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The missing link in early emotional processing

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Abstract

Initial evaluation structures (IES) currently proposed as the earliest detectors of affective stimuli (e.g., amygdala, orbitofrontal cortex, or insula) are high order structures i) whose response latency cannot account for the first visual cortex emotion-related response (80ms), and ii) lack the necessary infrastructure to locally analyze the visual features that define emotional stimuli. Several thalamic structures accomplish both criteria. The lateral geniculate nucleus (LGN), a first-order thalamic nucleus that actively processes visual information, with the complement of the thalamic reticular nucleus (TRN), are proposed as core IESs. This LGN-TRN tandem could be supported by the pulvinar, a second order thalamic structure, and by other extra-thalamic nuclei. The visual thalamus, scarcely explored in Affective Neurosciences, seems crucial in early emotional evaluation.

Keywords: Emotion, Visual Thalamus, Initial Evaluation, Lateral Geniculate Nucleus, Thalamic Reticular Nucleus, Pulvinar, Superior Colliculus

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1. Introduction

In certain and relatively frequent situations, the capability to rapidly evaluate and respond to salient stimuli, such as the abrupt onset or rapid approach of a dangerous animal or hazardous object, is crucial for survival. These and other salient stimuli cause, by definition, emotional reactions that manifest at the physiological, subjective and/or behavioral level. The term "emotional" will be employed hereafter to refer to salient stimuli as well as their inherent multi-level consequences (Carretié, 2014; but see different and more specific definitions of "emotion" and "emotional", from diverse theoretical frames, in Brosch et al., 2010). Regarding the behavioral level, each tenth of a second may be critical. Indeed, motor reactions clearly revealing a previous discrimination of emotional from non-emotional stimuli may occur between four and five tenths of a second in those tasks especially designed to favor rapid responses, such as Go/Nogo tasks (e.g., Zhang & Lu, 2012). Evidently, this emotional motor reaction is preceded by emotional neural processing, which should be also rapid.

Event-related potentials (ERPs) show that emotional modulation of the visual cortex occurs in humans before 100 milliseconds (ms) from stimulus onset. For example, C1, the first visual ERP component originated at the cortical level, presents increased amplitude in response to emotional stimuli (Acunzo et al., 2019; Elder et al., 2010; Pourtois et al., 2004). The onset of this component occurs around 50 ms (e.g., Di Russo et al., 2003), its peak being produced as early as 63 ms in response to certain spatial locations (e.g., Capilla et al., 2016), and in any case before 100 ms (Rauss et al., 2011). This is compatible with intracranial recordings in human patients, in which the V1/V2 response to visual stimuli is recorded at 60 ms (Krolak-Salmon et al., 2003). Emotional modulation of C1 is produced between 60 and 100 ms, peaking at 80 ms (Acunzo et al., 2019; Eldar et al., 2010; Pourtois et al., 2004; see also Pizzagalli et al., 1999). This component originates in V1 or striate cortex (both terms will be employed indistinctly) according to several studies (Capilla et al., 2016; Di Russo et al., 2003), although the contribution of early stages of the extrastriate cortex, concretely V2 and V3, cannot be discarded (Ales et al., 2010). It is unanimously assumed that visual cortices need the previous operation of brain structures that monitor visual inputs, evaluate them, and "label" or signal certain stimuli as worth

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receiving preferential processing. Several proposals exist for these initial evaluation structures (IES), the most recurrent and noteworthy being the amygdala (e.g., see reviews or meta-analyses in Adolphs, 2008; Costafreda et al., 2008; Ohman, 2002; Zald, 2003), due to the direct inputs it receives from the thalamus, an issue that will be discussed later. Mainly in human and non-human primates, ventral prefrontal -or orbitofrontal- cortex (vPFC) and insula have also been proposed as emotional evaluation structures (e.g., see reviews by Rudebeck & Murray, 2014 and Norman et al., 2011, respectively). All of them have in common their mutual direct interconnections, as well as receiving early visual inputs and sending direct efferences to the visual cortex so they may modulate its activity through attentional changes (see a review on the connectivity of these structures in Carretié et al., 2009).

Two critical issues regarding the current proposals on initial emotional processing motivate this review. The first one is related to time. If visual cortices show emotional modulation at 80 ms approximately (or maybe ~10 or 15 ms earlier, since 80 ms is the peak differentiation), these evaluative structures should previously present a distinctive activity for emotional stimuli (with respect to neutral). Moreover, this activity should occur with time enough to transmit their information to visual cortices prior to 80 ms. Human intracranial recordings of evaluation structures accumulated up to the present are not compatible with this prerequisite. Thus, the shortest ~~reported~~ responses sensitive to the emotional content of visual stimulation have been reported at 74 ms in the case of human amygdala, and only for faces; responses to other emotional visual stimuli were produced beyond 150 ms (Méndez-Bértolo et al., 2016). In the case of the other two structures mentioned above, the earliest reported saliency activations are produced over 80 ms: 120 ms in vPFC (for both faces and scenes: Adolphs et al., 2006), and 140 ms in the case of insula (only faces have been explored, to the best of our knowledge: Willenbockel et al., 2012). May information from amygdala, the fastest of these structures according to current data, reach V1 before 80 ms from stimulus onset? Taking into account the average conduction velocity in the cerebral middle-range neurons in humans, information from amygdala should take over 20 ms to reach V1 or V2 (Table 1). The probability that the other proposed evaluation structures, such as vPFC and insula (among others: Lee & Siegle, 2009),

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may act as IES and cause the emotional V1 peak response observed at 80 ms is even more remote (Table 1). In sum, and taking into account the available data, evaluative structures proposed up to present cannot be responsible for the emotion effect observed in V1 at 80 ms.

*** Table 1 ***

The second issue motivating this review is related to the architecture of IESs. These structures should be able to constantly monitor, evaluate and label (if pertinent) the ascending visual information. This requires an in situ processor of the visual input capable of recognizing certain visual features, such as shapes, colors or motion patterns. Ultimately, this visual processing would require modules that constantly analyze the visual information transmitted by the retinal ganglion cells. Each module would process a visual region or receptive field -RF-, which is the information unit transmitted by ganglion cells. These modules could be conceptualized as a sort of *focal* processors in terms of the total extension of the visual field. As explained in forthcoming sections, these focal processing modules, which indeed exist in different parts of the brain, consist of retinotopically organized visual processing cells. Parallely, IESs should also be capable of *global* processing. Global modules would transversally manage several focal modules to extract general information of the visual input, which often involves several focal RFs. For example, the shape of a spider close to us -its legs, its head, its abdomen- would involve several RFs (several focal processing modules), but the “spider shape” would require an in situ global processor that puts together the information of those individual RFs: Figure 1. These in situ processors should mark the ascending visual information if a relevant stimulus is detected, a “decision” that requires the capability of storing visual features that have been associated with emotional situations in the past. This storage should be also local, so initial evaluation may keep its speed.

*** Figure 1 ***

In summarized terms, IES should be visual processors. Amygdala, vPFC or insula have shown to increase their activity in response to certain visual stimuli (mainly emotional), and to

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receive direct inputs from visual cortices, but this is not equivalent to be visual processors. Many other brain areas also receive visual inputs and respond to them, such as the hippocampus, the anterior cingulate cortex, the motor cortices, etcetera, but they are not considered visual processors. Additionally, the infrastructure we are mentioning (retinotopy, focal and global feature processing) has not been described for them up to the present. A tentative explanation is that they are global processors (in the terms explained above), but this seems improbable, since global processors need to interconnect many focal modules to extract global features. This ramified interconnectivity with retinotopic structures of the brain has not been described for amygdala and neither for vPFC nor insula. However, the fact that these structures do not accomplish the necessary conditions to be IESs does not mean they are not crucial in emotional processing. The key issue is that they receive pre-processed (pre-evaluated) information (also the amygdala, the fastest responding among the three: Pessoa & Adolphs, 2010). The most probable roles of these structures, and the stage within emotional processing in which they may intervene, will be discussed in the final section. Therefore, we are before a “missing link” in emotional processing. Concretely, the IESs are yet to be defined.

2. The thalamus hypothesis

Sensory thalamus, and particularly the visual thalamus, is often conceptualized as a relay to which sensory information arrives from the retina and from which this information is transmitted to the visual cortex and other brain areas. This role as a relay is understood as passive, the capability of processing this information being assigned to other cerebral structures. In fact, as pointed out by Ghodrati and collaborators (2017), the models and representations of the visual processing route start at V1, never before. However, the capability of visual thalamus for processing and modulating the information it receives before transmitting it to other neural levels has been demonstrated in the cognitive field. For example, certain thalamic nuclei later described may filter or enhance the visual information they receive before sending it to the visual cortex as a function of attention (see reviews in Ghodrati et al., 2017; Halassa & Kastner, 2017; Saalmann & Kastner, 2011; Weyand, 2016). In other words, these thalamic structures may send different

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signals to visual cortices in response to exactly the same stimulus depending on whether it is attended or not. The proposal here is that this capability of the thalamus to process the information it receives may be extended to the emotional domain.

