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Review article

The neuroscience of social feelings: mechanisms of adaptive social functioning

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ABSTRACT

Social feelings have conceptual and empirical connections with affect and emotion. In this review, we discuss how they relate to cognition, emotion, behavior and well-being. We examine the functional neuroanatomy and neurobiology of social feelings and their role in adaptive social functioning. Existing neuroscience literature is reviewed to identify concepts, methods and challenges that might be addressed by social feelings research. Specific topic areas highlight the influence and modulation of social feelings on interpersonal affiliation, parent-child attachments, moral sentiments, interpersonal stressors, and emotional communication. Brain regions involved in social feelings were confirmed by meta-analysis using the Neurosynth platform for large-scale, automated synthesis of functional magnetic resonance imaging data. Words that relate specifically to social feelings were identfied as potential research variables. Topical inquiries into social media behaviors, loneliness, trauma, and social sensitivity, especially with recent physical distancing for guarding public and personal health, underscored the increasing importance of social feelings for affective and second person neuroscience research with implications for brain development, physical and mental health, and lifelong adaptive functioning.

1. Introduction

A "feeling" is a fundamental construct in the behavioral, neurobiological and social psychological sciences encompassing a range of subjective experiences. Many of these experiences relate to homeostatic aspects of survival and life regulation (Buck, 1985; Damasio and Carvalho, 2013; LeDoux, 2012; Panksepp, 2010; Strigo and Craig, 2016). Feelings may sometimes signify a sensation, an emotion, perception, a form of thought (e.g., judgement, sense), impression or opinion, an inclination to believe, or an overall physical (e.g., feeling ill) or

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psychological experience (e.g., feeling excluded). It is important to distinguish that feelings as affections "are categorically distinct from cognition and from feelings that are sensations which, unlike affections, have a bodily location and may inform one about the state of one's body" (Bennett and Hacker, 2003) (p. 199). Damasio and Carvalho (2013) argued that the bodily "viscera" are critical to many feelings or are distinct from specific emotions. Although feelings are fundamentally private, inner experiences, they nevertheless may be inferred from or perceived directly in the public behavior of people (e.g., behavioral criteria can be used to teach another person about complex social feelings; Bennett and Hacker, 2003).

A broad definition for feeling is a subjective experience that appears to emerge from perceptions and mental events involving processes inside and outside the central nervous system as well as physiological/bodily states (Damasio and Carvalho, 2013; LeDoux, 2012; Nummenmaa et al., 2016) in interpersonal and other environmental contexts. However, the full range of feelings is diverse. It has been posited that they can emerge from and with emotions (Buck, 1985; Damasio and Carvalho, 2013; Panksepp, 2010), levels of arousal, physical actions and activities (Bernroider and Panksepp, 2011; Gardiner, 2015; Kirsch et al., 2018), linguistic and social acts (Lindquist et al., 2012), hedonics (pleasure and pain) (Buck, 1985; Damasio and Carvalho, 2013; LeDoux, 2012; Panksepp, 2010), drives (Alcaro and Panksepp, 2011; Damasio and Carvalho, 2013), cognitions including perceptions/appraisals of self and others (Ellemers, 2012; Frewen et al., 2013; Northoff et al., 2009), motives (Higgins and Pittman, 2008), social interactions (Damasio and Carvalho, 2013; LeDoux, 2012; Panksepp, 2010) as well as reflective (Holland and Kensinger, 2010), emerging (*e.g.*, the importance of oscillatory activity to consciousness of the feeling component of emotion (Dan Glauser and Scherer, 2008)) and anticipatory perspectives (Buck, 1985; Miloyan and Suddendorf, 2015). Embodied and enacted experiences and activities create meaning through the visceral, haptic, kinesthetic and sensual systems that may well feed into feelings caused by or manifested in social situations. While Schilbach et al. (2013) and others have delineated how experiencing and interacting with others can be primary ways of knowing others, feelings likely play important roles in these social processes and may provide underlying mechanisms that influence and modulate behavior.

In this review, we consider social feelings, which we more narrowly describe as subjective experiences that arise in interaction with others or when being remembered and when recalling others' behaviors, thoughts, intentions or emotions. Specifically, we reviewed neuroscience research on social feelings that has been conducted. We considered whether the notion of 'social feelings' represented natural kinds of neurobiological processes that could be identifiable and conducive to scientific inquiry. That is, alongside emotion, attitudes and the self, feelings appear to be naturally occurring phenomena and especially prominent within social contexts (Mitchell, 2009). As part of this review, we (1) discussed the fundamental importance of social feelings for attachment, affiliation, empathy, influence and well-being, distinguishing it from emotions; (2) considered its emerging role in research areas of parent-child attachments, moral sentiments, interpersonal stress, and emotional communications, while acknowledging important neurotransmitter and neurohormonal modulators; (3) confirmed by meta-analysis the brain regions involved in social feelings, using the *Neurosynth* platform for large-scale, automated synthesis of functional magnetic resonance imaging (fMRI) data; (4) explored the rising importance of social feelings research in psychiatric disorders and in the era of expanding social media during periods when physical distancing has been required for guarding public and personal health; (5) reviewed the language that people use to express social feelings and whether those terms might inform the way we approach social neuroscience research (Fig. 1); and (6) identified the relationships that exist between social feelings and other areas of affective research within this special issue (i.e., Physiological, the Self, Anticipatory, Actions, Attention, Motivation, Anger, Fear, Happiness, Sadness, and Hedonics), summarizing future research needs in this burgeoning domain.[1]

2. The concept of social feelings

Social feelings occupy an important position in relationship to empiricial research and affect and emotion theory, particularly involving interpersonal contexts. Their presence and potential influence can vary from fleeting to long-term feeling states intertwined with complex chains of thoughts, emotions and behaviors. Temporal aspects of social feelings are not yet well understood. They can reflect psychological and viscero-somatic comfort and security as well as discomfort that has social origins (e.g., "cringing" at the remarks of another person (Müller-Pinzler et al., 2016). Social feelings may indicate one's current standing in relation to others, highlight the importance of the thoughts and feelings of other individuals and groups, have specific normatively and culturally constructed expressive forms, and contribute to a wide variety of effects and functions (Dan Glauser and Scherer, 2008). For example, a sincere apology because of a social faux pas can, once accepted by the person or group harmed, reduce feelings of regret and guilt about one's initial actions concerning another. It is also possible to be influenced by the emotions experienced by others not simply because they are other people but especially because they are members of one's own social group. The currency of shared and unexpressed feelings appears to potentially fuel, discourage as well as segregate many kinds of social actions and relationships. Yet, feelings are often not clearly considered or accounted for in many social neuroscience models although they are acknowledged as key component processes (e.g., Bickart et al., 2014; Porcelli et al., 2019).

Advances in affective research have revealed important distinctions between feelings and emotions. Feelings are considered an affective component/constituent of emotional responses. For example, fear as an emotion consists of a spectrum of automatically activated cognitive reactions and defense behaviors that co-occur along with "feelings of fear" that can encompass changes in hormonal, viscero-somatic and mental state processing. Emotions are distinguished from feelings in that they tend to be more complex, parcellated, cognitively elaborated and semantically filtered. It is also important to note that feelings are not limited to those that co-occur with specific emotions. Rather, feelings encompass a wide range of important mental experiences that may signify physiological need (*e.g.*, hunger), tissue injury (*e.g.*, pain), valenced features of behavior that are not always "felt" (Winkielman and Berridge, 2004), optimal function (e.g., well-being), discord, and dynamics of social synchrony such as increases or decreases in social status. We observed that feelings are not consistently defined in the social neuroscience literature, and that definitions for these terms can evolve with new discoveries. Moreover, while the natural occurrence of some social feelings may be universally experienced across cultures (*e.g.*, grief, affiliation, parental love etc.), we acknowledge that aspects of other social feelings may be culturally shaped. Their roles as influencers and modulators will be examined in several developing research lines.

Within psychology and the neurosciences, there is a growing awareness that feelings are an important but neglected topic that is

[1] This review of 'social feelings' was undertaken as part of the 'The Human Affectome Project', an initiative organized in 2016 by the non-profit organization Neuroqualia (https://www.neuroqualia.org). As part of the Human Affectome project, a series of overarching reviews is being published that summarize and critique much of what is currently known about affective neuroscience while simultaneously exploring the language that we use to convey feelings and emotions. The project is comprised of twelve teams that are organized into a taskforce focused on the development of a comprehensive and integrated model of affect that could serve as a common focal point for current and future affective research. Recent papers of this effort pertinent to social feelings include those on fear (Raber et al., 2019), self (Frewen et al., 2020) and anticipatory feelings (Stefanova et al., 2020).

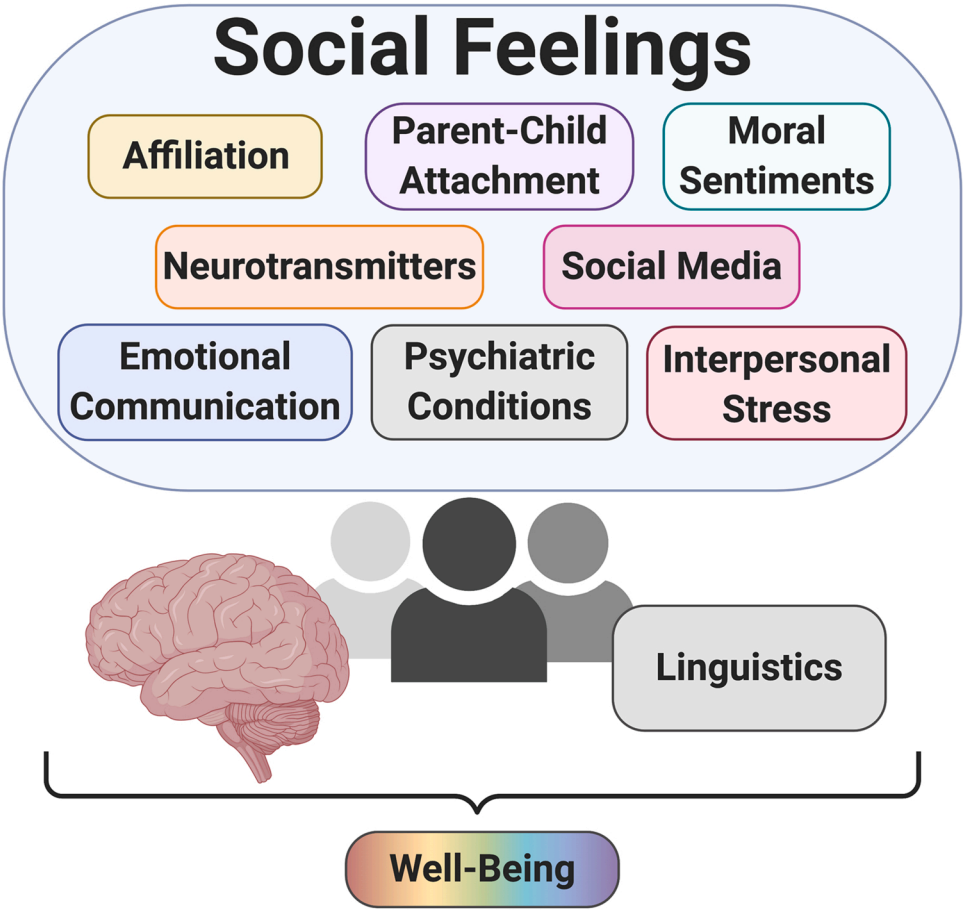


Fig. 1. Overview of the contents of the review. We discuss social feelings in the context of 5 major sub-categories: Affiliation, Parent-Child Attachment, Moral Sentiments, Interpersonal Stressors, and Emotional Communication. Throughout, we consider the known neurobiology related to social feelings and highlight where research is needed. Additionally, we review the language people use to express social feelings, and included a meta-analysis using Neurosynth software. This review is timely, considering the growth in social media and recent world-wide interest in the psychology of social interaction and social distancing, with their effects on overall well-being.

distinct from the topic of emotion. Similar to the many covert and overt dimensions of emotion (Cowen and Keltner, 2017), there is recognition that feelings also may serve overt as well as covert purposes. It has been hypothesized that feelings may guide caution or confirm cognitions in social and non-social settings (e.g., something doesn't feel right here, this person makes me feel uneasy). Recent ideas from the 'second person neuroscience' literature (e.g., Pfeiffer et al., 2013) have emphasized that interpersonal contexts can invoke social network processes, some of which may be experienced as involuntary (e.g., mirror neuron system and emotional contagion) and others as inferential, derived from prior experiences or mentalizing network activity associated with a multiplicity of social feelings. We are interested in addressing how the construct of social feelings relates to social cognition and social emotions. For example, reactive feelings to another in the case of some instances of stigma and disgust can be reduced by a shared social identity (Reicher et al., 2016), possibly indicating the greater importance of inhibitory processes as correlated lateral prefrontal cortex (PFC) and anterior cingulate cortical (ACC) responses increase (Krendl et al., 2006). Contagion remains an elusive and problematic concept (e.g., when understood as a kind of virus-like transmission between people and within groups), as the strength of involuntary sharing of feelings and emotional states with others can be influenced by age, context, and group dynamics. For this reason concepts such as influence and amplification of feelings are important to consider as there are implications for understanding how feelings may trigger a variety of mechanisms (e.g., approach, avoid, imagined social status) through which people affect and are affected by others. We suspect that these dynamics can be some of the key roles of feelings in social action and interaction.

Social feelings appear to relate to well-being pertinent to maintaining homeostasis. Social behaviors and interactions can be particularly susceptible to influence and modulation by feelings. This obtains for perceiving and evaluating the actions of others as well as deciding how to respond within social interactions (Gilam and Hendler, 2016). As important conceptual and methodological challenges, we first address emotional contagion, empathy, attachment and affiliation as mediating processes.

2.1. *Social feelings: contagion, empathy, attachment and affiliation*

Social feelings appear to be generated through a variety of mediating processes. Their effects can be fleeting or persistently impact mental experiences and behavior. Prominent explanations to date for generation of social feelings in relation to persons and groups have included contagion and empathy. The intentional communication and sharing of feelings involving others can lead to various forms of influence upon one another. Research on emotional contagion has revealed that experiences of emotional empathy, for example, facilitates "somatic, sensory, and motor representations of other people's mental states" (Nummenmaa et al., 2008) (p. 571). Explanations have focused on the proposed mirror neuron system and the automatic activation of motor and sensory system representations of observed behaviors of others with linkage to limbic system structures as a potential basis for some of the shared *feelings* of empathy (Carr et al., 2003; Nummenmaa et al., 2008; Keysers and Gazzola, 2009). Similar research in social contagion has examined some of the physiological correlates of synchronized feelings and shared social emotions that can occur in typical group settings (Ardizzi et al., 2020). While the neurophysiological bases of social feelings often arises in interaction with individuals, it is also important to explore instances of social influence in groups. This can include sharing feelings with a group and the experience of having one's feelings "amplified" by others when acting towards joint aims or goals (e.g., feeling empowered (Drury et al., 2005) or collective pride (Sullivan, 2017)).

Research on the neural systems responsible for processes of social contagion has been limited by experimental situations and tasks, but is still developing. When healthy participants viewed emotionally-charged social scenes and were instructed to empathize with a specific person in the scene (i.e., emotional empathy), for example, significant activations in the parietal (secondary somatosensory and inferior regions), fusiform, middle frontal and parahippocampal cortices as well as insula, thalamus and brainstem were detected than when instructed to empathize with a person in a non-emotional social scene (i.e., cognitive empathy) (Nummenmaa et al., 2008) (Fig. 2A). These systems might be involved in the experience of what the other person is feeling. Automatic and rapid generation of similar feelings may lead to further sharing, mimicry (expressive or communicative), matching of emotional behavior (e.g., smiling, celebrating), and coordination of social activities (e.g., group singing, coordinated actions).

A natural extension of influence, empathy and emotional contagion into the social domain pertains to the neuroscience of feelings of belongingness produced by bonding and identification at the group-level. These investigations have provided evidence of other brain regions associated with what can be described as 'like love' (Duarte et al., 2017) and may involve experiences of group-based pride. We would expect that the latter might activate similar regions as individual pride and include the right posterior superior temporal sulcus and left temporal pole (Takahashi et al., 2008) (Fig. 2B). An fMRI study of football fans watching videos of their team vs. a rival team reported higher levels of activation in a network involving the ventral tegmental area, substantia nigra, striatum, insula, hippocampus and amygdala (Duarte et al., 2017) (Fig. 2C). The results support an interpretation of activation of reward and affective processing systems. Similarly, such results demonstrate the difficulty of attempting to easily localize neural systems mediating feelings that are not intense enough, enduring or are not yet imbricated with reasons, goals and evaluations to be described in terms of emotions but often may still be of considerable psychological and social importance (Cikara and Van Bavel, 2014).

Although recent theoretical efforts have given feelings a central role in psychology (Cromby, 2015; Damasio and Carvalho, 2013), there remains a gap in understanding what contributes to a person's feelings being markedly different to many others. Cromby's analysis of the neurophysiological underpinnings of feelings of paranoia—that others are a potential or immediate threat—may be a useful example to consider here before exploring specific empirical studies (e.g., see Section 9 for examples of research social feelings and psychiatric conditions). Describing the resultant feelings as "unfounded fears" (Freeman et al., 2015) does not quite capture the diverse qualitative feelings associated with the experience of paranoia that include threat, disapproval, humiliation and powerlessness. For this reason, Cromby and Harper (2009) conclude "there is no account either of the variety of feelings related to paranoia, or of the ways in which they may be related" (p. 341). Freeman et al.'s approach emphasized multiple causal roles for paranoid delusional feelings (e.g., on-going stress, illicit drugs, and trauma). With regard to the links between suspected neural systems and such feelings, there have been only a few attempts in psychological research to associate these particular neural systems or any other embodied aspects of emotion with cognitive accounts of paranoia (Damasio, 1994) (p. 342). It is particularly important here that Comby and Harper highlight "impoverished notions of social influence" (p. 342) as a key problem for a convincing account of the affects accompanying paranoia.

