

## Review Article

# Neural pathways underlying the interplay between emotional experience and behavior, from old theories to modern insight

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**Abstract:** Emotions are specific psychological states brought about by neurophysiological changes associated with feelings, thoughts and behavioral responses. Emotions were considered as irrational experiences beyond the domain of logical perception because of their intertwinement with mood, temperament, creativity, motivation and personality. Through the centuries, emotions have been the focus of research among great classical philosophers, doctors, neuropsychologists, neuroscientists, neurologists and psychiatrists. The neurophysiological basis of behavior, such as emotional facial expression, and autonomic events in the physiological theory of William James and James-Lange and modified by Cannon-Bard, was followed by the two-factor theory of emotions of Schachter-Singer and Lazarus' higher-order cognitive evaluation. Four components that influence each other represent the concept of emotions and complete the overall emotional experience, and these are: autonomous (increase in heart rate, blood pressure); somatic (body language, facial expressions); cognitive (control, management), and subjective feeling (emotion, individual experience). The interplay between emotions and cognition has been the subject of research. Emotions can be evoked reflexively by simple physical stimuli (bottom-up), but can also be complex reactions involving cognitive, physiological and behavioral reactions (top-down). The amygdala, the “alert” or “neural alarm” structure, is responsible for conditioning fear, while the medial prefrontal cortex participates in emotion self-regulation and decision making.

**Keywords:** emotion; amygdala; prefrontal cortex; top-down; bottom-up

## INTRODUCTION

Through the centuries, great philosophers (Platon, Aristotle, Spinoza, Descartes), doctors (Aristotle and Galen), neurophysiologists (Broca, Papez and McLean), neuropsychologists, neurologists, psychiatrists etc., have considered emotions to be mysterious and irrational experiences, greatly contributing to the study of this phenomenon. In ancient Greece, emotions were named in a different manner, such as passion, feeling, affection, disturbance, movement, turnover, appetite, etc. [1,2]. Emotions (from the Latin *emovere*, movement, replac-

ing) are biologically based responses to life situations and are complex phenomena consisting of multiple changes in different relevant subsystems. Emotional episodes may vary in intensity, frequency, stability and clarity, assuming a central role in the human ability to understand and learn. Emotions represent short, transient episodes (phenomena) and a neurophysiological response to stimuli that evoke a system of components that include subjective experience, physiological reactions, expressive behaviors and cognition, which prepare the organism to respond, together determining

the organism's behavior [3,4]. Unlike short, strong, and instant responses to a specific recognizable cause or situation (emotion), an emotional state, which is milder and longer lasting than an emotion, and can last for hours, days or weeks, and is referred to as mood.

The major components of emotion affecting one another that create an emotional experience include (i) autonomous, visceral phenomena that are established through the activity of the sympathetic and parasympathetic nervous systems and include an increase/decrease in cardiovascular activity, muscle tension, sweating, pallor/redness of facial skin, etc. [5,6]; (ii) somatic, skeletal-motor interactions that manifest through "body language" such as posture and movement ("fight or flight") and represent nonverbal communication. Together with instinctive or inherited facial expression (the "language of emotions"), emotions appear as the consequence of physiological activity of the central and peripheral nervous systems [7]. The skeletal-motor component is part of simple or primary emotions (anger, fear, surprise and disgust, joy, sadness), but also other complex emotions (i.e. jealousy). (iii) Attention and evaluation are cognitive components of emotions, and they can change emotional reaction to provide better adaptation. Strong emotions can affect changed mental behavior and loss of control [8,9]. (iv) Personal experience or subjective feeling as an emotion component is an internal representation of changes, short-term, unconscious patterns of inter- and proprioceptive signals with a role in orientation. People often hide emotions such as shame, anger, fear, sadness, jealousy, contempt [10-12].

The number and type of components that participate in the structure of emotions as well as their integration and synchronization include sociocultural factors, motivation (the tendency towards increased activity), and have a philosophical component, etc. Emotions are generated by the fine coordination of expressive, neurobiological, physiological, experiential, behavioral and cognitive responses to stimuli. Sometimes, emotions can be harmful to mental or physical health [13-14].

