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EMOTIONAL ENGAGEMENT AND BRAIN POTENTIALS:
REPETITION IN AFFECTIVE PICTURE PROCESSING

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Chapter 1

Introduction

1.1. Emotions

1.1.1. Defining Emotion

Research on emotion has increased significantly over the past two decades with many fields contributing including psychology, neuroscience, and psychiatry. The numerous theories have attempted to explain the origin, neurobiology, experience, and function of emotions, suggesting different views regarding emotion.

Part of the complexity in studying emotion is defining it. Although most people have a rich vocabulary for describing their individual emotions, it is hard to find consistency between researchers regarding a single definition of emotion. Despite the absence of a clear definition of emotion, one point that many researchers accept is that the primary function of emotion is to motivate action. It is instructive that the word “emotion” stems from the Latin *movere*, meaning “something that moves one”.

Considering that the word “emotion” is generally used for describing events that are felt to be moving, generating an affective experience in humans, “motivation” is the term usually reserved in interpreting the actions of animals. There are some aspects that are shared by humans and other animals, such as responses that occur when an organism detects and responds to significant

events in the course of surviving. Emotions have been described as a result of evolution because the motivation to avoid threats and attain appetitive goals allowed our ancestors to survive and eventually evolve into what our species is today.

1.1.2. Historical Background

To begin, an historical overview of the main theories of emotions is presented, starting from the evolutionary perspective. Following, a discussion of contemporary theoretical approaches to studying emotion is reviewed, focusing on the motivational model proposed by Lang and colleagues, that is particularly relevant for the questions examined in the present work. Finally, due to the benefits of new technical instruments, findings of the recent studies which have employed peripheral and central physiological measures for studying affective response in humans are explored.

In the late 19th century, the publication of Charles Darwin's book *The Expression of the Emotions in Man and Animals* (1872) was the pulse for evolutionary perspectives on emotions. Darwin was one of the first to suggest that emotions are used as a goal for humans, in communication and also in supporting their survival. The Darwinian hypothesis highlights the innateness and universality of emotional expressions among different cultures, and they are the product of our evolution. Darwin also discussed the existence of parallel experiences between humans and animals, leading an increase of researches on animals to determining the neural substrate underlying emotion.

William James (1884), influenced by Darwin, emphasized a close relationship between physiology and emotion. Posing his famous question: "What is an emotion?", James suggested that emotions arise as a consequence of physiological changes. The most cited example proposed by James was the following: "we are afraid because we run" (James, 1884). In other words, this counterintuitive example stated that changes in bodily state precede the emotional experience rather than the other way around. According to the James-Lange theory, it is the self-perception of bodily changes that produces emotional experience. Consequently, specific emotions would have a specific physiology. Although this hypothesis prompted an intense psychophysiological research over the last century, the fact that bodily changes give rise to an emotion was not supported by a large number of empirical evidences.

An alternative idea was proposed by Walter Cannon (1927), who provided a more accurate understanding of the connection between emotion and somatic responses. One major criticism to the James-Lange theory was that physiological responses were too slow and often inappreciable to induce emotion. Cannon suggested that emotional events trigger both physiological and experiential aspects of emotion at the same time (Cannon, 1931). This idea was supported by the work on animals of Philip Bard (1934), contributing to elaborate the Cannon-Bard theory of emotion. This theory proposed that all sensory information had to pass through the thalamus, which simultaneously transmitted information to the cerebral cortex and the autonomic nervous system. Cannon-Bard's theory prompted a vast amount of research about the neural substrate of emotional

processing, which led to the formalization of the limbic system structures (Papez, 1937). These included the regions of the cingulate cortex, hippocampus, hypothalamus and anterior nucleus of the thalamus. The work of MacLean extended this idea to incorporate regions such as the amygdala and orbitofrontal cortex. These different regions were hypothesized to work together to produce an integrated “emotional brain” (MacLean, 1949).

Though almost all approaches agree that emotions are associated with the modulation of the physiological changes, radically different views have been expressed by distinct researchers. In particular, some investigators have emphasized the discrete nature of emotions, suggesting the specificity of the physiological changes associated with each emotion (e.g., Ekman & Friesen, 1971; Ekman et al., 1983; Levenson, Ekman, & Friesen, 1990). On the other hand, other researchers have emphasized dimensional approaches to the study of emotions to explain all range of emotional states (e.g., Russell & Barrett, 1999; Russell & Carroll, 1999; Russell, 2003), stressing the role of basic motivational systems in regulating behavior and physiological functions in humans and animals (e.g., Konorski, 1967; Bradley et al., 2001; Lang, 2010; Lang & Bradley, 2013; Rolls 2013; LeDoux, 2012).

1.1.3. Basic discrete Emotions Models

One way to conceptualize emotion is in terms of a set of diverse, discrete emotions, such as fear, anger, happiness and so on. Paul Ekman and his

colleagues studied the facial expression of emotion and suggested that there are six basic expressions of emotion, corresponding to anger, disgust, fear, happiness, sadness, and surprise. Ekman argued that each of these expressions is characterized by a unique subset of facial muscle and bodily changes, and the ability to convey them appears to be innate and universal across cultures (e.g., Ekman & Friesen, 1971, Ekman et al., 1983; Levenson, Ekman, & Friesen, 1990). Ekman (1992b) described nine characteristics that permit to consider an emotion as basic, and different from another.

- Distinctive universal signals: observing an individual's facial expression of disgust, it supposes that the individual is harmed by a smell, taste or sound, and this consideration is universally shared across cultures.
- Presence in other primates: some emotions are analogues between humans and primates, such as, fear, anger and joy (Chevalier-Skolnikoff, 1973; Redican, 1982).
- Distinctive physiology: different emotions, such as, fear, anger and disgust show distinct activity of the autonomic nervous system (ANS) (Ekman et al., 1983; Levenson et al., 1990)
- Distinctive universals in antecedent events: some stimuli will produce an universal response, e.g., sudden noise will produce fear.
- Coherence among emotional response: autonomic and expressive responses are not disconnected by nature, despite of individual differences.
- Quick onset: emotion can arise before the awareness of the individual, activating a really fast response to stimuli.

- Brief duration: the duration of an emotion is termed in several seconds, or minutes.
- Automatic appraisal: the emotional response induced by external or internal stimuli showed regardless the conscious awareness.
- Unbidden occurrence: an emotion happens without being consciously chosen.

However, the idea that emotions are related to specific response patterns and that these changes produce the subjective experience of emotion has been widely discussed, the main weaknesses are the following:

- 1) Researchers did not support the idea that individuals universally recognize basic emotions from signals on the face. In order to replicate the Ekman's findings, cross-cultural studies were performed, exploring the percentage of participants who matched the face with the predicted emotion. These results showed differences as a function of culture and language (Russel, 1994).
- 2) Evidence for emotion-specific autonomic and central patterning is inconclusive (Cacioppo et al., 1992; Barret et al., 2009; 2012).
- 3) Evidences suggest a lack of agreement about a common list of basic emotions. For example, Ekman described six basic expressions of emotion, but other many authors did not agreed with his list, and the literature is totally inconsistent regarding the criteria on how to define basic emotions (Izard, 1977; Plutchik, 1980).
- 4) There are many reasons about the impossibility to induce and, consequently, study basic emotions: a) each stimulus/event engages a lot

of emotions at the same time, and it is not possible to induce a single emotion in the laboratory context; b) it would be hard to compare basic emotions by controlling for the level of intensity. Differences between basic emotions might arise from the differences in the level of intensity/arousal. Almost all studies did not control (or manipulate) the level of intensity/arousal of the basic emotions which were examined compared, making it difficult to draw any conclusion from these findings.

- 5) Evidences do not support the idea that observers have an innate ability to produce discrete emotional displays (Barrett et al., 2009). For instance, congenitally blind infants (Fraiberg, 1977), children (Roch-Levecq, 2006), and adults (Galati, et al., 1997) do not produce the same facial spontaneous expressions of healthy children (Galati, et al., 2001). Also, there are evidences that even 4-month olds do not show specific facial displays, such as anger, fear, disgust, and sadness (e.g., Bennett et al., 2002; Camras & Fatani, 2008).
- 6) Evidences from animal research in supporting the basic emotions model, present relevant methodological problems (e.g. coarse electric stimulation techniques), and the emotional behaviors studied in animal research are not equivalent to human emotions (Barrett et al., 2009).
- 7) The physiology will vary with action, and actions associated with the same emotional state will also often vary. For example, a threatening cue can lead to freezing or escape, in relation to a contextual support and the organism's learning history. The somatic responses of fear in the context

of freezing will be different from the somatic responses of fear in the context of escape (Bradley, 2000).

These questions suggested that our emotions are not “on” or “off”, but are experienced on a continuum. Accordingly, some researchers suggested that emotional states may be better described by a limited number of continuous dimensions.

1.1.4. Motivational Models

The general idea embraced from the motivational perspectives is that emotions are established on the activation of neural circuits that evolved in the mammalian brain to ensure the subsistence of individuals and their progeny. Originally, these motivational circuits were activated by significant stimuli, that represent threats or supports to the organism’s survival. These stimuli engage systems that enhance attention and facilitate perceptual processing, and active a series of reflex responses that mobilize the organism for the motor actions.

Animal research described a number of structures involved in this survival network (Lang and Davis, 2006; Davis and Lang, 2003), stressing the key role of the bilateral amygdala. Some structures, such as, cortex, thalamus (sensory) and hippocampus (memory) send inputs to each amygdala. The implication of the central nucleus and extended amygdala (bed nucleus of the stria terminalis) lead a modulation of sensory processing (vigilance), enhanced related information processing, and the activation of autonomic and somatic structures.

Researches on motivated behavior in animal agreed that two basic parameters of *direction* and *intensity* control action (e.g., Schneirla, 1959; Hebb, 1949). Schneirla (1959), for example, initially noted that, in aplysia, bidirectional actions of approach and withdrawal characterize the basic behavioral responses supporting survival, with approach related to action towards stimuli necessary for life, and withdrawal connected to action away from stimuli that threaten life. Rodents may respond to a perceived menace by active avoidance; or showing “freezing”; or, depending on the specific context, aggressively approach to a conspecific (Blanchard & Blanchard, 1989).

These analogies have encouraged researchers to study other mammalian species in these contexts, in order to offer an animal model that can increase knowledge of human emotion. In other words, in the any organism, stimuli that promote survival (e.g., food, nurturance) elicit behaviors towards the eliciting stimulus, whereas those that threaten the organism prompt withdrawal, escape, or avoidance. Both kinds of behaviors can happen with varying strength, speed and vigor.

Studies from affective language confirmed the idea that different emotions might be arranged around simpler motivational parameters. Interestingly, a description of three primary dimensions of feelings: *Lust* (pleasure), *Spannung* (tension), and *Beruhigung* (inhibition), can be found in Wundt’s approach about the introspection (Wundt, 1896). In line with this issue, Titchener (1908) highlighted the primary dimension of pleasantness and unpleasantness. Some researchers later assessed this question empirically, by using evaluative responses of subjects to a series of stimuli. They found similar dimensions of

affective valence (pleasant, unpleasant) and arousal (calm, aroused) described by Wundt (Osgood, Suci, and Tannenbaum, 1957). Lately, it has been confirmed that these factorial dimensions organize the diversity of evaluative judgments (e.g., Mehrabian, 1970; Mehrabian & Russell, 1974; Russell, 1980).

In line with this reasoning, Russel proposed a two-dimensional structure for describing the affective domain (Russel & Barret, 1999). The Figure 1.2 shows a schematic structure of affect as the Cartesian space formed from the valence and activation dimensions. The data fall in a circular pattern, which positive affect (the right half of the figure) consists of a range of words that vary in level of activation, as does negative affect (the left half), and activation (the top half of the figure) consists of words that vary in valence, as does deactivation (the bottom half).

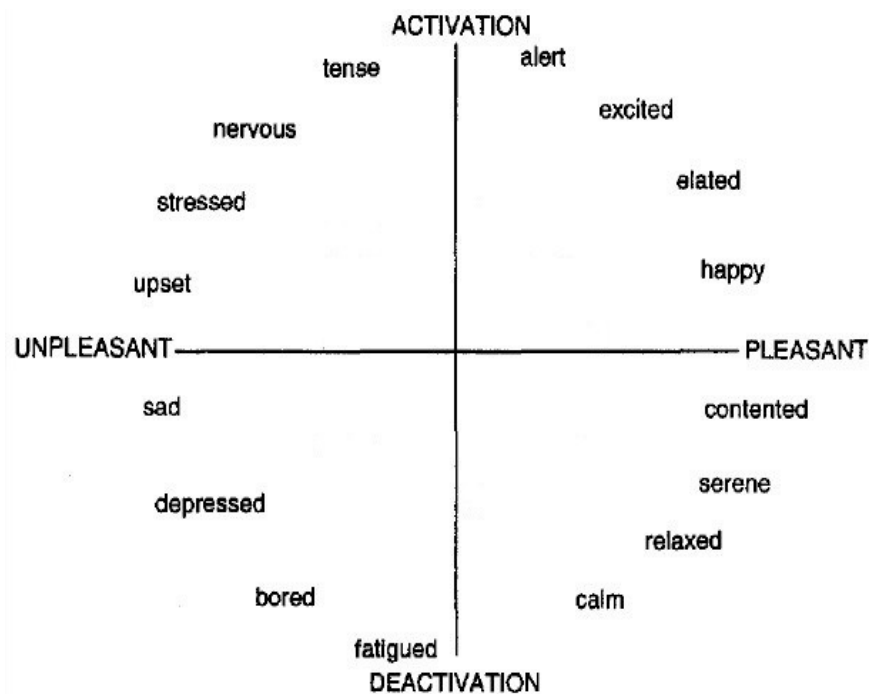


Figure 1.2: Two-dimensional structure of affect. This graph, on which activation is plotted on the vertical axis and valence on the horizontal axis, permits the depiction of the range of emotional states. Modified from Russel, 1998.

Russel suggested that emotional states could be understood as varying along the dimensions of activation and valence. For example, “sad” and “tense” are both unpleasant, but “sad” is not as activating or arousing as “tense”. “Excited” and “nervous” are both activating states, but “excited” is relatively positive and “nervous” is relatively negative. The model fit the data well, with Unpleasant Activation - Pleasant Deactivation/Pleasant Activation - Unpleasant Deactivation accounting for 87% of the variance in the valence factor and 82% of the variance in the activation factor (Barret, 2006; Barrett & Russel, 1999; Russel, 2003).

Using Hebb’s (1949) definition of motivation, it is the motivational circuitry that regulates both the direction and vigor of behavior in attainment survival’s goals. In other words, motivation’s directional function is wired in underlying subcircuits, one defensive, related with reports of unpleasant affect, and the other appetitive, related with reports of pleasant affect - both changing in the strength (or arousal) of their activation.

Konorski (1967) followed a similar motivational approach, stressing the survival role of the body’s unconditioned reflexes. These reflexes are preservative (e.g., ingestion, copulation, nurture of progeny) or protective (e.g., withdrawal from or rejection of noxious agents). He suggested that affective states are consistent with a preservative/protective organization: preservative emotions include affects as sexual passion, joy, and nurturance, whereas, protective affects include fear and anger.

Dickinson and Dearing (1979) developed Konorski’s distinction, renaming the two motivational systems aversive and attractive. These systems mediate a

different, but similar large set, of unconditioned stimuli which caused perceptual motor patterns and the course of learning.

More lately, Rolls (2003) proposed that emotions can be described as states elicited by rewards and punishers, which have particular functions. These functions are defined in what follows, and include working to obtain or avoid the rewards and punishers, respectively. A reward is anything for which an animal (or humans) will work. A punisher is anything that an animal will escape from or avoid. An example of an emotion might be the happiness produced by a particular reward, such as a pleasant feel, laud, or winning a wide sum of money. Another example of an emotion might be fear produced by the noise of a speedily approaching car, or the sight of a fearful expression on individual's face. These examples indicate how emotions can be induced by the delivery, omission, or termination of rewards or punishers, indicating how several emotions could be produced and classified in terms of the rewards and punishers received, omitted, or terminated (Rolls, 1999). Rolls described some types of emotion that may be elicited by different contingencies. The classification scheme created by the different reinforcement contingencies consists of: (a) the presentation of a positive reinforcer (S+); (b) the presentation of a negative reinforcer (S-); (c) the omission of a positive reinforcer (S+) or the termination of a positive reinforcer (S+!); and (d) the omission of a negative reinforcer (S-) or the termination of a negative reinforcer (S-!). Accordingly, each different reinforcer will produce different emotional states (see Figure 1.1).

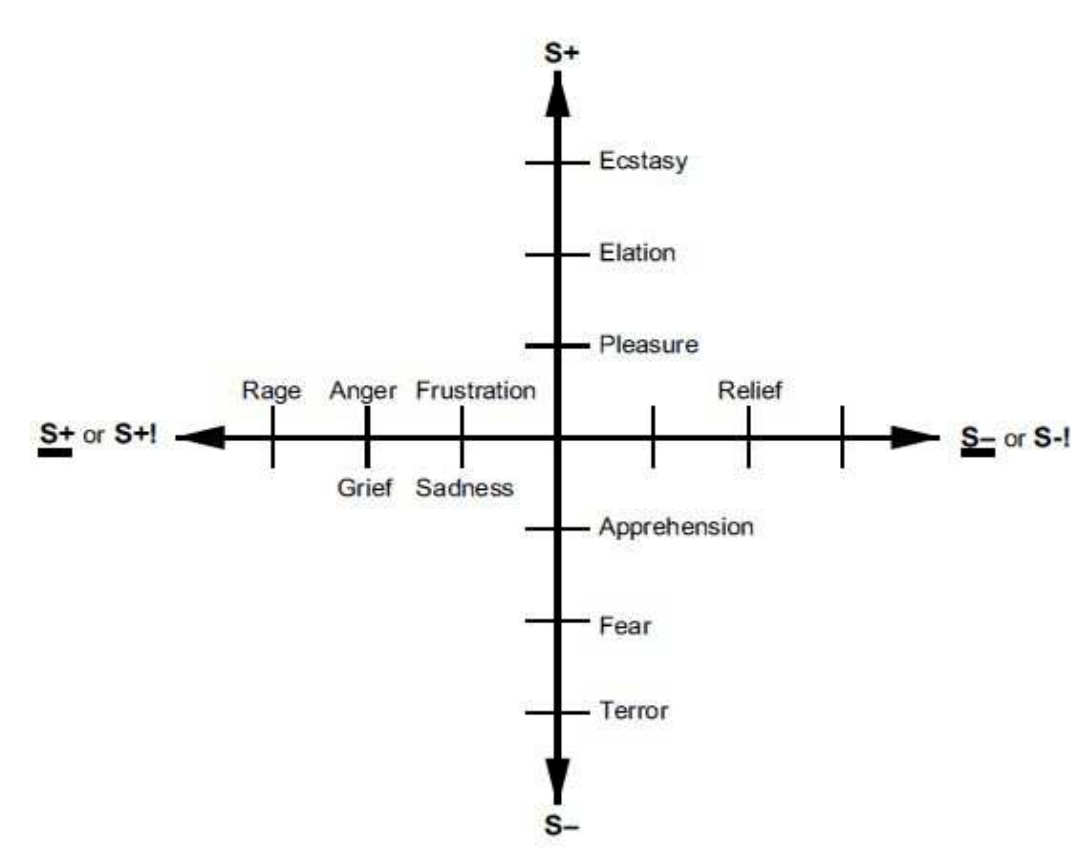


Figure 1.1: This diagram summarizes the types of emotion that may be elicited by different contingencies. Intensity increases away from the centre of the diagram, on a continuous scale.

An important part of Rolls' theory of emotion is the formalization of two processes involved in emotional behavior. (1) The first is stimulus-reinforcer association learning; emotional states are produced as a result. This process is implemented in structures such as the orbitofrontal cortex and amygdala (Grabenhorst & Rolls, 2011; Rolls & Grabenhorst, 2008). (2) The second is instrumental learning of an action made to approach and obtain the reward or to avoid or escape from the punisher. This is action-outcome learning, and involves brain regions such as the cingulate cortex when the actions are guided by the aims, and the striatum and part of the basal ganglia when the behavior becomes

automatic and habit-based, that is, uses stimulus-response connections (Rolls, 2005b; Rushworth, et al., 2011). Emotions are a result of these two processes, because they are elicited in the first stage by stimuli which are decoded as rewards or punishments. The motivation is to obtain the reward or avoid the punisher (the aims for the action). Indeed, primary or unlearned rewards and punishers are specified by genes which actually determine the aims for action (Rolls, 2013).

