LeDoux's Fear Circuit and the Status of Emotion as a Non-cognitive Process

Gregory Johnson

LeDoux (1996) has identified a sub-cortical neural circuit that mediates fear responses in rats. The existence of this neural circuit has been used to support the claim that emotion is a non-cognitive process. In this paper I argue that this sub-cortical circuit cannot have a role in the explanation of emotions in humans. This worry is raised by looking at the properties of this neural pathway, which does not have the capacity to respond to the types of stimuli that are generally taken to trigger emotion responses. In particular, the neurons in this pathway cannot represent the stimulus as a complete object or event, rather they represent the simple information that is encoded at the periphery. If it is assumed that an object or event in the world is what, even in simple cases, causes an emotion, then this sub-cortical pathway has limited use in a theory of emotion.

Keywords: Amygdala; Emotion; Fear; LeDoux; Non-cognitive Process; Thalamus

1. Introduction

In his book *The Emotional Brain*, Joseph LeDoux describes two neural pathways that direct fear responses in rats. One, which he calls the "high road," is a circuit from the thalamus, which receives sensory information, to the cortex, and from there to the amygdala. The second pathway, the "low road," is a direct route from the thalamus to the amygdala. The existence of the low road has been taken as evidence in favor of characterizing emotions in humans as non-cognitive processes. Essentially the argument is that since the low road does not pass through the cortex, there is nothing "cognitive" about this pathway, and therefore, emotions are ultimately, non-cognitive processes. In this paper I argue that the low road that LeDoux has identified cannot support this claim that emotions are non-cognitive processes.

Others have argued for a similar conclusion on the basis of the idea that even a simple process, as long as it is a process that manipulates information, should be considered cognitive (Lazarus, 1991; Scherer, 1993).[1] My argument depends on

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different considerations. In this paper I examine the direct thalamo-amygdala pathway that LeDoux has identified for auditory stimuli and a related pathway for visual stimuli. I argue that these two pathways do not have the capacity to respond to the types of stimuli that are generally taken to trigger emotion responses in humans. In particular, the neurons that compose these pathways cannot represent the stimulus as a complete object or event. If it is assumed that an object or event in the world is what, even in simple cases, causes an emotion response, then the low road is probably not involved—at least in the vast majority of cases—in the generation of emotion responses in humans. As an example take this simple case: an individual sees a large spider and this causes a fear response. This scenario is not one that could utilize the direct thalamo-amygdala pathway that LeDoux has identified. However, this observation runs counter to the way that this pathway has been treated by those who are committed to the non-cognitive position, and so in this paper I will explain why their position is mistaken.

First, I will outline the non-cognitive position and contrast it with the view that emotion is a cognitive process. In the sections that follow I will examine the direct pathway to the amygdala that carries auditory information and a similar pathway for visual information. This will provide the basis for the claim that the low road cannot carry out the emotion process in humans. I conclude with some observations on the neurobiology of emotion that are worth keeping in mind when looking at neurobiological evidence that might arbitrate between the cognitive and non-cognitive positions.

2. Cognitive and Non-cognitive Processes

The idea that emotions are non-cognitive processes has been argued for recently by Robinson (2004, 2005), Prinz (2004a, 2004b), and Delancey (2002), all of whom cite LeDoux's research in support of their position. Before explaining what they mean by non-cognitive, it will be helpful to make a distinction between processes and states. In a straightforward sense, processes occur or unfold over time and, neurobiologically, over a particular spatial scale. During the course of the process, information of one sort or another is manipulated such that the output that the process produces is different than the input it began with. In contrast, a state is something that is simply present or not present. A mental state, for example, a belief, has content and perhaps a causal or a functional role in a process, but the state itself is just present or not present in an individual.

The reason for pointing out this distinction is so that we can keep emotion states and emotion processes separate. An emotion state is simply the occurrence of a particular emotion, for example, being in a state of fear (or happiness, or sadness, or whatever), while the emotion processes is the process or processes that generate an emotion response.[2] The latter is a process insofar as it begins, at least in many cases, with the perception of an event and ends with the "bodily response." The process by which an emotion response is generated is what I am focusing on in this paper.

The larger context that this paper is situated within is the question of whether this process should be classified as cognitive or non-cognitive. We can orient ourselves to this question by noting two abilities that humans have, one of which is cognitive and one of which is non-cognitive. An ability that is clearly cognitive is language comprehension, while an ability that we would call non-cognitive is a reflex or a reflex like response such as the blink response when something touches the cornea.[3] Therefore, the claim that the emotion process is non-cognitive is a commitment to the idea that the emotion process belongs in the category with the eye blink rather than with language comprehension.