### **A historical overview of emotions through centuries**

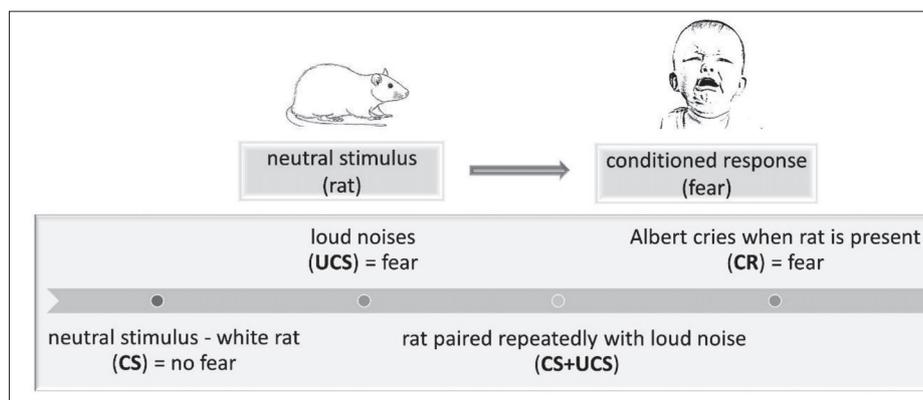
A historical understanding of the nature and functions of emotions is complicated and there is no consistent

definition of what emotions are in physiology, philosophy and mental health sciences. Aristotle in Ancient Greece (384-322 BC) believed that most feelings are active and involve cognitive elements, but the center of intelligence and emotions was the heart. He approached happiness as the most important goal that people strive after, and which contains two basic aspects, hedonic (satisfaction) and Eudaimonia, an essential element of a good life and fulfillment [1,15]. According to Plato (427-347 BC), three parts of the soul are analyzed as three layers: feeling, thinking and desire. Plato defined love as a philosophical instinct for ideas' comprehension, in which physical connection is excluded. Plato's relation to emotions has no dimension of his own corporeality [3,16]. According to Galen (130-200 AD), the brain ventricles are considered the centers of intellect and emotions according to the "theory of brain chamber emotions". Information that is the result of the five senses (touch, taste, smell, hearing and sight) would be processed in the cerebral ventricles and grouped together as a single perception in the circulatory system and "common sense" [17,18].

Leonardo Da Vinci (1452-1519) made a significant contribution to the development of neuroscience through neuroanatomy and neurophysiology. He dissected corpses and applied the theory of the four world forces (motion, mass, force and "percussion"). Da Vinci pointed at the correlation between brain structures and superior cerebral functions, and therefore he can be considered a forerunner of phrenology, a theory developed centuries later by the Viennese physician Franz J. Gall [18].

René Descartes (1596-1650) was a mathematician, philosopher and metaphysician. Descartes wrote about pineal neurophysiology, sharp mind and body dualism and the movement of the spirit through the pineal gland, which is the "seat of the soul". Body-soul dualism was determined by experiences such as feelings, pain, hunger, etc. He distinguished between six "primitive" emotions: wonder (most significant), love and hate, lust, happiness and sorrow [17].

In the 19th century, the first mapping of brain function was proposed by the phrenologist Franz Joseph Gall (1758-1828) who believed that the amount of brain tissue involved in cognitive functions determines human behavior. He thought that the brain



**Fig. 1.** The American psychologist John B. Watson (1878-1958), the father of behaviorism, is the founder of “affective neuroscience” and a philosophy. Neutral stimulus (rat, has become a conditioned stimulus (CS) that elicits a conditioned response, fear of rats (CR)). UCS – unconditioned stimulus is something that naturally and automatically triggers a response without any previous learning.

possesses about 35 specific cognitive functions, from basic ones such as speech and color perception, to transient feelings such as a sense of morality, and that each is supported by a specific area of the brain, observed on the skull as a nodule. He believed in the existence of specialized parts of the brain cortex that are responsible for the mind (intellect), since the brain is organized according to specific abilities and functions. Gall studied the relief structure of the skull that presumably follows the structure of the cortex, and by analyzing different patients (from lunatics to criminals), he described different personalities. The theories of Gall were called “craniology” (science of the head) and “phrenology” (science of the mind) [17-19].