It is relevant to note that the idea of the thalamus as a structure crucial in "emotional labeling" of sensory inputs is about one century old. Cannon (1927), for example, postulated that "the peculiar quality of the emotion is added to simple sensation when the thalamic processes are roused" (p. 120). A similar idea was previously defended by Head (1920). These sound proposals were based, due to the scientific limitations of the epoch, on very scarce data mainly obtained from behavioral observations, and lacked concretion on the mechanisms by which the thalamus evaluated sensory inputs as emotional, or on the nuclei involved. However, Lashley, explicitly referring to this proposal, indicated a decade later that "the supposed evidence that the thalamus adds the affective or emotional character to sensations breaks down completely when subjected to critical analysis" (Lashley, 1938, p. 60). Parallely, the first influential model of the emotional brain was published by Papez (1937). In it, the key structure in charge of evaluating and labeling sensory inputs as emotional was not the thalamus, but the hypothalamus and other brain structures: "the sensory excitations (...) receive their emotional coloring from the concurrent processes of hypothalamic origin which irradiate them from the gyrus cinguli" (p. 729). Later, MacLean (1949), whose model of the emotional brain was strongly settled on Papez's, successfully recovered the term "limbic" (coined by Broca in 1878), to refer to this "system" or circuit whose structures are in the *limbo* or intermediate area between brainstem and cortex. The limbic system, as the Papez's circuit, included the thalamus, but its function in both models was connective and secondary. The central element of the MacLean model was, instead, the hippocampus.

This "golden age" of the study of emotion within the field of Neuroscience (i.e., the first half of the XX century) was followed by a steady period in which the limbic system concept dominated and was not significantly compromised by new findings or proposals. The situation changed in the final years of that century, in which some influential postulates displaced the epicenter of the emotional brain from hypothalamus or hippocampus, as in Papez's or MacLeans'

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models, to other structures. For example, LeDoux (1992) signaled the amygdala as a core element of the emotional brain, proposing at the same time some strong and sound reasons to overcome the limbic system model, and Damasio (1994) stressed the crucial role of vPFC (whereas the amygdala was present in the MacLean's model -not in Papez's, who explicitly indicated that "its function is unknown", 1937, p. 742-, and also the vPFC, their role was not as central as in contemporary Affective Neuroscience). This is currently the dominant vision since, as indicated, these structures have repeatedly been proposed to be involved in the emotional evaluation and labeling of visual inputs. In any case, this current vision inherits from the Papez-limbic age the idea of thalamus as a mere connecting hub from sensory organs to other brain structures, or between different brain structures. Indeed, thalamic nuclei have been largely ignored as recording placement during the 60-year history of human intracranial exploration of emotion, despite they have been repeatedly accessed for stimulation scopes (see a review in Guillory & Bujarsky, 2014). Similarly, non-invasive studies employing hemodynamic techniques have focused their regions of interest -ROIs- on the thalamus only in exceptional cases, as we are about to see.

During the last century (1920-2020), the number of paper titles in which both the words amygdala and emotion appears is 399 according to Google Scholar, more than thirty times the number of those including the words emotion and thalamus or any of its visual nuclei, which is 13 (search made on April 2020). Already in 2008, 385 studies recording amygdala responses to emotional stimuli through PET or fMRI existed (Costafreda et al., 2008). Table 2 shows a summarized review of the human studies reporting significant differences between the thalamic response to emotional and to neutral visual stimuli. A total of 56 studies were detected after a systematic review (see details of the search procedure in Table 2 legend). Despite only a portion of these studies defined a ROI for the thalamus, as indicated (26.8%), several experiments employed a whole brain analytical strategy that allowed the analysis of its activity. As may be appreciated, the direction of differences is "Emo>Neu" in all cases, and it is observed regardless the type of emotional visual stimuli (faces, scenes, bodies, etc.) and the type of task (explicit -asking for the emotional categorization of stimuli- or implicit -asking for non-emotional

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characteristics, such as the gender of emotional expressions-). However, it is important to note that these studies employ haemodynamic techniques (fMRI or PET), and due to the spatial resolution limitations of the majority of scanners, this thalamic sensitivity to emotional stimulation is not located in specific nuclei except in a few studies (28.6%), the pulvinar (the biggest thalamic nucleus in humans and other mammals) being the most recurrent. This limitation, along with usual analytic strategies (e.g., defining relatively big cluster sizes), hinder the activity of small thalamic nuclei, such as lateral geniculate nucleus, to be detected (but see Van den Stock et al., 2011). More importantly, these recording techniques also present low temporal resolution, so brief responses are difficult to detect, and in any case, it is not possible to determine whether the recorded thalamic response is produced in the initial, ascending course of visual information or in later, recurrent phases (or in both). Scarce studies using electromagnetic brain signals, characterized by their high temporal resolution, point to the former possibility, whereas results should be taken with certain caution due to their limitations in spatial resolution. Thus, magnetoencephalographic (MEG) data show gamma band enhancement –an index of increased activity- in the thalamic area from 20 ms in response to fear facial expressions (Luo et al., 2007; this latency is not a discrete onset, but the beginning of the time-frequency analysis window), and another MEG study describes increased amplitudes of the thalamic response to emotional faces at 35 ms (Liu et al., 2015).

*** Table 2 ***

The part of the thalamus that processes visual information, or visual thalamus, comprises several structures that may be classified as first-order nuclei, which receive visual information mainly from the retina, and higher order structures, receiving main visual inputs from other brain areas. As described next, LGN, which is a first-order structure, as well as the pulvinar and the thalamic reticular nucleus (TRN), both second order structures, are the main nuclei of the thalamus in charge of processing visual information (but not exclusively visual, in the case of pulvinar and TRN): Figure 2. At least in the initial, fastest visual processing, which is the main focus of this review, pulvinar and geniculate routes are parallel and relatively independent. For obvious reasons, the physiological properties of these nuclei have been scarcely studied through

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intracranial recordings in humans, but data from non-human primates, relatively numerous mostly in macaques and marmosets, provide information widely generalizable to our species. Crucially, as we are about to see, the three structures are capable of modulating the information they receive so it may be amplified or filtered prior to its submission to other brain areas, and their structure and function make them solid candidates to be IESs.

*** Figure 2 ***

3. First-order visual thalamus: LGN

As schematized in Figure 2, LGN is an "U" shaped structure, its neurons presenting a retinotopic distribution. LGN receives direct inputs from the retina through ganglion cells, and the majority of geniculate neurons receiving them directly project to the visual cortex, with no intermediate neurons (Weyand, 2016). These geniculo-cortical neurons, also named relay neurons, are of three different types, parvocellular (P), magnocellular (M) and koniocellular (K), and are distributed in different layers. Each of these relay cells receive dominant inputs from one specific ganglion retinal cell, but also secondary inputs from other two or three ganglion cells (Ghodrati et al., 2017), even of different type (up to date, at least 17 types of ganglion cells have been described in the primate visual system: Grünert & Martin, in press). Relay neurons would act mainly as focal processors (Figure 1), but there are several differences among the three types. Thus, P cells are more sensitive than M to color, higher spatial frequencies, lower temporal frequencies, and have lower sensitivity to luminosity contrast, whereas M cells are more responsive to luminosity contrast, lower spatial frequencies, higher temporal frequencies, and are more involved in motion processing, among other processing differences (Derrington & Lennie, 1984; Schiller & Malpeli, 1978; DeYoe & Van Essen, 1988; 456 Maunsell & Newsome, 1987). K neurons, much less studied, are a physiologically heterogeneous group of cells, and some of them exhibit motion and orientation selectivity, others are more sensitive to color, and even part of them seem unresponsive to visual information (Martin & Solomon, 2019). In general, K cells present lower spatial selectivity and longer response latencies compared to P and M (Zeater et al., 2019). Geniculocortical projections are mainly directed to striate cortex -P, M and K cells reaching different layers of this cortical area-, but also to extrastriate visual cortex: V2, V3, V4

and MT receive geniculate inputs, mainly from K cells (Ghodrati et al., 2017). This direct transmission of information from the retina to visual cortices through a two-neuron design facilitates rapid transmission of information.