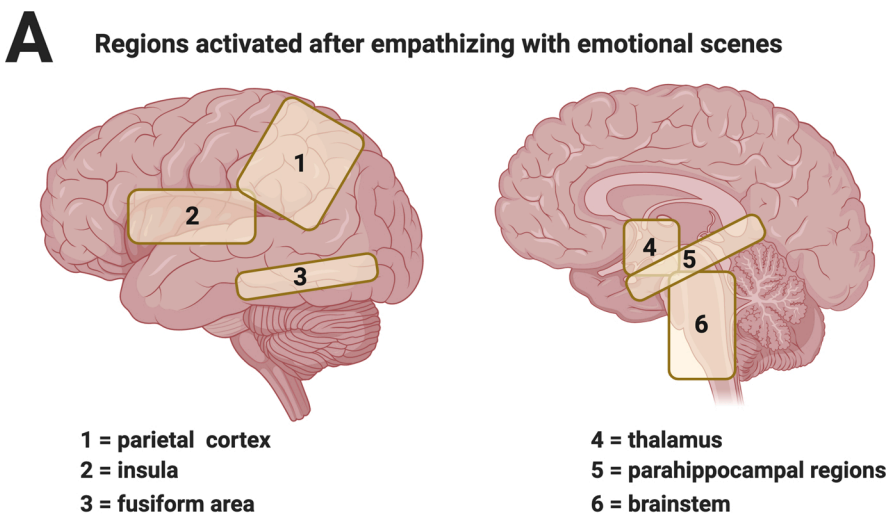
It is interesting to consider that we are not always aware of the processes that give rise to feelings. For example, irritability might be a measured response to the unreasonable actions of others, or it might be due to low blood sugar, tiredness or other non-social concern. Cromby and Harper (2009) also noted that we may not be aware of what prompted a particular feeling or our interpretation of it may be incorrect. This might be particularly true of social feelings (e.g., the thrill of being accidentally touched by someone might be interpreted inaccurately as the possible start of a relationship). Social interactions where there is a discrepancy between one's own feelings and those of another person pose an interesting research challenge as well. Neural systems involving the pregenual anterior cingulate cortex (pACC) may have a role in generating unpleasant feelings and have been associated with feelings of suffering (Vogt, 2005) such as when the presence or actions of another person are deeply distressing. Therefore, social feelings potentially have multiple ways of influencing and modulating actions that have individual or multi-person significance.

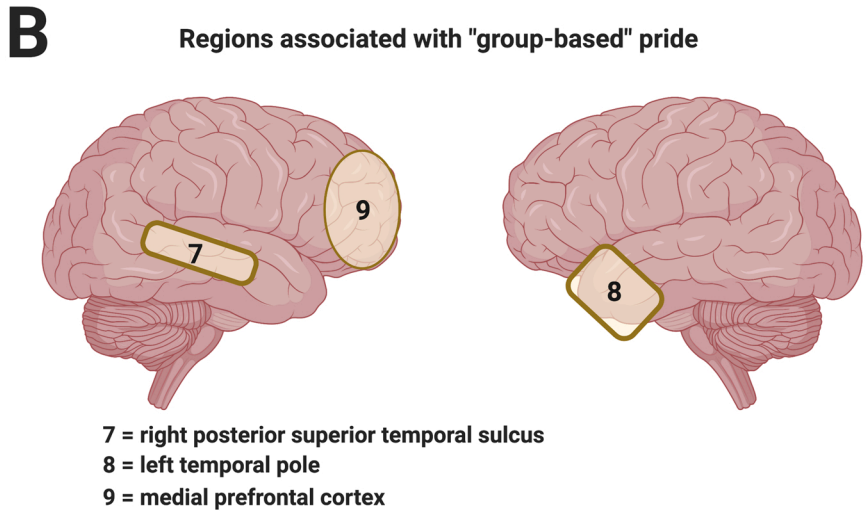
Among social feelings, so-called 'affiliative feelings' are purported to play a central role in interpersonal relations (e.g., parental, romantic, friendship, organizational), as they embed key building blocks for human attachment and bonding. These may be germane to the potential for effective adaptation and more complex social feelings such as guilt, compassion and gratitude. Affiliative feelings, moreover, may be a fundamental driving force undergirding socially motivated behavior that is associated with natural rewards (e.g., pride in the laudable behaviors of others one is closely related to) (Warnell et al., 2018).

Feelings also have been tightly linked to a wide spectrum of activities described as socio-moral. Feelings are said to be moral when they involve the interests or welfare either of society as a whole or at least of persons other than the judge or agent (Haidt, 2003). Because these feelings may help aggregate, civilly space or alienate humans, they are often categorized into a spectrum of prosocial and anti-social classes (Fontenelle et al., 2015; Thoits, 1989). Prosocial feelings are feelings related to positive interactions with others (e.g., cooperation, helping, reciprocity, reparative actions). Similarly, prosocial feelings are also related to social conformity and involve feelings such as guilt, embarrassment, gratitude and awe (Moll et al., 2008b) (Fig. 3). Prosocial feelings include varying degrees of affiliative feelings, which are key for social attachments, whether parent-infant, filial, friend, neighbor or other.

Attachment to nonhuman living beings (e.g., plants, homes, personal effects), cultural symbols, abstract ideas, and beliefs (the so-called "extended attachment") may contribute to the remarkable human inclination to cooperate beyond kinship boundaries, due to intrinsic reward, even when no evident reputation gains are at stake (Moll and de Oliveira-Souza, 2009). As such, affiliative feeling may be proposed a cornerstone for several prosocial emotions (i.e. guilt, gratitude and compassion) (Moll and Schulkin, 2009; Moll et al., 2011; Preston, 2013), but not for those that drive social conformity based on self-interested motivation (e.g., embarrassment) (James and Olson, 2000). In contrast, sentiments linked to interpersonal aversion – the other-critical sentiments (such as disgust, contempt and anger/indignation) – are experienced when others violate norms or one's rights or expectations, and endorse aggression, punishment, group dissolution and social reorganization (Haidt, 2003; Moll et al., 2005) (Fig. 3). In the latter study, neural activations evoked by social disgust, interestingly, overlapped to a large extent with those evoked by sensory (e.g., putrid taste or odor) disgust. Hence, a more reflexive, self-protective action may power a similar type of socially aversive feeling. Hence, acquired norms of social behavior may set parameters within which affects spur breaking off contact or affiliating with agents and/or their actions, as well as other approach-avoidance tendencies.

A key question that remained unsolved until recently was whether brain activation associated with affiliative feelings could be anatomically and functionally dissociated from general positive or negative emotional states. One recent study employed passive presentation of social narratives involving kin (i.e., associated with affiliative states) or not involving kinship (Moll et al., 2012) and confirmed the prediction that the septo-hypothalamic region would be engaged by affiliative states in both positive and negative emotional scenarios. Interestingly, activity in another basal forebrain region, the subgenual cingulate cortex, was only detected when modelling individual differences in how strongly participants perceived their own families as a distinctive social group in affiliative scenarios (Rusch et al., 2014). These results





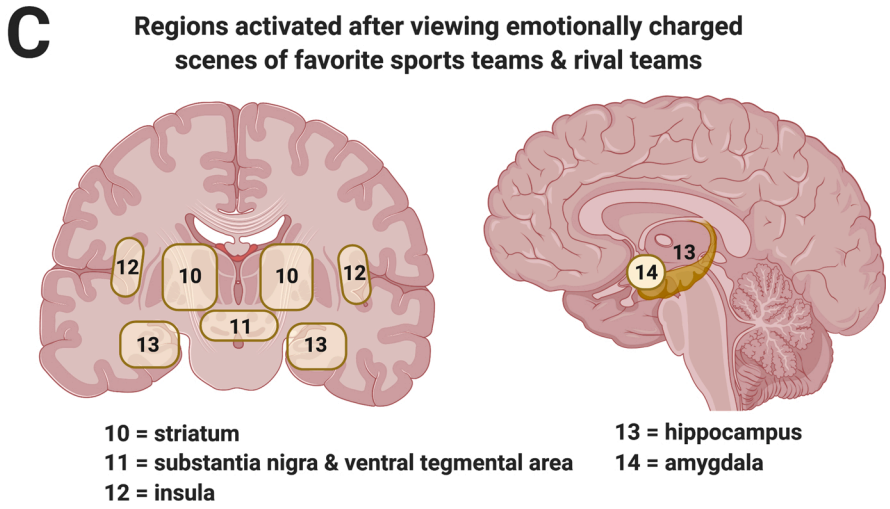


Fig. 2. Brain regions associated with empathy. A) People instructed to look at interpersonal scenes and empathize with a specific person in an emotionally-charged vs. neutral situation showed greater activation in premotor cortex, thalamus, primary motor cortex, and primary somatosensory cortex. Participants simultaneously reported feeling similar emotions to the "other" person (Nummenmaa et al., 2008). B) Evidence for "group" emotions point to activation of the right posterior superior temporal sulcus and the left temporal pole, regions that are similarly activated when individuals feel pride in themselves (Takahashi et al., 2008). C) Other investigations into "group" feelings have shown that the striatum, substantia nigra, ventral tegmental area, insula, hippocampus, and amygdala have an increase in activation when sports fans watch emotionally-charged clips of their favorite teams (Duarte et al., 2017).

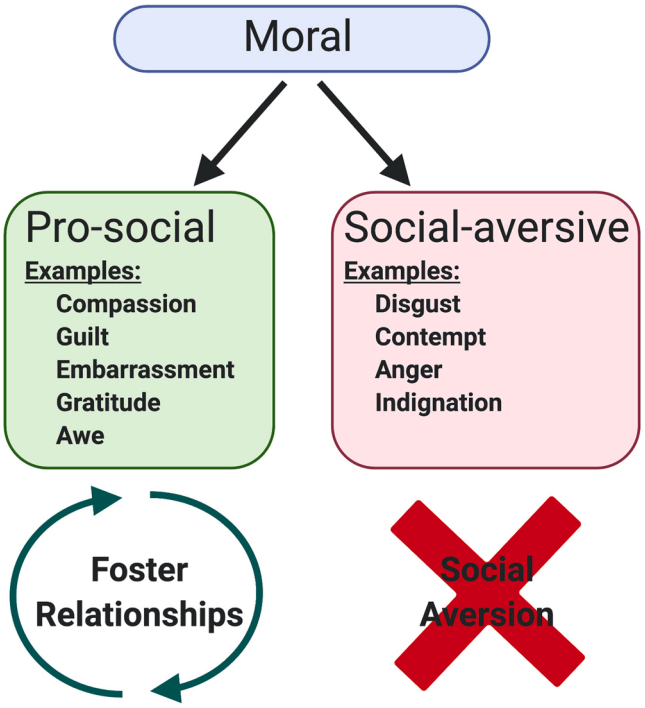


Fig. 3. Schematic illustration of one of the ways social feelings can be broken down. Feelings of affiliation greatly depend on the individual's perception of the other's feelings. Generally, these can be grouped as having a negative or positive valence, and being self- or other-oriented. Additionally, morality is a large component of shared feelings, which can be grouped widely into pro-social or social-aversive. Examples of pro-social affiliative emotions include compassion, guilt, embarrassment, gratitude, and awe, and serve to build & foster relationships. Examples of social-aversive affiliative emotions include disgust, contempt, anger, and indignation, which often lead to social aversion or a break-down of potential relationships.

suggested a more sophisticated role for the subgenual cingulate cortex in encoding social group belongingness. Bortolini et al. (Bortolini et al., 2017) confirmed the role of subgenual frontal areas in distinguishing between in- and outgroups by showing that the subgenual cortex was selectively activated for efforts benefitting anonymous fellow fans of one's soccer club compared with playing to benefit non-fans.

Activation of basal forebrain regions was also observed in fMRI experiments involving healthy participants witnessing the delivery of rewards to similar others ("vicarious rewards" (Anders et al., 2020a; Mobbs et al., 2009)). In this study, watching another player with whom one could identify receiving rewards was associated with activation of the ventral striatum and adjoining septo-hypothalamic area. Interestingly, when correlated with the perceived degree of similarity of shared values (a more complex construct), higher activity was observed in the subgenual frontal cortex.

Affiliative feelings, therefore, comprise subjective experiences associated with fundamental social behaviors (such as when parents hold offspring in their arms) as well as more elaborated ones in diverse social contexts associated with emotional overtones and sophisticated cognitive processing. The circuitry of the human brain that enables affiliative feelings has so far pointed to the importance of the hypothalamic, septal, striatal and subgenual frontal areas of the brain together with hormonal modulation influences and network interactions with other limbic system and cortical networks related to social behaviors.

An emerging framework for considering diverse forms of affiliation has proposed that the hippocampus and related structures map relational aspects of affiliation to help organize such information for behavioral actions (Montagrin et al., 2018; Schafer and Schiller, 2018). Mapping computations may organize conspecifics not only according to physical space but also according to social relational frames such as power, dominance hierarchy, familiarity, kinship, and other socially relevant processes that organize one's social networks within different settings and contexts. This can lead to new testable hypotheses utilizing computation approaches to increase understanding of social decision-making (Charpentier and O'Doherty, 2018). We anticipate that such studies will reveal affiliative feelings as being contributing factors.

3. Arginine, vasopressin, and oxytocin within the social behavior neural network

The neural network that mediates and influences social behavior has been referred to as the social behavior neural network (SBNN) (Newman, 1999) (Figs. 4 and 5). This large scale cortical-subcortical network includes frontomedial prefrontal cortex (PFC), cortex of the temporoparietal junction (TPJ), precuneus, amygdala and other structures or nodes that are strongly regulated by hormonal effects and are conserved across mammalian species. Of particular interest for this discussion are the nodes including the posterior bed nucleus of the stria terminalis (BNSTp), lateral septum (LS), medial preoptic area (MPOA), ventromedial hypothalamus (VMH), anterior hypothalamus (AH), and periaqueductal grey (PAG) (Fig. 4). Common characteristics of these nodes are that they all (1) contain gonadal hormone receptors, (2) are reciprocally interconnected, and (3) they have been recognized for their regulatory contributions to social behavior (including aggression, sexual behavior, social recognition memory, parental behavior and social communication (Adkins-Regan, 2009; Albers, 2012, 2015; Albers et al., 2002; Bosch and Neumann, 2012; Goodson and Kingsbury, 2013). This network appears to be evolutionarily conserved and exists in mammalian species and in non-mammalian vertebrates (Crews, 2003; Goodson, 2005; O'Connell and Hofmann, 2011), although important differences may exist in non-mammalian networks (Goodson and Kingsbury, 2013). The working hypothesis for researchers in this field is that social behavior across a wide range of species is influenced by interactions within the nodes of this network (Albers, 2015).

Within this network, there is a substantial evidence that arginine-vasotocin (AVT)/arginine vasopressin (AVP) and oxytocin (OT) neuropeptides have a significant influence on social behavior (Albers, 2015). In humans, polymorphisms in the genes encoding oxytocin and vasopressin peptides and/or their respective target receptors have been associated with variation in social recognition (Tobin et al., 2010), social attachment (Tickerhoof and Smith, 2017), parental behavior (Johnson and Young, 2017), affective disorders (Surget and Belzung, 2008) and psychiatric phenotypes such as autism (Cataldo et al., 2018)

There are two main classifications of vasopressin receptors (i.e., Avpr1 and Avpr2). Subtype Avpr1a is a transmembrane G-protein-coupled receptor found in several brain nuclei and is involved in the regulation a range of social behaviors, including sibling conflict, agreeableness and impulsive aggression (Mulholland et al., 2020; Phelps, 2010; Wilson et al., 2017). Avpr1b, by contrast, is quite localized within the brain (prominent in hippocampal CA2 pyramidal cells and in anterior pituitary corticotrophs) and is an important modulator of stress adaptation via the hypothalamic-pituitary-adrenal (HPA) axis (Caldwell et al., 2017; Roper et al., 2011), as well as aggressive behavior, and social memory (Stevenson and Caldwell, 2012).

The OT receptor (Oxtr) is a transmembrane G-protein-coupled receptor and the primary mechanism for oxytocin effects within the central nervous system (Caldwell, 2017). Brain regions dense in OT and OT receptors (among other neuropeptides and monoamines) include the pre-optic anterior hypothalamic area, the septal region and closely associated basal forebrain structures. OT and its receptors have been primarily associated with positive social behaviors, such as social reward learning (Dolen et al., 2013), regulating maternal behaviors (Marlin et al., 2015), social learning of trust (Xu et al., 2019) and social attachment (Carter, 2017) (see (Jurek and Neumann, 2018) for a full review). However, there is an increasing understanding that it also

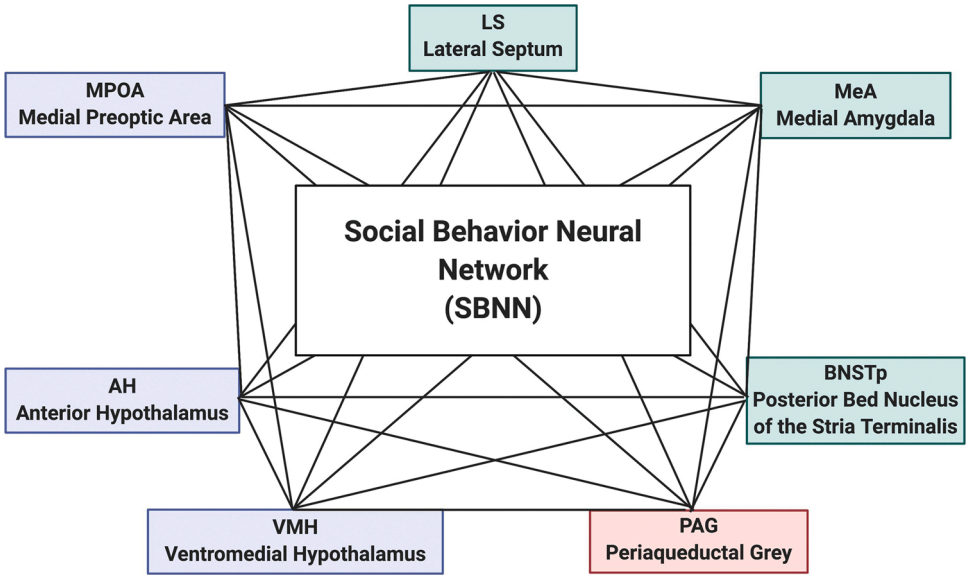


Fig. 4. The social behavior neural network (Adapted from Smith et al., 2019a,b): Green boxes represent cortico-striatal regions; red box represents midbrain region; blue boxes represent hypothalamic regions.