According to Charles Darwin (1809-1882), emotions represent basic patterns, universal and innate adaptive responses to situations in the environment. The evolutionary theory of emotions argues that emotions are naturally selected features and adaptive responses to threats, affording a greater chance of preservation to the human race (survival and reproduction). By questioning people in different cultures, Darwin realized that people have a limited set of general or basic emotions. Evolutionarily beneficial behavioral activities, such as eating, mating and protection, represent motivation and reward, and therefore have an increased probability of recurrence in the future [20-22].

The physiologist and psychologist Sigmund Exner (1846-1926) studied psychological perception from a physiological point of view using experimental animals. He devoted himself to research into the localization and functions of neural circuits, mechanisms of sensory events as well as their conversion to emotional behav-

ior, interactions of sensations of pleasure and repulsion that produce motor and autonomous responses, the functional architecture of the visual cortex, etc. [23].

Skinner Burrhus Frederick (1904-1990) thought that all forms of behavior (not just learning) could be explained as a reaction to the environment. Skinner and Watson were the founders of behaviorism according to which all human forms of behavior depend on the presence or absence of reinforcement (award) or punishment. They proved this theory experimentally by operant conditioning (strengthening and weakening of behavior) and by experimental “boxes” [24].

The most famous but also most controversial figure in modern history, Sigmund Freud (1856-1939), founded the psychodynamic interpretation of emotions and psychoanalysis a century ago. Freud’s first postulate called inertia is similar to today’s homeostasis (whereby the stimulated organism tries to return to the unstimulated condition by induced inertia). He defined sensitivity as a form of “energy” that must be expressed directly or indirectly [25].

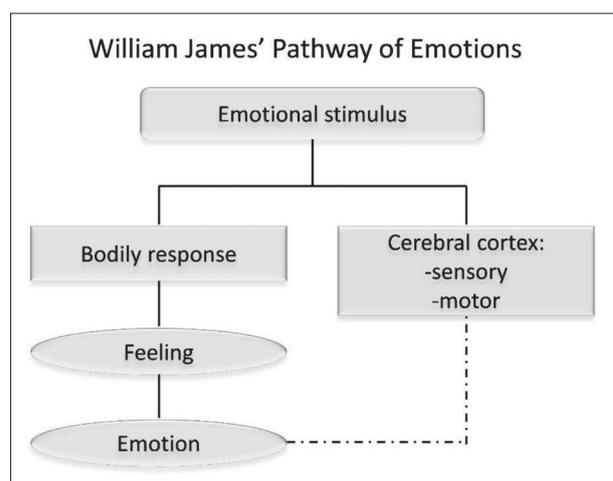
The American psychologist John B. Watson (1878-1958), father of behaviorism, was the founder of “affective neuroscience”. Behaviorism is an attempt to place psychology on a rigorously objective and scientific basis, with a shift in focus of research from humans to laboratory animals as subjects. Watson suggested that psychology can be objective only if it focuses on the study of observable behavior [26-28]. The ethics of Watson’s experiment on a 9-month-old infant (the Little Albert investigation) is criticized to this day and is the most controversial experiment in the history of psychology (Fig. 1). Albert’s classical

conditioning (loud noises, sudden discharge of the child, slight shaking while the child was sleeping, etc.) caused a revolution in the understanding and development of psychopathy (phobia). This experiment illustrated how phobias can form through classical conditioning. Due to emotional transfer, the fear of the white rat was transferred to other white furry objects that caused fear in the child although they had not caused fear before. For Watson, emotions represent a type of hereditary, unlearned behavior while the other type of such behavior is instinct. The Little Albert investigation was the last published research of Watson's academic career [27-29].

Hans Selye (1907-1982) set up the concept of general adaptation syndrome (in 1956) and adaptation diseases. A certain amount of stress is good (alarm response, adaptation and exhaustion for a given stimulus) but too much stress introduces pathology. Due to the difference in the perception of emotions, subjects' distinguished reactions to "positive" stress (satisfaction with received reward) or "negative" (a quarrel with an emotional friend). The brain cortex can recognize the difference between adrenocorticotrophic hormone and "corticoids" released under the influence of stress [30,31].

The neurosurgeon Wilder Graves Penfield (1891-1976) electrostimulated different parts of the cerebral cortex of awake patients with severe epilepsy during surgery under local anesthesia and asked them to describe their feelings [32]. By examining specific areas of the brain, such as the temporal lobe, he could provoke hallucinatory experiences, sleep, memory, certain smells, feelings of flickering light, caressing the back, *deja vu*, fear, loneliness, strangeness, entire memory sequences as well as famous songs. His work was used to make models of sensory and motor homunculus. [32,33].