This agree from various researchers strengthens the hypothesis that human emotions arise from an underlying animal biology, determining both the intensity (level of activation) of bodily mobilization, and the directional disposition (appetitive approach or aversive withdrawal) of following emotional responses. This hypothesis seems different from the neophenomenological perspective, based on the idea that response direction is a result of a rational, or appraisal process, and only activation is biologically determined.

On the basis of similarities in behavioral and physiological reactions between humans and animals, Lang and colleagues have offered a really influential model of human emotion, addressing issues about psychophysiological reactions of emotional perception of specific stimuli.

Lang (1997) proposed that the data of emotion that researchers can really assess are the following: (1) expressive and evaluative language, (2) physiological changes, and (3) behavioral responses. Expressive and evaluative language of affective experience comprise verbal descriptions (e.g., "I'm happy"), ratings of emotion (e.g., ratings of happy on scale of 1 to 10), reports of physiological

responses (e.g., identification of bodily changes), and other methods that elicit reports regarding awareness of affective reactions. Physiological changes comprise bodily events mediated by somatic and autonomic systems, which can be assessed using psychophysiological instrumentation. Behavioral responses (e.g. propensity of avoidance) are commonly measured in studies of motivated behavior in the animal laboratory.

Emotions result from the synergic contribution of language, behavioral, and physiological responses. This interplay supposes an underlying organizing factor (Lang, 1997). The conditioning literature of the 20th century indicates that this factor is biological and motivational. In line with Konorski (1967) and other Pavlovian researchers, emotions are activated by appetitive states, producing positively valent responses, such as approach and nurturant; and by aversive states, producing negatively valent responses, such as, defensive, and protective. Consistent with this neuroscience perspective, human emotion is considered disposition to action (Frijda, 1986; Lang, 1979, 1985), to detect events that threaten or sustain our life. In other words, emotions arise from the activation of the motivational circuits, which engage sensory systems, enhanced vigilance, reflexive autonomic and motor responses, that reacted to threats or rewards in the course of evolution. The defense system is engaged in situations that threaten the survival (e.g. flight, fight, damage). On the other hand, the appetitive system is activated in contexts that promote survival (e.g. sustenance, copulation, and nurturance). Despite of some reactions are only appetitive or defensive, it has been observed that many physiological and

behavioral responses are analogous in both situations of arousal, and are supported by the same neural structures. (Lang, 2010).

Thus, despite of a great number of emotional words, a really simple structure of affective language derived. What type of system is more activated by an external stimulus is deducted by its hedonic valence. The intensity of activation of the two motive systems depends on the amount of arousal elicited by a stimulus (Bradley et al., 2001).

In order to determine whether animal reactions when detect threat or reward are similar to human reactions, Lang, Bradley, and their colleagues have developed a set of stimulus materials for use of emotional research. The International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2001) included a series of visual stimuli defined by the evaluative reports of pleasure and arousal. The distribution of these stimuli in a Cartesian space defined by valence and arousal ratings resulted in a scatter plot (see Figure 1.3).

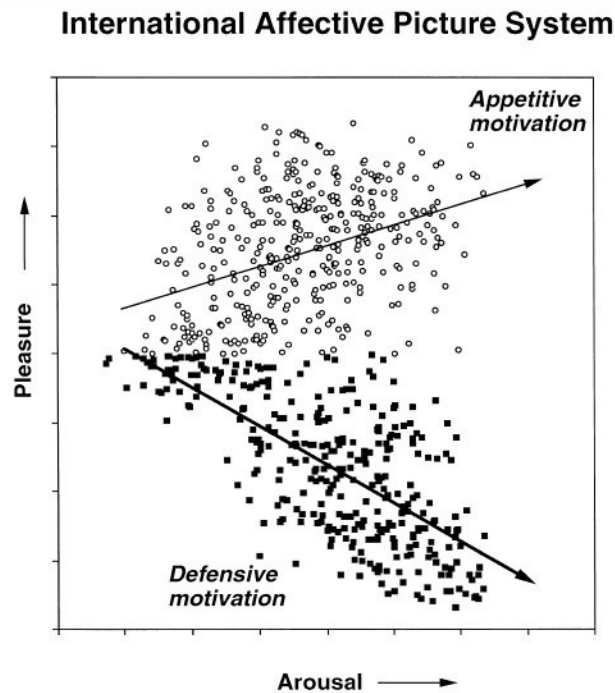


Figure 1.3: Affective spaces described by ratings of valence (y axis) and arousal (x axis) for natural scenes. Regression lines indicate the direction of appetitive and defensive motives. Modified from Bradley et al., 2001.

The basic idea is that affective percepts, such as images, act as motive cues that automatically engage old limbic circuits and reflex reactions. Accordingly, evaluative judgments of pleasure and arousal reflect the activation of two underlying motivational systems. In other words, if ratings of arousal increase, then defensive or appetitive motivation increase as well.

As a result, a number of researchers, by investigating behavior and physiological responses to this standardized stimulus material, have reported relevant evidences about the modulation of these responses as a function of the arousal dimension and, for the existence of the underlying defensive and appetitive systems. The present work makes use of the IAPS material and it will be further described in a later chapter (see Chapter 2).

Consistent with the physiological reactions to aversive visual stimuli in humans, it has been proposed a “cascade of reflex responses”, that have analogies with the animal responses (Lang et al., 1997, see Figure 1.4). The basic idea is that humans that are looking at a significant picture are behaviorally analogous to animals, prey or predators, which are looking a threat or reward at the distance. In other words, the common reaction between humans and animals is to arrest, look, and pay attention and, depending on the proximity and intensity of the stimulus, to react with appetitive or defensive actions (see, e.g., Löw, Lang, Smith, & Bradley, 2008).

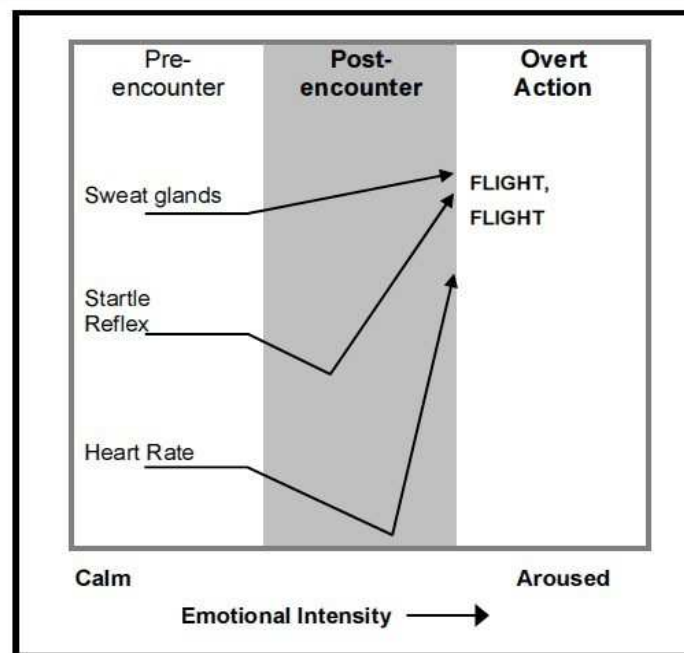


Figure 1.4: The defense cascade model. The graph shows specific physiological reactions observable in humans during picture viewing. Modified from Bradley et al., 2001.

Obviously, real life events are different from pictures in a human laboratory, thus, overt actions in response to emotional stimuli are not possible. However,

viewing pleasant or unpleasant pictures is enough to lead the activation of the specific motivational system, generating a series of physiological changes as a function of perceived arousal. Changes in electrodermal, heart rate activity, and startle reflex are typical indices measured during detection and processing of emotional slides. Taken together, these indices reflect an orienting response, that is, allocation of attentional resources to the stimulus and facilitated perceptual processing. A more detailed description about specific psychophysiological reactions to emotional pictures, and a discussion about the relationship between orienting and emotion will be offered in the following paragraphs (see 1.1.5; and 1.2.1).

In line with motivational models, more lately, Joseph LeDoux (2012) offered an interesting framework for thinking about some key phenomena related to emotion, without explaining or defining what emotion means. In common language, some mental states associated to feelings, are usually called emotions, leading an interchangeable use of “emotion” and “feeling” words. LeDoux highlights that some problems might arise when using “feeling” words (fear, happy, sadness etc.) to study emotion. In particular, the major complication derives when applying these words to the animal world.

In the last decade, neurobiological approaches have in fact used animal researches in order to understand emotional functions in the human brain. Thus, LeDoux suggested to set apart the general definition of emotion, and consider some important emotional phenomena that are shared by humans and other

animals. These phenomena include responses that happen when an organism is in the presence of a danger or a reward, both of them significant events.

LeDoux's idea is to focus on circuits that mediate functions that drive an organism to ensure survival, by detecting and responding to challenges and opportunities. These survival circuits and their adaptive functions are shared by all mammals, and have originated from early life forms. For example, bacteria have the ability to withdraw from harmful chemicals and to admit nutritional chemicals (Macnab & Koshland, 1972). Thanks to the evolution of multicellular and multisystem organisms, and the intervention of specialized sensory receptors, motor effectors, and central nervous system, these survival circuits have increased in complexity, leading to regulate bodily function and interactions with the environment (Shepherd, 1988).

Following LeDoux's reasoning, survival circuits are not considered to have a causal role in determining feelings, but they are accounted to influence feelings in an indirect way. The function of the survival circuits is to mediate behavioral interactions in specific situations, helping organisms to adaptive purposes.

The approach/avoidance motivation usually takes place in two stages: (1) an anticipatory/exploratory/search for target objects, and (2) the performance and consummatory responses (innate responses controlled by survival circuits) once target objects are usable (Tinbergen, 1951; Cardinal et al., 2002; Berridge, 1999, 2007).

Specific target objects activate survival circuits on the basis of innate programming or past experiences. Innate programming derived from genetically specified synaptic dispositions which are founded by natural selection. Past experiences derived from situations formed by the association of meaningless stimuli with significant events. Thus, meaningless stimuli acquire the capacity to activate the same survival circuits underlying the innate stimuli (LeDoux, 2012). In other words, the innate (unconditioned) triggers activate innate responses without the necessity of past exposures to the stimulus, in order to process challenges and opportunities indicated by innate trigger. On the other hand, learned (conditioned) triggers activate innate responses to stimuli after their association with innate triggers (by Pavlovian conditioning), in order to process challenges and opportunities indicated by learned trigger. In general, innate and learned emotional stimuli can be considered in terms of unconditioned and conditioned survival circuit triggers.

Moreover, the unconditioned and conditioned survival circuit triggers can also be described as incentives, stimuli that cause instrumental behavior. More specifically, innate (unconditioned) incentives enhance behaviors of approaches or avoidances toward a stimulus, in order to determine specific challenges and opportunities. Learned (conditioned) incentives conduct behaviors toward circumstances where challenges and opportunities can be determined.

In addition, the unconditioned and conditioned survival circuit triggers can be accounted as reinforcers, that is, stimuli that increase the probability that an instrumental behavior will be learned (reinforced) and also performed

(motivated), supporting the learning of Pavlovian or instrumental associations. Reinforcement and motivation are two words strongly related. Situations that motivate are usually reinforcing, and the other way around. Farther, if some situations have been experienced repeatedly to the individual, responses to these situations habituate and might substitute the incentive instrumental behaviors (Ledoux, 2012).

The effect of survival circuit activation is “generalized arousal” (Moruzzi and Magoun, 1949; Lindsley, 1951; Schober et al., 2011; Lang, 1994). As previously viewed, generalized arousal has been considered a relevant factor in many theories of emotion (e.g., Schachter and Singer, 1962; Schachter, 1975; Lang, 1994), and is also central in contemporary dimensional theories of emotion (Russell, 1980, 2003; Russell and Barrett, 1999). Generalized arousal is usually triggered in emotional situations, and might affect further processing.

Based on this idea, LeDoux summarizes a series of arousal reactions in response to the activation of survival circuit systems: (1) innate behavioral (related to the specific situation), autonomic nervous system and hormonal responses. Feedbacks to the brain from these behavioral, autonomic, and endocrine reactions give a contribution to the generalized arousal; (2) Excitability and neurotransmission in the brain from the activation of neuromodulatory systems; (3) the activation of motivational systems, depending on the goal-directed instrumental behaviors; (4) the contribution of sensory, cognitive, and memory systems. The individual’s organism becomes susceptible to significant stimuli in the environment, and new learning, memory representations, and learned

instrumental behaviors pertinent to the adaptive function are formed (see Figure 1.5). In LeDoux’s perspective, emotion, motivation, reinforcement, and arousal are strongly related arguments that appear together in reasoning about emotion.

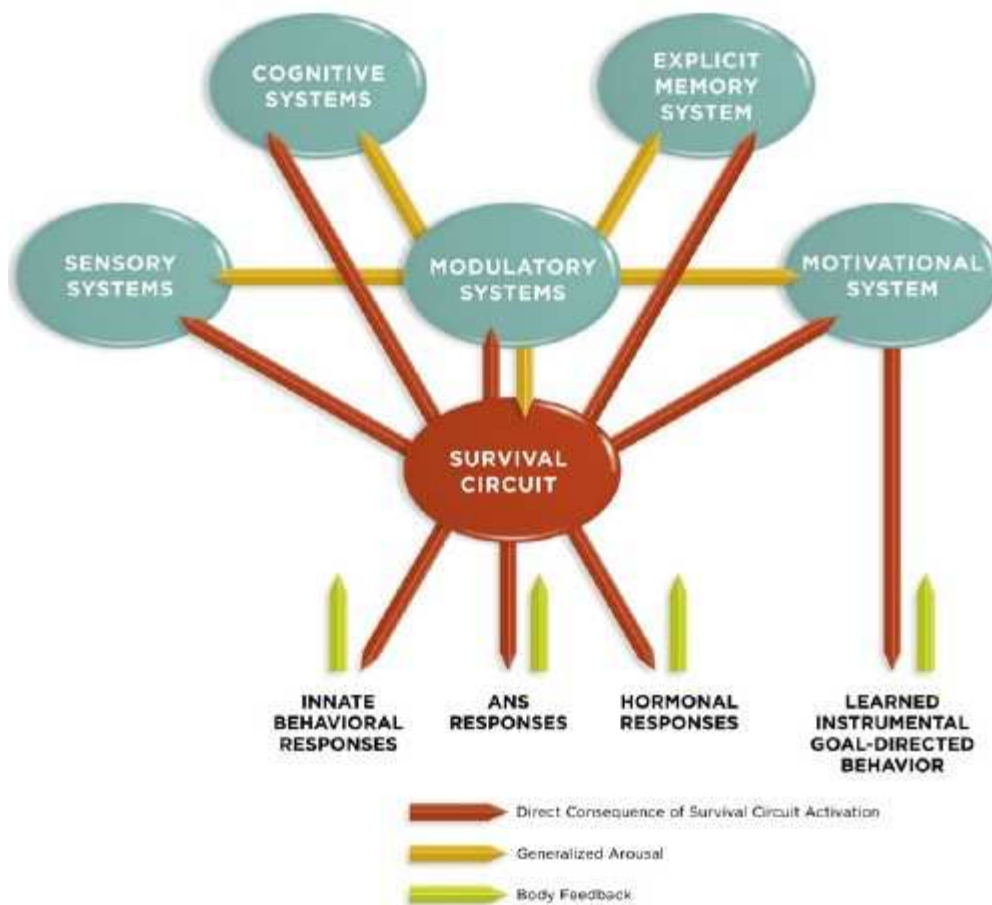


Figure 1.5.: Diagram of the effects of Survival Circuit Activation.

Since psychophysiological reactions to the visual processing of emotional stimuli are a very relevant topic for the present thesis, it will focus on studies that measured autonomic and somatic responses to the presentation of emotional pictures.

1.1.5. Physiological evidences of affective response

In studying autonomic and somatic reactions to emotional pictures taken from the IAPS, almost all researches have focused on cardiovascular, electrodermal, facial EMG systems, and startle reflex modulation. These reactions (e.g., heart, skin) of affective response are proximally controlled by the peripheral nervous system and the anatomical and functional distinctions between its parasympathetic ("homeostatic") and sympathetic ("fight or flight") branches have been relevant in the study of emotion. In the following paragraphs, the main peripheral responses will be described and linked to affective processing.

Cardiovascular reactions

Researches exploring emotion in perception assessed cardiovascular activity as a function of differences in stimulus intensity (e.g., Roessler et al., 1966; Epstein, 1971; Turpin & Siddle, 1983). Early studies reported that low-intensity sensory stimuli prompt heart rate deceleration, mediated by parasympathetic dominance, whereas intense stimuli prompt heart rate acceleration, mediated by sympathetic reactivity (see Sokolov, 1963; Graham 1979; Turpin, 1986). Following these results, sympathetic activity was associated with mobilization to respond to aversive events, whereas pleasant affect was associated with parasympathetic dominance (Arnold, 1960; Gellhorn & Loofbourrow, 1963; Schneirla, 1959).

On the other hand, other empirical evidences have demonstrated that some physiological measures (e.g., the heart) may differ as a function of the weighting of activation in the parasympathetic and sympathetic systems (e.g., see Berntson et al., 1994). For instance, Quigley and Berntson (1990)

demonstrated that heart rate acceleration to an aversive stimulus in the rat is larger than to a low-intensity stimulus because parasympathetic activity decreases with high intensity stimulation. Similarly, in humans, an aversive loud noise prompts a cardiac defense response that consists of an initial acceleration (4-6 s), followed by a decelerative component (17-23 s), and a later secondary accelerative component (31-76 s).

During picture perception, some researchers have found an heart rate deceleration to the presentation of unpleasant emotional events, contrary to the idea that these aversive events might prompt heart rate acceleration (e.g., Libby, et al., 1973; Klorman, et al., 1975; Klorman, et al., 1977; Hare, 1973; Hare et al., 1971). Based on these data, Lacey hypothesized that cardiac deceleration was an index of perceptual processing, reflecting sensory intake, whereas cardiac acceleration was an index of mental processing, reflecting sensory rejection.

Many recent studies have confirmed that the cardiac response during aversive picture viewing involves significant initial deceleration. During pictures viewing, unpleasant stimuli typically prompt more initial deceleration than pleasant or neutral pictures (Lang et al., 1993; see Figure 1.6, top left).

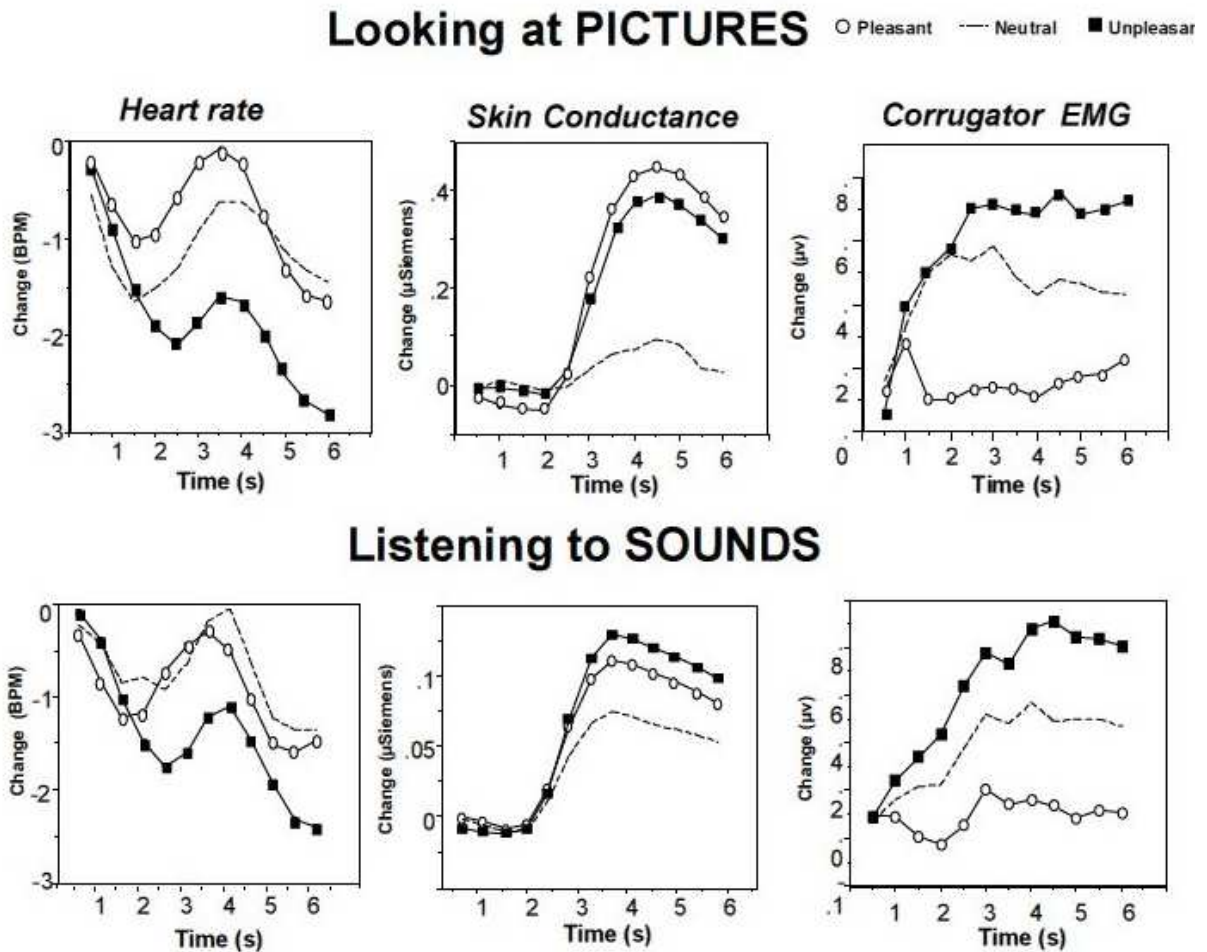


Figure 1.6: Heart rate, skin conductance, and corrugator EMG activity during perception of 6 s presentations of pleasant, neutral, or unpleasant pictures (top) and sounds (bottom) display similar emotional modulation. Modified from Bradley & Lang (2006).

