

THE NEUROIMAGING OF LOVE AND DESIRE:
REVIEW AND FUTURE DIRECTIONS

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Abstract

We review recent neuroimaging research on the experiences of romantic love and sexual desire, focusing specifically on the question of links and distinctions between the brain regions involved in these experiences. We conclude that although love and desire are associated with distinct patterns of brain activation, certain regions (such as the caudate, putamen, insula, and anterior cingulate cortex) have shown activation during both experiences, raising the possibility that certain types of love and desire may be relatively distinct from one another (on an experiential and neural level) whereas others are more interconnected. We outline several promising directions for future research on this possibility, for example testing for differences between the neurobiological bases of different types of sexual desires (i.e., those directed toward strangers versus romantic partners; those which are more “responsive” versus automatic, and those which are more or less dependent on an emotional context). We also discuss future research directions related to the study of female sexual desire and orientation.

Key words: romantic love, sexual desire, caudate, putamen, insula, anterior cingulate cortex, passion, fMRI, PET, EEG

Declaration of interest: none

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It is a truism that love and desire are fundamentally distinct, albeit fundamentally related. Sexual desire is typically defined as a “a wish, need, or drive to seek out sexual objects or to engage in sexual activities” (Regan 1998, p. 346) whereas romantic love is typically defined as “the constellation of behaviors, cognitions, and emotions associated with a desire to enter or maintain a close relationship with a specific other person” (Aron & Aron 1991). The degree to which romantic love and sexual desire are fundamentally integrated (and potentially identical) experiences has long been a topic of debate (Aron 2010). In particular, it has been thought that sexual desire is a necessary ingredient for the intense feelings of passion which characterize the earliest stages of romantic love (reviewed in Diamond 2003). Yet other researchers have argued that love and desire are functionally independent social-behavioral systems with distinct evolutionary functions and neural bases (Fisher 1998).

The increasing use of functional neuroimaging (most commonly fMRI, or functional magnetic resonance imaging, but also PET, or positron emission tomography, and less often EEG, or electroencephalography) to investigate the basic neurobiological architecture of love and sexual desire can make important contributions to this basic question. PET and fMRI techniques measure changes in blood flow and oxygenation in response to the presentation of visual, auditory, or tactile stimuli, under the assumption that these changes correspond to

regional neural activity. Responses to experimental stimuli are contrasted with responses to control stimuli in order to identify stimulus-specific patterns of brain activity (i.e., responses to sexually arousing photographs or to a photograph of one’s romantic partner). Several reviews have been published in recent years summarizing extant neuroimaging research on both sexual desire (Fonteille & Stoleru 2010, Maravilla & Yang 2008, Ortigue et al. 2009, Stoleru & Mouras 2007) and romantic love (Ortigue et al. 2010). In the present review, we focus on the question of *links and distinctions* between these experiences at a neurobiological level. This topic has not previously received explicit attention in neuroimaging studies (for example, no research has directly contrasted brain activity during romantic love versus sexual desire in the same group of subjects), but a sufficient number of studies have investigated either romantic love *or* sexual desire to allow for comparison of the brain regions involved, and consideration about how these complex experiences are related. In addition to reviewing this body of research, we highlight key directions for future study, especially in the understudied domain of sexual orientation.

Studies of love-specific neurobiological activation

The most relevant data on the neurobiological basis

of romantic love comes from studies conducted by Bartels and Zeki (2000), Aron and colleagues et al. 2011, Aron et al. 2005, Xu et al. 2010), and Ortigue and colleagues (Ortigue et al. 2007). The seminal early work of Bartels and Zeki (2000) focused on early-stage passionate love, and found that when participants viewed pictures of their loved one (versus viewing pictures of friends that were comparable to the loved one with respect to age, sex, and familiarity), activation was detected in the middle insula, anterior cingulate cortex (ACC), putamen, retrosplenial cortex, and caudate. In contrast, deactivation was detected in the amygdala. The insula and ACC are typically associated with emotion and attentional states, whereas the retrosplenial cortex is involved in episodic memory recall, imagination, and planning for the future. The putamen and caudate are associated with motivational states and reward, while the amygdala processes fear and experiences of threat.