As indicated, this relay role classically stressed for the LGN in the literature, and considered relatively passive, is actually modulated by several factors. First, only about 10% of synaptic inputs to LGN neurons proceed from the retina (Ghodrati et al., 2017). On one hand, the visual cortex sends feedback neurons to LGN and is able to modulate its activity (e.g., Marrocco et al., 1996). On the other hand, LGN neurons receive subcortical inputs, which account for approximately 30% of LGN synapses (Ghodrati et al., 2017). Interestingly, all subcortical structures innervating LGN reach K cells, which receive glutamate afferences from superior colliculus, gabaergic from the nucleus of the optic tract (NOT), cholinergic from both the parabigeminal nucleus and the pedunculopontine tegmentum (PPT), and histaminergic from the tuberomammillary nucleus (TMN) (Casagrande et al., 2005; Zeater et al., 2019). P and M cells also receive inputs from NOT, TMN and PPT (Casagrande et al., 2005; Zeater et al., 2019).

Second, retinal ganglion cells do not only innervate relay neurons (i.e., P, M and K cells), but they branch to also reach LGN interneurons, which represent approximately 25% of LGN neurons. These cells, of gabaergic (inhibitory) nature, are multidirectional (i.e., its neurites may act both as “dendrites” and as “axonic terminals” in different situations), and present a very complex pattern of connections with hundreds of other interneurons and different types of both retinal ganglion cells and relay cells (mostly M: Casagrande et al., 2005). Interestingly, due to this ramification, each interneuron processes an aggregation of numerous RFs that, together, may cover half visual field approximately (Morgan & Lichtman, 2020). This rich and variate synaptic architecture allows interneurons to participate in global processing (Morgan & Lichtman, 2020), and they may be conceptualized as in situ analyzers that strongly modulate the activity of LGN outputs (Govindaiah & Cox, 2006). Therefore, the possibility that interneurons constitute, at least partially, the global processor previously discussed (Figure 1), despite unexplored, should not be discarded. Interneurons can act at extremely high speed in response to ganglion inputs in certain circumstances (1 ms: Blitz & Regehr, 2005), so this global processing would not compromise the

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IESs requirement of short latency. However, as discussed later, current data point to another thalamic nucleus, TRN (alone, or coordinately with interneurons) as the probable main global processor linked to LGN activity.

This interconnectivity of LGN (ascending routes being summarized in Figure 3) enables its role as an active processor capable of modulating the information conveyed by retinal ganglion cells prior to its re-transmission to visual cortices. Thus, data from fMRI reveal that, similar to visual cortices, the activity of human LGN is enhanced towards attended stimuli and attenuated towards unattended stimuli (O'Connor et al., 2002). fMRI data show also that human LGN increases its activity in response to complex shapes and figure vs ground processing, regardless if these stimuli are attended or not (Poltoratski et al., 2019). Whereas fMRI data may reflect a recurrent cortico-geniculate activation (Poltoratski et al., 2019), electrophysiological LGN recordings in macaques point to the possibility of local, pre-cortical modulation in some circumstances. For example, the spike rate of M and P cells rapidly increases in response to attended stimuli -a bar with specific orientation- appearing in their corresponding RF, as compared to non-attended stimuli -a bar with another orientation- (McAlonan et al., 2008; macaque). The latency of the attended vs. non-attended response differences is rapid enough to discard the involvement of the visual cortex, at least in early stages, in this attentional effect: 26 and 37 ms average from stimulus onset in M and P cells, respectively. Together, these fMRI and intracranial data point to a key LGN role in sensory gain or sensory filtering as a function of extrinsic variables, such as the attentional demands of the ongoing task, or intrinsic to the stimulus, such as its configurational characteristics.

The way by which LGN modulates retinal inputs is, therefore, spike rate. Since LGN is less dense in spatial terms than retina, it compensates this deficit through richer signals in temporal terms than those transmitted by ganglion cells (Weyand, 2016). Depending on the visual characteristics of the stimulus in each RF, LGN relay cells may reproduce or not the spike arriving from ganglion cells, and in the former case, the temporal distribution of spikes varies to inform on different visual features (Weyand, 2016). This mechanism allows the thalamus to work similar to digital image processing, such as unsharp filters or local contrast increase (Hirsch et

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al., 2015). This spike activity, linearly related to the intensity of the stimulus, is called *tonic firing.* Importantly, as indicated above, this tonic firing may be modulated by extrinsic or intrinsic characteristics of current stimulation.

Tonic firing may be also modulated by relatively steady neural states. For example, data exist showing shorter response latency in LGN neurons when the brain presents a desynchronized state (characterized by a high-frequency / low amplitude electrical activity, reflecting enhanced vigilance) than in the synchronized state (low frequency / high amplitude, characteristic of lower vigilance situations), probably due to a global increase of membrane conductance in the former state (Wang, Chen et al., 2014). This shorter latency is also produced in different layers of V1, indicating an accumulative response speed in the visual pathway in vigilance situations. In relation to this, synchrony between LGN and V1 (this is a different concept from the global synchronized state of the brain, previously mentioned), particularly in the beta frequency, may enhance the transmission of visual information between both structures (see a review in Saalmann & Kastner, 2011). Another relatively steady, diffuse mechanism is the influence of certain neuromodulators, such as histamine (but also others such as serotonin), which reaches relay cells through neurons proceeding from the tuberomammillary nucleus, as already indicated, causing an increase in the LGN transfer ratio of information from the retina. According to Casagrande and collaborators (2005), “histamine release is often associated with negative stimuli. Thus, one might speculate that this pathway to the LGN functions to increase the transfer ratio of retinal signals in situations where potential danger exists” (p. 204).

Along with tonic firing, LGN produces *burst firing*, consisting of bundles of temporally close action potentials (one spike each 4-5 ms or less, as compared with the typical gap in tonic LGN activity, often over 10 ms: Sherman, 2001). Classically associated with sleep, when they are abundant (e.g., Livingstone & Hubel, 1981), they are also present in the awake state, whereas more sporadically. In the awake animal, it has been proposed to be a sort of “wake up call” (Guido & Weyand, 1995) that signals the appearance of a salient stimulus, LGN returning then to tonic firing mode to facilitate both the reliable transmission of information from ganglion cells to cortex and a more detailed information processing (Lesica & Stanley, 2004, Saalmann & Kastner,

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2011; Alitto et al., 2019). As in tonic firing, the temporal characteristics of burst spikes, namely the amount of burst spikes and the interspike interval, could inform on specific visual characteristics of the stimulus, such as the phase and the amplitude of spatial frequency (Ishii & Hosoya, 2020, regarding retinal bursts in salamanders, but probably generalizable to other visual levels and species).

As indicated, LGN is involved in complex feature processing. For example, it is able to categorize and prioritize stimuli -in terms of the firing rate towards visual cortices- according to their shape. Thus, P cells (M and K cells have not been explored at this respect) increase their spike rate, especially burst spikes, in response to a particular geometrical form but not to others 40 ms after their onset (Ortuño et al., 2014; macaque). This prioritization may be endogenous (i.e., primate subjects are conditioned -through juice or water administration- towards a particular shape) or exogenous (i.e., they are not instructed or conditioned towards a particular shape). In this latter case, an increase in burst occurrence rates is observed around 40 ms after the onset of novel shapes within a sequence of “standard” -more frequent- shapes (Ortuño et al., 2014). Also in the exogenous domain, burst firing increases also around 20 ms after luminosity or motion changes in naturalistic shapes -frames of forests or people- as compared to similar changes in artificial shapes -frames composed of black and white pixels randomly distributed- (Lesica & Stanley, 2004; cat). Despite only parvocellular cells (or X cells, in cats) have been explored up to the moment as regards shape recognition, similar results should be observed in other LGN relay cell types, as indicated by Ortuño and colleagues (2014). Whether emotional shapes are capable of activating LGN neurons to a greater extent than non-emotional has not been explored through intracranial recordings, but haemodynamic data in humans point to this possibility (despite this results could also reflect recurrent cortico-geniculate LGN activations rather than initial evaluation: Van den Stock et al., 2011). In sum, LGN appears to accomplish the main criteria to be an IES, adequate latency of response and visual processing architecture, but is likely complemented by other first or second order structures.