More specifically, the non-cognitive position is based upon the idea that the response is produced automatically upon the presentation of the relevant stimulus and without any sort of evaluation of the stimulus or judgment about the stimulus that could be called "cognitive." Further, it is claimed that the process does not require, and typically does not use, representations that have propositional or conceptual content. This position also emphasizes the similarity, or even the sameness, between emotions in humans and other animals, for which cognitive activity is perhaps not an option. Summarizing this position, Robinson says:

> Affective appraisals respond automatically to events in the environment (either internal or external) and set off physiological changes that register the event in a bodily way and get the agent ready to respond appropriately. An emotional response is a response set off by a non-cognitive affective appraisal. I speculated that there are probably a limited number of basic emotion systems each identified by a specific non-cognitive appraisal and the particular suite of behaviour it prompts. (2005, p. 89)[4]

The non-cognitive position contrasts with the claim that the process by which the perception of an event is transformed into an emotion response (i.e., a bodily response) is a cognitive process (Ellsworth & Scherer, 2003; Roseman & Smith, 2001; Scherer, 2001). The motivation for this position is that certain resources appear to be needed to explain the observations that (1) different emotions can be caused by the same event, either across different individuals or for the same individual at different times; and (2) a range of different stimuli which have no objective features or properties in common can cause the same type of emotion response. Both of these points suggest that the emotion response typically depends upon information or beliefs that the individual has prior to encountering the emotion causing stimulus. The information that the individual has prior to encountering the stimulus, plus relevant information about the stimulus, determine the type of emotion response that is generated. A simple example goes like this: if I am informed that my car has been stolen, this will cause an anger or sadness response, because I attached some value to my car and have certain beliefs about its importance in my life. However, if I believe that the car was a piece of junk and well insured, and I had been meaning to replace it, then the fact that it was stolen will cause a happiness response instead of anger. In both of these cases the stimulus is the same, but the additional beliefs and desires that I have about the car are an essential factor in determining the emotion response: anger or happiness.

These sorts of considerations suggest to those committed to the cognitive position that there must be a system in place that allows for more flexibility than just a direct response to the stimulus itself. Rather the system has to be able to combine these different types of information in a particular way. The idea that such a system is in place is the basis for the claim that the emotion process is a cognitive one.[5]

These descriptions of the cognitive and the non-cognitive positions have been laid out for explanatory purposes. There are substantial differences between the various non-cognitive theories, but these differences do not need to be explored here. Moreover, the argument that I am making, which focuses on the thalamo-amygdala pathway, does not depend upon the central differences between the cognitive and non-cognitive positions. In fact, the argument itself is neutral with respect to the two theories except insofar as those committed to the non-cognitive position have taken the direct thalamo-amygdala pathway as support for their position.

The central issue addressed in this paper is whether an emotion response in humans can be generated by this direct thalamo-amygdala pathway. The claim that it cannot is based upon the observation that the neurons in this pathway are at too early a stage of sensory processing to respond to the types of objects or events that typically cause an emotion response. If the direct thalamo-amygdala pathway does not generate emotion responses in humans, then it cannot be used as support for the non-cognitive position. This, of course, is not a refutation of the whole non-cognitive position, nor is it evidence for the cognitive position. However, the extent to which this work by LeDoux is used to support the non-cognitive position, this position is undermined.

3. LeDoux's Two Pathways

LeDoux has demonstrated with rats that when a tone, which has been conditioned to elicit a fear response, is heard, signals from the auditory thalamus are sent simultaneously to the auditory cortex and to the lateral nucleus of the amygdala (1995, 1996; Armony & LeDoux, 2000; Figure 1). After receiving input from the thalamus, the auditory cortex then transmits the signal to the lateral nucleus of the amygdala. Hence, the lateral nucleus in quick succession receives information directly from the thalamus, as well as the information that has passed through the cortex. From the lateral nucleus signals are then sent to the central nucleus of the amygdala which triggers the coordinated fear response in the rat.[6] The signal that is transmitted directly from the thalamus reaches the lateral nucleus of the amygdala as early as 12 milliseconds after the onset of the tone, while the signal that travels through the cortex reaches the lateral nucleus at least 20 milliseconds after the onset of the tone. Therefore, the direct thalamo-amygdala pathway has a speed advantage over the neural pathway that passes through the cortex.

Furthermore, lesion studies and single unit studies of the neurons in these areas indicate that the cortex is not necessary for the acquisition of the response to the conditioned stimulus. The conditioning procedure that LeDoux has used is a pure tone (the conditioned stimulus) followed by a footshock (the unconditioned stimulus).
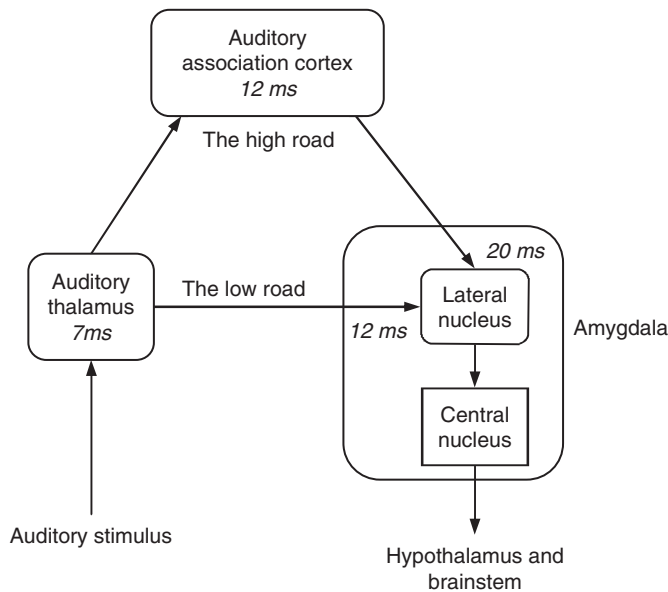
Figure 1. Pathways from the auditory thalamus to the latest nucleus of the amygdala and the minimum response times for a signal to reach each structure after the onset of a tone. Adapted from Quirk, Armony, & LeDoux (1997), Armony & LeDoux (2000).

