Article

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Abstract

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Emotional Attention for Erotic Stimuli: Cognitive and Brain Mechanisms

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ABSTRACT

It has long been posited that among emotional stimuli, only negative threatening information modulates early shifts of attention. However, in the last few decades there has been an increase in research showing that attention is also involuntarily oriented toward positive rewarding stimuli such as babies, food, and erotic information. Because reproduction-related stimuli have some of the largest effects among positive stimuli on emotional attention, the present work reviews recent literature and proposes that the cognitive and cerebral mechanisms underlying the involuntarily attentional orientation toward threat-related information are also sensitive to erotic information. More specifically, the recent research suggests that both types of information involuntarily orient attention due to their concern relevance and that the amygdala plays an important role in detecting concern-relevant stimuli, thereby enhancing perceptual processing and influencing emotional attentional processes. J. Comp. Neurol. 524:1668–1675, 2016.

INDEXING TERMS: erotic information; selective attention; motivational relevance; amygdala; reward

The multifarious environment we live in and our limited sensory resources make it difficult to attend to every single element around us. However, there are psychological mechanisms that enable us to focus on the most relevant information. Specifically, selective attention can orient us to the most crucial elements in the environment (Posner, 1980). It has been suggested that selective attention can be divided into three different processes: exogenous, endogenous, and emotional (e.g., Vuilleumier, 2005; Brosch et al., 2011). Whereas endogenous attention is voluntarily guided by the observer's momentary goals related to the task they are performing in a top-down attention process (e.g., looking for one's keys), both exogenous and emotional attention are automatic, involuntary, stimuli-driven, bottom-up processes orienting attention. However, whereas the former is modulated by the stimuli's low-level perceptual properties (e.g., its shape or color), the latter is influenced by the stimuli's emotional value being relevant for the specific concerns of an individual (e.g., a spider's representation of threat for a person suffering from arachnophobia) in order to satisfy a need (e.g., avoiding the potential threat).

Interestingly, it has long been posited that only negative, and in particular threatening, events involuntarily orient our attention (Öhman et al., 2001). In fact, it has been theorized that humans possess a "fear module" that underlies the rapid detection of potential threats in order to survive (Öhman and Mineka, 2001). Thus far, there has been a vast corpus of literature on the effects of negative threatening information on attentional processing and its neural networks (Vuilleumier, 2005). It has specifically been proposed that the

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amygdala is the brain structure responsible for detecting threats (Öhman and Mineka, 2001). According to this theory, only threat-related stimuli, and in particular those with an evolutionary significance, modulate the involuntary orienting of attention.

However, over the last 20 years, there have been new lines of research that are incongruent with this theoretical perspective. The notion that the amygdala is reserved for negative threatening information has been questioned, as it has been shown that the amygdala is not only involved in the detection of threats but also of positive rewarding stimuli (e.g., erotic stimuli[1] or food; Sander et al., 2003).[1]

Evolutionarily speaking, organisms have many needs, to survive and reproduce, rendering a plethora of stimuli motivationally relevant such as food, threat-related information, and erotic stimuli (Panksepp, 1998). However, biological relevance is not a sufficient explanation for emotional attention. Studies have shown that the amygdala is also engaged during the perception of stimuli that have acquired relevance through socialization such as money (Sescousse et al., 2013). Additionally, studies have shown that participants involuntarily orient their attention toward money like they do for other types of positive rewarding stimuli (Pool et al., 2015b). According to appraisal theories of emotion, after the perception of a stimulus, a relevance check occurs. If the stimulus is deemed motivationally relevant for the current concerns of the observer, then its properties will further influence cognitive processes to satisfy one's needs (Sander et al., 2003, 2005). Therefore, in line with those theories, our attention is not exclusively oriented toward negative threatening information but rather toward information deemed motivationally relevant to the current concerns of the observer (Brosch et al., 2007, 2008; Pool et al., 2014, 2015b).