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4. Second order visual thalamus

4.1. Pulvinar

Pulvinar, the largest structure in the thalamus, is crucially involved in a wide set of visual and cognitive processes, and its lesion causes important dysfunctions regarding saccades, orienting responses, filtering irrelevant visual information, or visually guiding motor behavior, among other alterations (Bridge et al., 2016, Saalmann & Kastner, 2011). The pulvinar is actually a set of nuclei, rather than a single nucleus, rostrally adjacent to LGN (Figure 2). Despite this proximity, and the similarities of some LGN and pulvinar cells at the connectivity and cytoarchitectonic level (Huo et al., 2019), no direct connections have been reported between both, but indirect through third-party structures, as explained later. Therefore, they seem to work largely in an independent and parallel fashion at least in early, ascending information processing. Pulvinar is only partially devoted to vision, and in humans and other primates, the visual pulvinar is located in its lateral (PL) and inferior parts (PI). These areas are relatively smaller in humans than in other primates (approximately ¼ vs ⅔, respectively, of pulvinar volume: Arcaro et al., 2015; Baldwin et al., 2017). The other two grand regions of pulvinar are anterior, involved in somatosensory processing, and medial (PM), bidirectionally connected to multimodal brain areas such as the amygdala, the prefrontal cortex, and several temporal and parietal regions (Bridge et al., 2016). This pulvino-amygdalar connection has been proposed as a short and fast route for emotional processing, enabling visual information to rapidly reach amygdala without the involvement of visual cortex. However, it is important to mention that, contrary to LGN, in which interneurons interconnect different relay neurons, local interconnections among different pulvinar nuclei have not been reported. Thus, a direct and local transmission from PI, the pulvinar portion that receives ascending visual inputs, to PM, which connects with amygdala (but seems not to receive these inputs in primates -data suggesting this possibility being controversial or not verified: Bridge et al., 2016)-, has not been reported. Communication among pulvinar areas is a scarcely explored issue, but it is probably carried out at the TRN and/or at the cortical level, both bidirectionally connected with several pulvinar areas as explained below. In other words, this path from retina to amygdala is not as direct and fast as sometimes assumed (see also the

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thorough review of Pessoa & Adolphs, 2010, at this respect), and may explain the relatively long response latencies in this structure.

Both PL and PI, devoted to visual processing as indicated, contain one or more retinotopic maps (Halassa & Kastner, 2017). The latter may be further subdivided into four or five regions, depending on the primate species (Baldwin et al., 2017). Although the nomenclature is variable from one author to another, the most common is, from the lateral to the midline PI: the lateral shell (PI_{LS}), lateral (PI_L), central (PI_C), medial (PI_M) and posterior (PI_P) parts (Cola et al., 1999; Gattass et al., 2018), with certain variations in humans (Figure 2; e.g., PI_P is absent in our species: Cola et al., 1999). Importantly, PI_M (present also in humans) is the only pulvinar subdivision receiving direct retinal (weak) inputs, along with superior colliculus (SC) inputs, and exclusively projects to the dorsal visual cortical pathway, concretely to area MT (Warner et al., 2010; marmoset): Figure 3. This retino/colliculo-pulvino-cortical route shows its peak functionality in newborns, and after a few months the LGN becomes the dominant thalamo-cortical visual output, axonal afferences from PI_M to MT experiencing then a swift anatomical regression (Warner et al., 2012). This route is significantly involved in visual processing in newborns, particularly in motion detection, and seems essential in the early acquisition of the idiosyncratic and sophisticated visomanual control in primates (Mundinano et al., 2018; marmoset). In adult primates, in which the superior colliculus (SC) is the main visual input, a residual of this pulvinar-MT path may remain, and is characterized by its fast transmission speed: total latency in the SC-Pulvinar-MT route is 5 ms average (Berman & Wurtz, 2010; macaque). In human adults, this route has been proposed to contribute to blindsight, a sort of unconscious vision caused by lesions in the striate cortex, although this contribution is controversial (see Kinoshita et al., 2019; but see Ajina & Bridge, 2018 or Schmid, 2010).

Some other PI areas also receive afferences from SC (PI_L is not among them, as later explained), which is the main ascending visual input of the pulvinar (Figure 3), and the reason to consider it a second-order visual structure (e.g., Usrey & Alitto, 2015). Being a second order structure is relevant to our purposes of describing an IES, since its processing latencies are longer than those of LGN (16 ms longer as an average: Bender, 1982, measuring the response

to the same stimuli in pulvinar and LGN; macaque). However, main visual inputs of the visual pulvinar are visual cortices. Thus, V1 to V4, or early ventral pathway, innervate PL and PI_L (the only PI subdivision directly connected to these visual cortices: Bridge et al., 2016), whereas MT and other early dorsal pathway areas send efferences to PI_M and PI_P (Bridge et al., 2016; Gattass et al., 2018). Innervations are mutual: these PI subdivisions send projections to the same visual areas from which they receive inputs. Thus, the pulvinar is mainly considered as a cortico-cortical intercommunication and coordination hub (Eradath et al., 2020; Jaramillo et al., 2019). Particularly, this role as a cortical hub could consist in regulating "cortico-cortical information flow by modifying synaptic efficacy within and across visual cortical regions, rather than by relaying visual features from one area to another" (Halassa & Kastner, 2017, p. 1673). Electrophysiological data provide another clue on the cortical preeminence over pulvinar, since part of the visual cortex (concretely V4) leads pulvinar in gamma synchrony, a sign of attention enhancement, during stimulus processing (Zhou et al., 2016; macaque).

Data from different lines of research point to a significant role of pulvinar in emotional processing. A recent review by Soares, Maior and colleagues (2017) reports enhanced firing rates of primate pulvinar neurons in response to emotional stimuli such as snakes or emotional faces. Forming a sort of tandem with pulvinar, SC seems also sensitive to the saliency of stimulation, as will be discussed in section 5. Despite an important part of pulvinar activity is "post-cortical", as indicated above, some data suggest a pre-cortical capability of pulvinar to discriminate salient stimuli, including emotional. Indeed, differences between faces and other visual stimuli are observed as early as ~50ms (Nguyen et al., 2013; macaque) or between snakes and other visual stimuli at ~55ms (Van Le et al., 2013; macaque), these latencies being incompatible with a cortically-mediated phasic intervention. Whereas the involvement of pulvinar in rapid emotional evaluation seems solidly backed by experimental data, the question on whether these latencies explain the initial V1 emotional discrimination in humans requires additional research. However, there are two complementary reasons that, together, and according to current data, make this unlikely. First, that latencies in the human visual structures could be longer than in the macaque (the accumulated difference in V1 is ~20ms; Pessoa &

Adolphs, 2010). Second, as previously explained and schematized in Figure 3, pulvinar nuclei innervating V1 and subsequent ventral visual cortex areas (PL and PI_L) seem not to receive ascending visual inputs (although this issue is controversial: Bridge et al., 2016), so something similar to what we explained above regarding SC-pulvino-amygdalar route occurs in this case. Thus, PI, the pulvinar area which receives visual ascending inputs (except PI_L, which does not receive them, as also indicated), can only indirectly trigger any activity at V1, V2 or V3, probably through TRN or cortico-cortical connections. In sum, the visual pulvinar could be a complementary IES acting with some delay with respect to LGN, and would send additional emotion-labeled information to both common and different structures to those reached by the LGN.

4.2. Thalamic reticular nucleus (TRN)

The TRN is a laminae of GABAergic neurons that surrounds the thalamus laterally (Figure 2). This sort of shell, close to, but not within the body of the thalamus, is indeed an intricate net or reticula that interconnect thalamic nuclei, and connects them with non-thalamic structures (Guillery & Harting, 2003; Kimura, 2014; 2017). Thus, each portion of the TRN is neurally and functionally linked to the thalamic nuclei it covers, often presenting a topographical organization (Halassa & Kastner, 2017). The visual portion, organized in retinotopic maps (Bragg et al., 2017), corresponds to its posterior part. It is bidirectionally connected with pulvinar and LGN, interconnecting them as already indicated (Saalman & Kastner, 2011). Additionally, this visual portion receives visual cortical information through collateral inputs from cortico-thalamic neurons (Bragg et al., 2017; Guillery & Harting, 2003). Globally, the TRN also receives direct afferences from brainstem nuclei, basal ganglia, ventral and dorsolateral prefrontal cortices, and amygdala (Ghodrati et al., 2017).

The interaction of visual TRN with LGN and pulvinar has been scarcely studied, especially in the latter case. With respect to LGN, despite TRN neurons are GABAergic, their final effects are more complex than exclusively inhibitory: their direct synapsis with LGN relay cells cause indeed inhibition, but, since they also innervate interneurons -whose effect is

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inhibitory-, they may also produce a disinhibitory effect on relay cells (Ghodrati et al., 2017). Each TRN neuron reaches multiple LGN cell types and layers regardless of their typology or ocularity, and this transversality and nonspecificity would enable interactions between different visual pathways (M, P, K), again pointing to the involvement of visual thalamus in relatively complex processing (Bragg et al., 2017). As regards its interconnections with pulvinar, which involve different TRN portions to those interconnected to LGN, data are scant. Recently, the pulvinar-TRN network has been involved, along with their cortical interconnections, in cognitive computations associated with decision making and, more concretely, with decision confidence (Jaramillo et al., 2019).