After a few pairings of the tone and the shock, the tone causes the fear response, which under normal circumstances would be caused by the shock. If either pathway is lesioned—the thalamo-amygdala or the cortico-amygdala—the fear conditioning still occurs by way of the other pathway. However, studies that recorded the activity of single neurons indicate that the conditioned response is acquired via the thalamo-amygdala pathway when both pathways are intact (Quirk et al. 1997).

And lastly, although it is not a feature that LeDoux has directly investigated, his work suggests that the thalamo-amygdala pathway is unable to discriminate between similar but different stimuli. For example, if two relatively similar tones are presented after conditioning, one of which is the conditioned stimulus and one of which is not, the neurons in the thalamo-amygdala pathway will respond in the same way to both (Bordi & LeDoux, 1994a; LeDoux, 1995).

These and other features of the thalamo-amygdala pathway seem to lend support to the non-cognitive position. The thalamo-amygdala pathway takes a stimulus at a low level of analysis, the signal travels directly to the amygdala, and the activity in this pathway can trigger a fear response prior to, and even without, the involvement of the auditory cortex. Thus, if the emotion process can be carried out by a modular, sub-cortical system, then that would suggest that the process does not include any sort of cognitive evaluation of the stimulus. Delancey, when arguing against the cognitive view, says the following:

> There are structural distinctions in the neuroanatomy underlying basic emotions and some other affects that are not consistent with cognitivism. This is a point well

illustrated, for example, by recent research by Joseph LeDoux, who has worked to map out the neural pathways of fear and show that there is a functional and anatomical separation between affective and cognitive processing systems. (2002, p. 41)

Delancey's conclusion is, I believe, too hasty. In what follows I will review the auditory and visual pathways that project to the amygdala without passing through the cortex in more detail. By tracing these pathways from the peripheral sensory receptors to the thalamus I will illustrate that what is represented in the thalamus are only the particular cues that these modalities encode at the periphery. These sub-cortical circuits do not have the capacity to carry anything but the simplest information from the periphery of the organism. The integration of these various cues into a representation of complete objects or events only occurs after processing in the cortex. Therefore, although these sub-cortical pathways do have a certain utility for the rat's response to potential threats, they cannot, at least in the vast majority of cases, have the same function for humans because humans generally require a more complex stimulus than do rats.

4. The Auditory Pathway to the Amygdala

Starting with the early part of the auditory system, sound waves are converted into electrochemical signals in the middle and inner ear. Hair cells in the inner ear drive the activity in the auditory nerve, which projects to the cochlear nuclei located in the brainstem. The auditory nerve carries information about the frequency and the intensity of the sound. Although most auditory stimuli (and our conscious perception of them) are complex sounds, they are encoded by the fibers of the auditory nerve as a series of pure tones (e.g., a vowel is typically composed of three
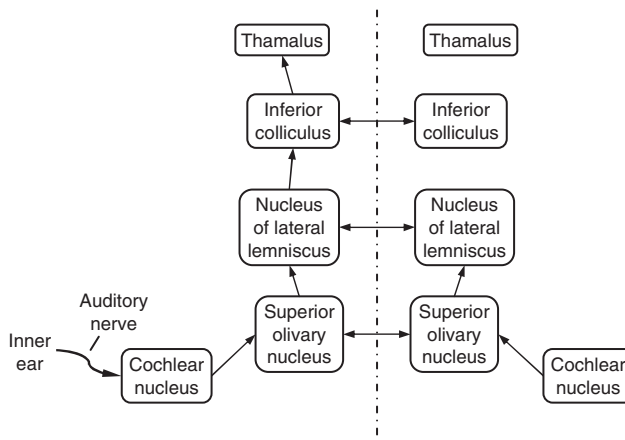

Figure 2. Auditory pathways from the inner ear to the thalamus. The dashed line represents the brain's midline. Adapted from Delcomyn (1998), Haines (2004).

dominant frequencies and each of the three is encoded separately at this early stage of the auditory process [Hudspeth, 2000]).

At low decibel levels the hair cells in the inner ear respond to a preferred sound frequency (the cell's characteristic frequency), although as the intensity of the sound increases the cells will respond to a greater range of frequencies. Since most of the nerve fibers that make up the auditory nerve (about 90–95% of them) carry signals from a single hair cell, information about frequency is transmitted to the cochlear nuclei as a function of which nerve fibers are active.[7] Frequencies below 2 kHz are also encoded by the timing of the action potentials in the auditory nerve which fire in phase with the sound wave, although an action potential will not fire at every peak of the sound wave. As the frequencies rise this timing cannot be maintained and so the response of the hair cells to their preferred frequency becomes more important for encoding the higher frequencies (Hudspeth, 2000; Kingsley, 2000).