Recently, a meta-analysis on attention orientation toward positive stimuli showed that reproduction-related stimuli had some of the largest effects on the biasing of attention (Pool et al., 2015b). Taking the reproduction concern into consideration, to increase the chances of finding a mating partner, the sensory system has to be able to guide the organism to the best options possible. Indeed, it has been shown that erotic stimuli, which are positive rewards and motivationally relevant for individuals' concerns, involuntarily orient attention (e.g., Most et al., 2007). Here, we review recent representative studies showing that attention is involuntarily oriented toward erotic stimuli and we propose that this process is based on cognitive and neural mechanisms that are common with the mechanisms that underlie involuntary attentional orienting toward threat-related stimuli. We also propose that this process is underlined by amygdala activity that allows 1) the detection of concern-relevant stimuli in the environment; and 2) amplifies the cortical activity related to perceptual processing of the motivationally relevant stimulus, rendering them more likely to access the limited attentional resources of organisms.

CEREBRAL STRUCTURES INVOLVED IN THE PROCESSING OF VISUAL EROTIC INFORMATION

Using functional neuroimaging techniques (e.g., functional magnetic imaging, positron emission tomography), various studies have investigated the neural substrates of erotic stimuli processing (e.g., Karama et al., 2002; Stark et al., 2005; Walter et al., 2008; Bianchi-Demicheli et al., 2011; Wehrum-Osinsky et al., 2014; see Fig. 1). They have shown two subcortical structures that seem to activate more for erotic information compared with neutral, less relevant positive or threat-related information: the hypothalamus and the ventral striatum (Karama et al., 2002; Stark et al., 2005; Walter et al., 2008; Wehrum-Osinsky et al., 2014). First, the hypothalamus has been associated with sexual motivation and the first stages of sexual arousal (Wehrum-Osinsky et al., 2014), and more specifically, stimulation of the posterior hypothalamus has been found to induce a copulatory behavior in animals (Redouté et al., 2000; Stoléru et al., 2012). Second, receiving rich sensory inputs from the amygdala and the orbitofrontal cortex (Redouté et al., 2000), the ventral striatum has been linked to the motivational component of sexual arousal and reward processing (Redouté et al., 2000; Stark et al., 2005; Walter et al., 2008; Stoléru et al., 2012; Wehrum-Osinsky et al., 2014). The motivational component, playing a crucial role in sexual desire, consists of the processes leading individuals to direct their behavior toward their sexual needs.

However, there are also cortical and subcortical neural structures that appear to be active during the visual perception of emotional stimuli in general. More specifically, activation of the orbitofrontal cortex, insula (de Gelder et al., 2004; Wehrum-Osinsky et al., 2014), parietal cortex, thalamus (Redouté et al., 2000; Stark et al., 2005; Walter et al., 2008), pulvinar nucleus of the thalamus (Redouté et al., 2000; Liddell et al., 2005), brainstem (Liddell et al., 2005; Stark et al., 2005), occipital cortex, and amygdala (Hamann et al., 2002; Stark

[1]It should be noted that in the present review, the term *erotic stimuli* represents highly arousing stimuli of a sexual nature such as images of naked women or men, couples during intercourse, or even sexually arousing words.

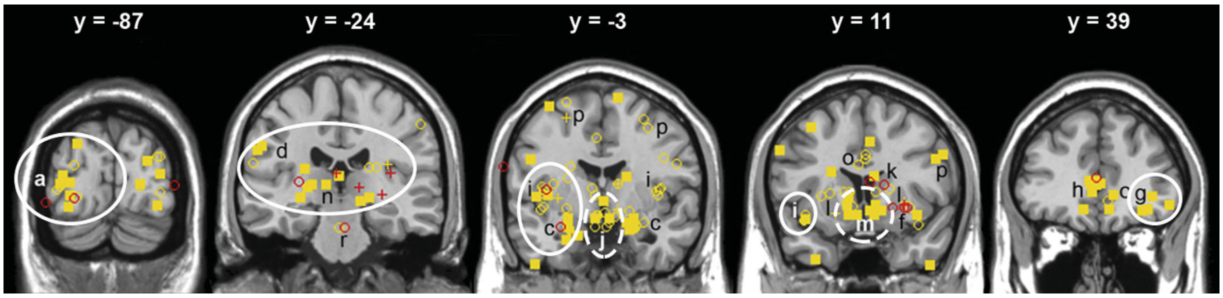

Figure 1. Brain structures active during the presentation of erotic stimuli across multiple studies. The geometric shapes (e.g., squares, circles) on each coronal slice (y-coordinate referring to MNI space) represent studies that have found activation for erotic stimuli at those sites. We have highlighted the brain regions involved in the processing of emotional stimuli in general (circled with solid lines) as follows: the (a) occipital cortex; (c) amygdala; (d) parietal cortex; (g) orbitofrontal cortex; (i) insula; and (n) thalamus; as well as those involved in the processing of positive rewarding stimuli (circled with dashed lines): the (j) hypothalamus and (m) ventral striatum/nucleus accumbens. Note: The different colors and shapes indicate the types of neuroimaging techniques (yellow, fMRI; red, PET) and stimuli (circle, video clips; square, photographs; cross, other stimuli) used in the studies. Reprinted and modified from Stoléru et al. (2012).