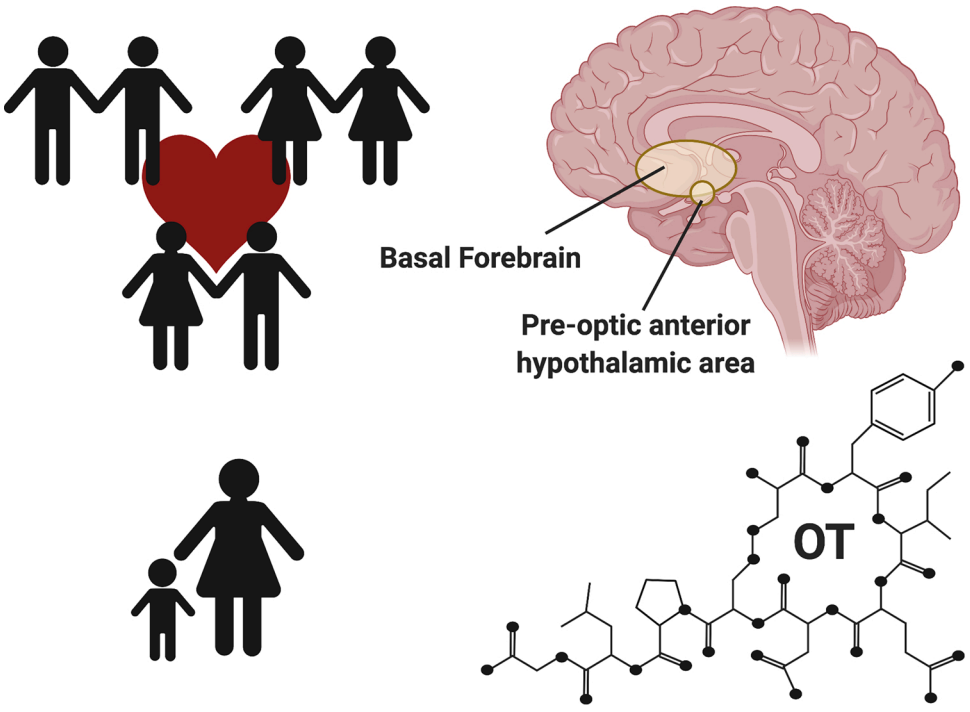


Fig. 5. Importance of oxytocin in pair bonding and maternal feelings. Oxytocin (OT) has been identified as an essential neurochemical in the formation of social attachment. Brain regions dense in OT and OT receptors (among other neuropeptides and monoamines) include the pre-optic anterior hypothalamic area, the septal region, and closely associated basal forebrain structures. Damage to this system interrupts naturally occurring monogamous pair-bonds in prairie voles, and formation of mother-child attachments.

mediates an important role in the avoidance of social contexts (Steinman et al., 2019), leading some to suggest that it plays a critical role in facilitating accurate discrimination between stimuli representing threat and safety (Janecek and Dabrowska, 2019). Together these neuropeptides have significant influence within this network and jointly modulate complex behaviors such as sexuality, the development of social bonds, and parenting, with effects varying depending on context and the background of the individual (Carter, 2017).

Some brain structures of the SBNN have been consistently implicated in social attachment mechanisms in animal models, including pair bonding and bonding between mother and offspring (Insel and Young, 2001; Stack et al., 2002; Swain et al., 2012). Experimental studies involving damage to the septal region in rodents and genetically-modified animals associated with reduced receptors for oxytocin (OT) in that region reported disrupted maternal caregiving (Febo et al., 2005). One can also include the preoptic-anterior hypothalamic area and associated basal forebrain regions (Stack et al., 2002) in this circuitry (Fig. 5). Data from experimental studies with OT in particular have supported its vital role in the formation and life-long maintenance of pair bonds of the prairie vole (Bosch and Young, 2018). These and similar mechanisms may be biological antecedents to romantic love in humans (Bosch and Young, 2018; Walum and Young, 2018). OT effects have been linked to behavioral changes that facilitate bonding processes such as social salience sensitivity in rhesus monkeys (Parr et al., 2018) and perception of a partner's responsiveness and gratitude in humans (Algoe et al., 2017). From investigations of

maternal and romantic love in humans using fMRI, overlapping activations in these regions have been reported (Aron et al., 2005; Bartels and Zeki, 2004; Swain et al., 2007b). Furthermore, OT receptor polymorphisms and prosocial temperament were demonstrated to be associated with individual differences in hypothalamic volume and function (Tost et al., 2010).[2]

The social behavior of maternal caregiving (discussed more below in 4.0) is related to a range of neuroendocrine systems, including OT (Feldman and Bakermans-Kranenburg, 2017) and cortisol (Swain, 2011). In a caregiving study (Elmadih et al., 2016), brain activation to infant cues was studied among healthy mothers at extremes of the maternal sensitivity spectrum. In this study, 15 mothers with the highest sensitivity (HSMs) and 15 mothers with the lowest sensitivity (LSMs) were selectively recruited from a pool based on mother–infant play interaction at 4–6 months postpartum. Brain responses to viewing videos of their "own" versus an "unknown" infant in 3 affective states (neutral, happy, and sad) were measured at 7–9 months postpartum. The participants' plasma OT was analyzed immediately following their free-play interactions with their infant. HSMs versus LSMs showed significantly greater brain activation in right superior temporal gyrus (STG) in response to own versus unknown neutral infant and to own-happy vs. own-neutral (Fig. 6C). Furthermore, the right STG activation in this contrast was negatively correlated with post-free-play OT responses in HSMs mothers. The right STG in LSMs was not differentially activated in response to own infant stimuli. In another example, dispositional personal distress was associated with greater cortisol reactivity to social evaluation stress in mothers, and mother's ventral ACC response to positive versus negative child feedback to their parenting decisions was inversely related to parenting-related cortisol reactivity (Ho et al., 2014). Perhaps further work will confirm these findings and reveal the directionality of brain and hormone physiology that relate to sensitive parenting and interventions (see 4.3).

4. Neurobiology of parent-child attachments

4.1. Evolutionarily conserved neuroanatomy/systems for response to infants

One of the landmarks of contemporary developmental psychology has been its focus on parent-infant attachment (Ainsworth and Bell, 1970; Bowlby, 1958, 1969; J., 1973) - a universal human phenomenon based on the need to form close affect-laden bonds, primarily between mother and infant. Attachment is mediated via an innate, evolutionarily conserved psychoneuroendocrinology promoting proximity-seeking between an infant and a specific attachment figure that increases the likelihood of survival to reproductive age. Parental care-giving behaviors, thoughts and feeling have a predictable time course and characteristic content (Leckman et al., 2004; Swain et al., 2007b, 2004).

Current approaches to investigating the human parental brain involve the use of infant stimuli for experimental paradigms that increasingly address relevant domains of parental function (Barrett and Fleming, 2011; Swain, 2011; Swain et al., 2007a). A prototypical context for studying the brain basis of parental functions is the naturalistic mother-infant interaction. This can be approximated in the maternal imitation of own vs. other infant facial expressions, which predictably activated their mirror neuron brain circuits, including insula and amygdala according to maternal reflective function (Lenzi et al., 2009). With an updated child face mirror task, requiring mothers to "empathically join" vs. "observe" own (vs. other's) child's joyful vs. distressed expressions, parenting stress was inversely associated with amygdala responses (Ho et al., 2020).

These studies are in accord with the literature on the key role of the amygdala and positive feelings in response to own infant face pictures (Barrett et al., 2012) and maternal-infant biobehavioral synchrony as approximated by using video vignettes as fMRI stimuli for healthy postpartum mothers (Atzil et al., 2011). In related work, responses of mothers to videos of interactions with their own 4–6-month-old infants also activated the dorsal anterior cingulate cortex (dACC), fusiform region, cuneus, inferior parietal lobule, supplementary motor area, and nucleus accumbens in study participants (Fig. 6A) (Atzil et al., 2014). Furthermore, dACC activation was correlated with mothers' own parent-infant micro-coded synchrony scores. In another brain imaging study aimed at approaching real-life circumstances, Ho et al. (2014) reported that maternal neural responses in the amygdala and hypothalamus were higher for children's negative (versus positive) feedback during a decision-making task that involved observing infant suffering. Brain responses were related to measures of dispositional personal distress, and salivary cortisol stress responses were buffered by activity in the social reward circuits of the ventral ACC and connectivity between hypothalamus and septum – a region important for stress-regulation and empathy (Fig. 6B). In sum, it appears feasible to incorporate naturalistic mother-infant interactions within a well-controlled experimental fMRI design to study brain systems that regulate behaviors and feelings.

Parental stress regulation in response to infant distress is a necessary aspect of sensitive parenting. For example, in response to their infants' cry, healthy human mothers are likely to pick up, hold and to speak to their infants - a specific complex of behavioral responsiveness that is known to calm them (Esposito et al., 2013). These behaviors, conserved across mammalian species and more than 180 societies, reduce infant crying (Lester and La Gasse, 2008) – supported by a prior randomized controlled trial (Hunziker and Barr, 1986). Perhaps because of their

[2] Systematic review and discussion of animal model studies of social feelings is beyond the scope of this paper. The authors recognize, however, that several key areas of human social feeling research has drawn on animal model studies. However, social feelings have been studied in some animal models. For example, social disorder models in mice can be linked to human social deficit syndromes, such as autism (Lahvis and Black, 2011; Young et al., 2002) and antisocial behavior (Sluyter et al., 2003). Increasing evidence supports that feelings like empathy are also present in animals, including rodents (Atsak et al., 2011; Bartal et al., 2011; Martin et al., 2015; Panksepp and Lahvis, 2011). Social recognition in mice is based on olfaction (Bielsky et al., 2004). This is different than social recognition in humans that is more based on visual cues (Haxby et al., 2002). In rodents, kin recognition, pair bond formation, selective pregnancy termination, territoriality and hierarchy depend on the ability to successfully differentiate olfactory signatures. In rodent social recognition, the olfactory investigation time decreases with repeated or prolonged contact with conspecifics. Mice deficient in oxytocin fail to develop social memory, and do not remember recently encountered adult animals. This is seen by longer sniffing times, despite normal olfactory abilities (Ferguson et al., 2000). In studies of social recognition, recognition can be investigated by introducing mice from another litter and pups from the parents' own litter to adult male and female mice and recording sniffing and licking as a measure for recognition. Typically, the mice spent more time sniffing the alien pup than the own pup, regardless of the age of pups at testing. Studies of aggressive behavior in mice have been undertaken to increase understanding about social conflict and social disorders such as psychosis or borderline personality disorder, in which aggression plays an important role (Miczek et al., 2001). There is direct evidence for a modulatory role of various serotonin 5-HT receptors in aggression. The 5-HT receptor modulates dopamine, noradrenaline and glutamate. Play fighting, offensive and defensive fighting, maternal aggression and predatory aggression exist in rodents. These behaviors are typically analyzed by observation and outcome measures like the proportion of animals fighting, tail rattling, chasing, latency for the first-attack bite, and the duration of attack bouts or flurries (Miczek et al., 2001). Two behavioral paradigms have been used commonly to study aggressive behavior in rodents. In isolation-induced aggression, a male mouse is singly housed in the home cage for a period of time, after which he is paired with an opponent (Malick, 1979). In the resident intruder paradigm, a male is introduced into the home cage of another male. Because of territorial instincts, animals do not need to be isolated prior to this test (Vivian and Miczek, 1993). These animal models increase our understanding of the pathways involved in social feelings and to develop behavioral and pharmacological therapeutic strategies to improve the well-being of those with disorders related to social feelings.

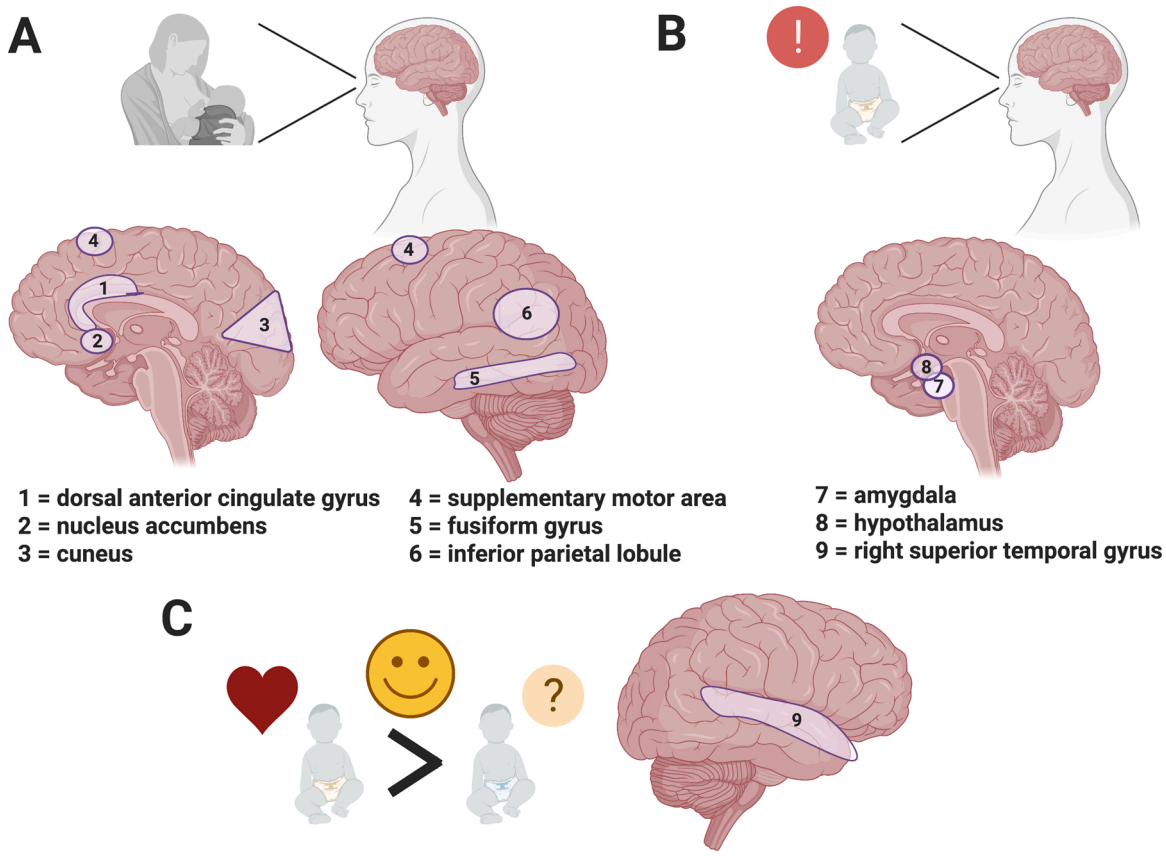


Fig. 6. The neurobiology of response to infant stimuli. Most of the literature investigating the neurobiology of mother-child attachment involves mothers watching scenes or videos of themselves with their children, or videos of their own babies or strange babies in various emotional states (*e.g.*, happy, distressed, neutral). A) When mothers watched videos of themselves interacting with their own children, fMRI research shows increased activation in the dorsal anterior cingulate cortex, fusiform gyrus, cuneus, inferior parietal lobule, supplementary motor area, and nucleus accumbens. B) When mothers watched videos of their children, they generated greater activation in the amygdala and hypothalamus when their child was distressed as opposed to happy. C) Some research has investigated "high sensitivity" and" low sensitivity" mothers based on plasma oxytocin levels immediately following mother-child play. When shown their own child and a stranger's child in neutral, happy or sad states, high sensitivity mothers displayed increased activation of the right superior temporal gyrus when their own child was happy compared to neutral. This was not seen in low-response mothers.

evolutionary advantage, as highlighted indeed by Darwin (Darwin, 1872), reactions toward infants distress are specific and automatic, widespread culturally, and embedded neurobiologically in mothers – and connected to parenting feelings. For example, human parents have specific implicit cognitive (Senese et al., 2013), autonomic (Esposito et al., 2014, 2015), and brain (Caria et al., 2012) reactions to human infant faces that differ from their responses to faces of human adults and faces of infrahuman mammal infants and adults. Recent study also confirmed that picking up and holding their infants are preferential maternal social caregiving behaviors across 11 countries and showed brain imaging evidence for common responses to infant cry in brain circuits that regulate the intention to move and speak across 3 cultures (US, China and Italy) (Bornstein et al., 2017).

4.2. *Affective neurocircuitry for mothers and fathers that connects to child outcome*

Recent research has begun to investigate how sensitive parenting and parental brain physiology in the first few postpartum months related to later child development (Kim et al., 2015b). In this study, associations between parental thoughts/actions and brain responses to baby-stimuli in mothers and fathers in the neonatal period were studied in relation to the child's social and emotional development at toddler age. Mothers (n = 21) and fathers (n = 19) were scanned while they listened to their own and unfamiliar baby's cry in the first month postpartum. Mothers' higher levels of anxious thoughts/actions about parenting in the first month postpartum, but not at 3–4 months postpartum, were associated with lower child socio-emotional competencies at 18–24 months postpartum. Maternal neural responses in motor cortex and substantia nigra were positively and negatively associated with their anxious thoughts and actions, respectively. In fathers, a more positive perception of being a parent during the first month postpartum, but not at 3–4 months postpartum, was associated with higher socioemotional competencies in toddlers at 18–24 months postpartum. Paternal neural responses in auditory cortex and caudate were also positively associated with their positive thoughts, perhaps because of enhanced sensory information processing. Although awaiting replication, this work implicated certain parent brain regions associated with very early postpartum parental thoughts and behaviors that potentially relate to their infant's future socioemotional outcomes. Possible sex differences and treatment implications in these findings require further research. A potential role for social feelings within parenting roles may be an important intervening variable that can be influential in shaping child outcomes (e.g., stress buffering) and conducive to modification in order to improve such outcomes.

Exploring the potential similarities and differences between mothers' and fathers' parenting-related feelings and brain function constitutes another promising direction of parental brain research (Rilling and Mascaro, 2017; Swain et al., 2014). Building on similar research in mothers, changes in fathers' brain structure using voxel-based morphometry analysis (n = 16) have been reported from 2 to 4 to 12–16 weeks postpartum (Kim et al., 2014a). Fathers exhibited an

increase in gray matter volume (GMV) in several brain regions putatively involved in parental motivation, including the hypothalamus, amygdala, striatum, and lateral prefrontal cortex. Conversely, fathers exhibited decreases in GMV in orbitofrontal cortex (OFC), posterior cingulate cortex, and insula. The findings suggest that neural plasticity in fathers' brains may be distinct from those of mothers reported previously (Kim et al., 2010).