Paul Ekman studied the facial expressions of people from different climates (the peoples of Fore from Papua New Guinea). He hypothesized that emotions vary on a pleasant-unpleasant scale and that they are a consequence of learned and social factors, and their meanings depend on culture [7,34]. He identified six universal basic emotions according to facial expressions that are genetically coded and different from each other (happiness, sadness, fear, anger, surprise,



**Fig. 2.** William James (1842-1910) said that "the greatest purpose of life is to be spent on something that will outlive us". Components of emotions according to James' theory: a mentally represented bodily state is an integral part of the emotional experience.

disgust-contempt). The stimulus that initiates a positive or negative emotion activates changes in many systems (central command), which includes facial expression, vocalization, the skeletal-muscular system, and activity of the autonomic nervous system [34,35].

### Hypotheses about the origin of emotions

The development of the regulatory, structural and functional systems involved in emotional processes, as well as the origin and regulation of emotions, are described in physiological, psychological and biological theories.

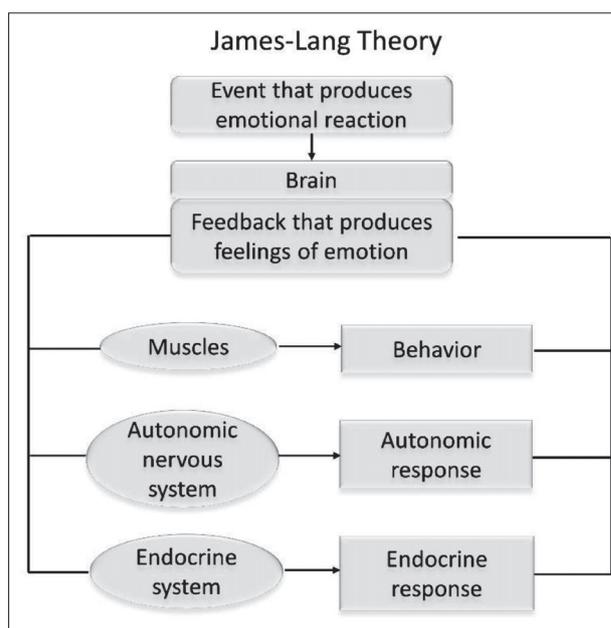
William James (1842-1910) was a lecturer in physiology, anatomy, philosophy (he was the founder of pragmatism and functionalism) as well as the founder of functional psychology and is the father of psychology in the US. James opposed the idea that emotions are useless, unpredictable and harmful phenomena, and argued that they are actually physical changes based on experience [36,37]. In response to a real or imaginary stimulus, the organism will react with a spectrum of physical changes (muscular, visceral, neurovegetative). Emotion is the feeling of these physical changes in the body during the very course of the changes, claimed William James, as did Charles Darwin [36] (Fig. 2).

According to James' theory, important life events cause emotions that are directly related to physical

changes in the individual (heart palpitations, shortness of breath, anxiety, activity of the facial muscles, etc.). The physical change will be felt first, and then the brain “understands” that it is a specific feeling (e.g. the emotion of fear). Every emotion becomes manifest through complex physiological changes and altered behavior (we are afraid of bears, and we should run, but we don’t run because we are afraid) [20,26,38,39].

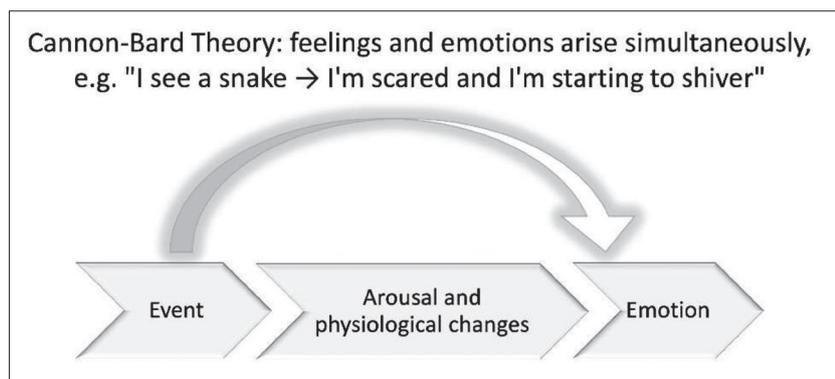
The organic or physiological theory of emotions of the Danish physician and psychologist Carl Lange (1885-1912) appeared almost at the same time as William James’s and is referred to as the James-Lange theory of emotions. The James-Lange theory provides “color and warmth”. According to the theory, without emotions, every environmental stimuli and experience would be pale and without content. By subjective and personal introspection, interpretation of that physical response further results in an emotional experience. [36,38]. Stimulatory events trigger physical responses, and our awareness of those responses is what emotions are. We become aware of emotions by interpreting the physiological reactions we have experienced (Fig. 3). There are linear sequences of events between perception and feeling (for example, sadness or anger), which are mediated by physical changes for each emotion; for example, when a person trembles and feels anxious, then the person feels fear. The James-Lange theory says that emotions are feelings that occur as a consequence instead of being the cause of physiological changes [40,41].