Aron and colleagues (2005) also focused on early-stage passionate love, and found that when participants looked at the face of their partner and thought about pleasurable, non-sexual events involving the partner, activation was detected in the right caudate and the ventral tegmental area (VTA), whereas the amygdala showed deactivation (similar to Bartels and Zeki's findings). Additionally, they found that the more passionately in love people reported feeling (using the Passionate Love Scale, Hatfield & Sprecher 1986), the greater the activation in the caudate. The caudate and the VTA are the most consistent regions associated with romantic love (Acevedo et al. 2011, Aron et al. 2005, Bartels & Zeki 2000, Ortigue et al. 2007, Xu et al. 2010), consistent with the fact that these dopamine-rich regions are strongly associated with reward and goal-directed behavior, supporting the notion of romantic love as an intense motivational state.

Research by Ortigue and colleagues (2007) used implicit representations of the beloved (i.e., subliminal priming with the partner's name versus a friend's name) and found further confirmation of the critical role of the caudate nucleus and VTA. They also compared brain activation in response to partner primes with responses to "generalized passion" primes (i.e., primes describing activities about which individuals had reported feeling passionately). This allowed for the identification of regions specifically associated with *romantic* passion. Results revealed love-specific activation in the bilateral fusiform regions and bilateral angular gyri, which are involved in the integration of abstract representations, particularly abstract representations of the self, and which call upon episodic retrieval processes. Hence, this work builds upon the emerging view of romantic love as a dopaminergically-mediated motivational state by demonstrating that love also fundamentally involves a self-representational component, consistent with Aron and Aron's (1986) model of love as involving the inclusion of the beloved into one's own self-concept. Finally, research using priming tasks (Bianchi-Demicheli et al. 2006, Ortigue et al. 2007) has demonstrated that the dopaminergically-mediated motivational state of romantic love has powerful effects on cognition, facilitating performance on lexical decision tasks. This body of work is particularly

important for demonstrating that although the experience of love may be localized in specific brain regions, its *effects* on other brain functions can be broad and pervasive due to a "love enhanced" neural associative network (Bianchi-Demicheli et al. 2006). As we will revisit below, this is particularly important for considering potential facilitative pathways between romantic love and sexual desire.

Studies of desire-specific activation

The results of studies of sexual desire show more variability than the results of studies of love, which may be attributable to the fact that studies of desire have used a much broader range of eliciting stimuli (reviewed in Fonteille & Stoleru 2010, Maravilla & Yang 2008, Ortigue et al. 2009; Stoleru & Mouras 2007). Whereas love studies have used pictures of the romantic partner or primes of the partner's name, studies of sexual desire have used a broad range of sexually explicit stimuli, and the form and intensity of participants' neurological response is likely influenced by multiple features of the stimuli (i.e., whether it is visual, auditory, or tactile; the use of still photographs versus videos; short versus long stimulus presentation; depiction of isolated individuals versus couples; depiction of nude bodies versus sexual activity, partnered versus unpartnered activity; the degree of physical activity involved, the emotional intensity and valence of the stimuli, attractiveness of the actors, etc.). It may be difficult or impossible to determine what specific features of the stimuli individuals are responding to: For example, a psychophysiological study of genital arousal conducted by Chivers and colleagues (Chivers et al. 2007) found that women showed substantially more genital arousal in response to videos depicting sexual activity than to videos showing single, nude bodies, regardless of the gender of the actors in the videos (i.e., lesbians showed sexual arousal to depictions of male-male sexual activity and heterosexual women showed arousal to depictions of female-female activity). For men, however, the gender of the actors proved more important than the presence or absence of sexual activity (gay men became more aroused to male actors whereas heterosexual men became more aroused to female actors). Such findings demonstrate the importance – and difficulty – of selecting stimuli which can be reasonably presumed to trigger comparable sexual responses across all participants. Further contributing to this problem, relatively few studies have incorporated detailed self-report assessments of participants' *subjective* responses to and interpretations of the stimuli (either during presentation or afterward) which might help to reveal the phenomenological basis for different patterns of neurobiological activation. In some cases, for example, post-experimental debriefing has revealed that some participants began imagining sexual acts after exposure to visual sexual stimuli (Moulier et al. 2006), and these elaborative fantasies may have included a range of additional contextual and affective features which might have influenced participants' brain activity.