et al., 2005; Walter et al., 2008; Wehrum-Osinsky et al., 2014) is common for multiple types of emotional stimuli, including threat-related and erotic images, compared with neutral stimuli. Whereas the parietal cortex and the thalamus have been suggested to subserve the guiding of visual attention and the orbitofrontal cortex has been suggested to be involved in integrating emotional processing and attentional control (Dominguez-Borras and Vuilleumier, 2013), the insula has been linked to interoceptive awareness (Stoléru et al., 2012). These cerebral structures have been linked to emotional attention, and it has been proposed that emotional stimuli are attended to because the amygdala renders the perceptual representation of emotional stimuli more salient and more likely to have access to the limited resources of individuals (Vuilleumier, 2005).

As previously mentioned, the amygdala is important not only for negative threatening stimuli but also for positive reward stimuli. For instance, it has been demonstrated that a specific subnucleus of the amygdala (the central amygdala nucleus), which has been shown to play a part in behavioral reactions to negative threatening stimuli (Amorapanth et al., 2000), is also involved in appetitive motivation for sexual stimuli in animals (Mahler and Berridge, 2012). More precisely, stimulation of this subnucleus increases the incentive salience of sex in rats, resulting in an increase of sexual investigatory behaviors toward potential sexual partners (Mahler and Berridge, 2012). In humans, Walter et al. (2008) compared erotic stimuli with less relevant positive stimuli (e.g., images of sport scenes) matched in arousal level and found greater amygdala activity for the former than the latter, ruling out the proposal that the amygdala is simply activated by high arousal content and suggesting that it might instead be necessary to appraise the relevance of information; the amygdala acting as a relevance detector (Sander et al., 2003; Ewbank et al., 2009; Cunningham and Brosch, 2012). In line with this notion, the previously mentioned studies (Stark et al., 2005; Walter et al., 2008; Wehrum-Osinsky et al., 2014) have all shown that the amygdala is activated for both erotic and threat-related stimuli compared with neutral or less relevant positive stimuli, both types being motivationally relevant to biological concerns such as survival and reproduction. Taken together, these studies underline the importance of the amygdala in the processing of erotic stimuli, which modulates the activity of the areas to which it relays information. Particularly, the amygdala can modulate the involuntary orienting of attention by providing specific information to the cortical areas it projects to, such as the occipital cortex and the orbitofrontal cortex (Vuilleumier, 2005).

It should be noted that although the present review focuses on the role the amygdala plays in emotional attention, it has been suggested that there are multiple parallel pathways involved in the visual processing of emotional stimuli. The orbitofrontal cortex, insula, and pulvinar nucleus of the thalamus are other important structures involved in the initial processing of emotional stimuli (Pessoa and Adolphs, 2010).

Visual erotic information, due to its concern relevance, is suggested to be detected by the amygdala and then further processed by structures associated with emotional attention (e.g., occipital, orbitofrontal, and parietal cortices) and reward processing (e.g., the ventral striatum). More specifically, it has been hypothesized that the amygdala favors the perceptual representation of emotional stimuli in sensory cortices, rendering it more salient to individuals (Vuilleumier, 2005). However, do erotic stimuli enhance perceptual processing?