This highly interactive structure, both at the thalamic (and visual-thalamic) and at the extrathalamic level, makes TRN a relevant global processor and modulatory element (Bragg et al., 2017). Indeed, it has been defined as an “attentional gate” that regulates the visual output of thalamus before reaching the cortex and other structures (McAlonan & Brown, 2002). In the case of visual processing, it could contribute to guide the attentional effects previously described in LGN relay neurons. Thus, while the visual input reaches M cells prior to TRN cells (P cells are reached after; K have not been studied), the effect of presenting an attended stimulus as compared to a non-attended one in the corresponding RF is observed 4 ms earlier in TRN cells than in M cells (22 ms and 26 ms average, respectively; 37 ms in P cells: McAlonan et al., 2008; macaque). The mechanism of action would start with a decrease in the disinhibitory effect of TRN. Thus, the arrival of the attended input triggers a reduction in TRN activity - as compared to the activity elicited by non-attended stimuli- and, since this nucleus is inhibitory in its direct synapses with LGN relay cells, the immediate consequence of this reduction is that they increase their activity (McAlonan et al., 2008).

These data are of extreme importance since they signal TRN not only as an in situ processor, but also as a fast and early processor compatible with the speed required for an IES. Relatedly, TRN plays an important role in the suppression of distractors during attentional focalization (Halassa & Kastner, 2017). Although these functions seem relevant in emotional processing, the involvement of TRN in it has not been explored yet, to the best of our knowledge.

However, this is highly probable taking into account the capability of emotional stimuli to capture attention (Carretié, 2014). The fact that, as indicated above, TRN receives inputs from emotional processing structures, such as amygdala and vPFC, point to this same hypothesis. Importantly, TRN shows long-term potentiation, which seems to be regulated by burst firings of thalamocortical cells (Sieber et al., 2013; rat), although this is a scarcely explored issue. This could imply a role of the TRN in mnemonic processes, which is a necessary element that allows the online comparison of the visual input with stored emotional features. Therefore, its role regarding initial emotional evaluation seems crucial and would complement the role of LGN and pulvinar.

5. First-order non-thalamic structures

Just as the thalamus has often been out of the focus of main models of cognitive and affective processing, and even out of models of visual processing, as indicated by Ghodrati and colleagues (2017), a possible limitation in any proposal on early emotional processing of visual stimuli could be to ignore other non-thalamic structures that may be involved. It is probable that each node within the ascending visual routes in which a synapsis is produced develops a certain level of processing or classification of stimulation as regards its potential risk or other saliency indicators, as well as a certain modulation of the information it receives. Therefore, the “missing link” in early emotional processing could be potentially extended to some first order visual structures.

Whereas the majority of retinal outputs travel through the optic nerve to LGN, there are a dozen brain nuclei that also receive direct ganglion fibers (Table 3). In most of them, the main role is associated with oculomotor function and/or motion processing, but some studies propose their involvement, to a greater or lesser extent, in cognitive functions such as attention or memory. Their involvement in affective processes has been scarcely studied (or not studied, in many cases), but the fact that dynamic stimuli are often emotional (predators, mates, approaching/falling objects, competitors, preys, etc.), leads to expect certain contributions at this level.

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*** Table 3 ***

5.1. Superior colliculus (SC)

This structure is located in the top (tectum) part of the midbrain, and is organized in six layers in mammals, the two external or superficial (SCs) receiving visual inputs from retina and other visual structures such as the visual thalamus, visual striate and extrastriate cortices, parabigeminal nucleus (a sort of SC satellite contributing to saccade control), pretectum nuclei (discussed in the next section) as well as from the locus coeruleus (involved in the regulation of arousal): Basso & May (2017). The SCs is organized retinotopically (Cerkevich et al., 2014) and sends projections to K layers and to pulvinar. It is involved in basic visual processing, mainly related to orienting and motion, and aimed at organizing orienting movements of the eyes and head (Krauzlis et al., 2013). Interestingly, SCs, despite not being connected to attention networks (such as fronto-parietal networks), responds differently as a function of physical stimulus saliency, what suggests an autonomous capability to detect it (White et al., 2017). Intermediate and internal layers (SCi), also organized topographically (Wurtz, 2009), are multimodal, since they receive visual inputs from SCs and non-visual sensory inputs as well. The SCi layers interact with many levels of the central nervous system including frontal and parietal cortices (but not with the visual thalamus), and would contribute to orienting behavior, and to cognitive processes such as attention or decision making (Basso & May, 2017, Krauzlis et al., 2013).

Several data suggest that SC is able to discriminate complex features. Through fMRI recordings in humans, SC responses to aversive stimuli are greater than to other visual stimuli (Almeida et al., 2015; Wang et al., 2020). Indeed, SC is proposed to form a sort of tandem with pulvinar as an early emotional detection mechanism, as indicated (Soares et al., 2017). Intracranial electrophysiological data also point to the SC capability to discriminate complex shapes. For example, it responds more intensely to certain fractal forms -varying in colors, forms and sizes- as a function of their hedonic value previously conditioned with juice administration (Griggs et al., 2018; macaque), a discrimination which is patent at 95 ms from stimulus onset. This relatively long latency may be explained by proposals from other lines exploring the involvement of SC in spatial attention. Concretely, the SC has been postulated to contain spatial

maps of the visual context rather than stimulus features, and therefore would need to intercommunicate with other cerebral structures that process and evaluate these features (Krauzlis et al., 2013). According to this, the SC would act as an indexing system that pools together the signals of those structures to determine the content of perception. This idea would imply that the feature evaluation carried out by the SC is fruit of recurrent information. In any case, electrophysiological data are very scarce up to the present, and additional research is needed to characterize, both in temporal and functional terms, the involvement of SC in emotional evaluation.

5.2. Other structures

As indicated, whereas the main targets of ganglion cells are LGN and, to a lesser extent, SC, several brain nuclei also receive direct retinal inputs (Table 3). Some of them seem less involved in rapid processing of visual stimulation, such as the suprachiasmatic nucleus of the hypothalamus, a key element in the control of circadian rhythms, or the pretectal olivary nucleus (PON), which controls the pupillary light reflex or triggers rapid eye movements during sleep. However, the majority of first-order nuclei, particularly those linked to oculomotor control, are indeed fast detectors of visual stimulation.

On one hand, the human accessory optic system (AOS) is a net of four nuclei also innervated by retinal ganglion cells which present large receptive fields and are direction selective (Fredericks et al., 1988). The AOS is involved in motion processing and in the control of oculomotor mechanisms, but it is also involved in cognitive processes such as spatial memory and attention (Giolli et al., 2006). On the other hand, the six nuclei that form the pretectum -PON, previously mentioned, is among them- also receive direct retinal inputs (Gamlin, 2006). One nucleus of the pretectum, the nucleus of the optic tract (NOT), is especially relevant since it receives inputs from visual cortex (along with retina) and projects to LGN, pulvinar and TRN, as well as to AOS nuclei and SC, among other structures (Büttner-Ennever et al., 1996). Functionally close to AOS, is also a part of the brain machinery that processes motion and

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adapts oculomotor activity to that motion (Gramlin, 2006). Indeed, and as AOS, the NOT participates in cognitive processes such as attention (Büttner-Ennever et al., 1996).

6. Discussion

Figure 3 summarizes the information provided in previous sections on the main ascending routes of visual information, and the approximate timings –from stimulus onset- in which each processing level (each synapsis) comes into play. The present review points to the visual thalamus, and likely other associated non-thalamic nuclei, as crucially involved in early emotional processing of visual stimulation. Concretely, the LGN seems to be a key IES, rapidly labeling the sensory inputs as emotional thanks to its contrasted capability to locally process relative complex stimuli, with the fast concourse of TRN as a global evaluator of visual features. This information, labeled as emotional if pertinent, would reach the visual cortex around 60-70 ms after stimulus onet. In parallel, but some milliseconds later, the SC-pulvinar tandem could also evaluate the ascending information. Whereas the SC-pulvinar tandem would probably not contribute to the initial V1 (or V2/V3) response to emotional stimuli, peaking at 80 ms, its action would reinforce and complement the LGN-TRN evaluation in ascending phases. Later, the visual input already marked as emotional would follow the routes shown in Figure 3 towards the visual cortices and, through TRN and cortical interconnections, to other brain areas well known to be involved in emotional processing such as amygdala, vPFC and insula (among others: Lee & Siegle, 2009). At this point, *deep evaluation* starts, since emotional stimuli are more sophisticatedly processed in these structures. Information would also travel back from these structures to LGN, TRN and pulvinar, among other brain areas. The recurrent information interchange among these elements is also characteristic of deep evaluation, and often derives in subjective (e.g., fear feeling), autonomic (e.g., increased skin conductance), motor (e.g., orienting or avoidance) and cognitive changes (e.g., mnemonic actualization), as a continuation of the *initial evaluation* reviewed here, of fast and (rudimentary) perceptual nature.