It is also not clear whether individuals' neurological responses to sexual stimuli can be interpreted as sexual *desire* versus sexual *arousal*. Many neuroimaging studies use these terms interchangeably, but desire and arousal are distinct subjective experiences with potentially distinct neurological substrates (Ortigue & Bianchi-Demicheli 2007). For example, sexual desire is commonly defined as a cognitively-mediated motivational state that leads individuals to pursue sexual activity with specific individuals, whereas sexual arousal is a physiological state of readiness for sexual activity which is often (but not always) accompanied by a subjective perception of sexual excitement (Basson et al. 2010). Given that neuroimaging studies typically use explicit sexual stimuli depicting strangers, rather than specific desired individuals, they are more appropriately considered studies of arousal than desire (to be sure, it may be ethically and logistically impossible to experimentally investigate the neural correlates of individuals' sexual desires for specific people, such as romantic partners, given that the "desire targets" would probably be unwilling to provide researchers with explicit sexual photos or videos of themselves!).

Despite diversity in stimulus properties and experimental protocols, certain regions do appear to be reliably activated in response to sexual stimuli, such as the hypothalamus, putamen, visual cortical areas and inferotemporal cortex, the orbitofrontal cortex, anterior cingulate cortex (ACC), parietal cortex, temporo-parietal junction, insula, ventral striatum, anterior temporal areas, inferior frontal and cingulate areas, amygdala, and basal ganglia (for comprehensive examples and reviews see Ferretti et al. 2005; Fonteille & Stoleru 2010; Karama et al. 2002; Maravilla & Yang 2007, 2008; Moulier et al. 2006; Redoute et al. 2000; Walter et al. 2008). Most importantly, studies of sexual arousal or desire have *not* detected the distinctive pattern of predominant caudate and VTA activation that reliably characterizes romantic love, supporting the notion that love and desire are distinct on both an experiential as well as a neurobiological level (Aron 2006). Yet equally important, some brain regions *do* show activation in studies of both love and desire, such as the caudate, insula, putamen, and ACC. The fact that these regions prove relevant for both love and desire provides a potential neurobiological basis for the fact that these experiences are often judged to be closely intertwined, and suggests pathways through which each type of experience might influence the other.

Given that the putamen and the caudate are both associated with motivational states and reward, their joint relevance for both sexual desire and romantic love likely reflects the fact that love and desire both involve strong motivation to seek the love object (albeit for different rewards: proximity in the case of romantic love, and sexual activity in the case of desire). The joint relevance of the ACC for both love and sexual desire is notable, given that the specific region of the ACC that was found to be activated in Bartel and Zeki's (2000) study of love-specific brain activation was the rostral or perigenual ACC (rACC), which is the same region found by Walter and colleagues (2008) to be particularly sensitive to the *emotional valence* of sexual stimuli.

This pattern of findings is consistent with the fact that the rACC is generally considered the "affective" component of the ACC (in contrast to the dorsal ACC, which is more relevant for cognition, attention, and motor control, and hence appears more important for physiological arousal). It is also notable that rACC activation has also been found to be related to the personal relevance and self-relatedness of stimuli (Heinzel et al. 2006, Phan et al. 2002), which is consistent with its role in romantic love.

Does love modulate the experience of desire?