TEMPORAL DYNAMICS AND PERCEPTUAL PROCESSING OF VISUAL EROTIC STIMULI

In humans (Pourtois et al., 2005) and monkeys (Sugase et al., 1999), it has been shown that the processing of negative threatening information is increased within perceptual pathways compared with neutral information. Investigating the temporal dynamics of erotic information, studies using electroencephalography (EEG) have demonstrated that erotic information processing benefits from more resources during early and late selective processing compared with neutral information (e.g., Schupp et al., 2004b). Early selective processing is more likely to reflect the role of automatic involuntary processes, whereas late selective processing is more likely to be influenced by controlled voluntary processes. Indeed, it has been found that the resources allocated to the perceptual processing of both erotic and threat-related images are augmented compared with lower arousal images of both valence and neutral images (Schupp et al., 2004a,b, 2013; Anokhin et al., 2006). More specifically, amplitudes for the early posterior negativity (EPN), appearing between 150 and 350 ms post stimuli onset over the temporo-occipital cortex, and the late positive potential (LPP), appearing between 300 and 700 ms post stimuli onset over the centroparietal cortex, have been shown to be enlarged for erotic images compared with a variety of images such as neutral images and less relevant positive images (e.g., kittens and flowers). These components are thought to index selective attention and sustained attention (Olofsson et al., 2008), respectively. Similarly to visual threatening stimuli, visual erotic stimuli seem to induce an early facilitation of the process leading to their perceptual representation, resulting in an involuntary attentional shift.

It has been shown that increased neural resources are available for the processing of positive images compared with neutral images during brief presentations (i.e., 120 ms; Schupp et al., 2004b). Furthermore, the authors demonstrated that a more pronounced negative EPN over temporo-occipital sites as well as larger LPP amplitudes over centroparietal sensors was elicited for erotic images over low arousal positive images. Therefore, akin to threat-related information, the amplified allocation of resources toward early processing seems to also occur when erotic content has been briefly displayed. The aforementioned studies suggest that more resources are quickly and involuntarily allocated toward the cortical processing of erotic information compared with neutral information and that the cortical activity is sustained over time.

Once more, it might be inferred that high arousal information receives prioritized allocation of resources considering that high arousal negative threatening and positive rewarding information are processed over low arousal and neutral information. However, van Lankveld and Smulders (2008) demonstrated that high arousal stimuli involuntarily orient attention only if they are relevant to the observer's biological concerns. On heterosexual men, they investigated the neural processing of images varying in arousal and valence. By comparing high arousal positive images (e.g., sports scenes) not relevant to biological concerns, with low arousal positive (e.g., kittens, flowers), high arousal negative (e.g., traffic accidents, snakes), low arousal negative (e.g., crying individuals, garbage), and erotic (e.g., nude women, heterosexual couples engaging in vaginal intercourse) images matched in arousal level with the positive high arousal images, they found an enhanced amplitude of the LPP for erotic images compared with all the other types of images. Additionally, Schupp et al. (2004a) found that erotic and threat-related images elicited an enhanced amplitude of the LPP compared with neutral images. Interestingly, the erotic images, which involved couples and individuals of the opposite sex, also produced a more positive LPP than any other positive images, including images of sports scenes. These studies thereby indicate that arousal is not the only factor influencing processing, rather it could be suggested that it is due to erotic content not only having a high arousal level but also being highly relevant to the biological concerns of the observer.

It has been demonstrated that the processing of erotic information is enhanced compared with low arousal positive and neutral information (e.g., van Lankveld and Smulders, 2008). As has been suggested for threat-related stimuli, one can posit that the neurocognitive mechanism responsible for favoring the perceptual representation of relevant emotional stimuli underlies emotional attention toward erotic stimuli. In this case, the increased perceptual salience of erotic stimuli should also influence the organism's behavior, by making erotic information more difficult to ignore and easier to attend to than other kinds of information that are less relevant for the current needs of the individual.

EROTIC INFORMATION AND BEHAVIORAL PERFORMANCES

Analogous to threat-related stimuli, studies have demonstrated that attention is involuntarily oriented toward erotic stimuli, influencing performance on tasks by affecting aspects such as speed or accuracy (e.g., Schimmack, 2005; Most et al., 2007). Anderson (2005) showed that erotic stimuli involuntarily orient attention more than neutral stimuli and low arousal positive stimuli. He used a dual target rapid serial visual presentation task (RSVP) in which word stimuli were rapidly (i.e., 100 ms) presented one after another while participants had to as accurately as possible relay two targets amid distractor items. A letter string of a single character (e.g., NNNNNNNN) was presented as the first target, and the second target consisted of an erotic (e.g., orgasm, foreplay), neutral (e.g., square, crowbar), or low arousal positive word (e.g., sky, flower). Distractor items, alphanumeric strings (e.g., @#$%&), were presented between the targets. It has been demonstrated that the fewer distractor items there are between the presentation of both targets, the timing being crucial, the more it becomes difficult to accurately determine the identity of the second target; this phenomenon is called an attentional blink. The attentional blink highlights the limitations of the temporal dynamics of attention as it becomes increasingly harder to perceive the second target the closer in time it is displayed after the first target. The results showed that the attentional blink was attenuated by the erotic words, reflected by an increase in accuracy compared with neutral and positive low arousal words. Similar results were found in two studies by Schimmack (2005): while participants were instructed to solve math problems, or determine the orientation of a line, different types of negative and positive stimuli varying in arousal were presented at the same time. Interference effects were found for the stimuli that elicited the highest arousal: threat-related images and images of women and men in underwear.