*** Figure 3 ***

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Therefore, the present proposal does not contradict previous data on the evaluative capabilities of amygdala, vPFC, insula, or other structures, which is backed by a solid background of concurrent and abundant data. However, their influence over visual cortices or other brain structures involved in visual processing would belong to deep evaluation rather than being the first markers of emotionality or IESs. Particularly, the role of amygdala, which in current models of emotional processing is often proposed as the cornerstone of emotional processing -also in humans-, should be discussed beyond the basic outlines mentioned in the Introduction. As indicated, initial evaluation, one of the main ingredients in this cornerstone role, seems not to be within the reach of amygdala mainly for three reasons. First, because the multisynaptic path that visual information needs to follow to reach this structure (four synapses minimum), causes latencies incompatible with observations. Focusing on faces -the stimuli evoking the faster amygdalar responses-, latencies are longer than required for any IES. Thus, the face-sensitive neurons of the macaque amygdala (i.e., they specifically react to faces and not to other visual stimuli) respond from 60 ms (Nakamura et al., 1992), and typically from 100 ms or beyond (Leonard et al., 1985; Sanghera et al., 1979; Wang, Tudusciuc et al., 2014). In humans, results are parallel but with the known increase in latency (Pessoa & Adolphs, 2010), and the earliest responses have been observed at 74 ms, as indicated in the Introduction (Méndez-Bértolo et al., 2016), and beyond 250 ms in several studies (Rutishauser et al., 2011; Mormann et al., 2008; Krolak-Salmon et al., 2004).

The second reason that distance amygdala away from being an IES is that it lacks the necessary cytoarchitecture. As mentioned in the Introduction, no amygdalar nuclei have been reported to incorporate focal processors in charge of specific RFs, which usually follow a retinotopic organization, or, alternatively, to include global processors connected to focal ones, in order to locally analyze visual features -shapes, forms, motion patterns, colors, etcetera- of the incoming stimulation, and hence to initially detect emotional stimuli. In other words, amygdala is not a visual processing structure. Indeed, amygdalar neurons responding to faces -but probably other amygdalar neurons- do not respond exclusively to visual information, an important part of them also responding to auditory stimuli (Kuraoka & Nakamura, 2007).

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The third reason is the relative specialization of amygdala in face processing (see the meta-analysis by Sergerie et al., 2008). While some amygdalar neurons specifically respond to other non-facial significant stimuli, such as food or animals (irrespective of their emotional valence), their response latency is usually longer (e.g., ~320 ms average in the case of stimuli depicting animals: Mormann et al., 2011; human). Relatedly, Méndez-Bértolo and collaborators (2016; human) showed that amygdalar differential activity between emotional and non-emotional stimuli is observed more than 100 ms later in response to non-facial than to facial stimuli (see Hariri et al., 2002, as regards the human amygdala advantage for facial over non facial emotional stimuli also in amplitude terms). Indeed, the amygdala is considered a key piece of the neural circuitry involved in social behavior (e.g., Amaral, 2003). However, and importantly, IESs should be also able to rapidly detect and label non-facial visual events, whose impact on survival may be even more dramatic.

Alternatively, amygdala it is directly connected with effector brain areas in charge of motor responses (PAG and striatum: Emery & Amaral, 2000), vegetative changes (hypothalamus: LeDoux, 2000), subjective (e.g., fear feeling, in which the bed nucleus of the stria terminalis is involved; Walker et al., 2003) and cognitive changes (e.g., hippocampal complex -memory- and visual cortices -attention-; see Dolcos et al., 2004 and Adolphs, 2004, respectively). Thanks to this map of interconnections, its main role would be to integrate sensory facial information with other associated information such as task demands, past experiences, reward value, or social context, and this integration would lead to a judgment about the emotion content of faces (Wang, Chen et al., 2014), a role that could be extended, later in time, to other visual stimuli. In sum, this multifaceted connectivity signal amygdala as a deep evaluator of the visual input. A similar role could be proposed for vPFC, insula or any other structure that receives direct inputs from visual cortices and connects, also directly, to effector systems (see a review on the connectivity of these structures in Carretié et al., 2009). In humans, vPFC and insula may even allow “greater resolution” in this integrative role and in the motor, subjective and cognitive outputs they may organize due to their richer connectivity (e.g., vPFC, but not amygdala, is connected to motor cortices: Emery & Amaral, 2000).

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As described in previous sections, three key prerequisites for an IES (short latency, visual feature processing architecture, non-specific content detection) seem to be accomplished by the LGN, which belongs to the main and fastest ascending route of visual information in humans. Data on its involvement in early emotional evaluation are scarce since it has been usually out of the scopes of research (i.e., it has not been a target in animal intracranial recordings or a specific region of interest in human fMRi in studies using visual emotional stimulation), but results from other lines of research provide some relevant clues. Regarding latency of response, LGN may modulate the visual input at ~40 ms from stimulus onset (~30 ms in macaques, as indicated: McAlonan et al., 2008). With respect to its capability to evaluate visual features, current data show that certain intrinsic characteristics of the stimulus, such as shape novelty (Ortuño et al., 2014), may modulate LGN responses, and we hypothesize that the idiosyncratic saliency of emotional stimulation may be among them. This modulation requires focal and global feature analysis, in order to detect shapes, colors, motion, etcetera, that could identify an emotional stimulus (Figure 1). LGN is undoubtedly capable of developing the focal analysis of the visual input through relay cells (P, M, and K), and global analysis, interconnecting several relay cells to increase the visual area to be processed, could be carried out by the TRN. Importantly, this nucleus is susceptible to long-term potentiation (Sieber et al., 2013), pointing to a capability to encode certain visual information and, ultimately, to the online comparison of incoming information with stored features corresponding to emotional stimuli. The participation of LGN interneurons -also interconnected to an important number and variety of relay cells- as a global processor is also probable at the light of the reviewed data. Labelling the stimulus as emotional would likely consist of a burst firing of LGN relay cells shortly after stimulus onset since, according to the information reviewed in previous sections, this type of activity marks relevant stimulation and privileges it in subsequent visual cortex processing. Additionally, TRN would distribute this information to other thalamic and cortical areas.

However, IESs likely consist of a network of complementary structures rather than a single node. Thus, whereas the LGN-TRN tandem is proposed here as the core IES, other structures may take part in the initial, ascending evaluation of stimulation. The involvement of

pulvinar, in close association with SC, in early emotional evaluation has been also reviewed. Two reasons have been mentioned suggesting that the pulvinar is probably not the core IES. On one hand, the main inputs to visual pulvinar are descending projections from different visual cortices, which shapes its main role as a hub that coordinates cortico-cortical activity (Eradath et al., 2020; Jaramillo et al., 2019). On the other hand, reported latencies of pulvinar enhanced activity towards emotional stimulation seem, up to the present, longer than required to explain initial visual cortex responses to emotional stimuli, as reviewed above. Whereas not a core IES, the involvement of pulvinar (or the SC-pulvinar tandem) in initial evaluation is backed by experimental data and may complement the LGN-TRN previous evaluation. The fact that the pulvinar reaches some different brain areas from those innervated by the LGN-TRN tandem, and that it conveys complementary information -more related to motion, both regarding the stimulus and the eyes/body themselves- to that processed in LGN, but also relevant to emotional processing, would indeed be a valuable contribution to early evaluation. Non-thalamic first order structures, such as the pretectum and AOS nuclei described in this review, can detect or evaluate certain aspects of stimulation as well, particularly those related to stimulus motion and motor behavior (e.g., eye pursuit), important parameters regarding many emotional visual events.

In sum, current data clearly show that a key lost link exists in emotional processing, which consists in defining the cerebral structures forming the initial evaluation system. While this gap seems evident, the candidates to be an IES are still to be experimentally explored. Our proposal on the key involvement of LGN-TRN in this initial, ascending evaluation, with the later contribution of SC-pulvinar, is based on the existing literature, but we are conscious this is still scarce and that further research is needed to confirm (or discard) it. In any case, the information reviewed here points to the crucial relevance of opening the focus of Affective Neuroscience to include the thalamus as a scope of research, as Cognitive Neuroscience is beginning to do in recent years. Two lines of research appear of special interest. On one hand, employing emotional stimuli in intracranial recordings of LGN (both relay and interneuron) and TRN cells of primates. On the other hand, designing fMRi studies in human subjects, also employing emotional stimulation, including LGN as a target region of interest. The susceptibility of TRN and

other visual thalamic nuclei to long-term potentiation is also a scarcely explored, but crucial, issue. Indeed, stimulus evaluation necessarily requires the storage of certain features that allow the identification of upcoming emotional events. In sum, it seems worth rescuing at least part of the protagonism the thalamus had in the first years of Affective Neuroscience.