Consideration of these "joint" love/desire brain regions raises the possibility that some forms of sexual desire might be more "romantic" than others (i.e., more sensitive to and perhaps dependent on emotional and interpersonal context), and that such differences are manifested neurobiologically as well as experientially. This possibility is consistent with the findings of Walter and colleagues (2008), who conducted one of the few studies seeking to disentangle the sexual versus emotional features of sexual stimuli. They found that the hypothalamus and the ventral striatum (VS) were specifically activated by sexually intense stimuli, independent of the stimuli's emotional intensity (participants rated the stimuli's sexual and emotional intensity after neuroimaging was completed). The relevance of the hypothalamus in this regard is consistent with the findings of numerous other studies of sexual arousal and desire (for examples and reviews see Fonteille & Stoleru 2010, Hamann et al. 2004, Karama et al. 2002, Maravilla & Yang 2008, Redoute et al. 2000). The relevance of the VS is consistent with the fact that this region is involved in motivation and predictive reward value (Kelley 2004, O'Doherty 2004). Walter et al's findings raise the possibility that sexual desires with little emotional context (i.e., directed toward highly arousing strangers or casual acquaintances) might involve relatively more hypothalamic and VS activity, reflecting more straightforward sexual motivation, whereas sexual desires *targeted to romantic partners* may evoke particularly high levels of rACC activation, given that such desires are likely to involve greater self-relevance and emotional context. Desires for romantic partners might also involve greater involvement of the temporo-parietal junction (TPJ), which has been implicated in interpersonal interactions and the capacity to infer/understand other people's intentions, beliefs and traits (reviewed in Ortigue et al. 2009). Such cognitively- and affectively-relevant processes are likely to prove highly relevant for sexual interactions with established partners.

Hence, in answer to the question of whether love and desire are distinct or interconnected at the neural level, the most accurate answer may be "it depends." Sexual arousal and desire clearly involve *both* "sex-specific" forms of neurological activity *as well as* more cognitively- and affectively-mediated forms of activity, the latter of which show more overlap with patterns of activation detected for romantic love. Hence, certain types of sexual desire might be more independent of romantic love than others (both experientially and

neurologically), and certain types of love might be more independent of sexual desire than others. Accordingly, one promising area for future research concerns pinpointing *conditions* under which patterns of sex/love brain activation prove more distinct versus overlapping. For example, just as sexual desire for passionate love partners might evoke more rACC and TPJ activation than desire experienced for strangers, strong feelings of passionate love for individuals who are *not* appraised as potential sex partners might also have a distinct neural signature. For example, as reviewed by Diamond (2003), there is extensive documentation of passionate but nonsexual infatuations developing between platonic friends, often in childhood or adolescence. Might these nonsexual infatuations evoke less “sexual” patterns of brain activation (i.e., characterized by less activation in joint “love/sex” regions such as the caudate, insula, putamen, and ACC), and more activation in regions typically associated with nonsexual, familial forms of love? For example, Bartels and Zeki (2004) contrasted brain activation in mothers viewing pictures of their own child versus a child they were well acquainted with, and they directly compared the activation patterns with their previous study on romantic love. They found overlapping patterns of activation for maternal love and romantic love in the putamen, globus pallidus, caudate nucleus, middle insula, and ACC, consistent with the view that that romantic and maternal love have a shared dopaminergic-motivational substrate reflecting their shared basis in the social-behavioral system of attachment (Carter 1998, Carter & Keever 2002).

Yet Bartels and Zeki only found hypothalamic and VTA activation for romantic love (consistent with the well-established role of the hypothalamus in sexual arousal, and also the fact that VTA activation has been found to correlate with sexual frequency and feelings of intense passion in long-term couples, Acevedo et al. 2011). Also, they only found periaqueductal gray matter (PAG) activation in maternal love. Notably, PAG activation has also been found to be associated with feelings of unconditional love (Beauregard et al. 2009) and in long-term couples, PAG activation is correlated with the duration of marriage (Acevedo et al. 2011). This suggests a potential role for the PAG in emotionally intense but nonsexual experiences of love. A promising direction for future research on links and distinctions between love and desire is to evaluate *changes* in patterns of neurological activation elicited by romantic partners over time. Both sexual desire and passionate infatuation are known to decline in long term relationships, but Acevedo and colleagues (2011) found that some long-term couples report experiencing – and show patterns of brain activation consistent with – the sort of passionate infatuation more typical of new couples (i.e., greater activation in the VTA, caudate, putamen, and posterior hippocampus). Future research should examine whether longitudinal changes in couples’ subjective experiences of their relationship (i.e., a shift from passionate infatuation to unconditional, companionate devotion) correspond to changes in the constellation of brain regions activated by the partner (i.e., reductions in VTA, caudate, and putamen activation and increases in PAG activation). Longitudinal changes might also occur in the brain regions activated during sexual desire in long-term rela-

tionships, perhaps reflecting a shift toward more emotionally- and cognitively-mediated forms of sexual response.