The physiological Cannon-Bard theory as an argumentative critique has significantly weakened the idea of the origin and visceral determinism of emotions according to the James-Lange theory. The research work of Walter Cannon (1871-1945) and his doctoral student Phillip Bard (1898-1977) revolutionized the study of emotions based on experimental decerebration of animals, and the observation that an intact hypothalamus elicits emotion (e.g., false anger) [42,43]. The Cannon-Bard psychoneurological theory argues that physiological changes in the body and the subjective experience of emotion occur simultaneously, and not one after the other. Canon claimed that the neurophysiological aspect of emotional expression is subcortical (“thalamic processes as a source of sensory experience”), and the specific quality of emotion is the result of neural activity. A

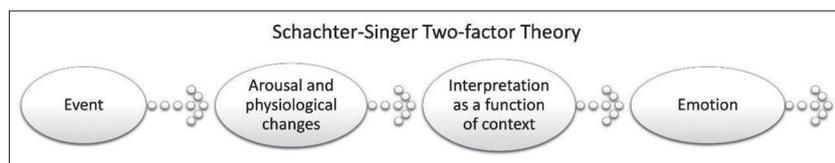


**Fig. 3.** The James-Lange theory provides “color and warmth”; without emotions, every environmental stimuli and experience would be pale and without content. By subjective and personal introspection, interpretation of that physical response further results in an emotional experience. James-Lange’s physiological theory: feelings are the result and not the cause of an emotional reaction.

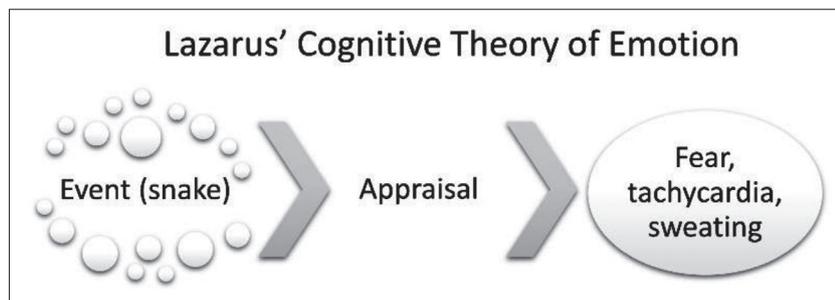
certain situation stimulates sensory receptors, initiating impulses that travel through sensory neurons to the thalamus where they are simultaneously divided and directed to the cortex (feeling of fear, anger, etc.). The thalamus is believed to both process information, as well as rely on the cerebral cortex and subcortical areas. The thalamocortical neurons receive sensory or motor information from the rest of the body and present selected information to the cerebral cortex. The thalamus is also connected with the hippocampus, mammillary bodies and the fornix, as well as with limbic system structures, allowing the thalamus to be involved in learning and episodic memory [44]. After a triggering event occurs, the thalamus sends signals to the amygdala, which is responsible for processing strong emotions such as fear, pleasure or anger. It also sends signals to the cerebral cortex, which controls conscious thought. Numerous signals are sent from the thalamus to the autonomic nervous system and skeletal muscles, controlling physical reactions manifesting a specific emotional state; these include sweating, shaking, or tensing of muscles. These processes then act according to patterns that correspond to the specific expression of emotions (Fig. 4). The Canon-



**Fig. 4.** Cannon-Bard's psychoneurological theory: changes in the body and the subjective experience of emotion occur simultaneously.