More specifically, all unpleasant contents, including both high arousal pictures (e.g. threat and mutilation), as well as, low arousal contents (e.g. pollution and loss) prompt a significant cardiac deceleration (Bradley et al., 2001a). This initial deceleratory response when viewing unpleasant pictures is analogue to the fear bradycardia elicited in animals to threatening stimuli. In animals, this decelerative reaction has been considered as reflecting increased sensory intake and orienting (see Campbell, et al., 1996). Consistent with this hypothesis,

highly arousing appetitive contents, such as erotica stimuli, prompt significantly more initial cardiac deceleration, than low arousing appetitive contents (Bradley et al., 2001a), suggesting that pleasant arousing contents can also draw heightened perceptual processing and sensory intake. Moreover, when using different stimuli, such as affective sounds, listening to highly arousing unpleasant sounds (e.g., bombs exploding) also prompt greater initial deceleration than listening to neutral sounds (Bradley & Lang, 2000; see Figure 1.6, bottom left).

Electrodermal reactivity

Whereas the heart rate is modulated by either parasympathetic or sympathetic activity (or both), the electrodermal system is innervated only by the sympathetic system.

In a series of induction contexts, electrodermal reactivity consistently varies with emotional intensity, with larger responses elicited in both unpleasant and pleasant, compared to neutral contexts.

During picture perception, for example, many studies have found enhanced skin conductance when viewing emotional, compared to neutral pictures, regardless of whether they are rated pleasant or unpleasant in hedonic valence (e.g., Lang et al., 1993; Winton, et al., 1984; see Figure 1.6, top middle). Equally, listening affective sounds (Bradley & Lang, 2000; Verona et al., 2004), skin conductance reaction increases to highly arousing acoustic stimuli, regardless of hedonic valence (see Figure 1.6, bottom middle).

This physiological measure has been interpreted as action disposition, that is mediated by sympathetic activity preparing the organism for fight, flight, and other appropriate appetitive and defensive behaviors. Thus, whereas the cardiac response reflects differences in sensory intake, the electrodermal response indicates the preparation for action, that is reflected in both motivation and emotion (Bradley & Lang, 2000).

Facial EMG reactivity

The most overt signs of emotional response are facial expressions, such as frowns, grimaces, smiles, and so on. Different branches of the facial nerve (e.g. temporal, zygomatic, buccal) innervate different facial muscles, with a series of activity in different muscles related to different facial expressions.

Identification of the facial muscle activity can be realized by measuring electromyographic (EMG) activity using electrodes placed over specific facial muscles. Indeed, different induction contexts prompt appropriate facial EMG activity that are mediated by changes in appetitive and defensive activation (e.g., Fridlund, et al., 1984; Tassinari, et al., 1989).

The corrugator muscles, located above and between the eyes, are responsible for lowering and contraction of the brows. Significant contraction of the corrugator muscle occurs when viewing unpleasant, compared to neutral pictures (Cacioppo et al., 1986; Lang et al., 1993), and shows similar modulation when people listen to unpleasant, compared to neutral, sounds, as figure 1.6 (right panel) shows. Moreover, pleasant arousing materials prompt relaxation below baseline activity over this muscle.

When assessing specific picture contents, Bradley et al. (2001a) found that all unpleasant picture contents prompted significant increases in corrugator EMG activity, with pictures of mutilations and contamination (i.e., disgust) prompting fairly greater changes than other unpleasant contents, for both men and women (Bradley et al., 2001b). The minimum corrugator EMG activity was observed for low arousing pleasant pictures, such as babies and families. The most arousing pleasant contents, such as erotica and sports, however, did not prompt significant relaxation from baseline.

Activity measured over the zygomaticus major muscle occurs when the cheek is drawn back or tightened (Tassinari, et al., 1989), and this muscle is involved in facial expressions of smiling. Cacioppo et al. (1986) found co-activation of the zygomaticus major and orbicularis oculi muscles when participants viewed pleasant, compared to neutral, pictures. Considering specific picture contents (Bradley et al., 2001a), co-activation in these facial muscles was described, and was most pronounced for low arousing pleasant pictures (e.g., pictures of babies, families, and food). Highly arousing unpleasant contents also prompt slight increases in activity measured over the zygomaticus major muscle (Lang et al., 1993). When exploring specific picture contents, Bradley et al. (2001a) found that unpleasant pictures prompt increased zygomatic activity with significant changes in both the corrugator, as well as, the orbicularis oculi muscles. This co-activation of these three muscles was most pronounced for pictures rated as disgusting, including mutilated bodies and contamination (e.g., spoiled food) scenes.

Startle Reflex modulation

In most mammals, a sudden sensory event will prompt a startle response, that is, a series of rapid extensor-flexor movements that fall throughout the body (Landis & Hunt, 1939). This reaction is a defensive reflex, facilitating escape in simpler organisms, providing a protective function in more complex animals (Yeomans, et al., 2000).

In animals, the amplitude of the acoustically elicited startle reflex is enhanced when elicited in the presence of a light previously paired with footshock (Brown, et al., 1951). Equally, humans display greater startle blink reflexes when exposed to cues previously paired with an aversive shock (Hamm et al., 1993). In particular, fast eye closure is one of the most clear index of the behavioral sequence of the startle response in humans. By placing sensors over the orbicularis oculi muscle beneath the eye, it is possible to measure electromyographically the associated blink reflex (see Figure 1.7).

Startle Reflex & Emotional Perception

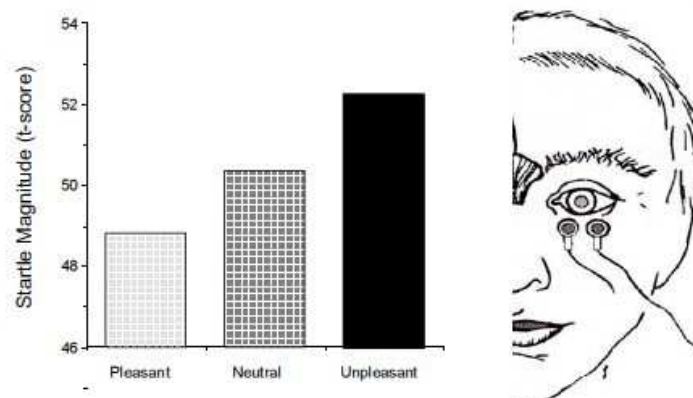


Figure 1.7: The startle blink reflex is modulated by hedonic valence, with potentiation for unpleasant pictures, and inhibition for appetitive pictures. Modified from Bradley et al., 2001.

During picture perception, blink responses are strengthened when viewing unpleasant pictures, and inhibited when viewing pleasant pictures, compared to neutral pictures (see Figure 1.7; Vrana, et al., 1988; see Bradley, Cuthbert, & Lang, 1999 for an overview). More specifically, startle potentiation is greatest for highly arousing unpleasant pictures (e.g., threat and mutilation), while startle inhibition is largest for highly arousing pleasant pictures (e.g., erotica and romance; Bradley et al., 2001a, Schupp et al., 2004).

Many studies have observed that the startle reflex is modulated by hedonic valence during picture viewing, regardless of the nature of the startle probe: visual, acoustic, or tactile (e.g., Bradley, et al., 1991; Hawk & Cook, 1997).

All together, these data suggest that emotional events prompt a cascade of physiological changes, reflected by cardiac, electrodermal, EMG, and startle responses, changing in different ways as a function of activation and hedonic valence.

It has already described autonomic and somatic reactions involved in affective picture processing. It will start the following section with presenting results from studies that investigated the processing of emotional pictures by measuring event-related potentials (ERPs), which provide excellent information regarding the time course of neural processing. The discussion of ERP results will only include the Late Positive Potential (LPP) component, that is modulated by emotionally significant stimuli.

1.1.6. The Late Positive Potential (LPP)

Event-Related Potentials (ERPs) are modulations of the electrical activity of the brain, which are classically analyzed in terms of components, defined as deflections of the ERP wave occurring at certain latency.

It has been described in many studies that emotional context, elicited by natural scenes, affects the amplitude of a late slow positive potential during random picture viewing, called the “Late Positive Potential” (LPP). More specifically, arousing pictures (both pleasant and unpleasant), compared to neutral scenes during their initial presentation prompt an increased positivity over centro-parietal sensors starting around 300-400 ms after picture onset. This affective modulation seems to be greater when viewing high arousing, compared to low arousing pictures (Cacioppo et al., 1994; Cuthbert, et al., 2000; Johnston, et al., 1987; Schupp et al., 2000; 2004; 2006, see Figure 1.8).

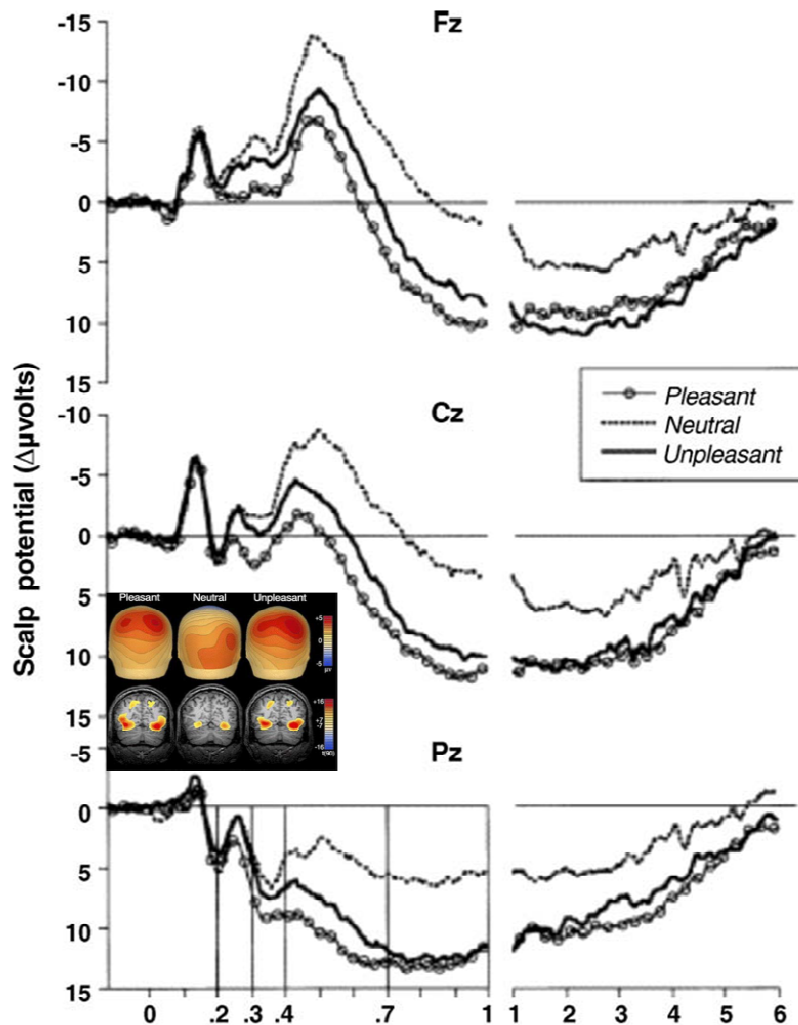


Figure 1.8: Grand-average event-related potential (ERP) waveforms for each picture valence category (pleasant, neutral, and unpleasant) from midline electrodes Fz, Cz, and Pz. Modified from Cuthbert et al., 2000.

These results suggested that motivationally significant stimuli are selectively processed, because they naturally engage attentional resources, as reflected in the LPP modulation (Lang et al., 1997).

A number of studies demonstrated that the affective modulation of the LPP component do not depend on voluntary evaluation of hedonic valence (Cuthbert et al., 1995; Codispoti et al., 1998; Junghoefer et al., 2001; Keil et al., 2002;

Schupp et al., 2003). In particular, by comparing LPP responses during passive viewing or an evaluative rating task, Chutbert and colleagues (1995) have found similar affective modulation of the LPP component in these two conditions, demonstrating that affective evaluation relies on obligatory process.

These results were obtained in experiments where each picture during affective picture processing was presented for a sustained time period (e.g. 6 s). Some researchers asked whether the exposure times of the picture may affect the affective response. In particular, by presenting pictures for short time periods (e.g. 25 ms), it has been demonstrated that brief presentations, as well as long presentations, are able to active the same LPP emotional modulation (Codispoti et al., 2001, 2002).

To extend these findings, it has been proposed that some features, like the color, under challenging perceptual conditions, could facilitate the process of recognizing the emotional content of natural scenes. It has been concluded that the recognition of the emotional content of pictures does not rely on color information, even when pictures were shortly presented, suggesting that when visual processing is partially degraded, affective stimuli are anyway recognized, as reflected in the affective modulation of the LPP (Codispoti et al., 2012).

Another important variable considered was the physical size of an encountered stimulus, because it defines the motivational relevance for the observant in the evolutionary sense. While early ERP components were modulated by picture size, the LPP affective modulation did not change as a function of picture size, demonstrating that at this phase a semantic representation of the stimulus has been already reached, and probably the LPP component reflects post-perceptual

stages of processing (De Cesarei & Codispoti, 2006). Similarly, another recent study have shown that, manipulating the understanding of natural scene contents by using spatial frequency filtering effects of a scene, LPP emotional modulation varied with picture identification similarly for high and low pass filtered pictures. These results suggested that the affective response, reflected by the LPP, did not depend on the compositional content of the pictures, but was due to the identification of the emotional content of the pictures (De Cesarei & Codispoti, 2011).

Taken together, these results suggest that the affective modulation of the LPP reflects the semantic identification of motivationally significant pictures, and is not due to bottom-up perceptual factors, such as exposure time, color, picture size, or spatial frequencies (Codispoti et al., 2001; 2002; 2012; De Cesarei & Codispoti, 2006; 2011).

1.2. Emotion, Attention, and Habituation

1.2.1. Emotion and attentional capture

Using some sentences of William James's book "Principles of Psychology" (1890), attention was defined as following: *"Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence."* This definition is focused on voluntary aspects of attention, that is, on the capacity to direct voluntarily the attention toward specific objects in the environment.

It is known that there are two different ways of how we attend to stimuli in the environment:

- Top-down or goal-directed manner concerns the influence of many factors, such as internal knowledge, goals, instructions, or interior states.
- Bottom-up or stimulus-driven manner refers to the intrinsic properties of a sensory stimulus.

The direction of attention arises from the dynamic interplay of these two ways of processing (Posner & Petersen, 1994).

In psychology laboratory, attentional processes are generally studied by varying instructions, tasks, or expectancies of neutral stimuli, such as tones, words or objects, providing an enhanced knowledge of the many facets of selective information processing.

In this work, motivation will be considered as a primary feature in driving attention, what has been called “motivated attention” (Bradley, 2009). In this perspective, human attention is examined as a process that engages the same procedures of selection and evaluation of motivationally significant stimuli that occur in animals. Accordingly, motivated attention in humans and animals is supported evolutionarily.

Due to their evolutionary importance, significant stimuli have the relevant feature of capturing attention. It has been demonstrated that emotional stimuli can automatically access to processing resources, regardless of the actual direction of attention of an individual (Dolan 2002). Some evidence seems to indicate that emotional stimuli are processed in a “preattentive” way, receiving priority in the processing, and this has been suggested from several empirical evidences. For example, during a serial search paradigm the time needed to detect a specific neutral target is related to the amount of irrelevant distractors. For emotional stimuli, conversely, the time needed to find them is independent of the amount of distractors, suggesting that these stimuli are quickly detected, due to a mechanism that operates without requiring attentional resources (Ohman et al., 2001).

Moreover, some investigators have observed that there is increased sensory processing of emotional stimuli compared to neutral stimuli (e.g. Dolan & Vuilleumier, 2003). To this regard, some researchers have found a nice way to compare the detection of emotional stimuli inside the focus of attention (task-relevant location) and outside the focus of attention (task-irrelevant location),

in order to demonstrate that the enhanced processing of emotional stimuli is independent of the actual direction of attention (Vuilleumier et al., 2001). More specifically, two stimuli of houses (both neutral stimuli) and faces (fearful versus neutral) were arranged in vertical and horizontal pairs. Participants were asked to focus their attention horizontally or vertically, and report whether these stimuli were the same or different, ignoring the other stimulus pairs. This type of experimental design offered the possibility to assess attentional and emotional effects independently. The main finding was that the activity of the fusiform area to faces was intensely modulated by the spatial attention locations. In addition to the effect of attention, fearful faces increased the activity of the fusiform area, suggesting additive effects of attention and emotion at this area. The amygdala, on the other hand, responded to fearful, compared to neutral faces, independent of this spatial manipulation of attention (Vuilleumier et al., 2001).

Evidence that there are special mechanisms for detecting a threat derived from research on classical fear conditioning in rats. This research shows that there are two pathways by which information about the emotional significance of a conditioned stimulus can reach the amygdala (LeDoux, 1997). The cortical pathway allows the stimulus to go through all stages of normal perception before reaching the amygdala; and the subcortical pathway skips some perceptual stages and allows the amygdala to make a fast and crude assessment of the emotional significance of a stimulus. It is suggested that this subcortical pathway provides an early warning system in the presence of potential danger (LeDoux,

1997). The evolutionary reasons for this are clear: it is certainly better to be safe than sorry if the potential consequence is physical harm or death.

A fascinating explanation regarding why attention and emotion are strongly related and why so much attention is required in emotion has been offered by Bradley and co-workers. The basic idea is that some physiological responses, which are considered as indices of orienting and attention, are mediated by defensive and appetitive motivational systems, which have evolved to assist survival behaviors of the individuals and the species. An interesting link between attention and emotion has been suggested by some analogies existing among the bodily changes appreciable when individuals process “novel” and “significant” events (Bradley, 2009).

Ivan Pavlov (1927) was the first to describe the behavioral manifestations of the so called “orienting reflex” during conditioning, observing his dog directing attention to the novel visitor instead of looking at the conditioned stimulus. A more detailed explication of the orienting reaction was performed by Sokolov (1963), who called orienting response (OR) a variety of physiological changes in response to novel stimulation. Sokolov’s idea was that novel stimuli that did not match items in the current “neural” model - that represents events in the environment at any instant - elicited an OR. His considerable work on the OR resulted in two main findings: (1) orienting responses were usually evoked in the repetition-change paradigm in which during a repeated presentation of the same stimulus, at certain intervals, a different stimulus was introduced; (2) orienting responses habituated with stimulus repetition.

Interestingly, among the variables that modulate the magnitude of orienting and the rate of habituation it was included the “relevance” or “significance” of a stimulus. However, a question arises spontaneously: what does “significance” mean? It has been proposed that “significance” could be operationally defined as a series of semantic judgments that an individual can make about stimuli (Maltzman, 1979). These semantic judgments, when submitted to factor analysis, individualize two dimensions of pleasure and arousal. These two dimensions have been considered as factors that organize the emotion human experience. Following this reasoning, the main link between emotion and attention arises from the definition of “stimulus significance” in terms of pleasure and arousal (Bradley et al., 2001).