Future directions: subtypes of desire and orientation

Understanding how different types and contexts of sexual desire are manifested neurobiologically can also make important contributions to basic research on female sexual desire and orientation. Among the most important recent developments in the clinical literature on female sexuality has been the movement away from traditional, male-based models of sexual response toward models designed to account for women’s distinctive experiences, particularly the “responsive” nature of female desire (Basson 2000, Brotto et al. 2010). Traditional models of the sexual response cycle posit that the “starting point” is innate and automatic desire, which presumably progresses to sexual arousal and motivates subsequent sexual behavior and release (Masters & Johnson 1966). Yet researchers have argued that among women, desire is a fundamentally *responsive* system, such that desires often only emerge *after* a woman encounters erotic stimuli (such as the initiation of sexual behavior) within a sufficiently facilitative context (Basson 2000, 2002). Little is known about the degree to which responsive sexual desires might have a different psychobiological basis than more automatic forms of arousal. One intriguing possibility suggested by extant neuroimaging research is that responsive desires are characterized by patterns of neurobiological activation indicative of more emotional and cognitive mediation, such as the TPJ, the rACC and the orbitofrontal cortex (OFC), which is implicated in appraising the sexual relevance and reward value of sexual stimuli (O’Doherty 2004). The insula may also be involved in responsive desire, given that it plays a role in mapping internal bodily states and in integrating somatosensory information with situational and emotional context (Singer et al. 2009). In contrast, more “automatic” forms of sexual desire might show more predominant hypothalamic activation, given the role of the hypothalamus in early stages of physiological sexual arousal (Fonteille & Stoleru 2010, Redoute et al. 2000, Stoleru & Mouras 2007).

Understanding potential neurobiological distinctions between automatic and responsive forms of sexual desire has broader implications for the understanding of female sexual *orientation*. Specifically, it might help to elucidate differences between women whose same-sex desires emerge relatively spontaneously, early in pubertal development, versus those whose same-sex desires emerge later in life, typically in response to intense emotional bonds formed with *specific* same-sex friends (reviewed in Diamond 2008). One way to characterize the difference between these two types of women is to posit that women in the former group experience *both* automatic and responsive forms of same-sex desire, whereas women in the latter group experience primarily *responsive* same-sex desires, in the absence of more automatic and spontaneous same-sex desires. The accumulating evidence for the high prevalence of

women in the latter group, relative to men (reviewed in Diamond 2008) is consistent with research suggesting a larger role for responsive desire in female than male sexuality more generally (Basson 2000, Brotto et al. 2010), and may play a role in women's greater sexual "plasticity" and "fluidity" (i.e., variability and sensitivity to context) relative to men (Baumeister 2000, Diamond 2008). For example, women are more likely than men to experience sexual arousal and desire for both sexes rather than for one sex exclusively, to report a late development onset of same-sex attractions, and to report changes in their degree of same-sex and other-sex attractions over time, sometimes triggered by single affectional relationships (see reviews in Baumeister 2000, Diamond 2003 2008). Perhaps most strikingly, Chivers and colleagues (Chivers & Bailey 2005, Chivers et al. 2004, Chivers et al. 2007) have documented that *both* lesbian-identified and heterosexually-identified women show genital arousal in response to *both* same-sex and opposite-sex stimuli, even when they report little *subjective* arousal to such stimuli. Notably, similar discrepancies between genital arousal in subjective response have also been found among bisexually-identified men (Rieger et al. 2005).