The intensity of the sound is also encoded in two ways. One is by the rate of the action potentials that the hair cell produces, which reflects the loudness of the sound; the more intense the sound the more frequent the action potentials. The second is by the number of hair cells (and hence, fibers in the auditory nerve) that are active at the same time. Since the hair cells respond to a wider range of frequencies at higher decibel levels, if more hair cells are active, this indicates that the sound is loud enough to engage a larger number of the cells—in which case the firing pattern of the action potentials is important for indicating the frequency (Hudspeth, 2000; Kingsley, 2000).

From the cochlear nuclei, signals are sent to the neurons that compose the superior olivary nucleus, which is in the middle region of the brainstem (the pons), and then to neurons that compose the nucleus of the lateral lemniscus (also in the pons), and the inferior colliculus, which is higher in the brainstem (in the midbrain). These areas are organized as tonotopic maps, meaning that for each brain area there is an orderly progression from one edge of the structure, where neurons respond to low frequencies, to the other edge, where the neurons respond to high frequencies. This organization is a feature of how the neurons are connected, which is basically in a one-to-one manner.[8] For instance, a neuron in the cochlear nucleus that is active when a particular frequency is heard will excite a neuron in the superior olivary nucleus, which will, therefore, also be active when that frequency is heard. That neuron in the superior olivary nucleus then projects to one in the nucleus of the lateral lemniscus that will likewise be active when that particular frequency is heard, and so on. Since this part of the auditory system utilizes tonotopic projections, the way in which the neurons (and hence the frequencies that they respond to) are organized in the cochlear nuclei is maintained all the way to the auditory cortex (Thivierge & Marcus, 2007).

After the cochlear nuclei, axons from the neurons in each brain area are sent up the brainstem as well as across the midline of the brain so that signals from each ear are combined. The convergence of inputs from each ear allows the timing and intensity differences in the signals to be used to identify from which side of the organism the sound is coming.

The final stage before an auditory signal reaches the thalamus is the inferior colliculus. This area is divided into three main regions, the central nucleus (ICC), the external cortex (ICx), and the dorsal cortex (ICd). The external cortex (ICx) and the dorsal cortex (ICd) of the inferior colliculus send efferents to the areas in the thalamus which then project to the amygdala (LeDoux, Ruggiero, & Reis, 1985; Linke, 1999), while the central nucleus of the inferior colliculus projects to the areas of the thalamus that project to the primary auditory cortex (Doron & LeDoux, 2000; Malmierca & Mierchan, 2004). As is illustrated in Figure 3, by the time afferents reach the thalamus they are moving through two separate auditory pathways. The main pathway sends information to the primary auditory cortex and the secondary pathway carries information directly to the amygdala. The secondary pathway also projects to the cortex, but not to the primary auditory cortex. Rather these areas of the thalamus send efferents to the auditory association cortex.[9]

In the main auditory pathway the cells in the thalamus are organized tonotopically and each responds to very narrow ranges of frequencies, thus preserving the information that has been encoded at the periphery (Jones, 1985; Merzenich, Colwell, & Anderson, 1982). In contrast, while some of the cells in the areas of the thalamus that project to the amygdala maintain the tonotopic organization (especially in the MGm), most cells will respond to such a wide range of frequencies—much wider than cells in the main pathway—that the tonotopic organization is not found.[10] Furthermore, most cells in these areas respond only to frequencies above 16 kHz, and some (especially in the PIN) only to loud sounds, about 40 dB and higher, which is a relatively high minimum threshold (Bordi & LeDoux, 1994a).

The main point I want to draw attention to here is that the cells in these areas of the thalamus that project directly to the amygdala are not set up to respond to stimuli that are very complex—a possibility that is essentially ruled out by the way in which stimuli are encoded at the periphery and then transferred to the thalamus. These neurons are responding to what could be emotionally salient cues, namely, frequencies that falls within a certain range and over a certain decibel level. However, it is the processing that occurs in the cortex that allows animals to respond
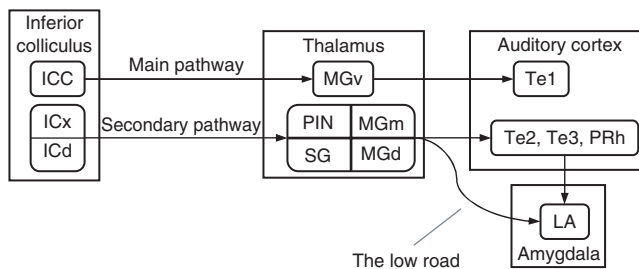

Figure 3. Primary and secondary auditory pathways. MGv: ventral division of the medial geniculate body; PIN: posterior intralaminar nucleus; SG: suprageniculate nucleus; MGm: medial division of the medial geniculate body; MGd: dorsal division of medical geniculate body; LA: lateral nucleus; Te1: temporal cortex, area 1 (primary auditory cortex); Te2 and Te3: secondary auditory cortex; PRh: perirhinal cortex.

to complex auditory stimuli such as changes in the frequency of a continuous sound (Harrington, Heffner, & Heffner, 2001) and species-specific calls (Heffner & Heffner, 1984), and to locate where in space a sound is coming from (Heffner & Hefner, 1990).[11]