4.3. *Parental affective neuroscience informed by psychopathology, stress, and interventions*

Parental stress and mood symptoms are issues of high concern given the impact on child development. Mother's amygdala activity may be hypo-responsive to certain standard cognitive neuroimaging challenges (Moses-Kolko et al., 2014) with depression and unresolved attachment trauma after viewing their own (but not unknown) infant's crying faces (Kim et al., 2014b). With a child face empathy task, depressed compared to healthy mothers displayed greater reactivity of the right amygdala, which was interpreted as emotional dysregulation (Lenzi et al., 2016). Finally, amygdala reactivity was increased in a self-focused baby-cry task designed to provoke brain responses in participants with a history of adverse early life experiences, sometimes described as a malevolent background "shark music" (Ho and Swain, 2017). These data support the hypothesis that amygdala response to infant stimuli is a function of the personal relevance of the stimuli. Variance in the properties of infant stimuli and context of presentation, along with research using hormone challenges may be helpful in clarifying the role of the amygdala in depression – especially given that often-used depression measures may not perfectly capture real-life parental dysfunction. For example, intranasal OT effects on amygdala response to infant crying was found to be moderated by attachment security of mothers, with OT decreasing emotional and amygdala reactivity only in mothers with insecure attachment representations (Riem et al., 2016). Thus, parents with insecure attachment, perhaps different from other attachment classifications and with different social feeling states, may have different brain mechanisms that render them amenable to OT interventions.

Recently, parental brain studies have begun to report findings related to childhood poverty and other parental stress. For example, childhood poverty impacts parents – and interestingly in a sex-specific manner in the brain (Kim et al., 2015a). In females, childhood poverty was associated with increased neural activations to infant cry in the posterior insula, striatum, calcarine sulcus, hippocampus, and fusiform gyrus, but with decreased neural responses to infant cry in the same regions in males (Fig. 7A). Furthermore, neural activation in these regions was associated with higher levels of perceived annoyance elicited by infant cries and reduced motivation to approach crying infants regardless of the gender of the participants (Kim et al., 2015b). This work underlines the need for special attention to the paternal brain as mentioned above. In a related study (Kim et al., 2016), lower income was associated with reduced responses to infant cry in brain circuits that are thought to evaluate emotional valence (medial prefrontal gyrus), regulate affect (middle prefrontal gyrus) and process sensory information (superior temporal gyrus). Furthermore, lower positive perceptions of parenting were associated with reductions in infant-cry response in the right middle frontal gyrus and superior temporal gyrus.

Characterization of parental brain function and dysfunction may also be informed by neuroimaging before and after parenting treatment such as the Mom Power (MP) intervention, which aims to promote maternal empathy, reflective functioning, and stress reduction skills (Muzik et al., 2015, 2017). In one study, MP treated mothers, as compared to untreated mothers, showed decreased parenting stress and increased child-focused responses in social brain areas highlighted by the precuneus and its functional connectivity with subgenual ACC – key components of social cognition. Furthermore, time-dependent reduction in parenting stress was related to concomitant increased child- vs. self-focused baby-cry responses in amygdala-temporal pole functional connectivity, which may facilitate maternal ability to take her child's perspective (Swain and Ho, 2017) (Fig. 7B). Finally, MP significantly increased maternal empathy-dependent amygdala responses for own versus other child's joyful expressions (Ho et al., 2020). Another intervention, Attachment and Biobehavioral Catch-up (ABC), was associated with larger increases in event related potential responses to emotional faces relative to neutral faces, which in turn was associated with observed maternal sensitivity (Bernard et al., 2015) and greater

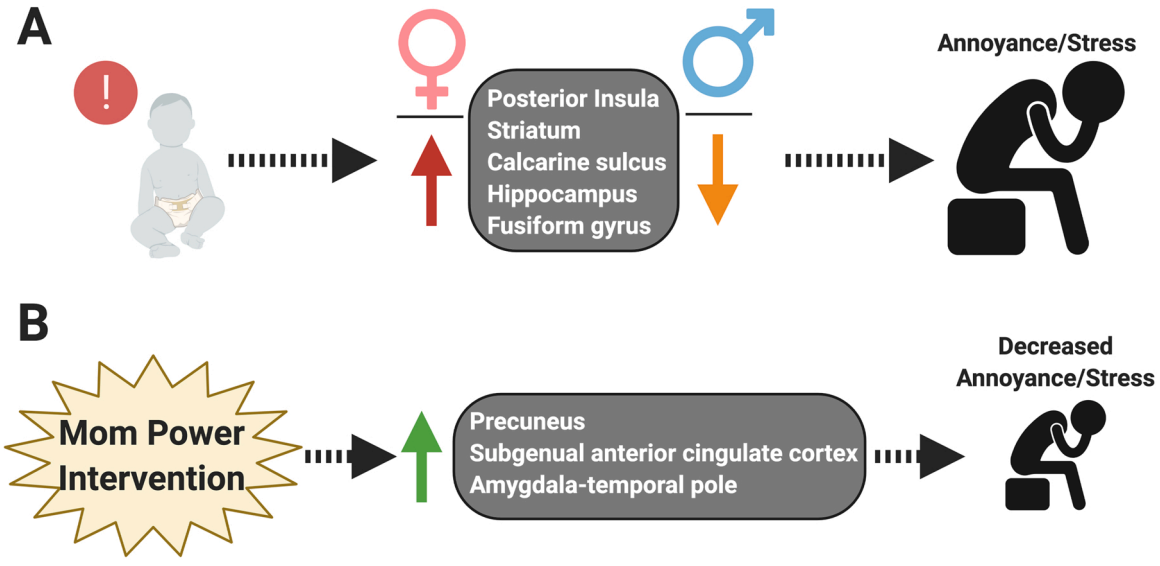


Fig. 7. Parental affective neuroscience and response to infant stress. Parent-child relationships – like any relationship – are influenced by outside factors, such as previous childhood poverty experienced by the parents. A) Response to a distressed child shows sex-specific brain activation in parents who had experienced childhood poverty. Specifically, women show increased activity in the posterior insula, striatum, calcarine sulcus, hippocampus, and fusiform gyrus, whereas men show decreased activation in these regions in response to infant cries. These neurobiological changes were associated with self-reported feelings of annoyance and reduced desire to approach infants in both men and women. B) Intervention, such as training programs for promoting maternal empathy and learning stress reduction skills (called "Mom Power"), was shown to increase activity in typical child-focused, social brain areas like the precuneus, subgenual anterior cingulate cortex, and amygdala-temporal pole functional connectivity. This training and altered brain activity was accompanied by decreased annoyance and stress felt by mothers.

responses for ~10 year olds to own mother picture cues in social cognition regions: precuneus, cingulate, and hippocampus (Valadez et al., 2020). Behavioral and brain imaging parameters of parental stress and empathy are also disturbed for mothers with substance use disorders such as the current epidemic of opioid use disorder. Opioids may modulate the maternal caregiving or behavior neurocircuits (Swain and Ho, 2019, 2021; Swain et al., 2019) – as developed from non-human research (Klein et al., 2014; Numan and Woodside, 2010). Such neurocircuits are hypothesized to govern human maternal behavior via two reciprocally modulating subsystems. These inhibit each other to either activate maternal caregiving behaviors when solicited by the infant or aggressive behaviors when the infant is threatened. Elucidating these and related mechanisms that could lead to more specific and effective treatments.

Thus, parenting may be conceptualized as a specific instance of altruistic social feelings that may positively influence health-related outcomes and is amenable to intervention (Brown and Brown, 2015; Ho et al., 2021; Konrath et al., 2015; Swain et al., 2012). Taken together, these results suggest that enhancing child-oriented altruistic social feelings may protect mothers from adverse effects of distress and stress related to caregiving - consistent with the hypothesis that prosocial motivation improves caregivers' well-being (Brown and Brown, 2015).

5. Moral sentiments as social feelings: neural considerations

5.1. History and definition of moral sentiments

Francis Hutcheson, his successor Adam Smith, and David Hume (Zahn et al., 2011b) highlighted the central importance of moral sentiments for moral behaviour. Adam Smith conceived "sympathy", as "man's capacity for fellow feeling with others", and considered it the most important moral sentiment (Lamb, 1974). Hutcheson stated that "benevolence" motivates virtuous actions and thereby provides "moral motivations" (Bishop, 1996). Modern authors use the term "moral emotions" rather than "moral sentiments". There is some disagreement about which emotions are considered moral (Eisenberg, 2000; Tangney et al., 2007a). Immanuel Kant, a contemporary of Hume, distinguished the ability to judge what is morally right and wrong ("principium diiudicationis") from the motivation ("principium motivationis") to act accordingly (Kant, 1786; Zahn et al., 2015). He was opposed to the notion that moral actions could be defined on the basis of experienced moral sentiments, which he considered as originating from the external senses. Instead he claimed that true moral actions are motivated directly by respect ("Achtung") for the moral law, which is self-generated and an act of free will (Kant, 1786). Thus, moral motivations as defined by the opposing schools of moral philosophy are either the respect for moral rules (Kant) or moral sentiments (Zahn et al., 2011a). Neuroscience and psychology research allows for developing theories and generating evidence about the structure and dynamics of subjective experiences and behavioural expressions of moral motivations, such as "respect for moral principles" or "feelings of guilt", and their neural underpinnings.

We use the terms "moral sentiments" and "moral feelings" synonymously, stressing the subjective and complex nature of moral sentiments which include cognitive ingredients such as causal attributions.

As recently reviewed (Zahn et al., 2020), although moral feelings have probably developed from affiliative feelings more generally, they are a distinct subset in that they enable humans to be motivated by other people's or societal needs in the absence of benefits to oneself or one's kin.

5.2. Brain lesions and impaired moral sentiments

By demonstrating which brain regions are necessary for moral and prosocial behaviour, lesion studies provide important insights, even if they relate to less confined anatomical areas and in some instances have to infer sentiments from observed behaviour. Already in the 19th century, Welt concluded that damage to the right medial orbital region was necessary to produce a change in moral character in a neuropathological case series (Zahn et al., 2015). In the 1980s, Eslinger and Damasio (1985) stimulated new interest in the neuroanatomy of the ventromedial frontal cortex (FC) by describing EVR, a patient with impaired moral and social behaviour. Around the same time, it was shown that frontotemporal dementia (FTD), particularly behavioural variant FTD (bvFTD) which regularly affects ventral frontal regions, can be diagnosed before death based on clinical features and was more common than originally thought (Snowden et al., 2001). Patients with FTD display impaired social behaviour (Bozeat et al., 2000). This was not only correlated with ventromedial FC, including the subgenual region, but also right anterior temporal lobe (ATL) damage (Liu et al., 2004). Ventromedial FC lesions that included subgenual sectors of the OFC were associated with a lack of guilt reported by caregivers (Koenigs et al., 2007). A study using fMRI and lesion information from patients with FTD showed that the ventromedial FC relates to the anticipation of negative consequences of social behaviour (Grossman et al., 2010), which is an important pre-requisite for experiencing guilt.

Septal damage in FTD was associated with diminished guilt and pity, but not embarrassment in an experimental task, whilst frontopolar damage was associated with impaired embarrassment in addition to guilt and pity (Moll et al., 2011). This showed that septal damage was associated with impairments of those moral feelings that entail empathic concern for other people, whilst frontopolar cortical damage was associated with prosocial feelings more generally, including embarrassment which is primarily related to upholding one's social reputation rather than concern for others (Eisenberg, 2000). In contrast to these associations of different moral feelings with different frontal-subcortical lesion patterns, another study showed that FTD patients with right ATL damage displayed selective impairments of abstract social relative to non-social conceptual knowledge (Zahn et al., 2009b) irrespective of the attached emotional valence. These lesion studies confirmed earlier fMRI evidence of partly dissociable representations of abstract conceptual social knowledge in the right superior ATL (Zahn et al., 2007) and different moral feelings in frontal-subcortical regions (Zahn et al., 2009c), which can independently contribute to impaired prosocial behaviour (Krajbich et al., 2009; Liu et al., 2004). Finally, meta-analytical evidence suggests that when frontomedian cortex is affected in bvFTD, it is associated with moral and social cognitive impairments. Analyses of empathic deficits in bvFTD have additionally identified pathology in the anterior insula and anterior cingulate regions (Schroeter et al., 2015, 2014).

5.3. Imaging the experience of moral feelings

The investigation of the neural correlates of subjective experiences of moral feelings in healthy people using fMRI has led to a number of interesting findings but can only be interpreted in light of brain lesion evidence. This is because fMRI also displays brain regions that likely are unnecessary for a given task or stimulus representation and merely reflect uncontrolled differences between experimental conditions.

Here, we focus on guilt and pity/compassion, given that the body of evidence on other moral sentiments is not large enough yet to draw conclusions. The anticipation of guilt is important in preventing moral violations and to motivate reparative actions (Eisenberg, 2000; Tangney et al., 2007a). Empathic concern is an essential ingredient of empathy—and is closely related to pity, sympathy, and compassion (Weng et al., 2015). Such feelings extend beyond perceiving, sharing or simulating other's emotions (e.g. sharing pain which is associated with anterior insula and dorsal cingulate brain activation (Lamm et al., 2011), requiring an extra step of feeling *for* the other person (de Vignemont and Singer, 2006; Decety et al., 2012). Frontal polar cortex activations emerge as most reproducible for both guilt (Basile et al., 2011b; Kedia et al., 2008; Moll et al., 2007; Morey et al., 2012a; Seara-Cardoso et al., 2016; Takahashi et al., 2004; Zahn et al., 2009c) and compassion (Fehse

et al., 2015; Ho et al., 2021; Immordino-Yang et al., 2009; Kedia et al., 2008; Moll et al., 2007) compared against equally unpleasant and complex emotions, such as indignation towards others. In addition, guilt was reproducibly associated with activations of the subgenual cingulate cortex (extending posteriorly to the adjacent septal area and the more anterior pregenual cingulate area in several studies) when compared with other complex negative emotions (Basile et al., 2011b; Green et al., 2012; Morey et al., 2012a; Zahn et al., 2009a,c). Septal and/or subgenual cingulate activations for guilt were reported in several studies, however, only when modelling individual differences in guilt proneness and empathic concern (Green et al., 2012; Zahn et al., 2009a,c).

Despite these reproducible associations of subgenual cingulate and septal activations with individual differences in guilt-proneness and empathic concern, two recent systematic reviews of fMRI studies probing guilt (Bastin et al., 2016; Gifuni et al., 2016) have failed to detect these regions. The reviews did not base their conclusions on studies controlling for individual differences in the experience of guilt-evoking stimuli, nor on those studies using optimised fMRI sequences for ventral frontal regions. It is not surprising, therefore, that subgenual cingulate/septal activations were not emphasized. This will be important in future systematic reviews.

5.4. *Converging evidence from fMRI and lesion studies on moral sentiments*

To summarise, lesion and fMRI data point to an important role for the septal region and ventromedial parts of the frontal cortex, in particular its subgenual cortex (BA25) component and the more anterior subgenual cingulate cortex, in processes of guilt and compassion (Fig. 8). Lesions to other cortical brain regions which were shown to represent goals of socio-moral behaviour, such as long-term consequences (frontopolar cortex, (Wood and Grafman, 2003) and conceptual quality of social behavior (right superior ATL, (Zahn et al., 2009b) led to changes in moral behavior as well (Zahn et al., 2009b) (Fig. 8) in keeping with the notion that moral behavior requires both socio-emotional qualities such as “affiliation” that have important elements of social feeling and the goal representations to which those sentiments are attached (Moll et al., 2008a).

6. Neurobiology of social feelings under interpersonal stress

A useful way to investigate whether social feelings are a naturally occurring neurobiological kind, identifiable and conducive to scientific inquiry, is to consider studies that directly induce real or imagined interpersonal stress (i.e., the presence of conflict or threat, or the loss or absence of belonging or connection) and ask participants to provide ratings for their emotional feeling states (Coan and Sbarra, 2015). Current understanding of the central neurobiology of social feelings in this context is limited because such studies have been dominated by a focus on peripheral physiology. However, this area provides unique opportunities to investigate social feelings in the context of integrated brain-body pathways.

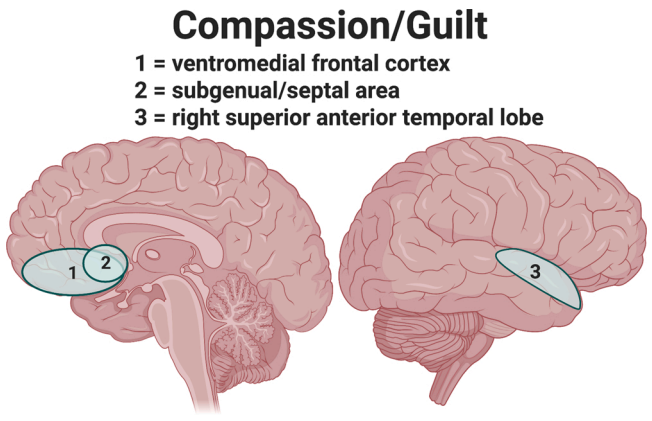


Fig. 8. Regions associated with empathy, as informed by lesion and fMRI studies. Feelings of guilt and compassion are strongly associated with typical functioning of the subgenual/septal region and ventromedial frontal cortex. Longer-term emotions, such as processing long-term consequences and conceptualizing quality of social behavior, activate the frontopolar cortex and the right superior anterior temporal lobe.

A relevant meta-analysis of studies that induced unpleasant feeling states using ecologically valid approaches (e.g., public speaking, marital conflict, films, music, mental re-experiencing) and measured peripheral stress, linked these physiological parameters to inferred feeling states (Denson et al., 2009). Specifically, nine judges were asked to mentally imagine themselves in the participant’s position and rate the intensity of feelings they imagined the stressor in each study would have provoked, including social feeling states (*e.g.*, submissive, fear of losing social approval, ashamed, guilty, embarrassed) (Fig. 9A). These ratings were then used to predict effect sizes for stress-induced changes in biological mediators. Statistically significant effects were observed for three of five social feelings. Stronger feelings of submissiveness and fears of losing social approval (as rated by the judges) predicted greater stress-induced increases in the endocrine hormone cortisol, an end-product of hypothalamic-pituitary-adrenal axis activation (Fig. 9B). Stronger feelings of embarrassment predicted greater stress-induced decreases in T-lymphocyte numbers, indicating a potential dampening of immunity (Fig. 9C). In contrast, two of the eight other feelings (*i.e.*, surprise and anticipation of a social encounter) showed statistically significant effects, predicting increases in cortisol and decreases in T-lymphocyte numbers, respectively.