Such variability contradicts conventional categorical models of sexual orientation, which posits only two "types" of sexuality — exclusive homosexuality or exclusive heterosexuality — both of which are presumed to appear early in life and to exhibit longitudinal stability (reviewed in Weinberg et al. 1994). Accordingly, individuals with variable patterns of sexual desire and expression have historically been characterized as repressing or misinterpreting their "true" desires (Rust 2000). Yet an alternative interpretation is that individuals who periodically experience desires that run counter to their overall pattern (such as women who fall in love with a single female friend, or those who consider themselves "mostly" but not completely heterosexual, Thompson & Morgan 2008) are experiencing a different *type* of desire, with a potentially distinct pattern of neurobiological activation. Just as sexual desires experienced for romantic partners might be characterized by more cognitively- and affectively-mediated processes than desires for strangers, this might also be the case for unexpected "cross-orientation" desires experienced within specific, emotionally-charged relationships. Women sometimes describe such "relationship-specific" desires as "feeling different" from other forms of desire and arousal, characterized by greater emotional and less genital intensity (i.e., coming from the "heart" rather than the "gut," Diamond 2005). Hence, a fascinating direction for future research would be to determine whether variation in the subjective quality and experiential context of such desires can be mapped onto different patterns of brain activation.

Suggestive evidence for this possibility comes from research indicating that different subtypes of sexual-minority women show different degrees of *hormonal* modulation of day-to-day sexual desires. Diamond and Wallen (2011) measured the intensity of sexual-minority women's same-sex and other-sex sexual motivation over a span of 10 days, during which time women also provided saliva samples for the

assessment of their estrogen levels. All women had been participants in a 13-year longitudinal study of sexual identity development. During women's peak estrogen levels (around which time ovulation is most likely to occur), women who had consistently identified as lesbian over the previous 13 years showed a significant *increase* in the intensity of their same-sex sexual motivation, and this increase was significantly larger than that observed among women who had consistently identified as bisexual for the previous 13 years or women who had alternated among different sexual identity labels (often basing their labels on the gender of their current partner) over that time. Furthermore, estrogen-related increases in same-sex motivation were significantly smaller in women who granted a larger role for situational and contextual factors in their sexuality. These findings indicate that some women's same-sex desires are relatively more hormonally-mediated, whereas other women's same-sex desires appear more context-dependent.

Might different types of desire have different neurobiological signatures?

Might these differences also be manifested neurobiologically? Notably, previous research comparing the neurobiological responses of premenopausal and postmenopausal women to visual sexual stimuli (Jeong et al. 2005) suggests a linkage between estrogen levels and the neurobiological substrates for sexual desire. They found that premenopausal women showed different regions of predominant activation in response to sexual stimuli than did postmenopausal women, focusing on the head of the caudate nucleus, putamen, cingulate gyrus, plenum of the corpus callosum, and inferior frontal gyrus. In contrast, the postmenopausal women's predominant activation was in the paralimbic area, which has proven less directly related to sexual arousal in previous research. Hence, the postmenopausal women's pattern of brain activation in response to sexual stimuli appeared to be less robustly "sexual" in nature, suggesting a role for hormonal modulation in differentiating different forms of sexual desire with different neurobiological substrates.

Links between the brain regions involved in love and desire provide another potential mechanism through which atypical, "responsive," "cross-orientation" desires might develop (Diamond 2003). Bianchi-Demicheli and Ortigue (2006) demonstrated that priming women with the name of their romantic partner significantly enhanced their speed on a lexical decision task, and that this effect was enhanced among women who reported that they were passionately in love with their partner. They interpreted their findings to suggest that the state of passionate love appears to involve a broad, unconscious associative network which functions to energize and enhance other goal-directed states via the associative recruitment of dopaminergic-rich brain regions. This suggests the possibility that the development of passionate feelings of love for individuals who are *not* initially targets of sexual desire might eventually *facilitate* the development of sexual desire, through the associative recruitment of dopamine-

rich brain regions that have shown shared love/desire activation (such as the caudate, putamen, and rACC). Hence, because love and desire have an overlapping neural architecture, the facilitative effects of the powerful motivational state of love extend not only to cognition (as shown by the lexical decision task) but also to sexual arousal and desire. Importantly, however, such facilitative effects may depend on the intensity of the love experience. As noted above, Bianchi-Demicheli and Ortigue (2006) detected significant greater performance facilitation among women who reported being passionately in love with their current romantic partners versus those who did not. Hence, as a relationship endures and as passion wanes, the potential for the dopaminergically-mediated motivational state of romantic love to facilitate other dopaminergically-mediated motivational drives (such as sexual desire) may wane. This associative linkage may also play a role in the time-dependent decline in passionate love typically experienced by new couples: As the intensity of partners' sexual desires for one another decline over time due to habituation, the potential for sexual desire to further enhance the motivational state of passionate love (again, via their shared dopaminergic-rich neural architecture), is also likely reduced.