5. The Visual Pathway to the Amygdala

It has been assumed (correctly) by emotion theorists that there is also a sub-cortical pathway to the amygdala for visual stimuli. For instance, Prinz uses this example when arguing against the cognitive position:

> It turns out that there is a subcortical pathway from the retina to the amygdala. This pathway probably mediates the fear response to coiled, snake-like objects. . . . According to LeDoux (1996), the response works as follows. First, we see a snake-like object. It reflects an image on the retinae of our eyes. The retinal image sends a signal through the optic nerve into the thalamus, which is the major subcortical hub for the senses before they send signals to the neocortex. The thalamus can register coarse visual features, but it cannot recognize objects. The thalamus sends information onto visual areas of the neocortex, which ultimately achieve recognition, but it also sends a signal directly to the amygdala. . . . The gross shape of a snake-like object, registered by the thalamus, is sufficient to initiate a full-fledged fear response. And there's the rub. If fear can occur without the mediation of the neocortex, then perhaps fear can occur without cognition. (2004a, p. 34)

Since there has been this interest in the sub-cortical visual pathway I will outline what is known about it, although it has not been studied as closely by LeDoux.

Outputs from the retina are carried by retinal ganglion cells. Each ganglion cell responds to light hitting a particular area on the retina. This area on the retina is the ganglion cell's receptive field, and in primates the receptive field of the ganglion cells range from 1/20 of a degree near the center of the retina to 5 degrees at the edge. Ganglion cells generate action potentials based on whether or not light is hitting this area, although different types of ganglion cells, on-center cells and off-center cells, will respond differently to light. On-center cells respond when light is hitting the center of the cell, and off-center cells respond when light is hitting the area around the center.

In addition to the distinction between on-center and off-center cells, another important way of classifying ganglion cells in primates is as M cells and P cells. The M cells have large receptive fields, are sensitive to small variations in contrast, and can respond to higher frequencies of stimulation than the P cells. Therefore, M cells respond better than the P cells to moving stimuli. The P cells have smaller receptive fields and display greater spatial resolution, which makes them more sensitive to detail than the M cells. P cells are also color sensitive, while M cells are not. Given these differences, the P cells are said to respond to the form or shape of the stimuli, while M cells respond to motion. (Livingstone & Hubel 1987; Tessier-Lavigne, 1991).

In the main visual pathway the axons of the retinal ganglion cells send efferents to the neurons in the lateral geniculate nucleus (LGN), which is the main visual area of

the thalamus.[12] The LGN then projects to the primary visual cortex (V1). The superior colliculus, an area located at the top of the brainstem (in the midbrain), also receives inputs from the retinal ganglion cells. It is the superior colliculus that projects to the areas in the thalamus that then project to the amygdala. This superior colliculus-thalamus-amygdala pathway seems to be the visual correlate of the auditory low road (Figure 4).

The superior colliculus is divided into six layers, and in the rat, retinal ganglion cells innervate the optic layer as well as the layers above and below it, the superficial gray and the intermediate gray (Linke, 1999; Linke, De Lima, Schwegler, & Pape, 1999). In the cat, the superficial gray layer and the optic layer receive retinal inputs from Y ganglion cells, cells that are similar to the primate's M cells, and which have large receptive fields and are sensitive to motion (Lo & Mize, 1998). This means that this pathway, which projects to the amygdala, only receives inputs from one population of the retinal ganglion cells: the ones that respond to motion.

The superficial gray and the optic layers transmit to the suprageniculate nucleus and the lateral posterior nucleus of the thalamus (Linke, 1999; Linke et al., 1999; Lo & Mize, 1998).[13] Both the suprageniculate nucleus and the lateral posterior nucleus contain neurons that project to the amygdala (Doron & LeDoux, 1999, 2000). And as is found in earlier parts of this pathway, the neurons in these parts of the thalamus have large visual receptive fields and respond well to quickly moving stimuli (Doron & LeDoux, 1999; Linke, 1999).

As was the case with the auditory areas of the thalamus that project directly to the amygdala, the visual areas of the thalamus that project to the amygdala are distinct from the main visual pathway. And the cells in the areas of the visual thalamus that project directly to the amygdala only respond to some of the cues that are encoded at the periphery. That is, cues that are indications that the stimulus is moving quickly and that it is "looming," but do not include any indications of the form of the stimulus. Prinz, and others who have looked to LeDoux's work to support the non-cognitive position, overstate the capacity of these areas of the thalamus. In particular, Prinz assumes that the form or shape of an object, or some other type of degenerated representation of the stimulus can trigger a fear response. However, we can now see that Prinz does not describe the process accurately. There is no point prior to cortical
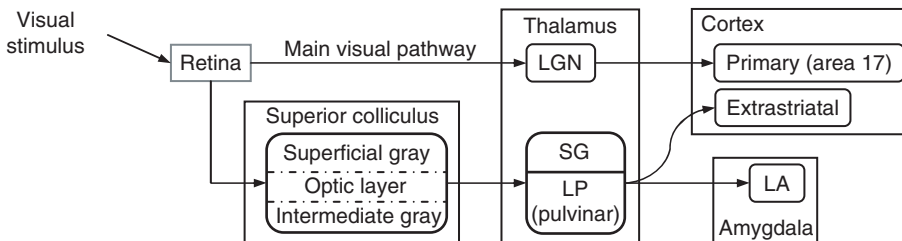

Figure 4. Primary and secondary visual pathways. LGN: lateral geniculate nucleus; SG: suprageniculate nucleus; LP: lateral posterior nucleus (the pulvinar is the primate equivalent of the LP); LA: lateral nucleus.

processing when the form of an object is represented.[14] The cells which respond to complete objects, not to mention full-fledged spatial maps that locate the object in space, are found in the cortex after a number of stages of processing through the cortical visual system (Van Essen & Gallant, 1994).