Considering the analogies between the effects of novelty and significance of a stimulus on the OR, it is useful to look at some main findings derived from physiological studies that have employed significant pictures as novel or repeated stimuli: (1) All novel pictures during their initial presentation in picture viewing paradigm engages OR. (2) Viewing arousing pictures increases the magnitude of the OR. (3) OR diminishes “differently” in the measured systems with picture repetition, suggesting that OR is not an unitary response. Consistent with these three main findings, it will be described the modulation of traditional indices of attention and orienting, such as skin conductance change, cardiac deceleration, and event-related potentials (ERPs) as a function of novelty and significance.

During picture viewing, heightened skin conductance and prolonged cardiac deceleration are evident when novel pictures are presented. Stimulus significance affects the magnitude of the orienting response in these two indices differently, showing increased skin conductance responses for pleasant and unpleasant, compared to neutral pictures, and, otherwise, a more pronounced cardiac deceleration only for unpleasant, compared to neutral and pleasant pictures.

It has been observed that different ERP components are modulated by stimulus novelty, such as an early mismatch negativity (Näätänen, 1979), N2b and P3a (e.g., Courchesne et al., 1975; Rohrbaugh, 1984). A more pronounced centro-parietal P3b amplitude is regularly observed for task-relevant stimuli, reflecting the amount of attention devoted to the stimulus (Johnson, 1986). Another late slow positive potential over centro-parietal sensors, the Late Positive Potential (LPP), is considered a reliable index of affective significance (see 1.1.7 for a detailed description).

These different indices habituate at different rates. Cardiac deceleration disappears very quickly after a single picture repetition (1 week later). On the other hand, electrodermal activity still shows affective modulation after a single picture repetition (1 week later), but decreased and then removed after multiple repetitions. In other words, skin conductance data show a slower habituation compared to heart rate data (Bradley et al., 1993).

Concerning the LPP component, despite repeated presentation of the same picture within the same session elicits a little reduction of the LPP emotional

modulation, its modulation is still significant after many presentations of the same picture, suggesting that the LPP is relatively resistant to habituation, because continued to show effects of significance after multiple repetitions (Codispoti et al., 2007). Taken together, these data indicate that these specific indices (skin conductance, heart rate, and LPP) are differentially modulated by relevance and repetition.

All these results prompt a reconsideration of the biological function of the orienting response. As early observed by Pavlov, the OR is important for the survival of any organism, in order to protect the animal life. If an unusual stimulus appears, it would be relevant to detect it to insure survival.

It has been proposed that a good way to define “novelty” is in terms of features shared to either short or long term memory representations. Consistent with Sokolov’s definition of the OR, many researchers, which used autonomic and ERP measures, suggested that the OR is enhanced when encountered events mismatch the current active short term memory representations (STM) (e.g. Gatchel & Lang, 1974; Gonsalvez et al., 2007). Almost all stimuli used in OR experiments are familiar to the individual, in the sense that, these stimuli are already encountered and represented in long-term memory (LTM) (Ohman, 1979).

Obviously, it would be informative to investigate orienting reactions to truly novel stimuli in humans. However, it is really complicated to find events or objects never been encountered before for humans, and, consequently it is hard to study reactions to truly novel stimuli in the adult human laboratory. It is

easier to find truly novel stimuli with children, or animals. In fact, it has been observed a series of behavioral reactions when primates were presented truly novel stimuli. The initial reaction of the animal is defensive, because the novel stimulus could be dangerous. Only after information is stored about the safety of the stimulus, “orienting” behaviors of exploration resulted (Dolin et al., 1965). In the animal and human literature, the cardiac deceleration is the first phase of orienting, and it has been considered an important index of the defensive response, reflecting perceptual processing. The second phase of orienting is to “prepare for action”, because the stimulus could be really dangerous. Due to the sympathetic role in supporting arousal and action, the skin conductance response has been considered another index of the orienting response.

Based on the mismatch model (Sokolov, 1963), orienting to novel stimuli will be largest for stimuli with low features shared with STM or LTM representations, and will be minimum for stimuli with great features overlapped.

In picture viewing paradigms, mostly used to investigate OR to motivationally relevant cues, unpleasant and pleasant pictures share some existing representations in LTM. Unpleasant pictures include associations to the defensive motivational system, producing increased perceptual processing (cardiac deceleration) and preparation for action (skin conductance change). Pleasant pictures, on the other hand, comprise associations to the appetitive motivational system, generating reduced cardiac deceleration and fast enhanced skin conductance change, because past memories lead to consider the pleasant stimulus as safe (Lang, 1984).

The late positive potential component is assumed as an index of significance detection. In other words, familiar pleasant and unpleasant pictures prompt enhanced LPP thanks to their natural associations with appetitive and defensive motivational systems. The basic idea about the LPP is that the repetition of the same picture (pleasant or unpleasant) does not remove the associative links to the appetitive and defensive motivational systems (e.g. Rescorla, 2001).

It has been described above that different indices of the OR mediate different adaptive reactions to novel and significant events, thus, their rates of habituation would be different. When the processes, reflected in the different indices, are not more engaged, these specific indices will fall out. For this reason, in this perspective, the habituation is not thought as a specific feature of the orienting response, but a “tool” to study the functioning of the processes underlying specific indices (Bradley, 2009).

1.2.2. Defining habituation

One relevant characteristic of an obligatory process is the resistance to habituation. Multiple exposures to a stimulus influence following attentional processes and orienting responses, leading to facilitate perceptual processing, and changes in subjective ratings of pleasantness and arousal (Sokolov, 1963; Bradley & Lang, 2000; Tulving & Schacter, 1990; Codispoti et al., 2006a). Although a single repetition of a specific stimulus leads to facilitate the following recognition (e.g. repetition priming), multiple repetitions lead to reduce the relevance of this stimulus.

Accordingly, habituation is operationally defined as a response decrement to repeated stimulation. An important aspect is that habituation is reversible: habituated responses exhibit spontaneous recovery (Harris, 1943).

The only authority to diverge from Harris' definition of habituation is Thorpe (1956), who considers it as a "relatively permanent waning of a response as a result of repeated stimulation. It will be observed that the time course for spontaneous recovery of an habituated response depends on several variables, thus, distinctions in terms of recovery time would seem somehow arbitrary. Obviously, Harris' definition has been largely appreciated.

Several authors have suggested a distinction between "short-term" and "long-term" habituation processes (Shapless & Jasper, 1956; Sokolov, 1955). Two peripheral mechanisms have often been assumed either explicitly or implicitly to account for response decrement: alterations in receptors or in effectors. A decrease in receptor activity will be called *receptor adaptation*, and a decrease limited to the effector response (including both effector and neuroeffector junction) will be termed *effector fatigue*. Following Harris (1943), response decrements that can be completely valued by these mechanisms will not be considered habituation. If a definition of learning such as "change in behavior under conditions of practice" is adopted, habituation must be included as an aspect of learning (Harris, 1943).

Studies of habituation may measure cellular or molecular responses or neuronal activity, including population activity, such as measures with EEG or functional imaging. These responses at the molecular, cellular or population levels may be

monitored in order to identify underlying mechanisms or they may be used as indices of habituation.

In the next paragraph, a description of specific features of habituation phenomenon will be presented.

1.2.3.Characteristics of habituation

Thompson and Spencer (1966) described nine characteristics of habituation, which will be noted in the brief summary that follows.

1. “Given that a particular stimulus elicits a response, repeated applications of the stimulus result in decreased response (habituation). The decrease is usually a negative exponential function of the number of stimulus presentations.”
2. “If the stimulus is withheld, the response tends to recover over time (spontaneous recovery).”
3. “If repeated series of habituation training and spontaneous recovery are given, habituation becomes successively more rapid” (this phenomenon might be called potentiation of habituation; see Figure 1.9).
4. “Other things being equal, the more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation.”
5. “The weaker the stimulus, the more rapid and/or more pronounced is habituation. Strong stimuli may yield no significant habituation.”
6. “The effects of habituation training may proceed beyond the zero or asymptotic response level” (see Figure 1.10).

7. "Habituation of response to a given stimulus exhibits stimulus generalization to other stimuli."
8. "Presentation of another (usually strong) stimulus results in recovery of the habituated response (dishabituation)."
9. "Upon repeated application of the dishabitulatory stimulus, the amount of dishabituation produced habituates" (this phenomenon might be called habituation of dishabituation; see Figure 1.11).

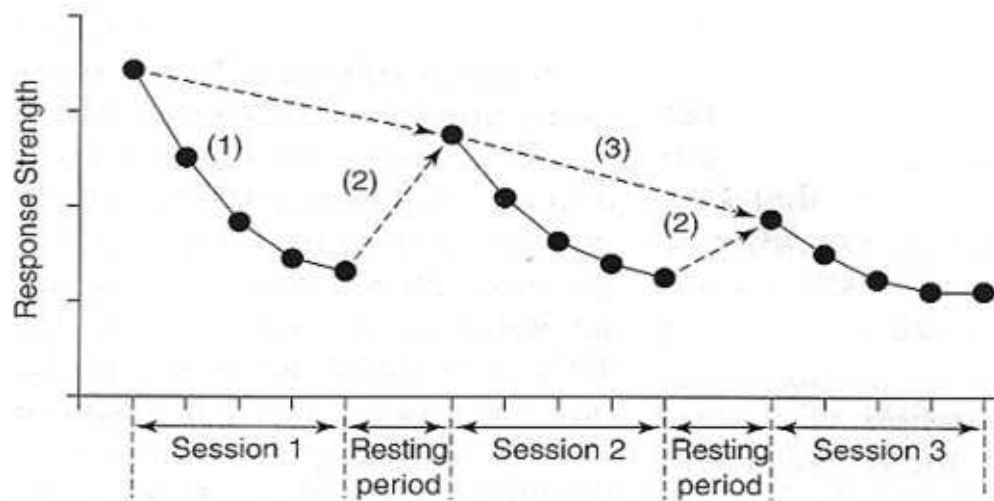


Figure 1.9: Characteristics of habituation: (1) short-term habituation; (2) spontaneous recovery; (3) long-term habituation.

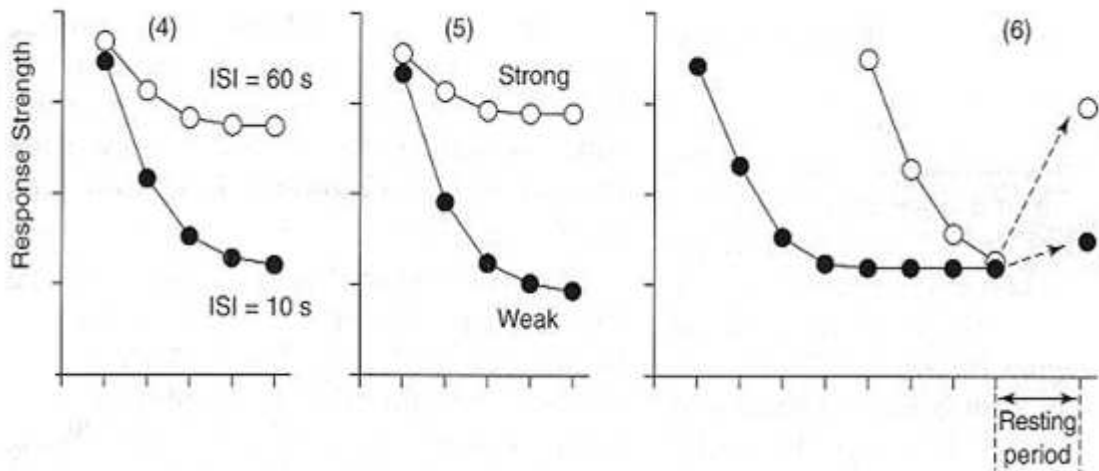


Figure 1.10: Characteristics of habituation: (4) the more rapid habituation with the more rapid frequency of stimulation; (5) the more rapid habituation with the weaker the stimulus; (6) habituation beyond the zero.

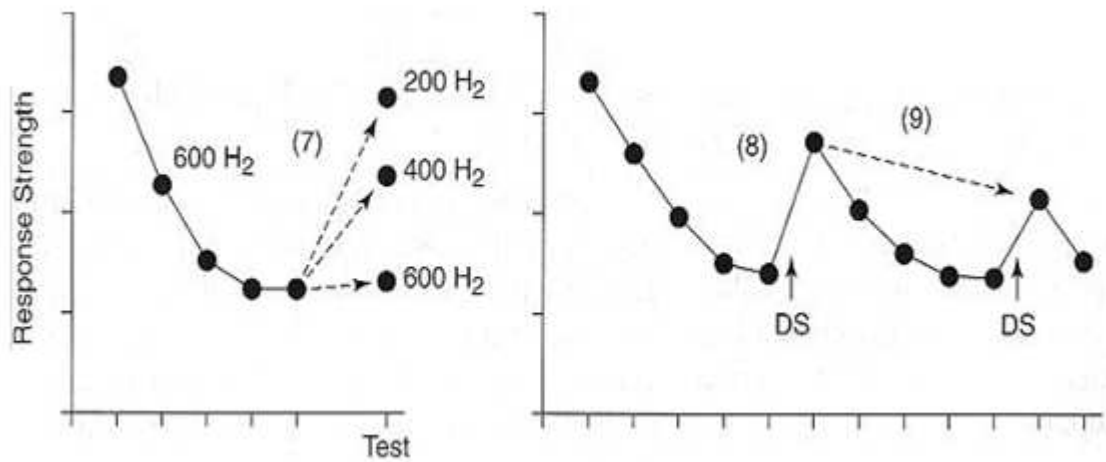


Figure 1.11: Characteristics of habituation: (7) generalization; (8) dishabituation; (9) habituation of dishabituation.

1.2.4. Habituation of emotional event-related potentials

In this section, studies that have investigated the influence of repetition on the affective response will be discussed in more detail. Recent researches have used

repetition paradigms in order to understand the nature of the processes underlying emotional processing.

The effects of picture repetition on the late positive potential component have been studied for the first time by Codispoti and coworkers (2006). The major prediction was the following: if the discrimination of affective stimuli is an obligatory process, the emotional modulation of the LPP should persist despite multiple repetitions.

More specifically, they compared LPP responses with autonomic measures, in order to clarify the specificity of each index of affective response as a function of repetition. They used pleasant, neutral and unpleasant pictures presented up to 60 times each, arranged in a habituation phase. In order to rule out effects linked to peripheral mechanisms, such as fatigue, they added a novel set of stimuli after the habituation phase.

In this study a clear dissociation between peripheral and central measures of the affective response emerges. Peripheral responses (both skin conductance and heart rate activity) were modulated by picture emotionality only at the beginning of the habituation phase, when pictures were only little repeated. The modulatory effect of picture emotional content on the autonomic nervous system was then eliminated after 60 repetitions of the same picture, as both skin conductance and heart rate responses did not show any differential activity as a function of picture content. In addition, all these responses showed an affective differentiation when, after the habituation phase, a novel set of

pictures was presented, excluding that the response decrease was due to peripheral mechanisms, such as fatigue.

The amplitude of the LPP component displayed an overall decrement during the habituation phase, suggesting a reduced attention allocation to repeated stimuli. On the other hand, despite this overall decrease, significant stimuli continued to elicit a greater LPP, compared to neutral scenes during the habituation phase.

These results clearly demonstrated that LPP and autonomic responses reflect different processes: autonomic responses reflect initial orienting reactions, with heightened sensory intake (heart rate) and preparation for action (skin conductance), which habituated rapidly, when the stimulus is easily recognized and no adaptive action is required, as it is the case for highly familiar (i.e. repeated) stimuli. On the other hand, the resistance to habituation of the LPP affective modulation suggests an obligatory processing of emotional stimuli, demonstrating that repetition did not alter the strong associations to appetitive and defensive systems (Codispoti et al., 2006).

In this study, a restricted analysis to ERPs waveforms at a few positions in the scalp, due to a small electrode array, did not permit to investigate the modulation of early ERP components over frontal and occipital sensors, and, to find a possible different modulation of early and late ERP components as a function of significance and repetition. Another important confound derived from the use of a long inter-stimulus interval (ISI; 10-20 sec), that might have

heightened the “novelty” of each stimulus despite its repetition, generating the resistance of the LPP emotional modulation during the habituation phase.

Thus, a new study investigated affective habituation using a dense sensor (60 channels) electroencephalographic (EEG) array and a shorter inter-stimulus interval (ISI; 2-3 sec) to further investigate repetition effects on the affective response (Codispoti et al., 2007). Neutral, pleasant and unpleasant pictures were repeated 90 times each across three blocks in a habituation phase. Similarly to the previous repetition study (Codispoti et al., 2006) the interpretation of reduced ERP amplitude due to fatigue was avoided by introducing a new set of pictures at the end of the habituation phase.

Consistent with previous results (Codispoti et al., 2006), the overall amplitude of the LPP decreased following multiple repetitions, but emotional pictures continued to prompt a greater LPP than neutral scenes, regardless of repetition. This effect supported the hypothesis about the activation of subcortical motivational circuits, that mediate the sensory and motor processes that support perception and action (Bradley, 2009). Thus, the hypothesis that a long inter-stimulus interval could be responsible for the recovery of the LPP emotional modulation during the habituation phase was disconfirmed.

In addition to the LPP, it has been described an early ERP component maximal in a window from 150 to 300 ms, that is modulated by emotional arousal, with emotional pictures prompting less negativity over frontal sensors and a corresponding less positivity over occipital sensors, compared to neutral scenes (e.g. Schupp et al., 2004).

Since both components have been considered as reflecting heightened attention to motivationally significant stimuli, the main purpose of the study was to clarify the precise nature of the processes involved in the modulatory effect of early and late ERPs (Codispoti et al., 2007). Results revealed that whereas both early and late components were similarly modulated by emotional arousal, picture repetition had different effects, suggesting different processes underlying these modulatory effects.

The early ERP component was partly affected by repetition, as reflected in a decrease across subblocks in the habituation phase. Interestingly, this component showed a complete recovery following a brief interval between blocks. The decrease within-block has been interpreted as reflecting increased perceptual fluency, due to a contribution of short-term memory representations (Jacoby & Dallas, 1981). These short-term representations are no longer available, generating a full recovery in the perceptual process following the interblock interval. This early ERP component has been interpreted reflecting perceptual processes involved in picture encoding.

Confirming previous data (Codispoti et al., 2006), both ERP components showed complete recovery when a new set of pictures were presented after the habituation phase, excluding that these components reflect a general decrease of vigilance.

These results were further supported by an additional analysis that implied the assessment of the temporal stability of these early and late ERP modulatory effects as a function of repetition and emotion. A new set of affective and

neutral pictures was presented to the same participants after ten days, with a procedure that was identical to that used in the first session. Whereas the late component showed stability between sessions, the early component did not, confirming that these two ERP components reflect different cognitive processes. More specifically, the LPP component seems to reflect enhanced attention to motivationally relevant scenes, while, early component is supposed to reflect low-level perceptual processing activated by the identification and recognition of relevant visual features (Ullman et al., 2002).

On the other hand, we should consider that in these previous studies picture repetition occurred among presentation of a variety of picture contents (distributed repetition) and this context in which repetitions were presented might have prompted the persistence of the LPP emotional modulation during the habituation phase. Thus, one hypothesis could be that the remaining LPP affective modulation was specifically prompt by the initial encoding required on each presentation, regardless of the high familiarity with the stimulus. For this reason, in order to investigate if it is motivational significance that mediates the persistence of the LPP emotional modulation despite repetition, Ferrari and coworkers (2011) investigated the effects of massed repetitions (the same picture repeated 30 times in row), on the modulation of the LPP.

Two other measures were employed in order to clarify the interpretations regarding the LPP modulation during massed repetition: the startle blink and the probe P3.

In general, an acoustic startle probe during affective picture viewing elicits changes in both the blink reflex and the P3 amplitude. It has been described that the P3 amplitude is generally smaller for acoustic probe presented during emotional, compared to neutral picture viewing, suggesting that this index reflects attention allocation. A plausible interpretation is that not much resource is available for processing the acoustic probe in an emotional context, due to an enhanced resource allocation to significant stimuli (Bradley et al., 2006; Bradley et al., 1999; Cuthbert et al., 1998). Differently, the reflexive blink response to the acoustic probe is modulated by hedonic valence, and it has been described that this modulatory effect of emotion persists despite repetition, indicating that this index reflects motivational significance (Bradley et al., 1993).

Results from this study showed that the amplitude of the LPP was affected by massed repetition particularly for emotional pictures, suggesting a decrease in attention allocation. However, enhanced LPP amplitude for emotional, compared to neutral pictures persisted even following massed repetition. The P3 amplitude to the acoustic probe increased with picture repetition, consistent with the idea that more attention is available to detect the probe when the picture has been already elaborated. More importantly, the difference in probe P3 amplitude between emotional and neutral pictures was reduced with massed repetition, indicating that the initial orienting and heightened attention allocation to emotional stimuli decreased with massed condition.