The possibility that there may be notably different forms of sexual desire, with different neurobiological underpinnings, also has implications for the understanding of bisexuality. Specifically, might bisexual individuals exhibit different patterns of neurobiological activation for same-sex versus other-sex partners? Most individuals who report attractions to both sexes claim that the quality and intensity of their same-sex and other-sex attractions are not identical (reviewed in Rust 2000). Psychophysiological research on bisexually-identified men confirms this to be the case for sexual arousal, as well, and in some cases bisexual men's arousal patterns diverged from their experience of subjective desire (Rieger et al. 2005). Neuroimaging data could make important contributions to understanding the nature of such discrepancies: Specifically, when bisexual individuals report more desire for one sex than the other (or when they show stronger *genital* responses to one sex than the other), how might this be manifested in their constellation of neurobiological activity? Given that several studies have found that exposure to sexual stimuli involves *disinhibition* of areas located bilaterally in the superior and middle temporal gyri and in the medial OFC which have been associated with moral judgment, guilt, and embarrassment (Bocher et al. 2001, Maravilla & Yang 2007, Redoute et al. 2000), one intriguing possibility is that some individuals with bisexual attractions gradually come to disinhibit some desires more successfully and consistently than others. Investigating such coordinated patterns of activation and deactivation, and how they relate to patterns of subjective and physiological arousal and desire experienced in different contexts and for different targets, has enormous potential to advance our understanding of human sexuality.

One final topic for future neuroimaging research concerns the frequent discrepancies that have been observed between individuals' physiological and subjective arousal (reviewed in Chivers et al. 2007).

Notably, these discrepancies take multiple forms: In some cases, individuals report much greater subjective than genital arousal. In other cases, they show the opposite pattern, and the direction of the discrepancies does not correspond systematically to individuals' self-described sexual identity (Rieger et al. 2005). One potential direction for future research is to investigate whether individuals with substantial discrepancies between subjective and physiological arousal show less activation in the insula during the presentation of sexual stimuli, given that the insula is typically associated with emotions and with the processing of somatosensory information related to bodily changes, such as genital arousal. As reviewed by Singer et al. (2009) the anterior insula is involved in detecting important changes in bodily states, visceral representation, and emotional expression, reflecting a subjective intensity of emotional experiences, whereas the right anterior insula is thought to map one's internal bodily states and integrate this information with the experiential context in order to produce a coordinated representation of emotional and physical activation. Hence, one possibility is that interindividual differences in the degree of correspondence between subjective and genital arousal may correspond to interindividual differences in insula activation. Such a finding would provide an important corrective to the notion that discrepancies between subjective and physiological arousal simply indicate "repression." Differences in insula activation would suggest, instead, that discrepancies between subjective and physiological arousal are better considered instances of incomplete *integration* of somatosensory information into the overall arousal experience (the reasons for which constitute additional important questions for future research).

Conclusion

Questions about the basic linkage between romantic love and sexual desire have long been debated by psychologists and philosophers: Neuroimaging research has the potential to significantly advance the sophistication of this debate, expanding the questions we can ask and offering provocative new answers. Although neuroimaging research obviously has well-documented methodological and logistical limitations (Aron 2006, Fonteille & Stoleru 2010, Maravilla & Yang 2008, Ortigue et al. 2007, Ortigue et al. 2010), thoughtful and creative experimental designs are likely to make critical contributions to our understanding of the complex chain of neurobiologically-mediated processes through which we become attracted to, fall passionately in love with, and sexually desire romantic partners. Although previous neuroimaging research has not focused specifically on the phenomena of sexual orientation, this represents one of the most exciting and promising areas for future research, with the potential to further deepen our understanding of the basic human capacity for love and desire.

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