In the thalamus there are only cells that respond to particular features of their receptive field, which for visual input is an area on the retina. A snake, or a snake-like object, will cause a number of retinal ganglion cells to respond in particular ways, depending on the light hitting the retina. These cells eventually project to the thalamus either by the main visual pathway or through the superior colliculus. But there is no place in the thalamus, or prior to reaching it, when the information that all of the cells are responding to is integrated or combined. Therefore, there is no way for these areas of the thalamus to respond to a snake-like form. More specifically, based on what I said above about the areas of the thalamus that project to the amygdala, if the snake is not moving, as seems to be the case in Prinz's example, then the cells in these areas of the thalamus would not respond at all because there are no cues for them to respond to. If it happened to be that the snake was in the process of striking, then some cells would respond to the rapid motion. It is perhaps interesting to know that rapid motion may cause a response without involving the cortex, but this only creates a very limited class of events that can cause responses via the sub-cortical pathway.

6. The Role of the Sub-cortical Pathways

I have given a simplified picture of the sub-cortical visual and auditory pathways. Even so, some obvious points stand out. First, the perception of the visual or auditory stimulus is organized as it enters the brain such that any one neuron encodes the information for its particular receptive field. For visual stimuli this is an area on the retina, for auditory stimuli this is a particular frequency. There is some processing of this sensory information before it reaches the thalamus. For instance, contrasting auditory inputs from both ears, which identifies the side of the organism that a sound is coming from, is a type of processing that occurs prior to the thalamus. However, there is nothing like the processing that would be required to respond to complete objects or events.

For both the auditory and visual areas of the thalamus, the cells in the regions that project directly to the amygdala do respond to emotionally salient information. The cells that respond to visual stimuli, respond to large and quickly moving stimuli, potentially dangerous characteristics of the environment. They do not, however, identify any particular form or the details of the stimulus (Doron & LeDoux, 1999). The cells that respond to sound (particularly in the PIN) are receptive to frequencies between 16–27 kHz, which is the same range that rats use for warning calls when they are threatened. These cells also prefer louder sounds (above 40 dB), which is an indication of how close the potentially threatening stimulus is (Bordi & LeDoux, 1994a, 1994b; Doron & LeDoux, 1999).

But while it is clearly the case that both the visual and auditory thalamo-amygdala pathways are important for responding to cues that may signal danger for the rat, these cues that are indications of danger are no more complex than what can be encoded at the periphery. It is not possible for a response generated by either the auditory or visual thalamo-amygdala pathways to be a response to any type of complete object, and certainly not a semantically meaningful stimulus that might signal danger. The cells that make up these pathways do not have the capacity to respond to objects—i.e., such information is not represented in these pathways. Of course, humans do respond to complex stimuli, but this requires the processing that occurs in the visual and auditory systems that are located in the cortex.

We can take a moment now to see where we stand. There are the features of the stimulus that are encoded at the periphery: individual frequencies, intensity of sound, light hitting a small portion of the retina, and other features of similar complexity for the other sensory modalities. Some of these features, taken individually, are going to be emotionally laden, especially for rats. We can also see how they might be emotionally significant for humans, for instance, a loud sound, or a sharp poke, might cause a fear response.[15] However, the vast majority of the cases that we want described by a theory of emotion are going to begin with the perception of a complete object. Thus, when we look at the neural circuits that carry out emotion processes we need a mechanism that includes cells that respond to fairly complete objects and events. For example, in the simple case of a fear response caused by seeing a spider, this process presumably includes cells that can respond to a spider qua spider, and these cells will be located in the cortex.[16]

With this distinction between the features of the stimulus that neurons in the thalamo-amygdala pathway can and cannot respond to, we can draw our first conclusion. The thalamo-amygdala pathway can only account for a very limited number of the instances when an emotion response is generated in humans, therefore, it is not a neurobiological case that describes the typical emotion process in humans. This is the weaker conclusion.

A stronger conclusion can be drawn by looking more closely at the relationship between the thalamo-amygdala pathway and a theory of emotion. This pathway only explains emotion responses that are caused by the simplest of stimuli, but we might wonder if this mechanism, although simple, is still useful for understanding more complex mechanisms. The question here is: Does what we know about the thalamo-amygdala pathway inform us about other, more complex mechanisms? We can answer this question by considering LeDoux's work in two different ways.