**Fig. 5.** Stanley Schachter and Jerome Singer are the initiators of a two-factor theory of emotions that focuses on the interaction between physical and cognitive arousal that lift emotions (1962).



**Fig. 6.** Richard Lazarus' (1922-2002) "cognitive-motivational-relational" theory of emotions. Theory of assessment argues that the event itself does not create emotions and that there is no emotional reaction to the situation until its significance is cognitively interpreted.

Bard theory points to a specific and mutual relationship between the "fight or flight" stress response and changes in the mind and body "homeostasis" [38,40].

The ideas of the Cannon-Bard theory were taken on by the neuroanatomist James Papez (1883-1958) who began a systematic study of the neuroendocrinology of emotional reactions. Paul Broca (1824-1880) was the first to use the term limbic (from the Latin word "limbus", meaning edge, ring). Starting from Papez's ideas, Paul MacLean (1913-2007) [45] introduced the term "limbic system" (MacLean's and Cannon-Bard's theory was supported by the Swiss physiologist Walter Hess (1881-1973), winner of the Nobel

Prize (in 1949) for the discovery of the functional organization of the diencephalon as a coordinator of internal activities) [18,42,45]. In his experimental work, Walter Hess conducted research in which electrodes were implanted in the hypothalamic area of cats. After electrostimulation of certain regions in the hypothalamus, he turned the cats from friendly animals into angry creatures with an "affective defense reactions", and from angry-emotional attacks to methodical predator-victim stalking [20,26].

Stanley Schachter (1922-1997) and Jerome Singer (1934-2010) [9] are the initiators of a two-factor theory of emotions that focuses on the interaction between physical and cognitive arousal. Schachter and Singer manipulated physiological arousal (spoken of by James), as well as the cognitive assessment of the situation. The Schachter and Singer theory focuses on the role of physiological arousal, which cannot be responsible for all emotional reactions and can be interpreted as any emotion. In other words, physiological arousal requires some kind of cognitive label, i.e. cognitive assessment and interpretation of a specific emotion in order to determine whether the state of physiological arousal will be defined as anger, joy, fear, etc. (Fig. 5). Thus, Schachter and Singer claim that emotional states are characterized by general physiological arousal of the sympathetic nervous system, and that the individual interprets and classifies the arousal state based on cognitive factors as the basis for perception and analysis of physiological arousal [9,46].

Richard Lazarus (1922-2002) improved the research of emotions through a specific psychodynamic and cognitive approach. He is considered the creator of the "cognitive-motivational-relational" theory of

emotions. According to Lazarus' theory of evaluation, a life event itself does not create emotions and there is no emotional reaction to the situation until its significance is cognitively interpreted, evaluated and processed as a physiological reaction to the event. Emotional reactions to events differ in the significance that the experiences have for us. Cognitive evaluation on a higher level and event evaluation have a specific effect on motivational, somatic, motor, and subjective components of emotions. Assessment also has an adaptive function, and it is significant for the way a person registers, decodes, transforms, stores, and uses stimuli from the environment to make decisions. Every individual will interpret emotions differently with regard to the significance of events and emotional reactions for their well-being. [47-49].

### **Neurophysiological determinants of emotions (bottom-up vs top-down)**

The conflict between emotions and cognition has a long history, with numerous attempts to understand their integration in the brain; it is considered that both emotion and cognition equally and conjointly participate in the regulation of behavior and thoughts. Emotions can be evoked in many ways, from reflex reactions to simple physical stimuli (from bottom to up, or bottom-up) to complex reactions that require interpretation (from top to down, or top-down). The generative and regulatory processes of both systems (bottom-up and top-down) are closely interdependent and overlap in neural processes that are in constant interaction. By experimental research on animal models and using the method of neurophysiological lesions, specific cortical and subcortical neural networks have been identified as a biological substrate for emotions [33,50,51]. Emotion regulation and control arise as a complex process in a network of neural groups that mediate cognitive, emotional and behavioral functions (the prefrontal cortex, limbic, and temporal regions). The development of emotions and their regulation include the interaction between a fast processing system (amygdala) that encodes the affective properties of the stimulus, and a control system that is carried out in the prefrontal cortex (PFC) and the anterior cingulate cortex (ACC). The relationship between the PFC and evaluative subcortical regions is reciprocal, and interactions are a function in "cognitive

repression of emotions" [52-54]. A polygraph or lie detector measures the increase in physical signs of anxiety in response to questions that would indicate that a person is lying. The method is unreliable and there are no definite physical markers of deception as people who do not feel ashamed/guilty can lie without changing their physical arousal, while honest people may be worried for reasons unrelated to deception [25,52,55-57].