This meta-analysis revealed an important role for social feeling states in peripheral stress physiology, especially feelings that arise when social status is threatened, and especially when compared to “fight-or-flight” feelings that are often the focus in studies of stress. In addition, it highlighted the variety of experimental approaches used to study social feelings under interpersonal stress. This raises an important question: Do social feelings and their underlying neural processes depend on different aspects of the experimental manipulation? This question is at the heart of the emerging area of second-person neuroscience (Redcay and Schilbach, 2019). The premise of this area is that the neurobiology of social processing varies as a product of two interpersonal dimensions: emotional engagement and interaction (Schilbach et al., 2013).

The emotional engagement dimension refers to the degree to which social stimuli are processed as self-directed and self-relevant (more emotional engagement), as opposed to from an observer’s perspective (less emotional engagement). Neuroimaging studies suggest that the affective and rewarding components of emotional engagement are particularly linked to the amygdala, the ventral portion of the medial prefrontal cortex (mPFC) (Schilbach et al., 2006) the temporo-parietal junction (Redcay et al., 2010, 2013) and striatal structures. The interaction dimension refers to the degree to which one is involved in a real or imagined interpersonal exchange (structured or dynamic), as opposed to being a passive observer of social stimuli (Krach et al., 2013; Schilbach et al., 2013). During direct interactions the mPFC, the posterior superior temporal sulcus and precuneus as parts of the mentalizing system as well as the anterior insula and ACC as part of a sharing system, are thought to be involved when we make sense of others’ states in the transition from social isolation to interpersonal exchange. Still very preliminary findings reveal evidence for greater activation of, and interactions among the mentalizing/sharing system and affect coding/-reward networks (Redcay et al., 2010; Redcay and Schilbach, 2019, p. 497) as participants move from processing social information that is low on emotional engagement and interaction versus high on emotional engagement and interaction. Further, it has been proposed that the mental state and neural qualities that are triggered by emotionally engaged interactions—termed “social immersion”—may persist after

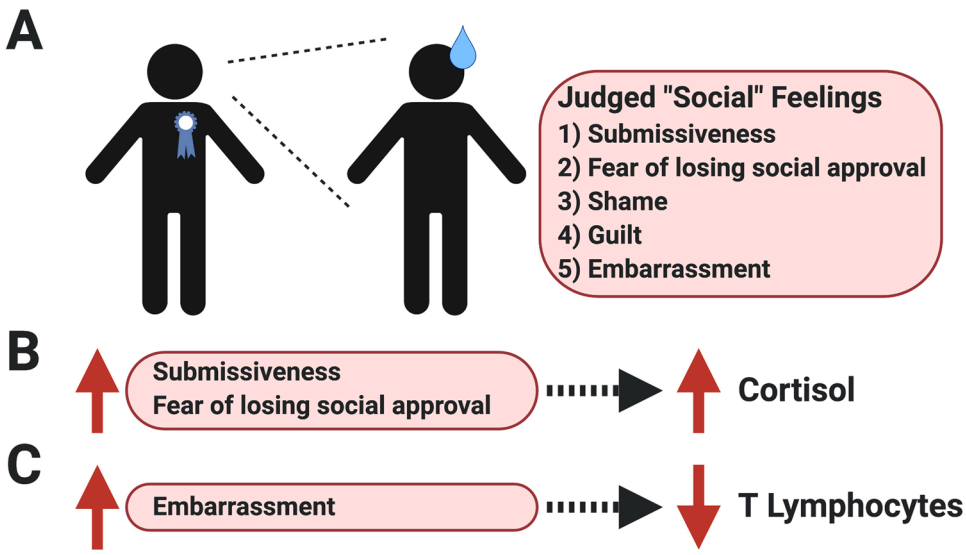


Fig. 9. Interpersonal stress and peripheral physiological responses. The physiological response to interpersonal stress has been investigated using a design where people were asked to "judge" another while imagining them in the judged-person's position and rate their social feelings and "other" feelings. A) Social feelings assessed included i) submissiveness, ii) fear of losing social approval, iii) shame, iv) guilt, and v) embarrassment. B) Judges' ratings of the other person's feelings of submissiveness and fear of losing social approval predicted a larger increase in the judged person's cortisol levels. C) Judges ratings of the other person's feelings of embarrassment predicted a decrease in T-lymphocyte numbers.

the social interaction ends (Krach et al., 2013, p. 427). Overall, this implies achieving clarity about the neurobiology of social feeling states will require teasing apart factors that differentially engage these two interpersonal dimensions (i.e., emotional engagement and interaction).

6.1. *Social-evaluative threat*

Grounded in animal models of social subordination stress, social-evaluative threat is a specific type of interpersonal stressor that involves potential loss of social status or social regard (Kemeny, 2009). Exposure to acute social-evaluative threat (e.g., solving math problems, estimating properties of a stimulus or giving a speech in front of a panel of deadpan evaluators) involves high emotional engagement in the context of a structured social interaction. Especially by manipulating the presence or absence of a judging audience, participants are motivated to think about others' evaluations and how one's performance might affect the impression others will have of them. In studies of social-evaluative threat that include measures of emotional states, participants are typically asked to rate momentary feelings (i.e., "How do you feel right now?") immediately before and after the experimental manipulation. Compared to participants assigned to solve math problems, estimate properties or give a speech either alone or with the mere presence of an inattentive person without any evaluation (Guerin, 1986), participants exposed to a judging audience showed greater increases in the endocrine stress hormone cortisol (Kirschbaum et al., 1993), along with the momentary feelings of shame and related feelings (e.g., humiliated, foolish) (Dickerson et al., 2008; Gruenewald et al., 2004) or embarrassment (Muller-Pinzler et al., 2015). Social feelings were accompanied by increases in salivary cortisol (Dickerson et al., 2008; Gruenewald et al., 2004) or pupil diameter as a correlate of affective arousal (Muller-Pinzler et al., 2015), and persons who reported greater increases in shame-related feelings (but not anxiety or fear) showed the greatest increases in cortisol.

Studies that induce social-evaluative threat using stressors that can be manipulated within the confined set-up of an fMRI have begun to address the central neurobiology of social feelings induced by social-evaluative threat. Mostly, these studies utilize cover stories or staged interactions with confederates to create ecologically valid social contexts. In one such study, participants discussed their positive and negative qualities while being videorecorded (e.g. "What are you most proud of?"); they were led to believe that another person (i.e., a confederate to whom they had been introduced prior to scanning) would view the recording in order to form an impression of them (Muscatell et al., 2015). Subsequently, and while in the scanner, participants were exposed to a combination of neutral, positive, and negative evaluative "social feedback" trials by viewing a cursor periodically selecting various adjectives (e.g., serious, shallow); they were led to believe that this feedback reflected the other person's impression of them based on the video recording. From the perspective of second-person neuroscience, this social-evaluative stressor can be characterized as high on emotional engagement (self-directed and -relevant), but low on social interaction. However, the paradigmatic set-up let participants immerse into the situation rendering the mental representation of oneself in relation to the evaluating other as essential. Exposure to the social feedback trials in aggregate (i.e., all neutral, positive, and negative trials) increased momentary feelings of social rejection and evaluation from before to after the scanning session, along with plasma levels of the cytokine interleukin-6 (IL-6), an immune system cell that has actions that promote inflammation. However, increases in social feelings and in IL-6 levels were not correlated. Moreover, these two responses were differentially related to neural activity during negative vs. neutral social feedback trials. Increases in momentary feelings of rejection (but not evaluation) were related to heightened activity in neural regions engaged by self- and social-processing, including mentalizing (i.e., mPFC, posterior cingulate cortex, and hippocampus). Increases in IL-6 levels were related to heightened activity in neural regions engaged by affective/threat-related processing (i.e., amygdala), and to greater functional connectivity between these regions and mentalizing-related regions (i.e., dorsomedial prefrontal cortex) (Muscatell et al., 2015; Muscatell and Eisenberger, 2012) (Fig. 10A). This study provides a preliminary look at the neural correlates of momentary stress-related social feelings under social-evaluative threat. However, specificity for social feelings cannot be determined because other feelings were not assessed.

This issue was addressed in an fMRI study in which participants received false negative, neutral and positive feedback about their cognitive estimation performance both privately and publicly. Specifically, in the public condition, participants were led to believe that three other persons whom they had met prior to entering the scanner, and who remained seated adjacent to the scanner during the entire session, could observe the feedback about the estimation performance given to the participants inside the scanner. In the private condition, estimation feedbacks were not projected outside to the audience (Muller-Pinzler et al., 2015). The feedback and private-public manipulation were delivered on a computer screen immediately following each cognitive estimation trial. After scanning, participants reported their social feelings (embarrassment, pride) and other feelings (anxiety, anger, sadness, happiness) for each trial type. The feeling of embarrassment was most affected by negative feedback (failure) that was observed by others (publicity), the two defining factors of embarrassment (Miller, 1996). Sympathetic nervous system

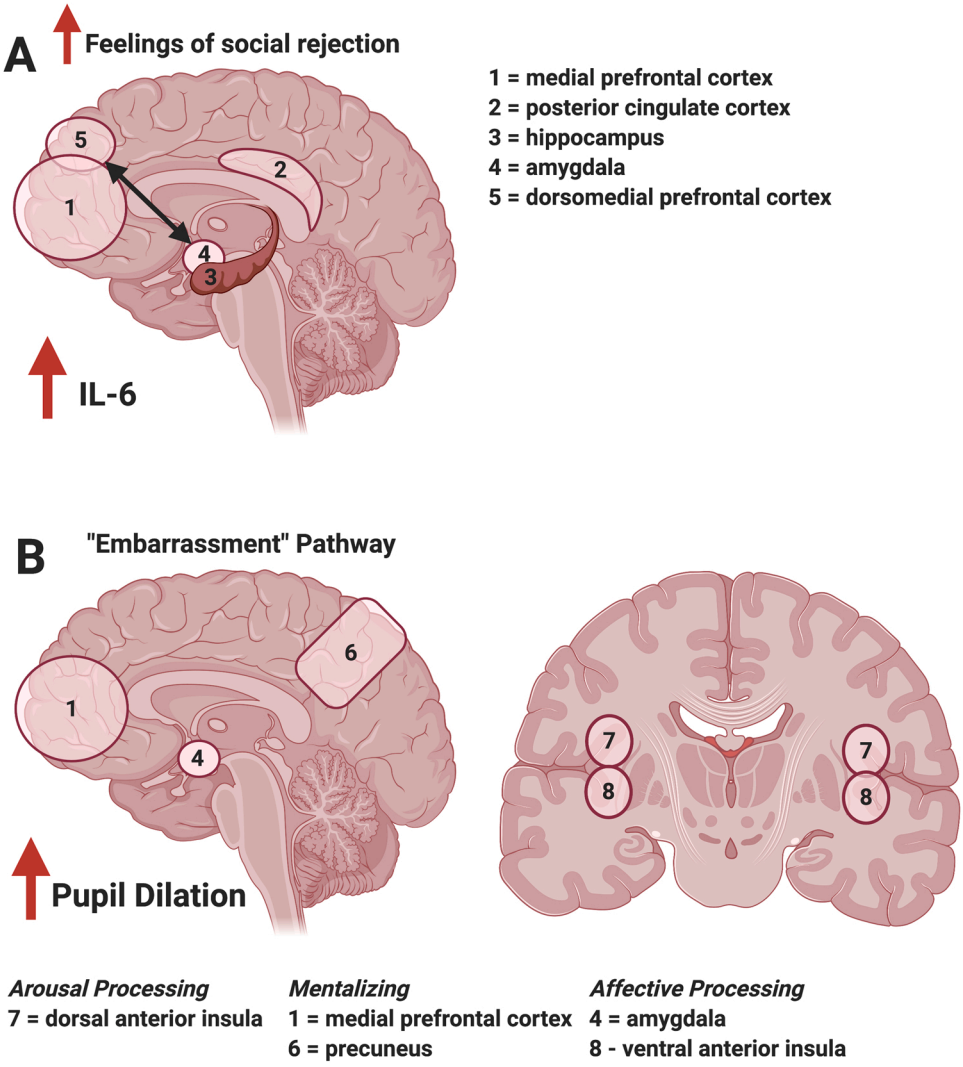


Fig. 10. Neurobiology of interpersonal stress. Participants in these studies were asked to discuss their positive and negative qualities on video; they were then placed into a scanner, where they received "social feedback" from another person watching their video, which indicated adjectives such as serious or shallow. A) Greater release of the cytokine IL-6 was seen following trials, regardless of feedback type. Increased activity in the medial prefrontal cortex, posterior cingulate cortex, and hippocampus was observed when subjects reported increased momentary feelings of rejection, as well as increased activity in the amygdala and functional connectivity between the amygdala and dorsomedial prefrontal cortex. B) Another study examined responses to negative, positive, and neutral feedback given publicly or privately. This research led to the identification of the "Embarrassment Pathway," which was most affected by negative feedback. This includes regions for processing the feedback, such as the dorsal anterior insula, processing the publicity, such as the medial prefrontal cortex and precuneus, and connectivity of these regions involved in affect processing, such as the amygdala and ventral anterior insula. These were also associated with increased pupil dilation.

arousal, indexed by pupil dilation, was also greater during the public versus private feedback and, while also increased during positive feedback, the interaction of failing in public was associated with the strongest pupil dilation. Further, during negative versus positive feedback, brain regions that were involved in processing negative feedback and related arousal (dorsal anterior insula), and those that were involved in mentalizing about the publicity (mPFC and precuneus), both showed greater functional connectivity with core affective processing regions (amygdala and ventral anterior insula) (Adolphs et al., 1995; Kelly et al., 2012) (Fig. 10B). Based on this pattern, the authors concluded that the integration of arousal, mentalizing, and affective/threat-related processing systems forms a "neural pathway of embarrassment" (Muller-Pinzler et al., 2015, p. 252). On the other hand, if the focus was on being successful during the cognitive estimation task, the experience of pride feelings was associated with increased activation of the brain's reward circuits in the striatum (Muller-Pinzler et al., 2015). As shown also in other studies, pride is elicited when humans achieve self-relevant goals. Studies suggest that its social function relates to the signaling of (real or imagined) status with potentially beneficial effects for both the displayer and observers (Bollo et al., 2018; Martens et al., 2012). Accordingly, on the neural systems level, the mPFC and precuneus, areas of the mentalizing network, are also implicated during pride experiences when participants reflect about their behavior and their evaluation in the eyes of others (Takahashi et al., 2008; Williams and DeSteno, 2008; Zahn et al., 2009c). However, according the mentioned study, the variability of pride was less affected by the presence/absence of the audience and accompanying positive evaluation of others (Muller-Pinzler et al., 2015). Rather than being affected by the publicity manipulation, pride feelings seem to depend on internal control beliefs when performing a task (Stolz et al., 2020). Further research might also reveal that different neural systems underlie the experience of authentic, positive pride and the more negative hubristic pride associated with arrogance and contempt.

6.2. Social exclusion

Social exclusion (also referred to as ostracism or social rejection) is a type of interpersonal stress that has received attention because of the centrality of social connections in human health and survival (Eisenberger, 2012). The neurobiology of social exclusion has often been studied using a virtual ball-tossing game (i.e., cyberball). From a second-person neuroscience perspective, this approach involves emotional engagement (i.e. self-relevance and self-directedness) and the sense of being involved in a social interaction (i.e. receiving and passing on of ball tosses). However, to induce the experience of social exclusion it is necessary to make participants believe and immerse into the set-up of social interaction. The typical feelings measured using this approach are those of momentary "social distress". Social distress is a composite that includes social feelings such as rejection, disconnection, not belonging, not liked, invisible, but also other feelings related to self-esteem and control that area less socially focused (Williams, 2009).

These "painful feelings associated with social disconnection" have also been described as "social pain" (Eisenberger, 2012, p. 421). In numerous studies, greater activity in various subregions of the ACC in response to social exclusion versus inclusion correlated positively with momentary feelings of social distress, with ACC subregion involvement being influenced by a variety of methodological factors (Eisenberger et al., 2003; Rotge et al., 2015). In addition, greater ACC activity during social exclusion, along with greater amygdala and periaqueductal gray activity, correlated positively with momentary feelings of social distress in response to social interactions in the natural environment (Eisenberger et al., 2007a). Further, activation of hippocampus and mPFC regions during social exclusion correlated positively with greater correspondence between momentary social distress in the natural environment and feelings of social distress as persons reflected over their day (Eisenberger et al., 2007a). From the perspective of second-person neuroscience, this pattern supports the hypothesis that persons who processed lab-based social exclusion with greater emotional and interpersonal engagement were more prone to translate this experience of social distress to everyday life social interactions in the natural environment.

In a different approach, voluntarily reliving a socially painful interpersonal stressor (e.g., a break-up, exclusion, or betrayal) as compared to a neutral interpersonal event, and as compared to a physically painful versus physically neutral event, was associated with greater activity in the dorsal anterior cingulate cortex (dACC) and anterior insula. The stronger feelings of social pain evoked by reliving interpersonal stress versus physical pain correlated positively with greater dACC activity. Further, the overall pattern reflected enhanced mentalizing, or processing of one's own and others' mental states, during reliving of interpersonal stress versus physical pain, as indicated both imaging data (i.e., greater activity in the dorsal mPFC) and behavioral data (i.e., more indicators of mental state processing in participants' written descriptions of the stressor) (Meyer et al., 2015). Another study showed that the secondary somatosensory cortex - an area usually involved in coding the sensory component of physical pain - was activated by the mere re-imagination and reliving of a romantic partner break-up triggered by viewing a headshot photograph of the ex-partner (Kross et al., 2011).