If we take LeDoux's work as being important because it illustrates a quick, sub-cortical, modular system, then what we know about the thalamo-amygdala pathway does not extrapolate to more complex mechanisms. Once we look at how even the simplest of the standard cases (e.g., the spider case) are carried out neurobiologically, we no longer have a quick, sub-cortical, modular system. Instead, we have to invoke cortical processing—at the very least for the visual processing of the stimulus.

The other way to answer the question is to take LeDoux's work as being important because of what he has discovered about the amygdala, while remaining agnostic for

the moment about where the significant projections to the amygdala come from (i.e., cortical areas or sub-cortical areas). If we go this way, then LeDoux's work does extrapolate to more complex cases. Advocates of the non-cognitive position have not, however, focused on this second way of looking at LeDoux's work—which, prima facie, would be neutral between the cognitive and the non-cognitive positions. Rather the defenders of the non-cognitive position have clearly focused on the thalamo-amygdala pathway because it is a quick, sub-cortical, modular system. While there are many aspects of LeDoux's work that are very significant, the thalamo-amygadala pathway itself does not appear to be, at least with respect to explaining how the emotion process is carried out in humans.

There is more that could be said here, but we can now state the second conclusion. The stronger conclusion is that the thalamo-amygdala pathway does not inform us, in any significant way, about the emotion process in humans. Therefore, this pathway cannot be used to support the non-cognitive position. This is to say, the thalamo-amygdala pathway cannot be invoked to explain the perception of objects without propositional or conceptual content. Nor can it be used to explain the generation of an emotion response to a snake or a spider without a "cognitive evaluation" of these stimuli. This is not to say that these tasks are not carried out somewhere in the brain, but it is a mistake to claim that the thalamo-amygdala pathway performs them.[17]

7. Two Final Comments

Insofar as advocates of the non-cognitive position have looked to neurobiology for support, I want to close with two more general comments on the status of sub-cortical brain structures. The first concerns how we think about the increased size of the brain in primates, especially humans, as compared to other species.[18] Even though mammals and most non-mammals share the same or similar brain structures, differences in the sizes of the structures, especially the expansion of the neocortex, is an important feature of the human brain. Characterizing this expansion as just giving primates more "computing power," or giving humans the capacity for language and other sophisticate skills is, however, too simple. The expansion of the human brain also appears to involve some reorganization and shifting of functional areas (both cognitive and non-cognitive). Berridge illustrates this point succinctly when he says, "Humans can be devastated, rendered into vegetative states, by large neocortical lesions, whereas a rat can lose its entire neocortex and continue on remarkably normal" (2003, p. 41). That rats are able to rely on sub-cortical processes to a much greater extent than humans implies that, although the same brain structures are present in humans and in rodents, these structures are doing different work for the different species. The neuropsychologist Richard Davidson, when commenting on the brain areas and the connections between them that are involved in emotion processes, makes a similar point:

> On the one hand, the rodent data have been essential in establishing some of the
> fundamental facts concerning the basic subcortical circuitry of emotion as

> Panksepp (1998) has illustrated. . . . However, we now know that many of the anatomical details of crucial components of this circuitry are different in rodents and primates. The organization and connectivity of amygdala nuclei are different (Amaral, Price, Pitkanen, & Carmichael, 1992), the anatomy of the prefrontal cortex is fundamentally different (Goldman-Rakic, 1987) and the connectivity and functional status of the anterior cingulate is also different (Bush, Luu, & Posner, 2000). These differences in anatomy imply differences in the nature, function, and complexity of emotions across species. (2003, p. 130)

For these reasons that Davidson mentions, some care must be taken when looking at neurobiological data from other animals to aid in the construction of a theory for a human psychological capacity. Neurobiological data are an important piece of the puzzle, and knowing the particular neural mechanisms that are used by humans is perhaps the ultimate goal with respect to understanding psychological capacities. However, it is a mistake to believe that neurobiological data from other animals can be used, without qualification, to describe how a psychological capacity is carried out in humans. This has relevance for the thalamo-amygdala pathway that I have been examining. Based upon the considerations just reviewed, it is reasonable to question whether such a pathway exists in humans at all.[19] At the very least, I want to suggest that it is not obvious that because the thalamo-amygdala pathway is present in rats that it is also present in humans.

This brings us to the second issue. Although the direct thalamo-amygdala pathway is not useful, and may not even be present in humans, this is not to say that the amygdala is not an important structure in the human emotion process. There is plenty of evidence that it is (e.g., Calder, Lawrence, & Young, 2001; Phan, Wagner, Taylor, & Liberzon, 2002). The non-cognitive position is motivated by the idea that it is only the cortex that participates in "cognitive" processes, while the amygdala, because it is a sub-cortical structure, only participates in "non-cognitive" processes. But, it is not clear that this is correct. Consider an area such as the hippocampus, which is not part of the neocortex,[20] but is critical for memory consolidation— presumably a "cognitive" process. The amygdala, which is at a similar level of the neural-axis as the hippocampus, should probably be thought of similarly—namely, as a sub-cortical structure that participates (or at least may participate) in cognitive processes. What is important is not just whether a structure is cortical or sub-cortical, but how the structure is connected to other areas of the brain. The amygdala in primates is well connected with higher order visual, auditory, and somatosensory cortical areas, and with the frontal cortex (Barbas, 2000; Carmichael & Price, 1995; Price, 2003). Therefore, if we think in terms of an emotion system, it may be reasonable to view this system as one that is composed of some areas that are cortical (e.g., parts of the frontal cortex) and some, like the amygdala, which are not part of the neo-cortex.[21]

These considerations and the examination of the visual and auditory thalamo-amygdala pathways do not amount to a full critique of the non-cognitive position. However, to the extent that the accounts offered in defense of the non-cognitive

position have relied on LeDoux's work for support, the issues examined here do raise serious doubts about this position.