The affective modulation of the blink reflex, on the other hand, was not affected by repetition. Like probe P3 amplitude, massed repetition affected the

amplitude of the LPP specifically for emotional stimuli, reflecting a decrease in attention allocation. On the other hand, like the blink reflex, affective modulation of the LPP persists despite massed repetition, suggesting that it indexes motivational significance. Taken together, these data support a two-process account of LPP modulation during affective picture viewing, in which the amplitude of the late positive potential reflects both attention and emotion.

1.3. The Research Problem

As previously described, the resistance to habituation of the affective modulation of the Late Positive Potential (LPP) suggests an obligatory processing of emotional stimuli, demonstrating that repetition is not sufficient to eliminate the strong associations to appetitive and defensive systems.

However, in previous studies participants were only asked to look at the pictures in a passive viewing context (e.g. Codispoti et al., 2006; 2007), during which attentional resources were fully available to process the pictures. One hypothesis is that, given that in a passive viewing experimental condition the emotional content of the pictures is the most relevant aspect of the context, participants might devote attention to the pictures in a voluntary manner, in the absence of any other task demand.

The specific aims of this thesis were:

- To investigate the processes that determine the resistance of the emotional modulation of the LPP following multiple repetitions. In other words, to assess the role of obligatory or voluntary processes on the affective processing.
- To study the nature of the processes underlying the reduction of the emotional modulation of the LPP with repetition. In particular, to clarify if this reduction involves only attentional processes, or a contribution of memory processes as well.

Chapter 2

Habituation and affective response

Study 1: Habituation of emotional pictures during a categorization task

The idea is that the resistance to habituation of the affective modulation of the late positive potential in a passive viewing context might be due to the absence of any other demanding processes, rather than reflecting a mandatory categorization of motivationally significant stimuli.

- 1) The main goal of study 1 was to investigate whether the impact of repetition on the emotional modulation of the LPP is affected by a competing task. We might expect that (a) a competing task does increase or reduce the effect of picture repetition on the LPP affective modulation, suggesting that the processing of highly familiar emotional pictures may depend on the availability of attentional resources; or (b) a competing task does not change the impact of picture repetition on the LPP amplitude, confirming that the affective discrimination of visual stimuli is due to obligatory processing.
- 2) It is possible that a specific category (pleasant or unpleasant) is more automatically processed when compared to the other one, suggesting a role of the hedonic valence on the emotional modulation of the LPP after

massive repetition. Following these considerations, another aim of the present study was to investigate the impact of a competing task on the affective modulation of the LPP as a function of pleasant and unpleasant pictures.

- 3) Another purpose of study 1 was to quantify the effects of repetition on the amplitude of the LPP. For this reason, the experimental paradigm included a real block of novel pictures before the habituation phase. This was to assess the impact of repetition on the amplitude of the LPP, by comparing the novel block with the first repetition block. In fact, previous studies did not sufficiently address this aspect, due to the presence of repeated pictures in the block of novel pictures, leading to an initial reduction of the LPP amplitude.
- 4) A related question of study 1 was: are there differences in the affective modulation of the LPP elicited by novel pictures between passive and active contexts? Previous studies have used passive viewing contexts in order to assess the LPP affective modulation elicited by novel stimuli. Another interesting goal of the present study is to investigate whether the emotional modulation of the LPP in response to novel stimuli, generally observed in a passive context, might be modulated by a competing task.
- 5) The last purpose of study 1 was to assess the effect of generalization (an important characteristic of habituation) of the LPP affective habituation.
 - (a) If generalization to other stimuli occurs, then a reduction of the LPP amplitude will persist when a set of novel stimuli are presented after the

habituation phase. (b) If the reduction of the LPP amplitude during the habituation phase is specific to the repeated pictures, then the LPP amplitude will show a full recovery to novel pictures. Previous studies showed a recovery of the LPP affective modulation when a new set of pictures was presented after the habituation phase. However, given that in the “so-called” novel phase pictures were also repeated over trials, it was impossible to estimate whether the recovery of the LPP affective modulation was complete, or instead there was a partial recovery due to a generalization process. Therefore, in the present study we introduced all novel pictures before and after the habituation phase, in order to assess the magnitude of the LPP recovery to novel pictures, and thus the effect of stimulus generalization in the habituation process.

Method

Participants

Participants were 33 students (19 females) from the University of Bologna who volunteered to participate in the study. They had normal or corrected-to-normal visual acuity. The study was approved by the Ethical Committee of the Department of Psychology at the University of Bologna, and prior to participating, all subjects signed their informed consent. Due to technical problems, one female participant was excluded from behavioral analyses, and three participants (two males and one female) were excluded from the EEG analysis.

Materials and design

The visual stimuli were 252 color pictures of natural scenes selected from various sources, including the International Affective Picture System (IAPS), and public domain pictures available on the Internet, depicting people in pleasant (erotic and romantic couples), neutral (portrait or multiple people in a daily context) and unpleasant (mutilated bodies and human attack) contexts. The number of picture exemplars was equally distributed across picture contents. In addition to these stimuli, 280 pictures depicting a variety of means of transportation (e.g. trains, cars, airplanes) were selected to serve as target stimuli in a categorization task. Stimuli were presented on a 21" CRT monitor at 800 x 600 pixel resolution and 85Hz refresh rate, subtending 22.6° horizontal x 17.1° vertical degrees of visual angle.

For each participant, two sets of 256 pictures (126 pictures of people + 140 pictures of means of transportation) were selected to be presented in two different experimental sessions, that took place one after the other, within the same day. In one session, participants were required to perform a categorization task, indicating whether the presented image contained a mean of transportation (target) or not. In this session, pictures of people (pleasant, neutral and unpleasant) served as non-target stimuli. The other session was identical to the previous one, except that participants were only required to simply look at each picture without an explicit response task (i.e. passive viewing condition), such that there was not an instructed distinction among

picture categories. The experimental structure was identical between the two sessions (see Figure 2.1).

Of the 126 pictures depicting people (42 pleasant, 42 neutral, 42 unpleasant), six (two for each affective valence) were selected to be repeatedly presented throughout the habituation phase, for a total of 50 repetitions for each picture, whereas the remaining 120 pictures were arranged into two blocks of only novel pictures. Pictures of means of transportation were always novel pictures throughout the study, as the same exemplar was never repeated.

In each session, pictures were arranged in seven blocks of 80 trials each. In each block, 20 pictures belonged to the category of mean of transportation, whereas the remaining 60 trials were equally representative of pictures depicting people in pleasant, neutral and unpleasant contexts. A series of five blocks constituted the habituation phase, during which each picture exemplar (two for each affective valence) was repeated ten times in each block. Two blocks of only novel pictures were presented, respectively, before and after the habituation phase.

The specific set of pictures serving as novel or repeated varied across participants, such that, across subjects, all pictures were used in all conditions.

The order of picture presentation was pseudo-randomized with the restriction that no more than two times consecutively the same picture or a picture of the same valence occurred. E-Prime software synchronized the presentation of the stimuli and triggered EEG recording on each trial.

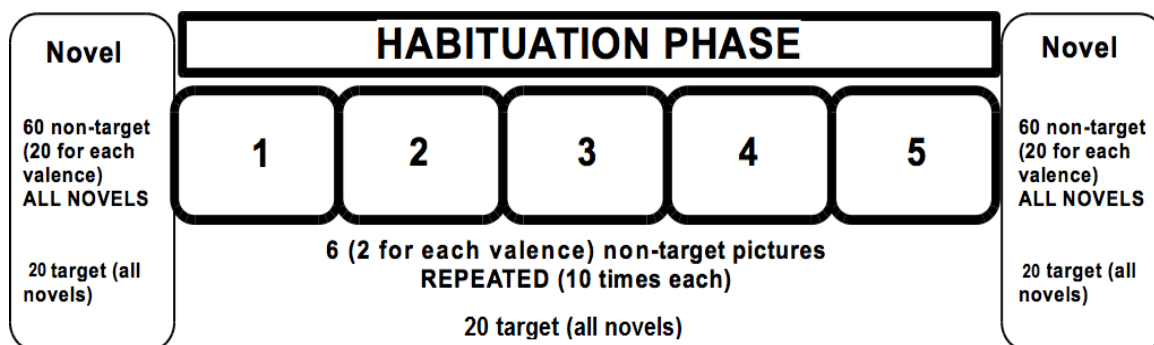


Figure 2.1: Experimental design in Study 1.

Procedure

After arrival at the laboratory, participants signed an informed consent form. Participants were then seated in a recliner in a small, sound-attenuated, dimly lit room, and the EEG sensor net was attached. In the categorization task, the participant was instructed to respond whether the presented image contained the target category (any mean of transportation) or not, by pressing one of two buttons on the keyboard (“z” or “m”) as fast and accurately as possible. For half of the participants, the letter-button mapping was reversed. In the passive viewing task, the participant was instructed that a series of pictures would be presented and that each picture should be viewed the entire time it was on the screen. Half of the participants performed the categorization task in the first session and the passive viewing task in the second session; the order was reversed for the other half. Between the two sessions, there was a 15 minutes break. Between each block, a 2-min break was given.

Participants sat in front of the computer monitor with their head supported by a chinrest. The distance between the eyes and the monitor was 100 cm for all subjects. During each trial, the image was displayed and remained visible for 1 s (see Figure 2.2). After picture offset, a grey screen was displayed for an amount of time ranging from 1500 to 2500 ms (intertrial interval, ITI).

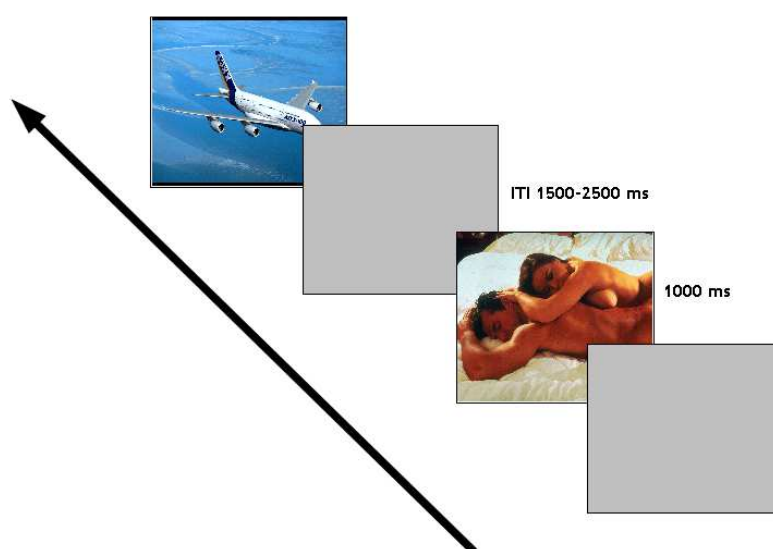


Figure 2.2: Sequence of events for all trials in Study 1.

EEG recording and processing

EEG was recorded at a sampling rate of 512 Hz from 257 active sites using an ActiveTwo system (Biosemi). The EEG was referenced to an additional active electrode during recording. Off-line analysis was performed using EMEGS (Peyk et al., 2011) and included filtering (40 Hz low-pass), removal of eye movement artifacts (Schlogl et al., 2007), artifact detection and sensor interpolation, and average reference. A baseline correction based on the 100 ms before stimulus onset was performed. Based on previous studies and on the maximal amplitude of the differential activity between emotional (average of pleasant and

unpleasant) and neutral, the Late Positive Potential (LPP) was scored over centroparietal areas as the average ERP amplitude in the 400-800 time interval.

Data Analysis

Given our main interest in investigating the impact of stimulus repetition on the affective modulation of the Late Positive Potential (LPP) as a function of task condition (categorization vs passive viewing), data analysis was performed only for pictures depicting people in pleasant, neutral and unpleasant contexts. These data were submitted to repeated measures analysis of variance (ANOVA; using the Greenhouse-Geisser correction) for within subject factors block (7 levels: 2 blocks of the novel phase, 5 blocks of the habituation phase), picture content (3 levels: pleasant, neutral, unpleasant), and repetition context (2 levels: passive, task). Also reaction times to non-target pictures (pleasant, neutral and unpleasant) were analyzed as a function of the blocks.

Results

Reaction Times

During the categorization task, reaction times to non-target pictures were affected by stimulus repetition [$F(6,186)=37.09$, $p < 0.0001$, $\eta^2_p = .55$; see Figure 2.3], with slower responses when pictures were novel compared to when they were repeated. More specifically, a progressive decrease of RTs was observed from Novel 1 to the end of the habituation phase [Novel1 vs Hab5: $F(1,31)=71$, p

< 0.0001, $\eta^2_p = .70$; Hab1 vs Hab5: $F(1,31)=36$, $p < 0.0001$, $\eta^2_p = .54$]; however, the presentation of a new set of novel pictures clearly prompted a significant RTs slowdown [Hab5 vs Novel 2: $F(1,31)=88.4$, $p < 0.0001$, $\eta^2_p = .74$], which did not differ from that observed in Novel 1 [Novel 1 vs Novel 2: $F(2,62)<2$, $p = 0.2$].

The effect of picture emotional content on reaction times was also modulated by stimulus repetition [$F(12, 372)=4.7$, $p<.0001$, $\eta^2_p =.131$]. As expected, the viewing of emotional pictures prompted slower reaction times compared to neutral pictures, but this was evident only when pictures were novel [both Novel 1 and Novel 2, $F(2,62)>20.3$]: RTs were slower for unpleasant stimuli compared to neutral and pleasant stimuli [$F(1,31)=27.43$, $p < 0.0001$, $\eta^2_p = .47$]. On the other hand, when pictures were repeated, RTs were no longer modulated by picture content [Hab1-Hab5, $p > 0.05$].

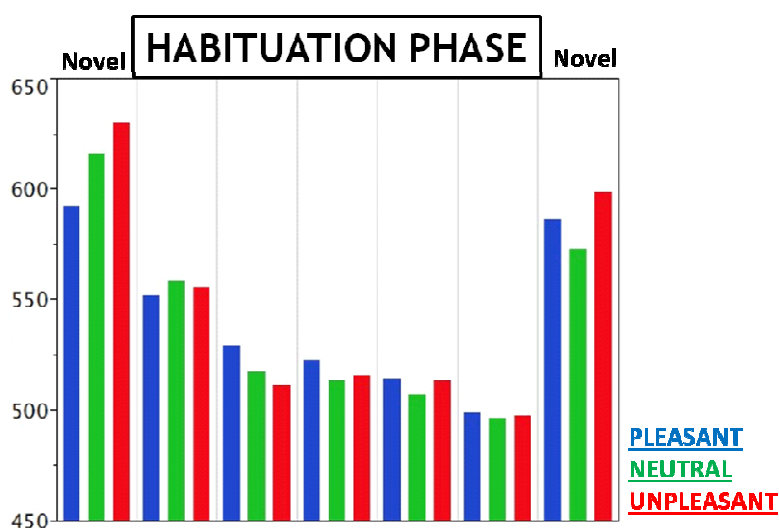


Figure 2.3: The effects of repetition on reaction times.

Late Positive Potential

In a passive viewing context, the Late Positive Potential (LPP) was modulated by picture content [$F(2,58)=80$, $p < 0.001$, $\eta^2_p = .73$], (see Figure 2.4, top portion), with pleasant and unpleasant pictures eliciting a more pronounced late positive potential compared to neutral pictures [$F(1,29) > 118$, $p < 0.001$, $\eta^2_p = .80$; $F(1,29) > 103$, $p < 0.001$, $\eta^2_p = .78$, respectively]. LPP magnitude for pleasant and unpleasant pictures did not differ [$F(1,29) < 1$, $p = 0.7$].

As expected, the affective modulation of the LPP was reduced by picture repetition, [$F(12,348)=4.2$, $p < .05$, $\eta^2 = .13$]. In fact, the enhanced positivity prompted by both pleasant and unpleasant pictures in the first novel block linearly decreased through the habituation phase [linear trend: Novel 1 to Hab5, $F_s(1,29) > 15.7$, $p < .0001$, for pleasant and unpleasant, respectively], such that the LPP affective modulation in the last block of the habituation phase was significantly smaller compared to that obtained with novel pictures [Novel1 vs Hab5, $F(2,58)=9$, $p < .005$, $\eta^2 = .24$] and the difference was specifically due to a decrease in the LPP for both pleasant and unpleasant pictures with picture repetition. After the habituation phase, a novel set of stimuli prompted a significantly larger affective modulation of the LPP compared to the last block of the habituation phase [Hab 5 vs Novel2: $F(2,58)=8.6$, $p < 0.005$, $\eta^2_p = .23$].

More relevant, the habituation pattern of the LPP affective modulation was very similar between the passive viewing and the task conditions (Task x Block x Picture content, n.s.). During the categorization task (see Figure 2.4, bottom portion), the LPP was clearly modulated by picture content [$F(2,58)=60$, $p <$

0.0001, $\eta^2_p = .67$], with larger LPP for both pleasant and unpleasant, compared to neutral, pictures [$F(1,29) > 125$, $p < 0.001$, $\eta^2_p = .81$; $F(1,29) > 47$, $p < 0.001$, $\eta^2_p = .62$, respectively], and this modulatory effect was preserved over the habituation block [$F(2,58)=34$, $p < 0.0001$, $\eta^2_p = .54$].

The task, on the other hand, prompted an overall larger centroparietal positivity for all conditions, compared to the passive viewing condition, [$F(1,29)=20$, $p < 0.001$, $\eta^2_p = .40$].

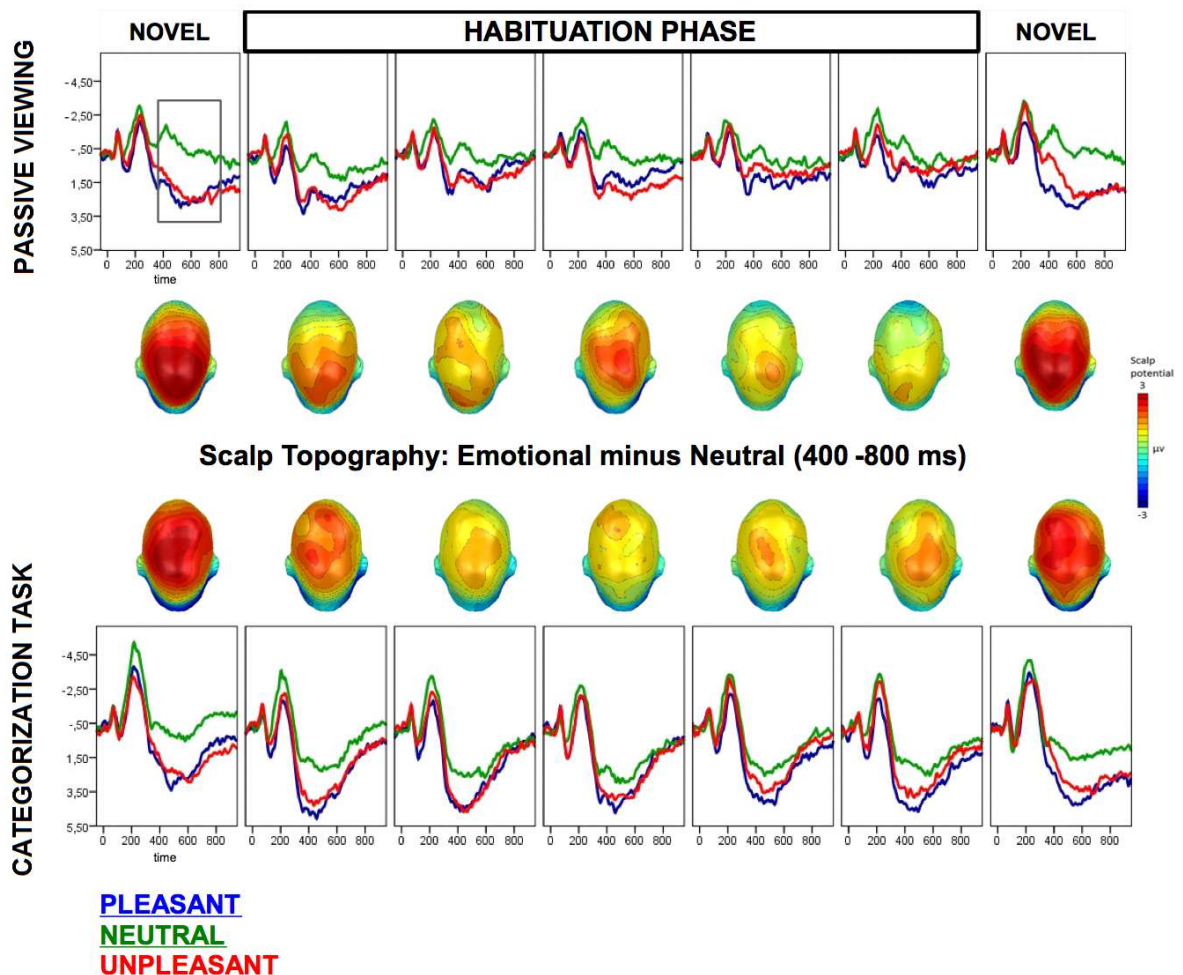


Figure 2.4: The effects of repetition on affective modulation of LPP during passive viewing (top portion) and categorization task (bottom portion).