6.3. Interpersonal transgressions

An intense aversive social feeling state that arises when we believe that we have behaved immorally or transgressively is guilt. Although guilt may also initially emerge in social isolation, its unpleasantness is mostly related to thoughts about the harm that one has caused to others and the fear of consequent rejection (Baumeister, 1994). Guilt thus involves an involuntary transgressive part, which then usually is followed by an approach-oriented and reparative part to fix the unpleasant situation (Fourie et al., 2012, 2014; Tangney et al., 2007b). While most neuroscience studies on guilt used script-based approaches and mental imagery (Basile et al., 2011a; Morey et al., 2012b; Shin et al., 2000; Takahashi et al., 2004), Fourie and colleagues used a clever set-up to directly induce states of guilt within the fMRI. To do so, they invited participants to a study allegedly examining prejudices among college students. Participants were told that they had been selected based on their overall positive explicit attitudes toward most social groups, but that there is usually a significant discrepancy between what people say they feel, and what they really feel, toward these groups. Participants subsequently performed an implicit association task (IAT) with neutral (sports, hair), positive (weight, religion) and negative (race, sexuality) response categories in the scanner. A preprogrammed feedback elicited guilt by providing participants information that contradicted their belief that they held egalitarian attitudes toward Black and physically/intellectually disabled people. The fMRI data indicated that this unpleasant feeling of guilt was associated with increased activity in anterior paralimbic structures, including the ACC and anterior insula, but also extended to areas associated with mentalizing, including the dorsomedial prefrontal cortex, posterior cingulate cortex, and precuneus. Although the IAT was performed in social isolation, the experience of guilt may have involved ongoing thoughts about one's own actions that caused harm to another person or group of people. Thus, it is not surprising that most studies found evidence for guilt-related activations of mentalizing areas, such as mPFC, posterior cingulate cortex, and precuneus (Basile et al., 2011a; Fourie et al., 2014).

Another study employed a more interpersonal approach to induce guilt in the MRI and studied guilt-associated reparative behavior (Yu et al., 2014). Participants played an interactive game with an alleged anonymous partner and were punished with painful stimulation when at least one of them responded incorrectly. In this case, participants were given the option to bear a portion of pain that would otherwise be delivered to the partner. Trials in which participants were solely responsible for the punishment elicited greater feelings of guilt, a higher sense of responsibility, higher levels of distress and higher willingness to receive a portion of the partner's pain, as compared to trials in which both partners were responsible for the punishment. These trials were further associated with activity of dorsal ACC and insula, again demonstrating the involvement of paralimbic regions in guilt states.

6.4. Resilience

Finally, there is preliminary evidence that social feelings with positive valence may confer neurobiological resilience to interpersonal stress. In an observational study, reports of more social interactions over 10 days with persons generally perceived as closer, more comforting, and more supportive were associated with less dACC activity during laboratory-based social exclusion vs. inclusion. This lower dACC activity, in turn, was associated with lower cortisol responses to laboratory social-evaluative threat (Eisenberger et al., 2007b). In an experimental study, the effectiveness of three interventions for reducing feelings of anxiety and peripheral stress mediators (cortisol, markers of inflammation, and indicators of autonomic nervous system (ANS) activity) in response to acute social-evaluative threat was assessed: dyadic training in cultivating positive social feelings (compassion, kindness, gratitude), dyadic training in cultivating cognitive perspective-taking on self and others, and individual training in focused attention and interoception (Engbert et al., 2017). The two dyadic trainings were motivated by evidence that rather distinct neural networks—empathy and mentalizing, respectively—are involved in these two modes of interpersonal understanding (Kanske et al., 2015). Compared to a no-treatment control, all interventions reduced feelings of anxiety in response to social-evaluative threat. None of the interventions reduced inflammatory or ANS responses to social threat. In contrast, dyadic training in cultivating positive social emotions, and dyadic training in cognitive perspective-taking when combined with individual training in focused attention and interoception, both reduced cortisol responses to social threat compared to the no-treatment control. The authors speculated that training in cultivating positive social feelings and social perspective-taking may build resilience to the shame response that is provoked by social-evaluative threat (Engbert et al., 2017). Unfortunately, however, measures of social feelings were not reported.

Overall, this emerging picture suggests that the neurobiology of social feelings ranging from concerns about social belonging and potentially diminished value in the eyes of others (i.e., submissiveness, loss of approval, shame, guilt, embarrassment, composite social distress)—or what might be termed lower "relational value" (Leary, 2015, p. 435)—to positive social feeling states such as pride, compassion or gratitude may play a key role in interpersonal states, even when compared to more basic emotions or feeling states that have traditionally been the focus in such studies. This evidence lends support to the idea that "social feelings" might be a neurobiological natural kind that is identifiable and conducive to scientific inquiry. Consistent with ideas from second-person neuroscience, results generally highlight the role of brain regions involved in emotional engagement (affective and reward-related

structures) and interaction (sharing and mentalizing related structures) in social feelings, although this varies by the specific paradigm for inducing interpersonal emotions, and by how and when social feelings are measured.

Recommendations for future research include measuring a range of social feeling states, and teasing apart composite measures of social distress, to ensure that results are specific to social feelings. This is particularly important given that neural regions may be involved in processing multiple feelings (e.g., Eisenberger, 2015). Measuring feelings both before and after stressors (or in response to different trial types) will also be important to ensure that any observed neural correlates are linked to stress-induced social feelings, rather than to stable individual differences in propensities to experience certain social feelings. Measuring stress-related social feelings in the natural environment, and beyond momentary time frames, will be helpful for establishing greater ecological validity for neural correlates. Related to this, because the second-person neuroscience framework predicts that degree of interpersonal closeness may modulate neural responses (Redcay and Schilbach, 2019), future research on this topic should involve measuring this or manipulating it in a laboratory setting (for an innovative approach of studying social touch related feelings see (Renvall et al., 2020)). Few studies of stress-related social feelings to date have included measures of both peripheral and central neurobiology, making it difficult to draw conclusions about integrated brain-body pathways. However, given that interpersonal stressors are among the most consequential stressors for health (Holt-Lunstad et al., 2017; Liu et al., 2017; Resnick et al., 1993), such approaches may yield important information about the role of social feelings in homeostasis and overall health.

7. Neuroscience of Social Feelings associated with emotional communications

Affective states are communicated overtly through physiological (blushing, sweating), behavioral (body posture, facial expression, modulation of the voice, interjections), and verbal ("I am really happy") signals. Perceiving another person's affective state can elicit various feelings in the perceiver (Fig. 11A). First, the perceiver might share the target's (actual or perceived) feelings (Keysers and Gazzola, 2007; Mayer et al., 2020; Paulus et al., 2013; Waytz et al., 2012). Second, perceiving another person's emotional state can lead to feelings of confidence in the perceiver if the perceiver is able to accurately decipher (and make sense of) the sender's emotion(s). Third, the perceiver might perceive the sender's emotion as appropriate or inappropriate in a given context (including the perceiver's own current affective state), leading to prosocial (e.g., affiliation, compassion) or aversive (e.g., anger, indignation) feelings. Fourth, if the perceiver views self and the sender

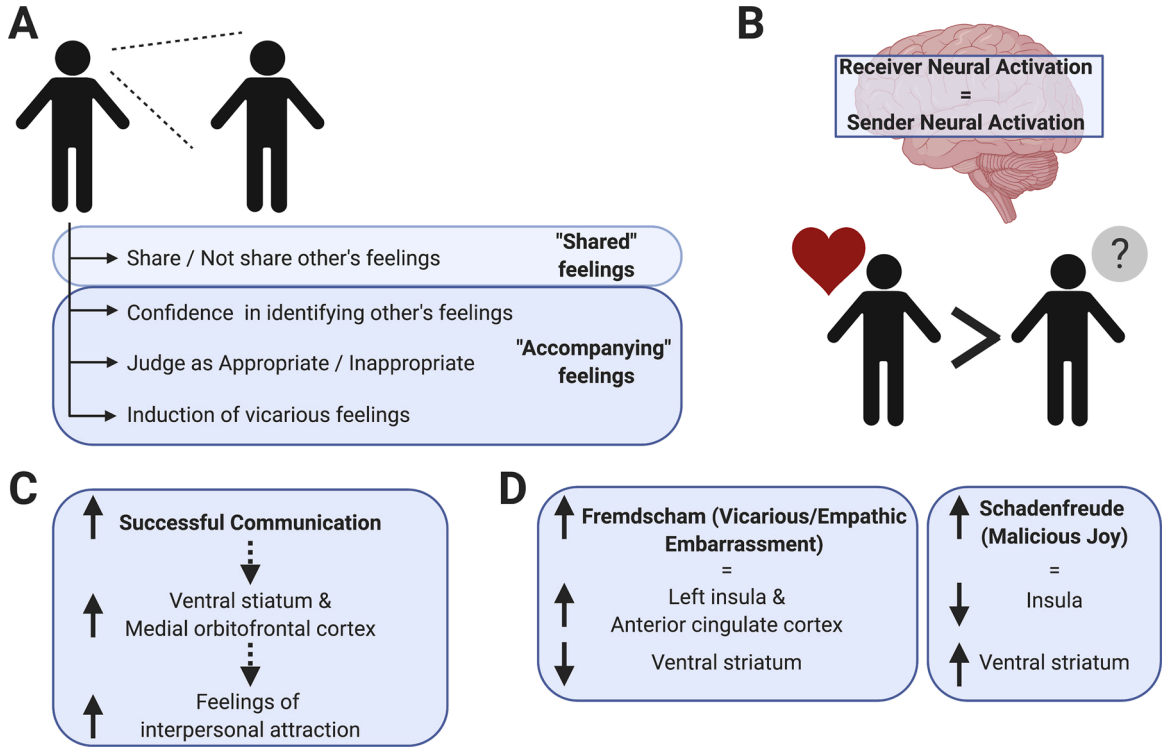


Fig. 11. Brain activity during emotional communication. A) When an individual perceives another person's emotional behavior, the feelings elicited in the observer can be characterized as "shared" or "accompanying." Accompanying feelings include pleasant feelings of confidence if the communication was successful (i.e. the feeling that one person correctly understood the other person's feelings), feelings elicited when one partner regards the other partners emotional behavior as appropriate or not, induction of one's own emotions regarding the other's response, and assessing confidence in if the person understands the other's feelings. B) Use of pseudo-hyperscanning allows researchers to l examine brain activity of a "sender" and a "perceiver" of emotional signals that can be temporally aligned. When a person is asked to communicate emotions via facial expressions, their communication partner shows similar neural activation. This is more pronounced between romantic partners than between strangers. The more similar the activation, the more shared feelings are reported (Anders et al., 2020b). C) Strangers viewing facial expressions of a sender show an increase in ventral striatum and medial orbitofrontal cortex activity that is correlated with the perceiver's confidence in having correctly understood the sender's emotion and predicts changes in interpersonal attraction (Anders et al., 2016). D) When people were asked to look at images of another person exhibiting publicly inappropriate behavior (a situation associated with self-reported feelings of Fremdscham or vicarious embarrassment caused by another's inappropriate behavior), greater activations in the left insula and anterior cingulate cortex occurred, and decreased activation in the ventral striatum was observed. In such emerging studies there is no overt communication of feelings or emotions (perceivers inferred the targets' feeling and emotional states from their actions in context or not at all), and the degree to which perceivers shared the targets' feelings are not specifically measured. Future studies, though, may develop more robust paradigms to address these issues.

as a social unit (e.g. friends) among more distant others, seeing the sender displaying emotional behaviors can elicit vicarious feelings in the perceiver (e.g. embarrassment or guilt when a close one behaves emotionally inappropriate towards others) (Müller-Pinzler et al., 2016). Although all of these feelings might occur in overlapping timeframes, the perceiver might not be aware of all feelings simultaneously, or might experience a blend of feelings rather than a set of distinct feelings.

Neuroscientific studies have been pursued to address the different types of feelings that can arise during emotional communication to very different extents. While numerous neuroimaging studies have focussed on the mechanisms and processes that might lead to shared feelings in the perceiver, neuroimaging studies investigating other types feelings that might occur during emotional communication (we call them "accompanying feelings" hereafter) are very rare. Here we will briefly review what is known about the neural processes that might give rise to shared feelings and accompanying feelings during emotional communication.

Early fMRI studies on shared affect compared neural representations of emotions (e.g. disgust) that arise during first-hand experience of that emotion (e.g., smelling an unpleasant odour) to those that arise during observation of the same emotion in another person (e.g., when observing another person's facial expression while they smell an unpleasant odour) in the same individual, bypassing the problem of having individuals communicating with each other during neuroimaging. While in these studies brain regions were identified that are activated during first-hand experience and observation of emotion (e.g., the anterior insula in the case of disgust, (Wicker et al., 2003)) they neither investigated communication (i.e., the exchange of information between brains) nor did they link neural activity to experiences (feelings). More recently, pseudo-hyperscanning has been used to investigate the neural basis of shared affective experiences during emotional communication. In pseudo-hyperscanning, a "sender" and a "perceiver" are scanned one after the other in the same scanner but are connected by audio or video recordings such that their brain activity can be temporally aligned after scanning. In one of these studies (Anders et al., 2011) female participants (senders) were asked to submerge themselves into cued emotional situations and to facially communicate their feelings as they arose to their male romantic partner (perceiver) whom they believed could see them online via a video camera while being scanned in a different scanner. Using classification techniques the flow of affective information between the sender's and the perceiver's brain was examined. This work showed that the senders' emotion-specific neural activity was reflected in corresponding neural networks of the perceiver's brain. Importantly, activity in these networks not only encoded prototypical emotional information, but information that was specifically related to the sender's specific affective state (Anders et al., 2011). Including more perceivers (who had not met the senders before) revealed that the sender's romantic partners simulated the sender's affective state more accurately in their own brains than strangers (Fig. 11B), and, importantly, that more accurate simulation was associated with a higher degree of shared affective feelings (Anders et al., 2020b). This study provided evidence that sharing another person's affective feelings during emotional communication might rely on between-brain neural simulation, i.e. the re-enactment of neural processes underlying the sender's affective state in the perceiver's brain.

A similar study (Anders et al., 2016) revealed that emotional communication was associated with accompanying feelings of confidence in the perceiver if the communication was successful, irrespective of the emotion that was being communicated. Short videos clips of six different senders experiencing sadness and fear from the pseudo-hyperscanning study described above were shown to $>$ 90 new participants. The participants' task was to decide, after each video clip, which emotion the sender had been experiencing, and to report how confident they felt about their judgement. Self-reported confidence covaried with (i) the re-activation of local networks in the anterior insula that were also activated when the perceivers experienced sadness and fear, respectively, themselves and (ii) neural activity in the ventral striatum and medial orbitofrontal cortex (mOFC) (two brain regions that play an important role in affiliation, see section 2. Furthermore, neural activity in the ventral striatum/mOFC and feelings of confidence during emotional communication were associated with increased feelings of attraction towards the sender after communication (Anders et al., 2016) (Fig. 11C). These findings are consistent with the hypothesis that seamless communication of emotional information can lead to affiliative feelings.

Successful emotional communication might not only elicit social feelings in the perceiver, but also in the sender. In a different study participants were asked to submerge themselves into happy or sad situations and to facially express their feelings. At the end of each trial a facial expression was shown that either matched or did not match the participant's facial expression. Facial expressions that matched the affective feeling expressed by the participants elicited stronger activity in the mOFC than facial expressions that did not match the feeling expressed by the participant, again irrespective of the emotion that was being communicated. Together, these studies suggest a link between neural activity in the ventral striatum/mOFC and positive feelings associated with understanding and being understood during successful emotional communication.

As described above, natural face-to-face communication is already difficult to implement in a neuroimaging environment. This is obtains further for face-to-face communication that would be embedded in multi-level social contexts able to elicit mixtures of higher order social feelings. We are not aware of any neuroimaging study that has successfully accomplished this in a robust scientific manner. With the large growth in video face-to-face communications due to the recent pandemic restrictions of social distancing, investigations of these various platforms may become more timely.

In an early study, circumvented this problem by linking interindividual differences in brain activity to trait levels of emotional awareness (the ability to recognize and differentiate affective feelings). They found that higher levels of emotional awareness (assessed by the Levels of Emotional Awareness Scale, LEAS (Lane et al., 1990)) were associated with more pronounced local activity in the anterior cingulate cortex (ACC) during emotional experiences. This pointed towards a role for the ACC in dissociating between different (and possibly conflicting) affective feelings.

In a simple approach, Krach and colleagues used contextual stimuli (visual sketches of social scenes) in combination with cued imagination to study neural processes associated with the self-related feeling of *Fremdscham* or vicarious embarrassment (i.e. embarrassment caused by another's inappropriate behaviour). Scenes associated with Fremdscham (compared to neutral scenes) elicited activity in the left insula and anterior cingulate cortex, and trait empathy correlated with activation parameters in those regions (Krach et al., 2011; Paulus et al., 2015) (Fig. 11D). In another study it was shown that neural activity in the ventral striatum depended on the perspective participants were asked to engage. If the task was to imagine another's inappropriate behaviour and assess one's vicarious feelings of embarrassment, activity in the ventral striatum was decreased compared to when participants were inclined to rate how funny they would find such predicaments (Paulus et al., 2018). However, as in the Lane et al. study, these experimental designs did not incorporate overt communication of emotion (perceivers inferred the targets' emotion from context or not at all), and the degree to which perceivers shared the targets' feelings was not measured. Studies investigating the neural processes underlying social feelings triggered by actions inferred to be emotionally intoned (perhaps indirect or covert forms of emotional communication) may eventually emerge.

Thus, neuroscientific studies on social feelings associated with the communication of emotion are currently heavily constrained by (i) the difficulty to elicit complex social feelings in the laboratory, and particularly in a neuroimaging environment, (ii) the challenges to measure complex, dynamically rising, changing and fading feelings in real life,

and (iii) the lack of analytical techniques and theoretical concepts of how neural and experiential data should be linked once they have been acquired. While the first problem might be tackled by increased use of fNIRS (functional near infrared spectroscopy), a technique that successfully has been used to measure neural activity of interacting brains (Cui et al., 2012) and that allows measurement of neural activity with portable devices that can be used over prolonged periods in many typical social situations (Piper et al., 2014), the second and third problems require more conceptual and methodological work (and interdisciplinary trained neuroscientists with a strong background in data analysis techniques).

8. Social feelings in psychiatric conditions

Social feelings are tightly linked to social interaction and communication. Atypical or dysfunctional social communication and interaction are at the core of various psychiatric conditions, which suggests that social feelings are also affected in individuals with neurodevelopmental disorders or mental health problems. Generally, this can manifest itself in an altered experience and expression of one's own social feelings, as well as in difficulties perceiving social feelings in others.