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Table 1. Estimated distance and transmission time between several human brain structures mentioned in the main text. Distances have been estimated using the Big Brain tool within the Human Brain Project web (humanbrainproject.eu), and using the MNI152 template. To approach real fasciculi shape and length we added 20% distance to the straight line distances calculated between structures. Conduction velocity (CV) varies enormously from neuron to neuron (from less than 1 m/s to several tens) depending on axonal diameter, myelination, arborization or number of varicosities (Debanne, 2004), but it has been computed here according to the following experimental information: i) the CV value of 8.75 m/s has been established per each µm of axonal diameter (Horowitz et al., 2015), ii) middle range neurons (e.g., uncinate fasciculus) as those more relevant here present an average diameter of 0.45 to 0.61 µm (Liewald et al., 2014), iii) the temporal gap between the human LGN and the V1 responses to the same stimulus is ~20 ms (Krolak-Salmon et al., 2003).These sources of information converge in yielding an average CV of **~4.5 m/s** in the type of fibers we are dealing with. Transmission times have been computed using this CV.

From	To	Distance (mm)	Transmission time (ms)
Posterior Thalamus (Pulvinar / LGN)	Amygdala	37.2	**8.3**
	Insula (anterior)	72	**16.0**
	Insula (posterior)	40.8	**9.1**
	vPFC (pole)	112.8	**25.1**
	vPFC (posterior)	62.4	**13.9**
	V1, V2	86.4	**19.2**
Amygdala	V1, V2	114	**25.3**
vPFC (pole)	V1, V2	195.6	**43.5**
vPFC (posterior)	V1, V2	144	**32.0**
Insula (anterior extreme)	V1, V2	153.6	**34.1**
Insula (posterior extreme)	V1, V2	111.6	**24.8**

Table 2. Studies reporting significant effects of emotional visual stimuli (as compared to neutral) in thalamic activity. Inclusion criteria: i) human adult participants free of affective or psychotic disorders (only control participants were taken into account if the study included clinical samples), ii) a neutral condition along with emotional, and iii) visual stimuli (faces, scenes, animals, etc.). The search was carried out in PubMed and Google Scholar until May 10, 2020. The search terms included different combinations of PET, fMRI, EEG, MEG, emotion, emotional, visual, neutral, thalamus, "lateral geniculate", pulvinar. A expanded version of this table (including more details on sample size, stimuli, task, observed effects or the coordinates showing peak effects is available at: https://osf.io/zvuj5/ .

Table Foot:

* As labeled by the authors.

Shaded lines: studies including a ROI in thalamus (whole brain strategy in the rest of studies).

Italic lines: studies employing PET (positron emission tomography); the rest employed fMRI (functional magnetic resonance imaging).

LGN: lateral geniculate nucleus, MD: mediodorsal thalamic nucleus, AL: anterolateral thalamic nucleus.

(Table 2 in next page)

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Authors	Year	Stimulus format	Type of task	Effects location*
Anders et al.	2004	Scenes	Indef.	Thalamus
Britton et al.	2006	Scenes (film clips)	Explicit	Thalamus
Bühler et al.	2008	Scenes	Indef.	Thalamus
Critchley et al.	2000	Faces	Impl-Expl	Pulvinar
Das et al.	2005	Faces	Indef.	Thalamus
de Gelder et al.	2004	Body gestures	Indef.	Pulvinar
de Gelder et al.	2006	Body gestures	Indef.	Pulvinar
Duan et al.	2010	Faces	Indef.	Thalamus
Dunsmoor et al.	2016	Faces	Explicit	Thalamus
Edmiston et al.	2013	Scenes	Indef.	Thalamus
Fichtenholtz et al.	2004	Scenes	Impl-Expl	Thalamus
Frank et al.	2014	Scenes	Indef.	MD, Pulvinar
Garrett & Maddock	2006	Scenes	Explicit	Thalamus
George et al.	*1995*	*Faces*	*Explicit*	*Thalamus*
Goldin et al.	2005	Scenes (film clips)	Explicit	Thalamus
Goldin et al.	2008	Scenes (film clips)	Impl-Expl	Pulvinar
Grosbras et al.	2006	Faces and hands	Indef.	Thalamus
Günther et al.	2017	Faces	Implicit	Thalamus
Hakamata et al.	2016	Faces	Implicit	Pulvinar
Hermann et al.	2007	Scenes	Indef.	Thalamus
Kang et al.	2016	Scenes	Indef.	Thalamus
Karama et al.	2011	Scenes (film clips)	Explicit	Thalamus
Kehoe et al.	2012	Scenes	Implicit	Thalamus
Kim et al.	2017	Scenes (film clips)	Impl-Expl	Thalamus
Lane et al.	*1997a*	*Scenes (film clips)*	*Explicit*	*Thalamus*
Lane et al.	*1997b*	*Scenes*	*Explicit*	*Thalamus*
Lee et al.	2005	Faces, Scenes	Explicit	Thalamus
Liberzon et al.	*2000*	*Scenes*	*Impl-Expl*	*Dienceph.*
Lichev et al.	2015	Faces	Implicit	Thalamus
Liddell et al.	2005	Faces	Implicit	Pulvinar
Lindner et al.	2015	Conditioned geometrical shapes	Indef.	Thalamus
Mizuno-Matsumoto et al.	2013	Scenes + sounds	Indef.	Thalamus
Morris et al.	*1998*	*Faces*	*Explicit*	*Pulvinar*
Morris et al.	*1997*	*Faces*	*Implicit*	*Pulvinar, AL*
Mourão-Miranda et al.	2003	Scenes	Explicit	Thalamus
Norris et al.	2004	Scenes	Explicit	Thalamus
Nummenmaa et al.	2008	Scenes	Explicit	Thalamus
Padmala et al.	2010	Faces	Implicit	Medial Pulvinar
Phillips et al.	1997	Faces	Implicit	Thalamus
Pichon et al.	2008	Body gestures	Implicit	Thalamus
Sambuco et al.	2020	Scenes	Indef.	Post. Thalam.
Schlochtermeier et al.	2013	Scenes	Explicit	Thalamus
Siman-Tov et al.	2008	Faces	Implicit	Pulvinar
Stark et al.	2005	Scenes	Explicit	Thalamus
Stark et al.	2004	Scenes	Explicit	Thalamus
Stark et al.	2003	Scenes	Indef.	Thalamus
Straube et al.	2010	Scenes (film clips)	Indef.	Thalamus
Surguladze et al.	2003	Faces	Implicit	Thalamus
Suslow et al.	2010	Faces	Implicit	Thalamus, MD, Pulvinar
Takahashi et al.	2004	Scenes	Explicit	Thalamus
Van den Stock et al.	2011	Body gestures	Implicit	LGN, Pulvinar
Walter et al.	2008	Scenes	Implicit	Medial thalamus
Wehrum et al.	2013	Scenes	Explicit	Thalamus
Williams et al.	2001	Faces	Implicit	Thalamus
Winston et al.	2003	Faces	Implicit	Lat. Post. Thalamus
Wright et al.	2004	Scenes	Indef.	Thalamus

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Table 3. First order (i.e., receiving direct retinal inputs) non-thalamic nuclei in the human brain.

Nucleus	**Location**
Superior colliculus	Tectum (midbrain)
Suprachiasmatic nucleus	Hypothalamus
Medial terminal accessory nucleus	Accessory optic system (spread, but mainly Tegmentum - midbrain/pons-)
Lateral terminal accessory nucleus	
Dorsal terminal accessory nucleus	
Interstitial nucleus of the superior fasciculus	
Olivary pretectal nucleus	Pretectum (midbrain)
Nucleus of the optic tract	
Anterior pretectal nucleus	
Medial pretectal nucleus	
Posterior pretectal nucleus	
Posterior limitans nucleus	
Commisural pretectal area	

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Figure legends

Figure 1. Schematic representation of the initial evaluation characteristics. From left to right: stimulus onset, retinal projection, and initial evaluation structure (IES). At the retina level, ganglion cells detect and transmit the visual input to a specific area: ganglion receptive field (RF). Axons of all ganglion cells, forming the optic nerve (continuous gray arrows), send this information to IESs, and may experience partial crossings or a few of intermediate synapses (discontinuous gray lines). This information is not modulated by cognitive or affective factors yet. At the IES level, two types of cells are present: focal and global processors. The former are organized retinotopically, but are less numerous than in the retina, so their RFs are bigger. Their activity (represented as different gray tones) depends on the visual input to its RF. Each global processor is connected to a great number of focal processors, so they manage several RFs and, hence, a big portion of the visual scene. As a function of the features they decode, they are able to modulate focal cells output to subsequent processing areas of the brain, including V1.