Discussion

During passive viewing, the presentation of novel pictures elicited a larger positivity for emotional (both pleasant and unpleasant) compared to neutral pictures. This modulatory difference was largely reduced by picture repetition, due to an overall reduction in attention to repeated stimuli. However, the affective content of the stimuli continued to prompt a larger LPP, despite repetition (Codispoti et al., 2006; 2007, Ferrari et al., 2011). The present study clearly indicated that the presence of a categorization task, in which repeated pictures were non-target stimuli, did not change the impact of picture repetition on the emotional modulation of the LPP. Indeed, the impact of repetition on the emotional modulation of the LPP was similar between the passive and the task context, suggesting that this effect is not specific to a passive viewing context. Thus, the categorization of motivational pictures seems to be an obligatory process that does not depend on voluntary processes.

In the current study, during the categorization task, reaction times (RTs) to repeated pictures were faster compared to novel pictures. This remains consistent with the hypothesis that attention to the picture declines with stimulus repetition. Additionally, RTs to non-target pictures (emotional and neutral scenes) were modulated by picture emotionality only with novel pictures, with slower RTs to emotional (specifically for unpleasant scenes), compared to neutral pictures. These results suggest that emotional stimuli processing requires enhanced attention allocation, compared to neutral scenes, that is usually interpreted as reflecting attentional capture. RTs when pictures

were repeated were not modulated by picture content, suggesting that the familiarity of the stimulus probably reduces the impact of attentional capture on the behavioral response. A clear dissociation between behavioral and physiological responses were observed, reflected in the maintenance of the affective differentiation across the whole habituation phase of the LPP. One hypothesis is that RT and LPP emotional modulation may reflect different processes related to emotional processing. In order to investigate this possibility, future studies could assess this dissociation.

Overall, these data seem to support a two-process hypothesis of LPP modulation during affective picture viewing. The amplitude of the late positive potential reflects both differences in initial motivated attention, attenuated by repetition, and motivational significance (the activation of fundamental appetitive and defensive motivational systems), that is not affected by picture repetition (Bradley, 2009; Ferrari et al., 2010).

Study 2: Habituation to emotional pictures over time

In study 1, a repetition paradigm was used to investigate the processes underlying the affective processing. Study 2 was conducted in order to explore the contribution of attentional or memory processes involved in the reduction of the emotional modulation of the Late Positive Potential (LPP) with repetition. Previous studies have evaluated the impact of picture repetition on emotional response using only single session paradigms, for this reason:

- 1) The main purpose of study 2 was to investigate long-term effects of affective habituation, by assessing the affective response after 1-day interval. We might deduce that (a) the attenuated emotional modulation of the LPP elicited by stimulus repetition in the last block of session one is similar in magnitude to that elicited in the first block of session two, suggesting that effects of repetition on the emotional modulation of the LPP involve long-term memory representations. (b) Alternatively, the emotional modulation of the LPP might fully recover to its initial level after 1-day interval, indicating that the effects of repetition on the affective response involve only attentional processes.
- 2) A related, important aim of study 2 was to explore the trend of the emotional and neutral pictures during the habituation phase after 1-day interval, by comparing the habituation pattern of the first session with that observed in the second session. We might expect that (a) the

habituation pattern to emotional and neutral pictures of session two does not change from that observed in session one, indicating that repetition effects on the affective response remain stable over time. (b) On the other hand, the habituation pattern in session two might show a substantial decrease, as repetitions proceed, compared to that observed in session one, suggesting that repetition produces further effects over time on affective processing.

Method

Participants

27 participants (16 females) from the University of Bologna took part in the present study in exchange for a monetary reward. They had normal or corrected-to-normal visual acuity, and signed an informed consent prior to begin the experiment. The study was approved by the Ethical Committee of the Department of Psychology at the University of Bologna. Due to technical problems, two participants (one female and one male) were excluded from the EEG analyses.

Materials and design

The visual stimuli used in the present study were 126 images selected from the same pool of stimuli used in study 1. Pictures belonged to three different categories: people in pleasant (erotic and romantic couples), neutral (portrait or multiple people in a daily context) and unpleasant (mutilated bodies and human

attack) contexts. The number of picture exemplars was equally distributed across picture contents. Stimuli were presented on a 21" CRT monitor at 800 x 600 pixel resolution and 85Hz refresh rate, subtending 22.6° horizontal x 17.1° vertical degrees of visual angle.

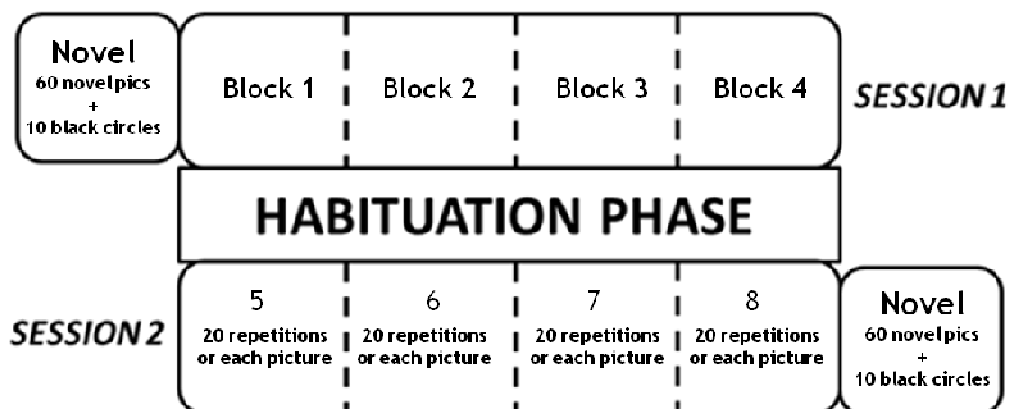
A picture with a black circle (2° x 2°) presented on the center of a grey background was also presented to serve as "dummy" target in order to make sure that participants were paying attention to the visual stimuli on the screen.

Participants took part into two different experimental sessions (one day apart). In each session, participants were presented with a block of novel pictures and a series of blocks of repeated pictures (habituation phase). For each participant, of the 126 pictures, six (two for each affective category) were selected to be repeatedly presented throughout the habituation phase, whereas the remaining 120 pictures were presented only once throughout the study (novel pictures). Of these novel pictures, half were selected to be presented in session one, whereas the other half was presented in session two. For each participant, the same set of six pictures was used in the habituation phase of both sessions. The specific set of pictures serving as novel or repeated varied across participants, such that, across subjects, all pictures were used in all conditions.

As shown in Figure 2.5, session one began with the presentation of a block of only novel pictures (20 pleasant, 20 neutral, 20 unpleasant), which was followed by the habituation phase, during which the same six pictures (2 pleasant, 2 neutral and 2 unpleasant) were repeatedly presented for a total of 80 repetition each. These repetitions were arranged in four blocks of 120 trials each. Session

two began with the habituation phase, which was identical to that of session one, followed by a block of novel pictures. Between each block, a 2-min break was given. In each block, the presentation of pictures of natural scenes (either novel or repeated) was sometimes (25%) interrupted by the appearance of a black circle that served as dummy target.

The order of picture presentation was pseudo-randomized with the restriction that no more than two times consecutively the same picture or a picture of the same valence occurred. E-Prime software synchronized the presentation of the stimuli and triggered EEG recording on each trial.



In each Block of the Habituation phase:
 - 6 pictures (2 for each valence) repeated 20 times
 - 20 black circles

Figure 2.5: Experimental design in Study 2.

Procedure

The experimental procedure was identical between the two sessions (one day apart). Subjects were seated in a chair in a dimly lit sound-attenuated room. After filling out the informed consent form, the EEG was attached. In addition, before starting session two, participants were asked few questions regarding

possible relevant events that might have occurred during the time interval elapsed since the end of session one until that moment.

The participant was instructed to look at a series of pictures presented on the screen, and press a button on the keyboard (“space”) whenever a black circle appeared on the screen (25% of the times). Pictures were presented on a screen located approximately 100 cm from the participant’s eyes. During each trial, the image was presented and remained on the screen for 2s (see Figure 2.6). After picture offset, a grey screen was presented (ITI) for about 1500 - 2500 ms.

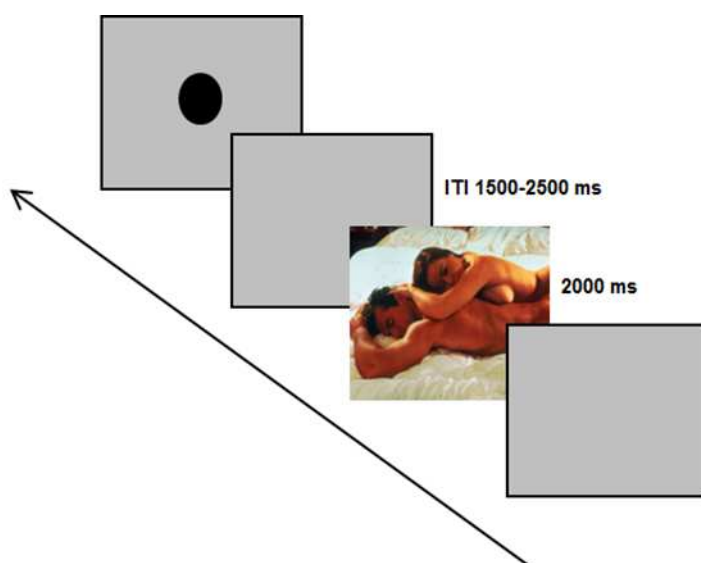


Figure 2.6: Trial procedure of Study 2.

EEG recording and processing

EEG was recorded at a sampling rate of 512 Hz from 257 active sites using an ActiveTwo system (Biosemi). The EEG was referenced to an additional active electrode during recording. Off-line analysis was performed using EMEGS

(Junghofer et al., 2006) and included correction of eye movements from the EEG signal (Miller, Gratton, & Yee, 1988), low-pass filtering at 40 Hz, artifact detection, and sensor interpolation (Junghofer, et al., 2000). Finally, the signal was re-referenced to the average of all channels, and the mean of the 100 ms preceding stimulus onset was subtracted from each waveform. Similar to study 1, the LPP was scored as the average amplitude of the ERP in the 400-800 ms time window over centro-parietal sensor sites.

Data Analysis

The LPP was analyzed in a repeated measure analysis of variance (ANOVA) using block (10: one block of novel pictures, eight blocks of the habituation phase, and one final block of again novel pictures), and picture hedonic content (3: pleasant, neutral, unpleasant) as factors. Greenhouse-Geisser corrections were applied where relevant. The eta squared statistic (η^2_p), indicating the proportion between the variance explained by one experimental factor and the total variance, has been calculated and is reported.

Results

LPP

Figure 2.7 illustrates the ERP waveforms averaged over centro-parietal sensors for pleasant, neutral, and unpleasant pictures in session 1 and session 2.

An overall interaction Block x Hedonic content [$F(18,432)=8.1$, $p<.0001$, $\eta^2_p=.3$] showed that the affective modulation of the Late Positive Potential (LPP) was

significantly affected by stimulus repetition. As expected, novel pictures prompted a clear modulation as a function of picture content, with larger positivity for emotional (both pleasant and unpleasant) compared to neutral pictures [$F_s(2,48) > 68$, $p < .0001$, $\eta_p^2 = .7$]. The LPP to pleasant and unpleasant pictures did not differ. With picture repetition, however, this modulatory effect was strongly reduced for pleasant and unpleasant over the eight block of the habituation phase [$F_s(7,168) > 10.5$, $p < .0001$, $\eta_p^2 > .3$]. On the other hand, the LPP to neutral pictures was unaffected by picture repetition ($p > .05$).

In particular, in day 1, the effect of repetition on the LPP was evident over the first two blocks of the habituation phase [Novel vs Block 1: $F_s(1,24) = 4.2$, $p = 0.05$, $\eta_p^2 > .15$; Block 1 vs Block 2: $F_s(1,24) = 24$, $p < 0.0001$, $\eta_p^2 > .50$, for pleasant and unpleasant, respectively]; in the following block, the modulatory difference remained stable.

Interestingly, after one-day break, the LPP prompted by the same set of pictures repeatedly presented in day 1 was similar to the one observed at the end of the previous habituation phase [Block 4 vs Block 5: $F(2,48) < 1$] (see also Figure 2.8). Although in the last two blocks of the habituation phase in day one the LPP was unaffected by stimulus repetition, in day two there was a further linear decrease in the LPP to pleasant and unpleasant pictures over the remaining blocks of the habituation phase [linear trend Block 5 to Block 8: $F_s(1,24) > 11$, $p < .001$]. In the last block of the habituation phase of day two, which corresponded to a total of 80 repetitions of the same picture, the difference between emotional (both

pleasant and unpleasant) and neutral pictures was still significant [$F(2,48)=5.3$, $p < 0.05$, $\eta^2_p = .183$; see Figure 2.7].

Finally, the introduction of novel pictures following the habituation phase elicited a significant reinstatement of cortical positivity [Bock8 vs Novel: $F(2,48)=18.31$, $p < 0.001$, $\eta^2_p = .43$], and the affective modulation of the LPP amplitude during the novel phase of the session 2 was not statistically different from that elicited in the novel phase of day 1 [$F(2,48)<1$].

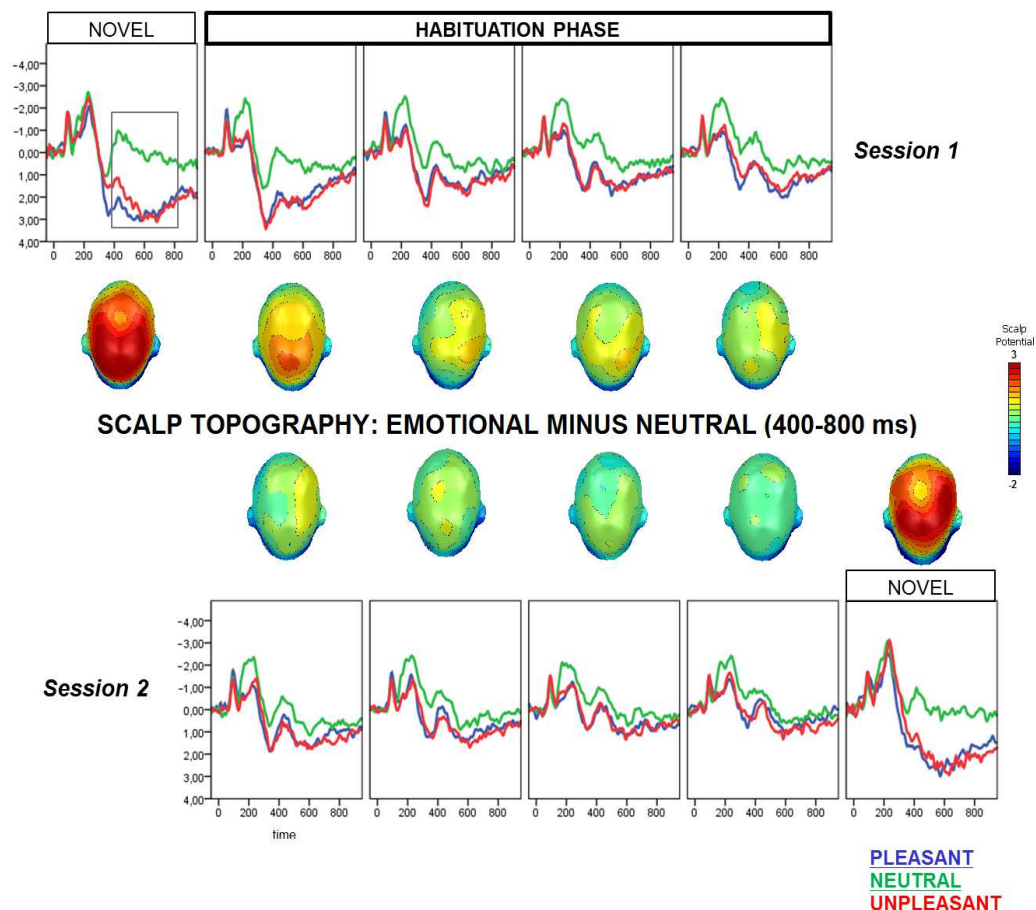


Figure 2.7: The effects of repetition on the LPP affective modulation during session 1 (top portion) and session 2 (bottom portion).

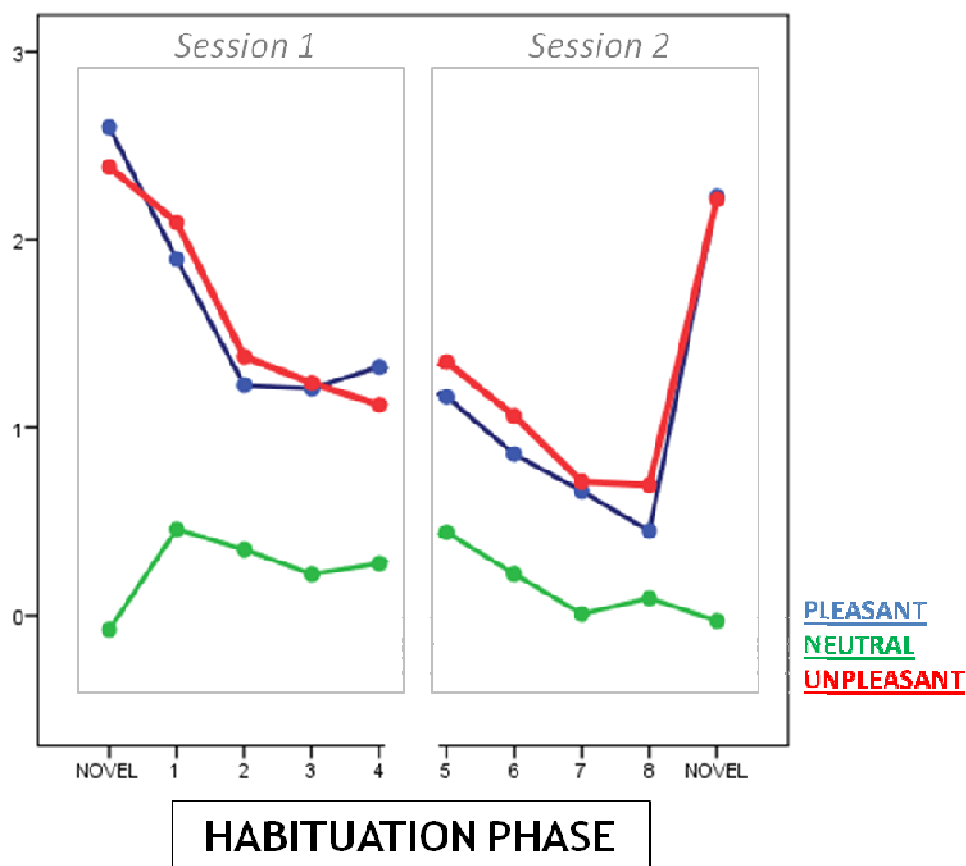


Figure 2.8: Different illustration of the LPP affective modulation as a function of repetition.

Discussion

The results of study 2 replicated and extended those obtained from study 1. As observed in a number of previous studies, during the presentation of novel pictures, a larger positivity for emotional (both pleasant and unpleasant) compared to neutral pictures was observed. This affective difference decreases during the habituation phase, consistent with the idea that familiar stimuli prompt a reduction in attentional allocation (Codispoti et al., 2006; 2007, Ferrari et al., 2008; 2011). In the present study, the persistence over time of

repetition effects on the emotional modulation of the LPP was investigated. These results clearly indicated that repetition effects on the LPP affective response might persist after a one-day interval. In particular, the magnitude of the emotional modulation of the late positive potential elicited by stimulus repetition in the last block of session one was very similar to one elicited in the first block of session two. This finding suggests a contribution of long-term memory representations on the affective habituation. Moreover, whereas the habituation pattern to emotional pictures during session one was relatively stable, the habituation pattern to emotional pictures during session two showed a substantial decrease as repetition proceeded. This finding suggests that the repetition might produce further effects on the affective response after a 1-day interval. More importantly, after eighty repetitions of the same picture, although all pictures were highly familiar, a larger LPP continued to be elicited by affective, compared to neutral stimuli, confirming the idea concerning the obligatory processing of those stimuli. These results are consistent with the interpretation that stimulus repetition does not change the associative strength of connections to subcortical motivational systems (appetitive and defensive), as reflected in the LPP modulation (Lang et al., 1997).