8.1. Autism spectrum disorder

A prominent example of these kind of psychiatric conditions are autism spectrum disorders (ASD), which are characterized by persistent deficits in social communication and social interaction, as well as restrictive, repetitive patterns of behavior (American Psychiatric Association, 2013). A key feature of ASD are difficulties in understanding others' mental states, especially in situations involving complex social information (Brewer et al., 2017; Senju, 2013). Although meta-analytic evidence suggests a general deficit in emotion processing in ASD, results are heterogeneous and it is unclear whether this supposed deficit depends on the type of emotion under consideration (Uljarevic and Hamilton, 2013). Behavioral studies have shown that individuals with ASD perform equally well to control samples in tasks examining recognition of social emotions such as embarrassment, guilt, or pride (Hillier and Allinson, 2002; Williams and Happe, 2010). This has been related to possible compensation strategies that are able to mask emotion recognition difficulties (Williams and Happe, 2010). Neuroimaging studies could show atypical neural processing of others' social feelings in individuals with ASD which could underlie these difficulties. An fMRI-study demonstrated that individuals with ASD showed decreased activation in brain areas related to affective sharing, the anterior insula and ACC, as well as decreased physiological markers of arousal, when confronted with embarrassing scenarios (Krach et al., 2015). Similarly, another study reported significantly decreased activation in the anterior insula and posterior superior temporal sulcus in individuals with ASD when inferring others' social emotions (Aoki et al., 2014).

Few studies have also focused on the experience and expression of social feelings in ASD. For instance, one study showed that children with ASD, compared to typically developing children, were less likely to report reasons for their feelings, specifically self-conscious emotions like guilt and shame, and provided more script-like accounts of emotional experiences (Losh and Capps, 2006). However, this could not be shown in adults with ASD (Williams and Happe, 2010). Also, the majority of research in ASD is based on the study of individuals without intellectual disability. This is even more evident for the study of social feelings in individuals with intellectual disabilities that is almost entirely neglected. One of the few studies in this field targeted "social" abilities underlying observational learning and correlated performance measures with cortical thickness (Foti et al., 2018). So far, there is no study addressing the neurofunctional level of social interaction and related feeling states in ASD with intellectual disabilities.

8.2. Social anxiety

Another psychiatric condition where the experience of social feelings depends on the social domain is social anxiety. Social anxiety is characterized by excessive and persistent fears of embarrassment and corresponding concerns about others evaluations or criticism. There is evidence that socially anxious individuals have a distorted and negatively biased self-image, that, if confronted with an observing and potentially judging audience, could lead to strong evaluative threats and to social withdrawal in the long run. Although the social aspect lies at the core of the symptomatology, so far most studies examined social anxiety in social isolation (Blair et al., 2010, 2011) and showed that the processing of fearful faces was associated with increased activations of the amygdala, ACC, or insula. Only few studies tried to translate the investigation into real socially interactive scenarios and thereby trigger what is at stake in social anxiety.

One example is a study by Yoshie and colleagues who investigated the effect of social monitoring on skilled motor performance. In an interesting fMRI set-up participants were asked to squeeze a pressure sensor to a certain target level within 5 s, displayed in a thermometer like fashion (Yoshie et al., 2016). After this initial period, participants were enforced to uphold the same force for another period of 15 s, however now with the thermometer being replaced by a video footage showing the faces of two experimenters sitting in the MRI control room, either with averted gaze (unobserved) or directly observing the participant (observed). The authors observed a significant increase in the grip force in socially anxious participants especially during observation. On the neural level, deactivation of the left inferior parietal cortex predicted both inter- and intra-individual differences in socially-induced change in grip force and could show that being observed was linked to enhanced activation within the posterior superior temporal sulcus, a region commonly associated with mentalizing processes (Frith and Frith, 2006). A similar modulation of neural activity under social observation was described above in the study by Müller-Pinzler and colleagues (Muller-Pinzler et al., 2015). There, failing in the presence of an audience was associated with longer gaze dwell time on social cues and increased activations of the mentalizing network in socially anxious participants. Notably, the association of social anxiety and mentalizing activation was mediated by the dwell time on social cues. In a follow-up study by the same group, the authors extended on their earlier findings by showing that socially anxious participants also exhibited more negatively biased self-related learning, especially when they were exposed to a judging audience (Muller-Pinzler et al., 2019).

8.3. Schizophrenia and bipolar disorder

Although schizophrenia and bipolar disorder are both associated with emotion processing deficits, Tabak et al. (2015) identified that measures of feeling states in these conditions were strongly related to daily functioning. Specifically, a clarity of feelings subscale in the schizophrenia sample was significantly correlated with independent living ability. In the bipolar disorder sample, higher attention to their subjective feelings was significantly associated with better social functioning. Ospina et al. (2019) took the approach of investigating alexithymia in similar patient samples. Alexithymia refers to difficulty recognizing and describing emotional experiences of the self. It can include symptoms such as impairment in identifying and describing feelings as well as distinguishing feelings from bodily sensations. Results indicated that both schizophrenia and bipolar samples were significantly impaired on an alexithymia scale sensitive to describing and identifying feelings, which was predictive of social functioning in the bipolar disorder sample. Interestingly, neuroanatomical correlates to alexithymia symptoms include the medial prefrontal cortex and anterior cingulate (both component structures of the social brain network) in bipolar disorder as well as control samples. These results align well with the broader model recently proposed by Porcelli et al. (2019) that

identified social withdrawal as a core, underlying deficit in diverse conditions in which social dysfunction comprises a dominant disability including schizophrenia, major depression and Alzheimer's disease. As part of this impairment, we hypothesize that social withdrawal results from emotional detachment, lack of emotional engagement (i.e., lack of "knowing others" through emotional engagement and interaction) and attenuated social feelings (experiencing and responding to).

9. Social media

The growth of social media appears to be fueled by natural and strong social motives and drives. These novel platforms continue to proliferate and evolve with increasingly mobile and easily accessible technology to the point where 2 billion users around the globe participate in hundreds of types of social networks. Important generational differences may exist that have implications for social-emotional functioning and neurocognitive architecture based on exposure during sensitive developmental periods (Crone and Konijn, 2018). For example, contemporary American adolescents are estimated to be involved in 6−9 hours of social media on a daily basis (excluding home- and schoolwork) (Rideout, 2015).

From a neuroscience perspective, many important questions quickly arise such as the neural substrate that supports and rewards such social media behaviors, and how similar and different it is from typical, direct social action/interaction. The ease of access, variety of social media platforms, and constantly changing trends and topics may provide fertile opportunities for activation of the seeking system (Panksepp and Biven, 2012). In this review, our focus is on discussing what is currently known about social feelings in relation to social media behaviors its neural correlates.

From a theoretical perspective social media would appear to share a good deal of overlap with processes of social cognition (such as mentalizing, theory of mind, empathy), social emotions (e.g., awe, contempt, gratitude, embarrassment) and social feelings (e.g., trepidation, affiliation, disgust). Digital resources have even devised attempts to provide some forms of visual signals (e.g., emoticons) to enhance transmission and perception of salient emotional and feeling states to mimic natural appearances. Why go through all these efforts? The opportunities to connect with more people in quick, efficient ways that one can control (and potentially portray and modify impressions, opinions, and influence) can bring rewards (Tamir and Mitchell, 2012). These can take the forms of 'Likes' and other feedback that may be highly motivating (Meshi et al., 2013).

Meshi et al. (2015) identified 5 key social media behaviors: broadcasting information, receiving feedback on information, observing the broadcasts of others, providing feedback on the broadcasts of others, and comparing oneself with others. Considering what is known about the social brain network, they argued that mentalizing was likely to be invoked by several of these behaviors, along with self-referential as well as self-other processing. These have been linked to the social brain network regions including the dorsomedial and mPFC, superior temporal sulcus, temporoparietal junction, anterior temporal lobe, and posterior cingulate/precuneus.

The motivating force of social media was supported by fMRI data generated from a sample of healthy adolescents and young adults. These individuals provided 'Likes' to posted pictures and experimentally received 'Likes' to pictures they posted in a simulated social media posting paradigm. Providing 'Likes' to posted pictures was associated with activations in the ventral striatum and ventromedial prefrontal cortex as well as the dorsal striatum and portions of the thalamus, limbic system and frontal-parietal cortices (Sherman et al., 2018). In contrast, when receiving feedback of 'Likes' on posted photos, activations were detected in the dorsal and ventral striatum, thalamus, brain stem/VTA, frontal lobe, occipital lobe and cerebellum. Conjunction analysis revealed 2 large clusters: (1) bilateral ventral and dorsal striatum, thalamus, hippocampus, brain stem and VTA; and (2) left lateral occipital/fusiform cortex, temporo-occipital cortex, and parahippocampal gyrus.

In addition to social media, social feelings are also being studied as part of the attraction to reality TV programs (Lewis and Weaver, 2015). For example, observing violations of social norms or others embarrassing themselves activated brain regions associated with theory of mind, empathy, and social identity (Melchers et al., 2015).

10. Extracting neural networks related to social feelings with quantitative meta-analyses

We conducted meta-analyses across imaging studies from the literature with Neurosynth (http://www.neurosynth.org; Yarkoni et al., 2011) to quantitatively extract the neural networks of mental processes relevant for social feelings as discussed in the review. Neurosynth is a platform for large-scale, automated synthesis of fMRI data including 507,891 activations from 14,371 studies (30th April 2020). As an automated brain-mapping framework Neurosynth applies text-mining and meta-analysis techniques to generate a large database of mappings between neural and cognitive states.

Activation coordinates and frequently terms are automatically extracted from published neuroimaging articles. The entire database of coordinates is divided into two sets for each term of interest, these that are reported in articles containing the term, and those that are reported in articles not containing the term. Thereafter, the meta-analysis compares the coordinates reported for studies with and without the term of interest. Images are corrected for multiple comparisons with a false discovery rate (FDR) of 0.01. We included only positive results and report results for the association test regarded as more reliable than results for the uniformity test. Here, the association test map reports z-scores from a two-way ANOVA testing for the presence of a non-zero association between the term used and voxel activation, whereas the uniformity test map shows z-scores from a one-way ANOVA testing whether the proportion of studies that report activation at a given voxel differs from the rate that would be expected if activations were uniformly distributed throughout the gray matter. Consequently, the association test maps allow making more confident claims that a given region is involved in a particular process, and is not only involved in almost every task (corresponding approximately to "reverse" and "forward inference" maps; for details see http://www.neurosynth.org). Eventually, association test maps show whether activation in a region occurs more consistently for studies that mention the current term than for studies that do not mention it. Resulting maps were downloaded and visualized with MRIcron (http://www.mricro.com; version 1st June 2015). For methods applied, please refer also to two other papers using the same approach in this volume (Frewen et al., 2020; Stefanova et al., 2020).

Meta-analyses were conducted for the terms affective (748 studies identified; 28,542 activations reported), emotional (1708; 58,326), empathy (187; 7913), feelings (149; 5414), moral (87; 2806), social cognition (220; 8247), social interactions (123; 4900), stress (321; 8294), and theory mind (181; 7761).

The quality of individual extracted studies in the database may be low, because of the automated uncontrolled process. Here, quality means controlling for strict fulfilment of inclusion and exclusion criteria (for further discussion see last paragraph of this chapter). Moreover, not all journals are covered and terms covered in the database are limited. Hence, results represent an orientation to be proved by other better controlled meta-analytic approaches. To adjust for this bias, at least partly, we considered only terms that were based on at least 100 studies. Only for moral the number of studies was below that threshold. Moreover, we chose the term with the maximum number of studies if terms covered related concepts, i.e. affective (not affect), emotional (not emotion), feelings (not feeling), social interactions (not social interaction) and theory mind (not mentalizing). Furthermore, we applied a strict FDR of 0.01 and reported only results for the association test

regarded as more reliable than the uniformity test. Finally, we conducted conjunction analyses to further strengthen the validity of our findings. These analyses correspond to overlap analyses for significant function-associated regions (for more detailed explanation see below).

As illustrated in Table 1 and the left part of Fig. 12 networks included frontomedian cortex and ACC, subcallosal area, frontolateral cortex and OFC, temporo-parietal junction, temporal pole, precuneus, insula, amygdala, midbrain and pituitary gland. The globus pallidus and mammillary bodies were only identified in one mental function, respectively. Obviously, there was a separation in rather "hot" or emotional-affective social functions, i.e. the neural correlates of the terms affective, emotional, feelings, stress, and empathy, and the neural correlates of "cold" cognitive social functions such as moral, social cognition, social interactions and theory of mind. Table 1 illustrates both concepts and their neural correlates in orange ("hot") and blue color ("cold" functions). Note that some regions, as illustrated in light color, could intermediate between "hot" and "cold" social functions, i.e. the temporal pole and precuneus as well as the amygdala and midbrain. Related social functions are feelings, empathy, social cognition and social interactions with intermediate nature between "cold" and "hot" social functions. Moreover, frontomedian cortex and ACC, subcallosal area, OFC, and insula were relevant for both, "hot" and "cold" social functions. Remarkably, the pituitary gland, involved in secretion of socially-acting hormones such as OT and vasopressin, was also highlighted by three functions, i.e. stress, empathy and social interactions.

Moreover, we conducted a conjunction analysis across the neural networks of all investigated mental functions to extract brain regions that reached significance with the chosen threshold (FDR corrected) criterion of 0.01 for more than one function. This conjunction illustrates regions, where results for single meta-analyses overlap, i.e. several meta-analyses showing significant findings there. Results are illustrated in the right part of Fig. 12, and in related movies in the supplementary material. This conjunction analysis confirmed for "hot" social functions, as shown in orange color, the frontomedian cortex and ACC, subcallosal area, OFC, insula, and amygdala as the most consistent hubs in this neural network. The conjunction analysis for "cold" social functions as shown in blue color identified the frontomedian cortex and ACC, subcallosal area, frontolateral cortex and OFC, temporo-parietal junction, temporal pole and precuneus as the associated network. Finally, we conducted a meta-analysis across all social functions, i.e. including both, "cold" and "hot" social functions (spectrum colors), which revealed as relevant networks the frontomedian cortex and ACC, subcallosal area, frontolateral cortex and OFC, temporo-parietal junction, temporal pole, precuneus, insula, amygdala and midbrain. In sum, the conjunction analysis confirmed findings of the single meta-analyses shown in Table 1.

As already mentioned, Neurosynth has limitations regarding the quality of individual extracted studies, because of the automated uncontrolled process to extract activation coordinates and frequently used terms from papers, and because it covers a limited number of journals and terms. Hence, results shall be proved by other better controlled meta-analytic approaches. Then, study selection shall be based on systematic screening in databases like PubMed / Medline and by applying strict inclusion and exclusion criteria, where study's suitability is checked by two independent reviewers (see preferred reporting items for systematic reviews and meta-analyses – PRISMA – guidelines (Moher et al., 2009). One might also cross-validate findings by using other quantitative techniques such as activation likelihood estimation (ALE) or seed-based d mapping (SDM; formerly coined signed differential mapping) meta-analyses, or conducting analyses in the better controlled

Table 1
Neural networks related to social feelings and related mental functions as revealed by the Neurosynth database.[1]

Anatomical Region	Stress	Affective	Emotional	Feelings	Empathy	Social Cognition	Social Interactions	Moral	Theory Mind
	"Hot" emotional-affective social functions					*"Cool" cognitive social functions*			
Frontomedian cortex		X	X	X	X	X	X	X	X
Anterior cingulate cortex		X	X	X	X	X	X	X	X
Subcallosal area		X	X	X		X	X		X
Frontolateral cortex			X		X	X	X		X
Orbitofrontal cortex		X	X	X	X	X	X	X	X
Insula		X	X	X	X		X	X	X
Temporo-parietal junction					X	X	X	X	X
Temporal pole				X	X	X	X	X	X
Precuneus				X	X	X	X	X	X
Globus pallidus			X						
Amygdala	X	X	X	X	X	X	X		
Midbrain		X	X		X	X	X		
Pituitary Gland	X				X		X		
Mammillary bodies	X								

[1] Dark colors illustrate regions where more than one-half of "hot" or "cold" social functions showed activations. Light colors illustrate regions that were intermediate between "hot" and "cool" social functions, i.e. temporal pole and precuneus as well as amygdala and midbrain. Note that the frontomedian cortex and anterior cingulate cortex, subcallosal area, orbitofrontal cortex, and insula were relevant for both "hot" and "cool" social functions.