Based on the findings of these studies, it has been suggested that erotic stimuli affect emotional attention due to their high arousal level (Anderson, 2005; Schimmack, 2005). However, it might not be solely due to arousal: Most et al. (2007) have shown that erotic stimuli can involuntarily orient attention even more than threat-related stimuli. In this version of the RSVP paradigm, erotic and threat-related images, inducing the same level of arousal, as well as neutral images were used as critical distractors in a rapid stream of neutral images, the emotional critical distractors hypothetically hindering the detection of the neutral target stimulus (i.e., rotated images of buildings and landscapes) depending on the number of items between them. The authors found that participants were less accurate in identifying the target when the emotional critical distractors appeared two items prior to the target compared with the neutral critical distractors, the emotional critical distractors thereby impairing the perception of the subsequent target. However, when given an indication about the target in order to identify it with more ease, only the performance for the neutral and threat-related trials improved. This was not the case when erotic critical distractors were presented, even with a monetary incentive to ignore the distractors. Therefore, erotic stimuli are hard to consciously disregard, but they might be even harder to disregard than threat-related stimuli.

Considering that Most et al. (2007) controlled for the degree of arousal the erotic and threat-related images induced, it could be suggested that the erotic stimuli were harder to ignore due to the relevance of the stimuli for the participants' sexual concerns. Indeed, Jiang et al. (2006) have shown that subliminal erotic stimuli influence attention and performance only if they are relevant to the individual's sexual concerns (e.g., sexual orientation). To subliminally present the images, the authors used interocular suppression, a procedure in which two different sets of images are displayed to each eye; the dominant eye is presented with two noise patches, whereas the nondominant eye is presented with an erotic image and a scrambled image. Displaying different images to each eye at the same time causes a binocular rivalry to occur; the dominant eye is able to consciously perceive the displayed image, whereas the other, the nondominant eye, is unaware of the image being displayed. Through this paradigm, they demonstrated that subliminal erotic stimuli can affect a participant's performance during a Posner cuing paradigm depending on the viewer's sexual orientation. During this task, the participants had to report whether a Gabor patch, presented after either an erotic image or a scrambled image, was tilted clockwise or counterclockwise. The authors found that, depending on the participants' sexual concerns, their attention was involuntarily oriented toward subliminal erotic stimuli, rendering them more accurate in detecting a target. For heterosexual men, when targets were located at the same site as the previously presented erotic images of women, participants were more accurate in detecting the orientation of the target. As for homosexual men and heterosexual women, their accuracy was greater when an erotic image of a man was presented in the same location as the subsequent target. This is interesting for two reasons, the first being that concern relevance appears to be essential for attention to be involuntarily oriented. Not all erotic stimuli will involuntarily orient attention: participants' attention was only involuntarily oriented when images of their sexual preference were presented; thus only the stimuli that were relevant for their sexual concerns influenced their attention. Second, the erotic stimuli were presented subliminally and participants were thus not aware of perceiving them, yet they were still influenced.

All these studies taken together imply that erotic information involuntarily orients attention and influences