The reduction of the LPP amplitude during the habituation phase was not due to general fatigue but rather was specific to highly repeated stimuli, as shown by the recovery of the LPP when a new set of pictures was presented in the novel phase of session 2. Furthermore, the affective modulation of the LPP amplitude during the novel phase of session 2 was comparable in magnitude to that

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observed during the novel phase of session 1, excluding a possible generalization effect.

Chapter 3

Discussion

This present thesis directed a number of experimental questions regarding the cortical correlates of affective stimulus elaboration during repetitive picture viewing. This last chapter discusses main findings of the present research by underlining their importance for the initial experimental aims.

Study 1 aimed at investigating the role of obligatory or voluntary processes on affective processing, by introducing a competing task during repetitive exposure of the affective stimulus. Even when participants devoted their attentional resources to target stimuli, and emotional and neutral pictures were non-target stimuli, the habituation pattern of the affective response was analogous to that usually observed when participants passively look at the pictures. In other words, the impact of repetition on the affective modulation of the late positive potential was very similar between the passive and the task contexts. This finding suggests that the affective processing of visual stimuli may reflect an obligatory process that still occurs regardless of the specific categorization task.

Evidence shows that using a categorization task in which arousing pictures were presented either as target or as non-target stimuli, task relevant or inherently significant (emotional) stimuli showed similar cortical changes, as indexed by late positive potential. This suggests that directed and motivated attention

share analogous mechanisms. Moreover, the influence of task-relevance and content seems to be independent and additive (Ferrari et al., 2008). Similarly, when using different categories (high-arousing erotica and mutilation versus low-arousing control images) as target or non-target category served in separate runs, the LPP affective modulation was larger in the task context. This shows that explicitly directing attention toward an emotional dimension of the pictures may increase the processing of emotional picture content (Schupp et al., 2007). In line with Ferrari et al. (2008), Weinberg and coworkers (2012) confirmed the additive nature of emotional and target effects on the late positive potential, using a modified emotional oddball task, in which pleasant, neutral, and unpleasant pictures served as both targets and non-targets stimuli. In particular, the magnitude of the late positive potential was greater for both emotional (pleasant and unpleasant) pictures compared to neutral, and for target compared to standards.

Although different experimental procedures were used in various studies, it has been observed that LPP affective differentiation is preserved despite competing cognitive tasks (e.g. Codispoti et al., 2006; Hajcak et al., 2007). In particular, it has been described that emotional pictures - compared to neutral pictures - prompted a larger LPP, despite the fact that participants were engaged in an unrelated categorization task (animal target condition.) This suggests that the emotional modulation of the LPP was maintained even when emotional pictures acted as distractors (Codispoti et al., 2006). Along similar lines, Hajcak and colleagues (2007) investigated the modulation of the late positive potential to

emotionally arousing stimuli during a concurrent task difficulty (performing mathematics), reporting that this modulation was not susceptible to competing task demands. By manipulating task relevance, all these results suggest that the facilitated processing of motivationally significance stimuli seems to be mandatory and might not depend on the availability of attentional resources. Recently, an alternative view was proposed by Wiens and colleagues (2013), supporting the idea that directing attention away from emotional stimuli declines motivated attention. They manipulated directed attention by instructing participants to attend to either the emotional pictures (pictures task) or the surrounding letters (letter task,) showing that the effect of arousal on the LPP amplitude decreased when participants directed their attention to the letters. This decrease was higher for pleasant compared to unpleasant distractors. The results from study 1 are clearly consistent with the studies that describe a maintenance of the LPP affective modulation despite competing tasks (Codispoti et al., 2006; Hajcak et al., 2007).

Another important aim of study 1 was to investigate the effect of a competing task on the affective response as a function of a specific valence category. The present results suggest that the late positive potential is larger for emotional, both pleasant and unpleasant pictures, compared to neutral scenes, even when participants directed their attentional resources to the processing of target stimuli. In line with previous findings (Bradley et al., 2001; Cuthbert et al., 2000; Ferrari et al., 2008, 2010), these data indicate that the presence of a categorization task did not modify the sensitivity of the LPP to arousing pictures

(pleasant and unpleasant). With regards to this aspect, there is evidence that the late positive potential is modulated by the hedonic valence. In particular, it has been suggested that unpleasant stimuli might capture attention more automatically than both pleasant and neutral pictures, calling this effect “negativity bias” (Delplanque et al., 2004; Ito et al., 1998b; Smith et al., 2003). However, it has been demonstrated that the negativity bias in the LPP occurs only in specific experimental procedures, in which (a) unpleasant pictures were compared to low arousing pleasant pictures, that elicit a really small late positive potential, (b) and a modified emotional oddball paradigm was used, in which the emotional content of a picture determines its status as target or non-target (Weinberg et al., 2012). The present results do not show any evidence for a negativity bias in the magnitude to the LPP, corroborating the idea that pleasant and unpleasant pictures did not differ from one another when matched for motivational salience (Schupp et al., 2004; Weinberg and Hajcak, 2010).

The late positive potential, maximal in a 400 to 800 ms window over centro-parietal sensors, decreased in magnitude across the habituation phase. This confirms the hypothesis that minor attentional resources were allocated to the repeated pictures as a function of their familiarity. More interestingly, a significantly greater reduction in the late positive potential amplitude was observed by switching from the block of novel pictures to the first block of the repeated pictures. This suggests that 20 repetitions of the same picture are enough to lead to a substantial decrease of the LPP amplitude. Although previous studies found an overall decrement in the LPP amplitude with multiple

presentations of the same picture (e.g. Codispoti et al., 2006; 2007), it was not possible to quantify the impact of repetition on the amplitude of the LPP due to the absence of a comparison with a block of novel pictures at the beginning of the experimental design. In line with one of our aims, we have been able to quantify the contribution of repetition on the amplitude of the late positive potential, due to the comparison between the block of novel pictures and the first block of repeated pictures.

Although the presence of a competing task prompted an overall larger centro-parietal positivity in all blocks, the magnitude of the emotional modulation of the late positive potential to novel pictures during the categorization task condition was very similar to that observed during the passive viewing condition. Although they had different experimental procedures, Cuthbert et al. (1995) confirmed that the passive viewing condition elicits similar modulation of the late positive potential as an explicit evaluative task.

Almost all previous studies make use of a passive viewing condition, in which participants were only asked to look at the pictures in order to assess the magnitude of the late positive potential as a function of emotional arousal (e.g. Cacioppo et al., 1994; Cuthbert et al., 2000; Schupp et al., 2000). One of our hypothesis stated that the differential processing of emotional pictures, compared to neutral ones during passive viewing of novel pictures, may vary to that observed during a categorization task. This seemed to be due to the fact that participants needed to direct their attentional resources to the processing of target stimuli. The results of the present study showed that during novel

pictures presentation, even when participants were engaged in a categorization task, motivationally significant stimuli prompted a similar LPP affective modulation to the one generally observed in passive viewing context. This suggests that emotional processing is relatively unaffected by task demands and seems to rely on mandatory evaluation.

The last aim of study 1 was to assess the effect of generalization on the affective modulation of the late positive potential. In general, when habituation to a specific stimulus led the habituation to other stimuli, generalization occurred. The present results demonstrate that generalization did not take place in study 1, as shown by a comparison between the two blocks of novel pictures before and after the habituation phase. More specifically, the emotional modulation of the late positive potential to the second novel block was comparable in magnitude to the one elicited in the first novel block, demonstrating that the recovery of the LPP amplitude after the habituation phase was specific to the repeated pictures. In line with these results, previous studies showed a recovery of the affective differentiation when new pictures were presented after the habituation phase (e.g. Codispoti et al., 2006; 2007), but it was not possible to disentangle the effect related to generalization from the one relative to the specific repeated pictures on the LPP amplitude. In these studies the affective response elicited to new pictures has been compared with the response elicited in the initial block of the habituation, which shows an initial reduction of the LPP amplitude. Thus, in study 1, the comparison between the two novel blocks (before and after the habituation phase) allowed us to

exclude generalization effect on the LPP affective modulation. Consistent with previous studies, we have ruled out the contribution of peripheral mechanisms, such as fatigue, as affective modulation was recovered during the presentation of a new set of pictures after the habituation phase (e.g. Codispoti et al., 2006; 2007).

Study 2 aimed at investigating the nature of the processing underlying the reduction of emotional modulation of the late positive potential after multiple repetitions. In particular, the contribution of attentional and memory processes on the affective habituation was assessed. In order to respond to our first experimental aim, findings of the present study suggest that repetition effects on the LPP affective response persists after one-day break, showing a similar reduced magnitude of the emotional modulation of the LPP between the last block of the habituation phase of session one, and the first block of the habituation phase of session two. One hypothesis is that multiple repetitions of the same pictures produce a long-term memory trace of these emotional pictures, leading to maintenance of the affective habituation after a one-day break. These results seem to exclude an exclusive role of attentional processes on the reduction of emotional modulation of the LPP with repetition and suggest an interplay of attentional and memory processes on affective habituation. These results go beyond those of previous studies in indicating that the consolidation of arousing memories serves an adaptive function (e.g., McGaugh, 2000). Building on the evolutionary importance of assessing the imminence of a threat or an appetitive affordance, highly arousing-threatening or -sustaining

stimuli such as mutilated conspecifics or sexual mates are good candidates for memory storage (Bradley et al., 1992).

The second purpose of study 2 was to explore the habituation pattern to emotional and neutral stimuli during session two. These results showed a different trend of the emotional pictures during the habituation phase between the first and the second session. More specifically, during session two, the habituation pattern decreased progressively compared to session one, as repetitions of emotional pictures proceed. One hypothesis is that in session two, the presentation of the same pictures repeatedly presented in session one, produced a consolidated long-term memory trace, leading to a faster recognition and greater habituation of these stimuli.

It is important to emphasize that these results have important implications for our understanding of emotional processing. Our results suggest the existence of long-term effects of repetition on the affective response, leading to a major understanding of the mechanisms underlying the effects related to the repetitive exposure of emotional pictures.

It would be interesting to explore the exact duration of time in which consolidation of emotional pictures takes place. Future studies could assess the effects of repetition on the LPP emotional modulation after a longer time break. For example, it is possible that effects of affective habituation may persist after a week interval, providing a clinical instrument with which clinic individuals can be studied.

The present findings seem to suggest that even after a massive repetition, these affective cues engage the appetitive and defensive motivational systems, which have evolved to adaptively mediate interaction with the environment. The affective modulation of the LPP during repetitive exposure persisted even when participants were engaged in a competing task. This indicates that categorization of affective stimuli is an obligatory process and that repetition did not alter the strong associations of these cues to appetitive and defensive systems. Finally, the present findings seem to suggest that the effects of repetitions on the affective modulation of the LPP involve long-term memory processes. Future studies should further clarify the memory and affective mechanisms affecting these brain responses, and may explore the role of these motivational mechanisms in clinical populations.

Bibliography

- Arnold, M. B. (1960). *Emotion and personality* (Vols. I and II). New York: Columbia University.
- Bard, P. (1934). On emotional experience after decortication with some remarks on theoretical views. *Psychological Review*, 41, 309-329.
- Barrett LF. (2012). Emotions Are Real. 12 (3), 413-429.
- Barrett, L.F. (2001). Was Darwin Wrong About Emotional Expression? *Current Directions in Psychological Science* 20 (6), 400-406.
- Barrett, L.F. (2006). Solving the emotion paradox: Categorization and the experience of emotion. *Personality and Social Psychology Review*, 10, 20-46.
- Barrett, L.F., & Russell, J.A. (1999). Structure of current affect. *Current Directions in Psychological Science*, 8, 10-14.
- Barrett, LF. (2009). The Future of Psychology: Connecting Mind to Brain. *Perspective Psychology Science*, 4(4), 326-339.
- Bennett, D., Bendersky, M., & Lewis, M. (2002). Facial expressivity 4 months: A context by expression analysis. *Infancy*, 3, 97-113.
- Berntson, G. G., Cacioppo, J. T., Quigley, K. S., & Fabro, V. T. (1994). Autonomic space and psychophysiological response. *Psychophysiology*, 31, 44-61.
- Berridge, K.C. (1999). Pleasure, pain, desire, and dread: hidden core processes of emotion. In Well-Being, D. Kahnemann, E. Diener, and N. Schwarz, eds. (New York: Russell Sage Foundation).
- Berridge, K.C. (2007). The debate over dopamine's role in reward: the case for incentive salience. *Psychopharmacology (Berl.)* 191, 391-431.
- Blanchard, R. J., & Blanchard, D. C. (1989). Attack and defense in rodents as ethoexperimental models for the study of emotion. *Progressive Neuro-Psychopharmacological & Biological Psychiatry*, 13, 3-14.
- Bradley, M. M. & Lang, P. J. (2000). Affective reactions to acoustic stimuli. *Psychophysiology*, 37, 204-215.

- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: SAM and the semantic differential. *Journal of Experimental Psychiatry & Behavior Therapy*, 25, 49-59.
- Bradley, M. M., & Lang, P. J. (2007). Emotion and motivation. In J. T. Cacioppo, L. G. Tassinary, & G. Berntson (Eds.), *Handbook of psychophysiology* (3rd ed., p. 581-607). New York: Cambridge University Press.
- Bradley, M. M., Codispoti, M., & Lang, P. J. (2006). A multi-process account of startle modulation during affective perception. *Psychophysiology*, 43, 486-497.
- Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion*, 1 (3), 276.
- Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001a). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion*, 1, 276-298.
- Bradley, M. M., Codispoti, M., Sabatinelli, D., & Lang, P. J. (2001b). Emotion and motivation II: Sex differences in picture processing. *Emotion*, 1, 300-319.
- Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1991). Startle modification: Emotion or attention? *Psychophysiology*, 27(5) 513-522.
- Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1999). Affect and the startle reflex. In M. E. Dawson, A. Schell, and A. Boehmelt (Eds.) *Startle Modification: Implications for Neuroscience, Cognitive Science and Clinical Science* (pp. 157-183). Stanford, CA: Cambridge.
- Bradley, M. M., Lang, P. J., & Cuthbert, B. N. (1993). Emotion, novelty, and the startle reflex: Habituation in humans. *Behavioral Neuroscience*, 107, 970-980.
- Bradley, M.M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology*. 46, 1-11.
- Bradley, M.M. and Lang, P.J. (2000) Emotion and motivation. In: Cacioppo, J.T., Tassinary, L.G. and Berntson, G. (Eds.), *Handbook of Psychophysiology* (3rd ed). Cambridge University Press, New York.
- Bradley, M.M., Codispoti, M., Cuthbert, B.N. and Lang, P.J. (2001) Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion*, 1: 276-298.
- Bradley, M.M., Greenwald, M.K., Petry, M.C., and Lang, P.J. (1992). Remembering pictures: Pleasure and arousal memory. 8 (2), 379-390.

- Brown, J. S., Kalish, H. I., & Farber, I. E. (1951). Conditioned fear as revealed by magnitude of startle response to an auditory stimulus. *Journal of Experimental Psychology*, 32, 317-328.
- Cacioppo, J. T., Berntson, G. G., & Crites, S. L. (1996). Social neuroscience: Principles of psychophysiological arousal and response. In E. T. Higgins and A. W. Kruglanski (Eds.) *Social psychology: Handbook of basic principles*. (pp. 72 -101). New York: Guilford Press.
- Cacioppo, J. T., Uchino, B. N., Crites, S. L., Snyder-Smith, M. A., Smith, G., Berntson, G. G., & Lang, P. J. (1992). Relationship between facial expressiveness and sympathetic activation in emotion: A critical review, with emphasis on modeling underlying mechanisms and individual differences. *Journal of Personality and Social Psychology*, 62, 110-128.
- Cacioppo, J.T., Crites Jr., S.L., Gardner, W.L. and Bernston, G.G. (1994) Bioelectrical echoes from evaluative categorizations: A late positive brain potential that varies as a function of trait negativity and extremity. *J. Pers. Soc. Psychol.*, 67: 115-125.
- Campbell, B. A., Wood, G., & McBride, T. Origins of orienting and defensive responses: An evolutionary perspective. In P. J. Lang, R. F. Simons & M. T. Balaban (Eds.) *Attention and Orienting: Sensory and Motivational Processes*. (pp. 41-68). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Camras, L.A., & Fatani, S. (2008). The development of facial expressions: Current perspectives on infant emotions. In M. Lewis, J. Haviland-Jones, & L. Feldman Barrett (Eds), *Handbook of emotions* (3rd ed., pp.291-303). New York, NY: Guilford.
- Cannon, W. B. (1927). The James-Lange theory of emotions: A critical examination and an alternative theory. *American Journal of Psychology*, 39, 106-124.
- Cannon, W. B. (1931). Again the James-Lange and the thalamic theories of emotion. *Psychological Review*, 38, 281-295.
- Cardinal, R.N., Parkinson, J.A., Hall, J., and Everitt, B.J. (2002). Emotion and motivation: the role of the amygdala, ventral striatum, and prefrontal cortex. *Neuroscience Biobehavioral. Rev.* 26, 321-352.
- Chevalier-Skolnikoff, S. (1973). Facial expression of emotion in nonhuman primates. In P. Ekman (Ed.), *Darwin and facial expression*. New York: Academic Press, pp. 11-83.
- Codispoti, M., Bradley, M.M. and Lang, P.J. (2001) Affective modulation for briefly presented pictures. *Psychophysiology*, 38: 474-478.

- Codispoti, M., Bradley, M.M., Cuthbert, B.N., Montebarocci, O. and Lang, P.J. (1998) Stimulus complexity and affective contents: startle reactivity over time. *Psychophysiology*, 35: S25.
- Codispoti, M., De Cesarei, A. and Ferrari, V. (2011). The influence of color on emotional perception of natural scenes. *Psychophysiology*. 49:11-16.
- Codispoti, M., Ferrari, V. and Bradley, M.M. (2006a) Repetitive picture processing: autonomic and cortical correlates. *Brain Res.*, 1068: 213-220.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2006). Repetitive picture processing: Autonomic and cortical correlates. *Brain Research*, 1068, 213-220.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2007). Repetition and event-related potentials: Distinguishing early and late processes in affective picture perception. *Journal of Cognitive Neuroscience*, 19, 577-586.
- Codispoti, M., Mazzetti, M. and Bradley, M.M. (2002) Exposure time and affective modulation in picture perception. *Psychophysiology*, 39: S62.
- Courchesne, E., Hillyard, S. A., & Galambos, R. (1975). Stimulus novelty, task relevance and the visual evoked potential in man. *Electroencephalography and Clinical Neurophysiology*, 39, 131-143.
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., McManis, M., & Lang, P. J. (1998). Probing affective pictures: Attended startle and tone probes. *Psychophysiology*, 35, 344-347.
- Cuthbert, B.N., Schupp, H.T., Bradley, M.M., Birbaumer, N. and Lang, P.J. (2000) Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biol. Psychol.*, 52: 95-111.
- Cuthbert, B.N., Schupp, H.T., McManis, M., Hillman, C., Bradley, M.M. and Lang, P.J. (1995) Cortical slow waves: emotional perception and processing. *Psychophysiology*, 32: S26.
- Davis, M., & Lang, P. J. (2003). Emotion. In M. Gallagher & R. J. Nelson (Eds.), *Handbook of psychology*, Vol. 3: Biological psychology (pp. 405-439). New York: Wiley.
- De Cesarei, A., and Codispoti, M. (2006) . When does size not matter? Effects of stimulus size on affective modulation. *Psychophysiology*. 43 (2), 207-15.
- De Cesarei, A., and Codispoti, M. (2011). Scene identification and emotional response: which spatial frequencies are critical? *Journal of Neuroscience*. 31: 17052-17057.