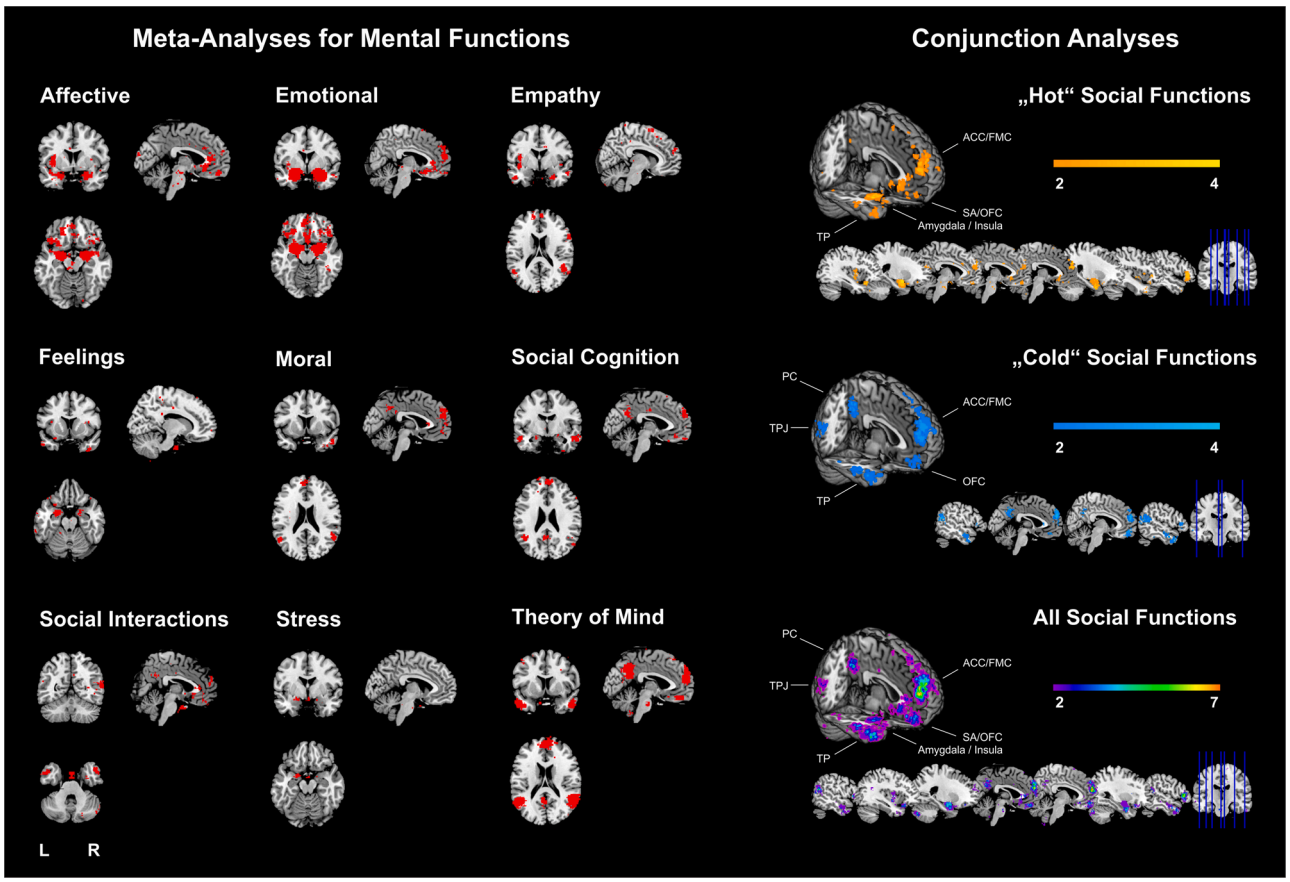


Fig. 12. Neural networks of mental functions related to social feelings as revealed by the Neurosynth database. ***Left:*** Maps extract regions, marked in red, where activation occurs more consistently for studies that mention the term than for studies that do not. ***Right:*** Conjunction analysis indicating regions where neural networks overlap for two or more mental functions. Results are shown separately for the five "hot" and four "cold" mental functions (orange or blue color, respectively), and for all nine mental functions together (spectrum colors). Number of regionally overlapping functions is color coded as shown on respective scale. ACC anterior cingulate cortex, FMC frontomedian cortex, L left, OFC orbitofrontal cortex, PC precuneus, R right, SA subcallosal area, TP temporal pole, TPJ temporoparietal junction. Results for conjunction analyses are additionally illustrated in respective movies in the Supplement.

Brainmap database (Albrecht et al., 2019a, b; Schroeter et al., 2020, 2014). We checked systematically whether studies compared directly Neurosynth with other meta-analytical approaches, such as ALE or SDM (systematic search in PubMed on 1st July 2020: keywords (i) neurosynth activation likelihood estimate meta-analysis, (ii) neurosynth signed differential mapping meta-analysis, (iii) neurosynth seed-based d mapping meta-analysis). Although a systematic comparison is missing and a desideratum for the future, two studies using both techniques, Neurosynth and ALE, demonstrated consistent findings (Andrzejewski et al., 2019; Parro et al., 2018). Moreover, smaller brain structures such as the septum might not be detected in imaging-based meta-analyses due to limited spatial resolution of these methods. While keeping these constraints in mind, we regard the meta-analytical findings as relevant to the neurobiology of social feelings.

11. Linguistics

To better understand the range of verbally articulated feelings that are expressed in the English language, a task team within the Human Affectome Project led a computational linguistics research effort to identify feeling words (Siddharthan et al., 2018). Results were extracted from the Google n-gram corpus (which includes roughly 8 million books (N and Reips, 2019) and then manually annotated by more than one hundred researchers from this project. This resulted in 9 proposed categories of feelings and a new affective dataset that identifies 3664 word senses as feelings. Of relevance to this review is a category related to "Social", which was defined as follows:

> Feelings related to the way a person interacts with others (e.g. accepting, ungrateful, etc.). feelings related to the way others interact with that person (e.g. appreciated, exploited, trusted, etc.), or feelings of one person for or towards others (e.g. sympathy, pity, etc.) that are not covered by other categories (specifically, does not include feelings of Anger, Fear, Attraction or Repulsion).

This subset of the results included about 637 feeling word senses (see Supplemental data accompanying this review). It was not within the scope of this effort to undertake a formal analysis of this dataset, but we reviewed these feelings words and attempted to roughly organize the words into discernable categories. Initial steps were undertaken to identify and classify such a semantic class and differentiate it from other feeling word classes. We identified eight major social domains where feelings could be categorized. These included: (1) social communications, (2) own behaviour, (3) reaction to others, (4) reaction of others, (5) social affiliation, (6) social power, (7) treatment of others, and (8) treatment by others.

These domains can be applied to agents, recipients, and interaction contexts. Subcategories were further identified for more specific feelings associated with disapproval, trusted, betrayal, compassion, friendly, loving, dominant etc. Positive and negative interactions, by intention and by outcome, constitute additional axes.

Caution should be exercised in the interpretation of this list since it

was created only to provide an initial sense of how feeling words related to one another. Although these remain far from a validated set of stimuli and identifiable categories for experimental application, developing a standardized set of 'social feeling words' may have a place in stimulating research on the underlying parameters of social feelings.Thus, we have included this dataset in the supplemental materials. In our opinion, the list warrants more in depth exploration and may deepen our understanding of the feelings in this domain.

Other approaches to further linguistic analysis can consider neurolinguistics. For example, 'wronged' as a social feeling word appears related to the specific action of another. There is a similar sense to feeling 'ostracized', 'bruised, and insulted' which all can result from the specific words and actions of others. In contrast, 'gratitude', 'compassion', and 'malice' are descriptive state terms that refer to attitudes and behavioral characteristics. Studies in patients with cerebral lesions have demonstrated that the neural mediation of actions words (i.e., verbs) is quite different from nouns. Correlation to lesion sites indicated that deficits in generating such words are associated with the inferior frontal lobe and temporal lobe, respectively (Piras and Marangolo, 2007). These findings raise the possibility that the semantic representation of certain social feelings may be distributed in a neural network that varies with the properties of what gives rise to the feelings, e.g., the specific actions of another on the perceiver vs. encountering another's behavioral characteristics indirectly, by differing valence, and in-group/out-group effects, among others.

12. Interactions and directions

There are several areas of important interactions with other Human Affectome team inquiries within this special issue that relate to social feelings. These are highlighted briefly below.

12.1. Anger

Anger is associated with diverse feelings that are directed towards another (or others) based on their actions that are perceived as unfair and/or disruptive to one's plans, goals and expectations. Anger has been considered to be a basic and a social emotion. Hence, there typically are suspected strong neurobiological foundations linked to personal well-being and adaptation but also social expectations, coordination and removal of social obstacles (Williams, 2017). Untoward reactions may take the form of hostility and aggression towards others (e.g., Klimecki et al., 2018). Such reactions may be mediated in part by specific social factors such a power status that may sway feelings regarding potential actions and consequences (Li et al., 2016). The social contexts of anger and the mediating role of feelings associated with power status, other types of relationship and other social factors leads to new hypotheses regarding the role, intensity and resolution of anger behaviors. Regulation of angry feelings may play an important mediating role in many forms of social interaction and decision-making (Gilam et al., 2015). The factors and variables contributing to individual differences in this area require further investigation.

12.2. Attention

There appear to be strong interactions between attentional and social brain mechanisms that are beginning to be identified and characterized. For example, social stimuli can attract first saccades more frequently along with a larger portion of visual attention to scenes (Rosler et al., 2017). Direct gaze can act as a type of prime for socially-relevant actions, particularly when combined with precise body movements that engage interaction (Betti et al., 2018). Furthermore, viewing patterns of social stimuli (for own species and cross-species) were discovered to be individual and species-specific in human and nonhuman primates, and possibly based on natural characteristics as well as experiential factors that develop through adaptation (Kano et al., 2018). These initial observations suggest several hypotheses regarding the alerting, arousing, saliency and adaptive value of social stimuli and social experience on environmental monitoring, allocation of attentional resources, and the affective/reward value of such processing. Within those computations, feelings associated with integrated forms of attention and social processing can be examined and tested.

12.3. Hedonics

Feelings of pleasure from engagement within certain social contexts have been thought to provide reinforcing and rewarding associations, though such mechanisms remain largely unknown. Touch has been associated with a variety of reported hedonic feelings (e.g., pleasure, pain, disgust, and comfort) and linked to both the endogenous opioid system and oxytocin mediation among others (Nummenmaa et al., 2016). Both context and motivation for touch appear to have substantive influences on the social aspects of the hedonic feelings that are beginning to be delineated (e.g., Ellingsen et al., 2015). In an intriguing experiment, Manninen et al. (2017) investigated whether social laughter, as an example of larger group social bonding activity, might activate the μ-opioid-receptor in a similar way as touch and grooming have been linked to endogenous opioid production. Results revealed that laughter was associated with endogenous opioid release in several brain regions linked to reward and arousal (thalamus, caudate nucleus), with baseline endogenous opioids levels predictive of social laughter and detectable in structures such as the amygdala, ventral striatum, and frontal and cingulate cortices. In contrast, experimental paradigms that manipulated social inclusion/exclusion identified limbic system activations associated with distress and feelings of rejection. Recurrence of distress and associated limbic system activation were also detected with reminiscence about past interpersonal stressors.

Areas of promising research pertinent to social feelings are emerging across the lifespan spectrum as well.

12.4. Parental neuroscience

The study of the parental brain requires a combination of well-established paradigms and innovative, realistic probes that incorporate consistent terminology on affect. More naturalistic and personally relevant stimuli must be pursued to carefully assess real-time parental brain functioning, thoughts and behaviors (Kim et al., 2013) to include the richness of parental feelings and real-time nature of parent-infant interactions (Safyer et al., 2020). For example, brain activity in response to own baby-cry was correlated with a measure of mental state talk, but not with more global aspects of observed caregiving (Hipwell et al., 2015). Current literature suggests mixed evidence for anatomical and functional correlations. Thus far, one human study suggests structural changes occur in the maternal brain over the early postpartum, including correlations with positive perception of baby (Kim et al., 2010) – a construct well connected with feelings.

High-stress environments such as poverty, being a single or teenage parent, high marital conflict, and substance exposure are significant risk factors for maternal insensitivity toward infants (Magnuson and Duncan, 2002; Roubinov and Boyce, 2017; Sripada et al., 2014; Sturge-Apple et al., 2006). This calls for more specific studies from brain imaging perspectives to determine specific mechanisms. Such specificity, as well as more work on healthy parents, will be critical for developing targeted interventions and treatments that are effective to prevent psychopathology for those at risk, improve symptoms of psychopathology among parents already affected and cross generations to improve offspring mental health.

12.5. Social isolation and loneliness

Being socially distanced or socially isolated negatively affects health and mortality risk (Pantell et al., 2013; Singer, 2018). This may be

related in part to a change in social feelings. These effects have been a special concern for elderly living either in retirement communities and nursing homes or alone at home More recently, the relevance and potential toll of social isolation has been highlighted for persons of all ages by events associated with the coronavirus pandemic in 2020. In addition to objective social isolation, however, feelings of loneliness have been associated as well with poorer physical health (Cacioppo et al., 2014) and with elevated risk for premature mortality (Holt-Lunstad et al., 2017). Dementia is also an increasing scourge in aging societies (Fox and Petersen, 2013). The combination of coronavirus restrictions and dementia can be considered as a "double hit" for many patients and their families, as loneliness, social withdrawal and isolation are already concerns for patients with dementia (Wang et al., 2020). Even in the digitally-experienced younger generations, the effects of sustained social distancing on physical and mental health may be evoking odd and unusual social feelings. Digital social networks clearly are not the same as interacting in person, but the shared experiences of social distancing may prove beneficial to certain innovations in occupational, educational, health care delivery and other interpersonal activities. Studies of recent unprecedented social isolation and its varied consequences deserves more specific attention from the perspective of social feelings.

12.6. Interpersonal trauma

With respect to social feelings and interpersonal stress, an important future direction is to extend this research to persons exposed to interpersonal trauma. Trauma-related disorders have traditionally been conceptualized as fear or anxiety-related disorders. However, exposure to interpersonal trauma, and especially trauma that occurs in close relationships, is also associated with social feelings such as betrayal, shame and humiliation during the immediate aftermath of the event (Kaysen et al., 2005), as persons reflect back on their experience (Amstadter and Vernon, 2008), and in response to subsequent social threat (Platt and Freyd, 2015). Moreover, these social feelings may help explain the more severe mental health symptoms reported by persons exposed to interpersonal versus non-interpersonal trauma (Badour et al., 2017; La Bash and Papa, 2014), and the severity of specific symptom clusters such as avoidance and emotional numbing (Kelley et al., 2012). Studies of the neurobiology of these social feelings may further identify mechanisms of illness in interpersonal trauma, and targets for intervention.

12.7. Social sensitivity feelings

A curious defect in social feelings may be hallmark of certain individuals identified as psychopathic. Such individuals may be described as callous, unfeeling, cold, and taking pleasure from the pain of others. Despite the apparent lack of social feeling for other's pain and well-being, such individuals may nonetheless display preserved moral reasoning and knowledge, at least upon formal questioning (e.g., know right from wrong by cultural standards). Yet, such knowledge does not drive or regulate their actions. Hence, an identifiable cognitive deficit has not been consistently identified in these cases, with some hypotheses positing that the defect emanates from a fundamental emotional, empathic and/or social feeling deficit (e.g., Cima et al., 2010). This in turn prevents experiencing a sense of guilt, embarrassment or shared pain that one might expect from intentional violent harm perpetrated on others. The neurobiological and psychological bases for a 'feeling defect' requires further investigation.

13. Conclusions

In this review, we considered social feelings from a neuroscience perspective and propose that the notion of social feelings represents natural kinds of neurobiological processes that can be distinguished from emotion and are conducive to scientific inquiry. Feelings play important roles in social experiences and appear to signal underlying mechanisms that influence and modulate behavior. Feelings in general are geared toward aiding homeostasis, adaptation and well-being. Social feelings are particularly germane to navigating, adapting and thriving within a complex and changing social world, which is a major facet of contemporary life. The spectrum of the social world is quite broad, ranging from the most intimate types of relationships to common home, community, educational or occupational settings and even larger societal concerns that each require managing spontaneous social interactions and a social self.

We defined social feelings as subjective experiences that arise in interaction with others or when being remembered and when recalling others' behaviors, thoughts, intentions or emotions. As such, social feelings have been invoked in studies of emotional contagion, attachment, affiliation, empathy, influence and well-being as well as disorders of such processes. There remain a variety of challenges to address, including the role of the mirror neuron system, identifying in what ways social feelings are *influencers* on others, how social feelings mediate belongingness as well as loneliness, and the mechanisms of extended attachments beyond kinship that are based on shared social feelings. It is particularly important to investigate how these processes modify decision-making, adjustment and computational neuroscience models.

Feelings are beginning to be considered in social neuroscience research and models as key component processes. They are being identified as contributors to mother-infant attachments and more broadly to parenting behaviors, moral sentiments, interpersonal stress including social evaluative stress, social exclusion, interpersonal transgressions, and emotional communications. There is increasing interest in understanding the social feelings dimension of psychiatric disorders (e.g., autism spectrum, social anxiety, schizophrenia, bipolar disorder), and the underlying dysregulation that affects social adaptation. Animal model research has been most prominent in identifying important neurotransmitter and neurohormonal modulators involving key structures within the social behavior neural network. Throughout the neuroscience literature reviewed, there is increasing evidence that social feelings are mediated, at least in part, by structures associated with the social brain network. There appears to be extension, though, to a broader network of structures throughout the paralimbic (e.g., subgenual, insula), limbic (e.g., septum, amygdala) and midbrain regions that likely mediate important effector mechanisms for mental and embodied experiences of socially-relevant feelings. These proposed associations were confirmed by the meta-analysis of brain regions involved in social feelings which utilized the *Neurosynth* platform for a large-scale, automated synthesis of functional magnetic resonance imaging (fMRI) data. Converging methods of structural and functional neural network analyses will be needed to confirm these initial observations. Intriguing avenues of emerging research concerns the evolving social media landscape, pandemic mandated video-education experiences, and work-from-home occupational modifications many people have experienced.

Increasingly powerful experimental and neuroimaging methods are being combined with meaningful and nuanced assessment of the feelings of social life in order to provide a more comprehensive account of what drives, regulates and maintains adaptive and healthy social behavior. This will require an integration not only with neuroanatomical and neurophysiological mechanisms but also constructs of cognition and emotion in order to delineate both typical, adaptive processes and various pathological forms of social feelings. Towards that end, we have identified relationships that exist between social feelings and other areas of affective research within the special issue "Towards an Integrated Understanding of the Human Affectome" (i.e., Physiological, the Self, Anticipatory, Actions, Attention, Motivation, Anger, Fear, Happiness, Sadness, and Hedonics), summarizing future research needs in this burgeoning domain.

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Author contributions

All authors contributed substantially to this work, including providing critical review and editing of the manuscript, with specific contributions as follows: LL organized the Human Affectome conference in 2016 and the coordination of this systematic review including collaboration among the team pertinent to this manuscript and other reviews within the special issue, developed the study concept design, drafted the section on vasopressin and oxytocin and the social behavior neural network, analyzed the feeling words for the Linguistic section, and drafted the Linguistics section. PJE organized the initial collaborative team and sections of the manuscript, drafted the introduction, social media section, portions of the psychiatric conditions, directions and interactions section, conclusions, and coordinated feedback among team members. SA drafted the neuroscience of social feelings associated with emotional communications section. JM drafted the neural substrate of shared interpersonal feelings section. TLN drafted the neurobiology of feelings under interpersonal stress section. JES drafted the neurobiology of parent-child attachments section and parental neuroscience subsection. GBS drafted the social influence and social affiliations sections. RZ drafted the moral sentiments as feelings: neural considerations section. JR drafted the study of social feelings in animal models section and was instrumental in coordinating final integration of all sections. SK and AVM drafted the section about social feelings in psychiatric disordersand provided important contributions to the section about interpersonal stress and emotional communication. MS and TB performed the meta-analyses, MS drafted the respective section in the manuscript. SB and JR developed the design and finalized most figures. AVM generated the list of abbreviations. All authors approved the final version of the manuscript for submission.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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