Acknowledgments

Notes

[1]   Lazarus and Scherer are responding to LeDoux (1989), which covers the same material.

[2]   What I am calling the *emotion response* includes the bodily response, for instance, the raised heart rate, trembling, sweaty palms, a particular facial expressions, and so on. The emotion response may have other components as well, one of which is presumably the individual's conscious awareness of the emotion.

[3]   The distinction between language comprehension and the eye blink reflex is rather stark, but it seems to be consistent with the exclusive distinction with which the debate in emotion has been cast (i.e., cognitive versus non-cognitive).

[4]   Robinson is using *affective appraisal*, *non-cognitive affective appraisal*, and *non-cognitive appraisal* interchangeably.

[5]   The accounts of emotion as a cognitive process typically do not suggest that the process is conscious or under the individual's control. The term *cognitive* in this sense is used in the same way as it is for a cognitive task such as language comprehension. However, this is different than the way in which *cognitive* is used in some areas of philosophy, e.g., metaethics.

[6]   A response that includes freezing, blood pressure changes, heart rate changes, and hormonal changes.

[7]   There are two types of hair cells, inner hair cells and outer hair cells. The inner hair cells synapse on about 20 fibers of the auditory nerve, but each of those fibers will only be innervated by one or two inner hair cells. This preserves (redundantly) the frequency that the inner hair cell encodes. The other 5–10% of the nerve fibers receive inputs from about ten outer hair cells, which means that these fibers carry less specific information about frequency.

[8]   This contrasts with convergent connections (many-to-one) and divergent connections (one-to-many) between neurons. Each of these types of connections—topographic, convergent, and divergent—transfers information in a different way (see Thivierge & Marcus, 2007).

[9]   This includes temporal cortex, area 2 (Te2); temporal cortex, area 3 (Te3); and parts of the perirhinal cortex.

[10] In particular, cells in the PIN respond to a much wider range of frequencies (i.e., have much broader tuning curves) than cells in MGv.

[11] These three studies all used macaque monkeys.

[12] Visual information is also organized topographically in the LGN where the organization of the neurons preserves the pattern of stimulation that the retina receives.

[13] It seems to be the case that the lateral posterior nucleus (pulvinar) projects to the extrastriate cortex. This has been suggested as the pathway for blindsight in humans (Guzeldere, Flanagan, & Hardcastle, 2000).

[14]   Note that Prinz also seems to be saying that projections to the amygdala are from the area in the thalamus that is part of the main visual pathway, which is not accurate.

[15]   But keep in mind that if the emotion response is generated solely by the activity in the thalamo-amygdala pathway, then the process that generates the response is a modular one (ie., *mandatory* and *encapsulated* in Fodor's [1983] terms for a modular process). This means that it can only be one of the simple cues that causes the emotion response, and not one of these cues combined with other information, for instance, information about the context of the event. Intuitively, it is easy to see how a fear response might be generated by a sudden loud sound when an individual is walking alone through a dark alley. The stimulus, however, in this case would be much more than just the particular sound. The stimulus would include the dark alley and knowledge about such locations. Again intuitively, it seems hard to image that any of these simple cues that are encoded at the periphery do consistently cause emotion responses by themselves.

[16]   Discussing the location of neurons that respond to whole objects is beyond the scope of this paper, but I have in mind the explanation of the visual system that is put forward by Van Essen and Gallant (1994). In whatever way we might conceive of the function of the neurons in V4 and in the inferotemporal areas (in the cortex), which Van Essen and Gallant describe as responding to complex patterns and shapes, these neurons seem to be necessary parts of a mechanism that can respond to a spider qua spider.

[17]   Note that removing the thalamo-amygdala pathway from the debate alters the resources available to the advocate of the non-cognitive position. One can suggest that a psychological process is not utilizing conceptual content, and then point to a sub-cortical pathway that could be carrying out the process to support this claim (e.g., see the quote from Prinz in Section 5). If, however, this sub-cortical pathway is not available, then this claim is much less compelling.

[18]   Or, to be more precise, encephalization in humans, which is a function of the ratio of brain size to body weight, and this ratio compared to other animals (Jerison, 1976, 1977).

[19]   ''Pathway'' in this context becomes a difficult term to pin down. Some neural connectivity between the thalamus and the amygdala is not what we are after. Rather, something like the same degree of connectivity (i.e., numbers of axons relative to brain size) and performing a similar function is perhaps closer to what seems to be in order.

[20]   I.e., the six-layer cortex. The hippocampus is part of the archicortex (three layer cortex), which is the oldest part of the cortex.

[21]   And of course, areas in the brainstem that drive the bodily changes.

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