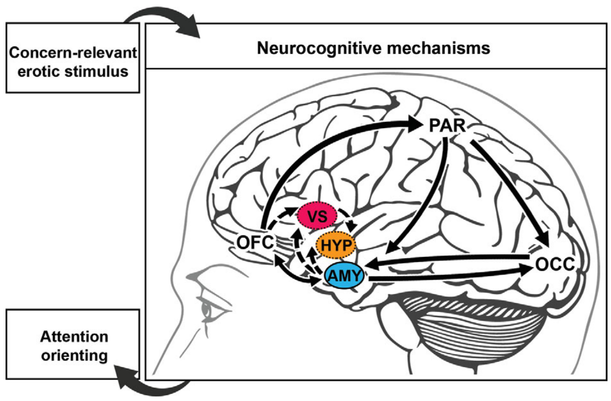

Figure 2. Schematic illustration of the key neurocognitive mechanisms we propose are involved in emotional attention toward erotic stimuli (solid arrows) as well as the structures known to be involved in reward processing (dashed arrows). Based on existing sexual concerns of the individual, the erotic stimulus is perceived and detected as relevant to the viewer's concerns, with the amygdala playing an important role, increasing the perceptual salience of the erotic information, which leads attention to be rapidly and involuntarily oriented toward it. The perceptual representation of erotic stimuli is later modulated by other structures involved in reward processing such as the orbitofrontal cortex, hypothalamus, and ventral striatum as well as by attention-related structures such as the parietal cortex. It should be noted that for purposes of simplicity, not all projections are depicted in the illustration, which was based on Haber and Knutson's (2010) review of the circuitry involved in reward processing. AMY, amygdala; HYP, hypothalamus; OCC, occipital cortex; OFC, orbitofrontal cortex; PAR, parietal cortex; VS, ventral striatum.

behavior (e.g., affecting organisms' speed and accuracy in detecting targets) just as much as threat-related information, even without awareness being necessary (Jiang et al., 2006), and that relevance might be a crucial underlying mechanism in emotional attention.

CONCLUSIONS AND FUTURE DIRECTIONS

This literature review suggests that erotic stimuli, because of their concern relevance, involuntarily orient attention just as much as other concern-relevant positive stimuli, or threat-related information, and we propose the following neurocognitive mechanisms by which this phenomenon occurs.

It seems likely that erotic stimuli share key cognitive and brain mechanisms with threat-related stimuli to involuntarily orient attention (Fig. 2), as it has been shown that: 1) erotic stimuli activate both the amygdala and perceptual areas (e.g., occipital cortex) more than neutral or less relevant positive stimuli, suggesting that the amygdala amplifies the resources allocated toward the perceptual representation of erotic information; 2) the enhancement of the representation of erotic stimuli occurs during the early stages of perceptual processing; 3) they can rapidly influence the involuntary attentional orienting even before consciousness appears; and 4) they depend on the current concerns of the observer. Taken together, the literature therefore suggests that erotic stimuli, which automatically and involuntarily orient attention due to their emotional value as biologically concern-relevant stimuli, are able to orient emotional attention, independently of exogenous and endogenous attention systems.

Although there has been evidence of erotic information involuntarily orienting attention, further investigations are needed. While it has been suggested that the amygdala favors the perceptual representation of emotional stimuli (Dominguez-Barras and Vuilleumier, 2013), and evidence has consistently shown that the amygdala is critically involved in the perception of erotic stimuli and that the activity in perceptual areas is amplified during their perception, the functional connection between these two areas remains to be proved for erotic stimuli.

Furthermore, there are many research lines to be elucidated. For instance, a recent model developed in affective neuroscience has posited that reward processing is not unitary but rather two components that can be dissociated: wanting, the effort individuals are willing to mobilize to obtain a reward; and liking, the hedonic pleasure felt during the consumption of the reward (Berridge and Robinson, 2003). It has been proposed that this distinction is important to understand reward processing in humans (Pool et al., 2015a, in press), and in particular to understand the processing of sexual stimuli (Toates, 2009, 2014). The wanting component of sexual stimuli has been suggested to be underlain by the orbitofrontal cortex, ventral striatum (including the nucleus accumbens), anterior insula, anterior cingulate cortex, amygdale, and the midbrain, whereas the liking component has been suggested to be underlain by the lateral hypothalamus, ventral pallidum, anterior insula, middle cingulate cortex, frontal operculum, inferior parietal lobule, and occipitotemporal cortex (Georgiadis and Kringelbach, 2012). A growing body of literature has demonstrated the powerful influence the wanting component has on behavior and cognition related to rewards. These studies suggest that wanting determines the behaviors of reward seeking, independently of the liking component (Wyvell and Berridge, 2000). However, it has yet to be demonstrated which component determines orientation of attention toward erotic stimuli. This line of research could have clinical implications, as it could improve the understanding of the underlying mechanisms of sexual desire disorders such as hypoactive sexual desire disorder and hypersexuality.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interests to report.

ROLE OF AUTHORS

Manuscript preparation: VS. Critical revision of the manuscript: EP, SD, TB, FBD, DS.

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