- Delplanque, S., Lavoie, M.E., Hot, P., Silvert, L., Sequeira, H., 2004. Modulation of cognitive processing by emotional valence studied through event-related potentials in humans. *Neuroscience Letters* 356, 1-4.
- Dickinson, A., & Dearing, F. (1979). Appetitive-aversive interactions between appetitive and aversive stimuli. *Psychological Bulletin*, 84, 690-711.
- Dolan, R.J., and Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of Sciences*. 985, 348-55.
- Dolan, R.J. (2002). Emotion, Cognition & Behavior. *Science*, 298, 1191-1194.
- Dolin, A. O., Zborovskaya, I. I., & Zamakhovev, S. M. (1965). On the role of the orienting-exploratory reflex in conditioned reflex activity. In L. G. Voronin, A. N. Leontiev, A. R. Luria, E. N. Sokolov, & O. S. Vinogradova (Eds.), *Orienting reflex and exploratory behavior* (pp. 54-69). Washington, DC: American Institute of Biological Sciences.
- Ekman, P. (1992b). Facial expression of emotion: New findings, new questions. *Psychological Science*, 3, 34-38.
- Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology*, 17, 124-129.
- Ekman, P., Levenson, R. W., & Friesen, W. V. (1983). Autonomic nervous system activity distinguishes among emotions. *Science*, 221, 1208-1210.
- Epstein, A. N. (1971). The lateral hypothalamic syndrome. In E. Stellar & J. M. Sprague (Eds.), *Progress in physiological psychology* (Vol. 4, pp. 264-318) New York: Academic Press.
- Ferrari, V., Bradley, M.M., Codispoti, M., and Lang, P.J. (2011). Repetitive exposure: Brain and reflex measures of emotion and attention. *Psychophysiology*. 48, 515-522.
- Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2010). Detecting novelty and significance. *Journal of Cognitive Neuroscience*, 22, 404-411.
- Ferrari, V., Codispoti, M., Cardinale, R., & Bradley, M. M. (2008). Directed and motivated attention during processing of natural scenes. *Journal of Cognitive Neuroscience*, 20, 1753-1761.
- Fraiberg, S. (1977). *Insights from the blind: Comparative studies of blind and sighted infants*. New York, NY: Basic Books.
- Fridlund, A. J., Schwartz, G. E., & Fowler, S. C. (1984). Pattern recognition of self-reported emotional state from multiple-site facial EMG activity during affective imagery. *Psychophysiology*, 21, 622-637.

- Frijda, N. H. (1986). *The emotions*. Cambridge, England: Cambridge University Press.
- Galati, D., Miceli, R., & Sini, B. (2001). Judging and coding facial expression of emotions in congenitally blind children. *International Journal of Behavioral Development*, 25, 268-278.
- Galati, D., Scherer, K.R., & Ricci-Bitti, P.E. (1997). Voluntary facial expression of emotion: Comparing congenitally blind with normal sighted encoders. *Journal of Personality and Social Psychology*, 73, 1363-1379.
- Gatchel, R. J., & Lang, P. J. (1974). Effects of interstimulus interval length and variability on habituation of autonomic components of the orienting response. *Journal of Experimental Psychology*, 103, 802-804.
- Gellhorn, E., & Loofbourrow, N. (1963). *Emotions and emotional disorders: A neurophysiological study*. Harper and Row: New York.
- Gonsalvez, C. J., Barry, R. J., Rushby, J. A., & Polich, J. (2007). Target-to-target interval, intensity, and P300 from an auditory single-stimulus task. *Psychophysiology*, 44, 245-250.
- Grabenhorst, F., & Rolls, E. T. (2011). Value, pleasure, and choice in the ventral prefrontal cortex. *Trends in Cognitive Sciences*, 15, 56-67.
- Graham, F. K. (1979). Distinguishing among orienting, defense, and startle reflexes. In H. D. Kimmel, E. H. van Olst, & J. F. Orlebeke (Eds.), *The Orienting Reflex in Humans*. (pp. 137-167) Hillsdale, N. J.: Lawrence Erlbaum Associates.
- Hamm, A. O., Greenwald, M. K., Bradley, M. M., & Lang, P. J. (1993). Emotional learning, hedonic change, and the startle probe. *Journal of Abnormal Psychology*, 102, 453-465.
- Hare, R. D. (1973). Orienting and defensive responses to visual stimuli. *Psychophysiology*, 10, 453-463.
- Hare, R. D., Wood, K., Britain, S., & Shadman, J. (1971). Autonomic responses to affective visual stimulation. *Psychophysiology*, 7, 408-417.
- Harris, J.D. (1943) Habituated response decrement in the intact organism. *Psychological Bulletin*, 40, 385-422.
- Hajcak, G., Dunning, J., and Foti, D. (2007). Neural response to emotional pictures is unaffected by concurrent task difficulty: An event-related potential study. *Behavioral Neuroscience*, 121 (6), 1156-1162.
- Hawk, L.W. & Cook, E.W.(1997). Affective modulation of tactile startle. *Psychophysiology*, 34, 23-31.

- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*. New York: Wiley.
- Ito, T.A., Larsen, J.T., Smith, N.K., Cacioppo, J.T., 1998b. Negative information weighs more heavily on the brain: the negativity bias in evaluative categorizations. *Journal of Personality Social Psychology* 75, 887-900.
- Izard, C.E. (1972). *Patterns of Emotions*. New York: Academic Press.
- Jacoby, L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General*, 3, 300-324.
- James, W.(1884). What is an emotion? *Mind*, 9, 188-205.
- Johnson,R. Jr. (1986). A triarchic model of P300 amplitude. *Psychophysiology*, 23, 367-384.
- Junghoefer, M., Bradley, M.M., Elbert, T.R. and Lang, P.J. (2001) Fleeting images: a new look at early emotion discrimination. *Psychophysiology*, 38: 175-178.
- Junghöfer, M., Elbert, T., Tucker, D. M., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology*, 37, 523-532. doi: 10.1111/1469-8986.3740523
- Junghöfer, M., Peyk, P., Fleisch, T., & Schupp, H. T. (2006). Neuroimaging methods in affective neuroscience: Selected methodological issues. *Progress in Brain Research*, 156, 31-51.
- Keil, A., Bradley, M.M., Hauk, O., Rockstroh, B., Elbert, and Lang, P.J. (2002) Large-scale neural correlates of affective picture processing. *Psychophysiology*, 39: 641-649.
- Klorman, R., Weissberg, A. R., & Austin, M. L. (1975). Autonomic responses to affective visual stimuli. *Psychophysiology*, 11, 15-26.
- Klorman, R., Weissbert, R. P., & Wiessenfeld, A. R. (1977). Individual differences in fear and autonomic reactions to affective stimulation. *Psychophysiology*, 14, 45-51.
- Konorski, J. (1967). *Integrative activity of the brain: An interdisciplinary approach*. University of Chicago Press, Chicago, IL.
- Landis, C., & Hunt, W. A. (1939). *The startle pattern*. New York: Farrar and Rinehart.

- Lang PJ (1985): The cognitive psychophysiology of emotion: Fear and anxiety. In: Tuma AH, Maser JD, editors. *Anxiety and the Anxiety Disorders*. Hillsdale, NJ: Erlbaum, pp 131-170.
- Lang, P. J. (1979). A bio-informational theory of emotion imagery. *Psychophysiology*, 16, 495-512.
- Lang, P. J. (1984). Cognition in emotion: Concept and action. In C. Izard, J. Kagan, & R. Zajonc (Eds.), *Emotion, cognition & behavior*. New York: Cambridge University Press.
- Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology*, 30, 261-273.
- Lang, P. J., & Davis, M. (2006). Emotion, motivation, and the brain: re-examinations in animal and human research. *Progress in Brain Research*, 156, 3-29.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2001). International affective picture system (IAPS): Instruction manual and affective ratings (Technical Report No. A-5). The Center for Research in Psychophysiology, University of Florida.
- Lang, P.J. (1979). A bio-informational theory of emotional imagery. *Psychophysiology*, 16, 495-512.
- Lang, P.J. (1994). The varieties of emotional experience: a meditation on James-Lange theory. *Psychol. Rev.* 101, 211-221.
- Lang, P.J. (2010). Emotion and Motivation: Toward Consensus Definitions and a Common Research Purpose. *Emotion Review*, 2 (3), 229-233.
- Lang, P.J., & Bradley, M. M. (2013). Appetitive and Defensive Motivation: Goal-Directed or Goal-Determined? *Emotion Review*, 5 (3), 230-234.
- Lang, P.J., Bradley, M.M. and Cuthbert, M.M. (1997) Motivated attention: affect, activation and action. In: Lang, P.J., Simons, R.F. and Balaban, M.T. (Eds.), *Attention and Orienting: Sensory and Motivational Processes*. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ, pp. 97-135.
- LeDoux, J. (2012). Rethink the Emotional Brain. *Neuron*, 73, 653-668.
- LeDoux, J.E., and Muller, J. J. (1997). Emotional memory and psychopathology. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*. 352, 1719-26.
- Levenson, R. W., Ekman, P., & Friesen, W. V. (1990). Voluntary facial action generates emotion-specific autonomic nervous system activity. *Psychophysiology*, 27, 363-384.

- Libby, W. L., Jr., Lacey, B. C., & Lacey, J. I. (1973). Pupillary and cardiac activity during visual attention. *Psychophysiology*, 10, 270-294.
- Lindsley, D.B. (1951). Emotions. In *Handbook of Experimental Psychology*, S.S. Stevens, ed. (New York: Wiley), pp. 473-516.
- Löw, A., Lang, P. J., Smith, J. C., & Bradley, M. M. (2008). Both predator and prey: Emotional arousal in threat and reward. *Psychological Science*, 19, 865-873.
- MacLean, P. D. (1949). Psychosomatic disease and the "visceral brain"; recent developments bearing on the Papez theory of emotion. *Psychosomatic Medicine*, 11, 338-353.
- Macnab, R.M., and Koshland, D.E., Jr. (1972). The gradient-sensing mechanism in bacterial chemotaxis. *Proc. Natl. Acad. Sci. USA* 69, 2509-2512.
- Maltzman, I. (1979). Orienting reflexes and significance: A reply to O'Gorman. *Psychophysiology*, 16, 274-282.
- McGaugh, J. L. (2000.) Memory: A century of consolidation. *Science*, 287, 248-251.
- Mehrabian, A. (1970). A semantic space for nonverbal behavior. *Journal of Consulting and Clinical Psychology*, 35, 248-257.
- Mehrabian, A., & Russell, J.A. (1974). The basic emotional impact of environments. *Perceptual and Motor Skills*, 38, 283-301.
- Miller, G. A., Gratton, G., & Yee, C. M. (1988). Generalized implementation of an eye movement correction procedure. *Psychophysiology*, 25, 241-243.
- Moruzzi, G., and Magoun, H.W. (1949). Brain stem reticular formation and activation of the EEG. *Electroencephalogr. Clin. Neurophysiol.* 1, 455-473.
- Naatanen, R. (1979). Orienting and evoked potentials. In H. D. Kimmel, E. H. van Olst, & J. F. Orlebeke (Eds.), *The orienting reflex in humans* (pp. 61-75). Hillsdale, NJ: Erlbaum.
- Öhman, A. (1979). The orienting response, attention, and learning: An information-processing perspective. In H. D. Kimmel, E. H. van Olst, & J. F. Orlebeke (Eds.), *The orienting reflex in humans* (pp. 443-471). Hillsdale, NJ: Erlbaum.
- Öhman, A., and Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*. 108, 483-522.

- Osgood, C. E., Suci, G. J., & Tannenbaum, P. H. (1957). *The measurement of meaning*. Chicago: University of Illinois Press.
- Papez, J. W. (1937). A proposed mechanism of emotion. *Archives of Neurology & Psychiatry*, 38, 725-743.
- Pavlov, I. P. (1927). *Conditioned reflexes*. Oxford, UK: Oxford University Press.
- Peyk, P., De Cesarej, A., & Junghöfer, M. (2011). Electromagnetoencephalography software (EMEGS): Overview and integration with other EEG/MEG toolboxes. *Computational Intelligence and Neuroscience*, 861705.
- Plutchik, R. (1980). A general psychoevolutionary theory of emotion. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, Research and Experience*, vol 1 (Theories of Emotion), pp. 3-31. New York: Academic Press.
- Posner, M.I., Deane, S. (1994). Attentional networks. *Trends in Neurosciences*, 17, 75-79.
- Quigley, K. S., & Bertson, G. G. (1990). Autonomic origins of cardiac responses to nonsignal stimuli in the rat. *Behavioral Neuroscience*, 104, 751-762.
- Redican, W.K. (1982). An evolutionary perspective on human facial displays. In P. Ekman (Ed.), *Emotion in the human face* (2nd edn). Elmsford, New York: Pergamon, pp.212-280.
- Rescorla, R. (2001). Retraining of extinguished Pavlovian stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 115-124.
- Roch-Levecq, A. C. (2006). Production of basic emotions by children with congenital blindness: Evidence for the embodiment of theory of mind. *British Journal of Developmental Psychology*, 24, 507-528.
- Roessler, R., Burch, N. R., & Childers, H. E. (1966). Personality and arousal correlates of specific galvanic skin responses. *Psychophysiology*, 3, 115-130.
- Rohrbaugh, J. W., & Gaillard, A. W. K. (1983). Sensory and motor aspects of the contingent negative variation. In A. W. K. Gaillard & W. Ritter (Eds.), *Tutorials in event-related potential research: Endogenous components* (pp. 269-310). Amsterdam: North-Holland Publishing.
- Rolls, E. T. (1999). *The brain and emotion*. Oxford, UK: Oxford University Press.
- Rolls, E. T. (2003). Consciousness absent and present: A neurophysiological exploration. *Progress in Brain Research*, 144, 95-106.

- Rolls, E. T. (2005b). *Emotion explained*. Oxford, UK: Oxford University Press.
- Rolls, E. T. (2013). What Are Emotional States, and Why Do We Have Them? *Emotion Review*, 5 (3) 241-247.
- Rolls, E. T., & Grabenhorst, F. (2008). The orbitofrontal cortex and beyond: From affect to decision-making. *Progress in Neurobiology*, 86, 216-244.
- Rolls, E.T. (2013). What Are Emotional States, and Why Do we Have Them? *Emotion Review*, 5 (3), 241-247.
- Rushworth, M. F., Noonan, M. P., Boorman, E. D., Walton, M. E., & Behrens, T. E. (2011). Frontal cortex and reward-guided learning and decision-making. *Neuron*, 70, 1054-1069.
- Russell, J. A. (1980). A circumplex model of affect. *Journal of Personality and Social Psychology*, 39, 1161-1178.
- Russell, J. A., & Carroll, J. M. (1999). On the bipolarity of positive and negative affect. *Psychological Bulletin*, 125, 3-30.
- Russell, J. A., & Fehr, B. (1994). Fuzzy concepts in a fuzzy hierarchy: Varieties of anger. *Journal of Personality and Social Psychology*, 67, 186-205.
- Russell, J. A., & Feldman Barrett, L. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*, 76, 805-819.
- Russell, J. A., & Mehrabian, A. (1977). Evidence for a three-factor of emotions. *Journal of Research in Personality*, 11, 273-294.
- Russell, J.A. (2003). Core affect and the psychological construction of emotion. *Psychol. Rev.* 110, 145-172.
- Schachter, S. (1975). Cognition and centralist-peripheralist controversies motivation and emotion. In *Handbook of Psychobiology*, M.S. Gazzaniga and C.B. Blakemore, eds. (New York: Academic Press), pp. 529-564.
- Schachter, S., and Singer, J.E. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychol. Rev.* 69, 379-399.
- Schlögl, A., Keinrath, C., Zimmermann, D., Scherer, R., Leeb, R., & Pfurtscheller, G. (2007). A fully automated correction method of EOG artifacts in EEG recordings. *Clinical Neurophysiology*, 118, 98-104.
- Schneirla, T. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. Jones (Ed.), *Nebraska symposium on motivation* (pp. 1-42). Lincoln, NE: University of Nebraska Press.

- Schober, J., Weil, Z., and Pfaff, D. (2011). How generalized CNS arousal strengthens sexual arousal (and vice versa). *Horm. Behav.* 59, 689-695.
- Schober, J., Weil, Z., and Pfaff, D. (2011). How generalized CNS arousal strengthens sexual arousal (and vice versa). *Horm. Behav.* 59, 689-695.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Hillman, C. H., Hamm, A. O., & Lang, P. J. (2004). Brain processes in emotional perception: Motivated attention. *Cognition & Emotion*, 18, 593-611.
- Schupp, H.T., Cuthbert, B.N., Bradley, M.M., Cacioppo, J.T., Ito, T. and Lang, P.J. (2000) Affective picture processing: the late positive potential is modulated by motivational relevance. *Psychophysiology*, 37: 257-261.
- Schupp, H.T., Junghofer, M., Weike, A.I. and Hamm, A.O. (2003) Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. *Neuroreport*, 14: 1107-1110.
- Schupp, H.T., Stockburger, J., Codispoti, M., Junghofer, M., Weike, A.I. and Hamm, A.O. (2006) Stimulus novelty and emotion perception: the near absence of habituation in the visual cortex. *Neuroreport*, 17: 365-369.
- Schupp, H.T., Flaisch, T., Stockburger, J., and Junghofer, M. (2006). Emotion and attention: event-related potential studies. *Progress in Brain Research*, 156, 31-51.
- Shupp, H.T., Stockburger, J., Codispoti, M., Junghofer, M., Weike, A.I., and Hamm, A.O. (2007). Selective Visual Attention to Emotion. *Journal of Neuroscience*, 27 (5), 1082-1089.
- Sharpless, S., & Jasper, H. Habituation of the arousal reaction. *Brain*, 1956, 79, 655-682.
- Shepherd, G. (1988). *Neurobiology*, Second Edition (Oxford: Oxford University Press).
- Smith, N.K., Cacioppo, J.T., Larsen, J.T., Chartrand, T.L., 2003. May I have your attention, please: electrocortical responses to positive and negative stimuli. *Neuropsychologia* 41, 171-183.
- Sokolov, E. N. The higher nervous activity and the problem of perception. *Proceedings of the XIX International Congress of Psychology*, Montreal, 1955.
- Sokolov, Y. N. (1963). *Perception and the Conditioned Reflex* (S. W. Waydenfeld, Trans.). New York: Macmillan. (Original work published 1958).

- Tassinary, L. G., Cacioppo, J. T., & Geen, T. R. (1989). A psychometric study of surface electrode placements for facial electromyographic recording: I. The brow and cheek muscle regions. *Psychophysiology*, 26, 1-16.
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, 73, 16-43.
- Thorpe, W. H. Learning and instinct in animals. London : Methuen, 1956.
- Tinbergen, N. (1951). *The Study of Instinct* (New York: Oxford University Press).
- Titchener, E. B. (1908). *Lectures on the Elementary Psychology of Feeling and Attention*. New York: MacMillan Co.
- Tulving, E. and Schacter, D.L. (1990) Priming and human memory systems. *Science*, 247: 301-306.
- Turpin, G. (1986). Effects of stimulus intensity on autonomic responding: The problem of differentiating orienting and defense reflexes. *Psychophysiology*, 23, 1-14.
- Turpin, G., & Siddle, D. A. T. (1983). Effects of stimulus intensity on cardiovascular activity. *Psychophysiology*, 20, 611-624.
- Ullman, S., Vidal-Naquet, M., & Sali, E. (2002). Visual features of intermediate complexity and their use in classification. *Nature Neuroscience*, 5, 682-687.
- Verona, E., Patrick, C.J., Curtin, J. J., Bradley, M. M., Lang, P. J. (2004). Psychopathy and physiological response to emotionally evocative sounds. *Journal of Abnormal Psychology*, 113, 99- 108.
- Vrana, S. R., Spence, E. L., & Lang, P. J. (1988). The startle probe response: A new measure of emotion? *Journal of Abnormal Psychology*, 97, 487-491.
- Vuilleumier, P., Armony, J.L., Driver, J. and Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*. 30, 829-41.
- Weinberg, A., Hajcak, G., 2010. Beyond good and evil: the time-course of neural activity elicited by specific picture content. *Emotion* 10 (6), 767-782.
- Wienberg, A., Hilgard, J., Bartholow, B.D., and Hajcak, G. (2012). Emotional targets: Evaluative categorization as a function of context and content. *International Journal of Psychophysiology*, 84 (2): 149-54.

- Wiens, S., and Syrjanen, E. (2013). Directed attention reduces processing of emotional distracters irrespective of valence and arousal level. *Biological Psychology*, 94 (1), 44-54.
- Winton, W. M., Putnam, L. E., & Krauss, R. M. (1984). Facial and autonomic manifestations of the dimensional structure of emotion. *Journal of Experimental Social Psychology*, 20, 195- 216.
- Wundt, W.(1896). *Grundriss der psychologie* (6th ed.). Leipzig: Engelman.
- Yeomans, J. S., Steidl, S., & Li, L. (2000). Conditioned brainstimulation reward attenuates the acoustic startle reflex in rats. *Social Neuroscience Abstracts*. 30, 1252.