### **Cognitive-emotional interaction: creating emotions from the bottom up**

The bottom-up approach is focused on subcortical structures, the hypothalamus and the amygdala, which are important generative evaluation systems. The direct pathway for rapid connection with the amygdala as a "center of fear" represents an evolutionary pathway for detecting threats that manifest instantly, automatically. Biologically prepared responses of a defensive, innate reaction outside of conscious perception occur in response to a potential danger. Two steps in creating an emotion "from below" to "above" are as follows: (i) biological stimuli from the environment or under laboratory conditions (sight, sound, painful stimuli, etc.), and (ii) emotions that occur instantaneously (e.g. fear). The amygdala is a neural alarm structure based on genetic coding that bypasses the cerebral cortex with shorter neural firing of information directly to the thalamus (12 ms). The amygdala has a role in carefully detecting and recognizing affectively visible stimuli (such as faces expressing sadness), learning, creating behavioral and visceral responses, modulating declarative memory, unconscious procedural memory, integrating sensory information that attaches adequate emotional importance, establishing positive or negative activation of stress hormones, etc. [12,25,57].

### **Creating emotions "from above" to "below" (top-down)**

The architecture of cognitive emotion control depends on the interaction between the PFC (ventrolateral and dorsomedial) and ACC cortical control systems that are responsible for many cognitive aspects of emotional responses. Cognitive control of emotional stimuli activates a wide neuronal network that in-

cludes the medial prefrontal (MPFC) cortex, which is in comodulation with the amygdala and has a “general” role in the processing of emotions (assessment, experience, etc.); the ventrolateral prefrontal cortex (VLPFC), which is involved in episodic memory and reducing the response to social exclusion (need for belonging and control); the dorsomedial prefrontal cortex (DMPFC), which creates subjective experience and memory, and the dorsolateral prefrontal cortex (DLPFC), which supports goal orientation and working memory [52-57].

The corticolimbic circle represents the interaction between the prefrontal regions of the cortex and amygdala (top-down system) that regulates emotional reactions in the direction of delayed, slow, detailed and accurate responses, as the result of precise and conscious analysis of events. Emotion regulation is defined as the process that individuals use to change the quality (type, intensity, timing) of their emotional experience, enabling better coping in new situations. The “top-down” approach includes a prefrontal cognitive system for selective attention, working memory, speech, emotional processing control by inhibition (extinction), as well as long-term memory. With subcortical structures (amygdala), conscious and thoughtful decisions in different emotional situations can be made about the manner of expression of emotions through speech. Working memory is the temporary manipulation of information where attention is directed, information is selected, the stimulus is cognitively assessed, and the meaning of the stimulus is reassessed in order to make better decisions and choose the right reactions. Activating assessment has an adaptive value and enables behavior to situations related to the goals of the individual, giving the body the strength and flexibility to respond to internal, mental as well as external and physical demands. Emotions “from above” to “below” occur in three steps: (i) occurrence of stimuli, (ii) thinking patterns that provide information about what is happening, and (iii) a feeling that occurs based on thoughts about the stimulus. Cognitive theories of emotion contribute to top-down regulation processes [12,25,49]. Neural circuits are inextricably linked and contain mechanisms for establishing emotions, reconsideration, cognitive distancing, suppression of behavior, control of attention, and reassessment through which emotions can be changed – cognitive change of the emotional experience.

## CONCLUSIONS

In psychology and psychophysiology, emotions are usually defined as a complex state of body and mind that has a strong influence on thinking and behavior. Major theories used in the study of emotion include: (i) physiological theories suggesting that changes in our body are responsible for emotions; (ii) neurological theories proposing that brain activities cause an emotional response; (iii) cognitive theories which argue that thoughts and mental activity contribute to emotion formation. Despite our understanding that emotions play a key role in every decision we make and the way we act and behave in the world, there is still much mystery as to why we have emotions. Research on emotions continues because emotions are a complex interplay of different feelings and physical changes that affect our lives.

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