Figure 2. The left human thalamus, highlighting the structures described in the text. **A)** Thalamus location in a transparent lateral-posterior view of the brain and main external thalamic nuclei. Dashed lines show the coronal sections depicted in B and C (TRN, thalamic reticular nucleus; LGN, lateral geniculate nucleus; see other acronyms, not mentioned in the text, at the end of this figure legend). **B)** Coronal section of the human pulvinar (PL, lateral pulvinar; PM, medial pulvinar; PI, inferior pulvinar; subscripts: LS, lateral shell; L, lateral, C, central, M, medial. **C)** Coronal section of the human LGN (P, parvocellular layer; M, magnocellular layer; K, koniocellular layer). Whereas schematized, coronal sections of LGN and pulvinar are represented with the approximate shape they present in humans (see Usrey & Alitto, 2015, and Cola et al., 1999, respectively). Other acronyms: anterior (A), mediodorsal (MD), anterior dorsal (AD), posterior dorsal (PD), ventral anterior (VA), lateral ventral (LV), ventral posterior (VP) and medial geniculate (MG) nuclei.

Figure 3. The ascending route from retina to the main visual and emotional processing structures in adult humans, including an approximate temporal scale regarding the arrival time of information to each processing level. Only forward and “horizontal” connections are represented (note that rich backward projections exist, as explained in the main text, not represented). Rectangular and colored structures: thalamic; circular: subcortical visual processing nuclei; arcuate: visual cortices; hexagonal: emotion processing structures. Dashed line= vestigial ascending route. Thick line= preferential ascending route. [SC= superior colliculus, LGN=lateral geniculate nucleus, TRN=reticular thalamic nucleus, vPFC=ventral prefrontal cortex]. PI_L , one of the subdivisions of inferior pulvinar, does not receive SC nor retinal inputs, and projects to visual cortices, so its connections are common to lateral pulvinar (¬ means “not”).

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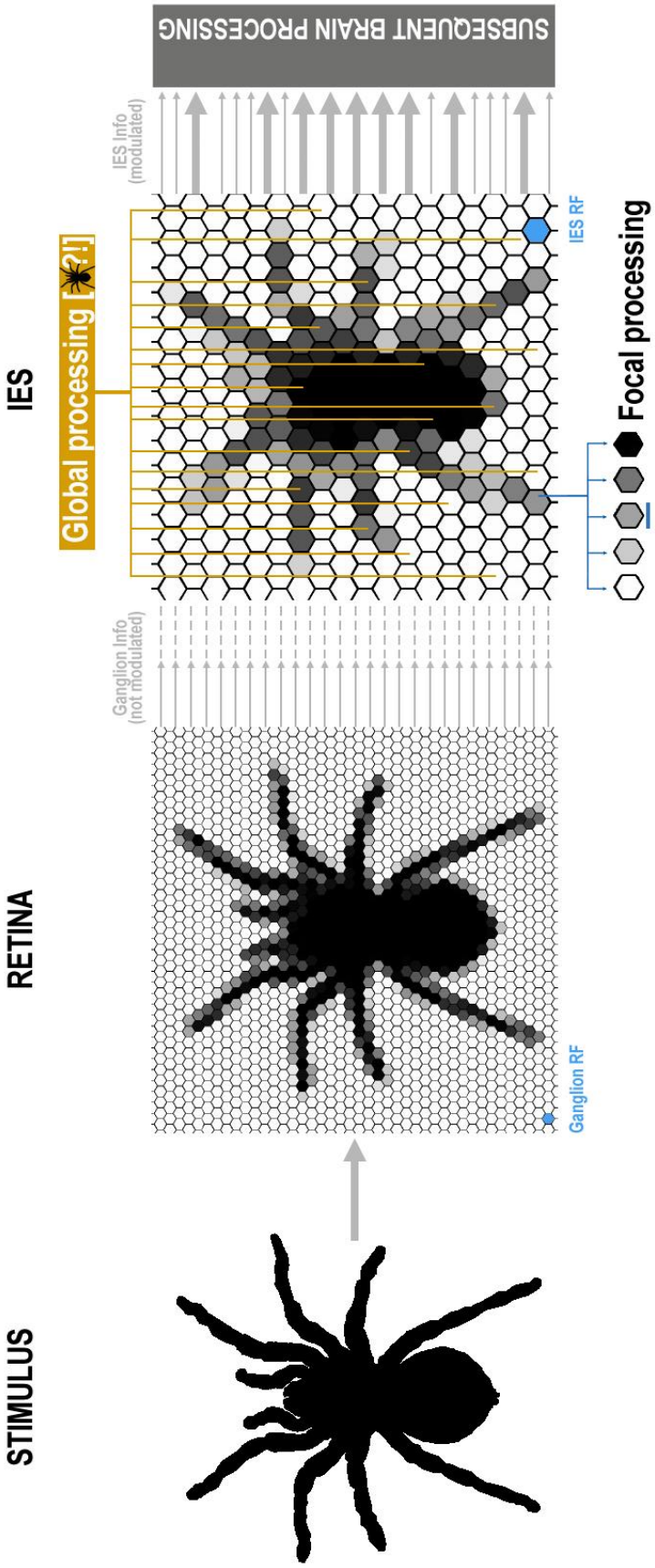

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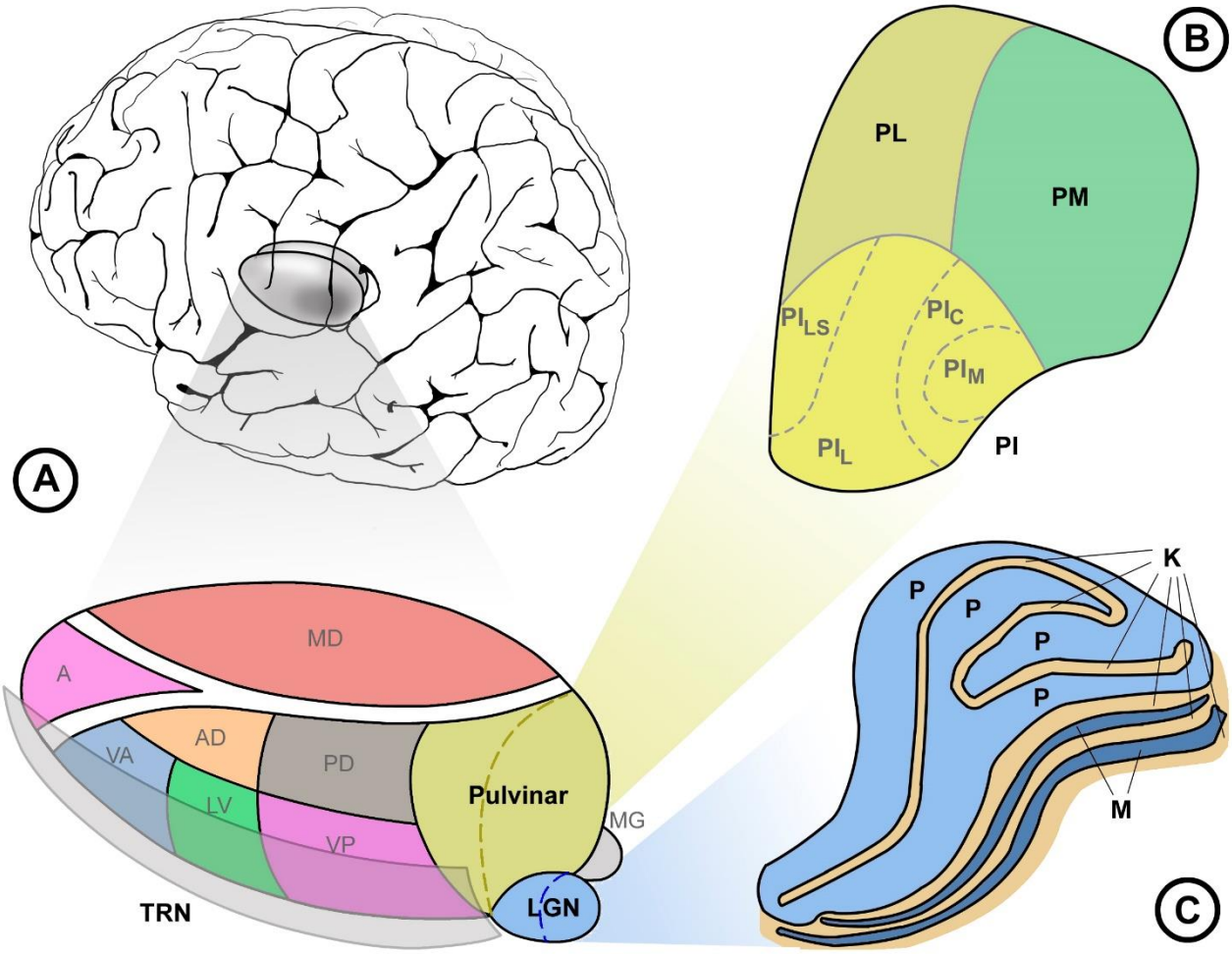

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