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A functional neuro-anatomical model of human attachment (NAMA): Insights from first- and second-person social neuroscience

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ABSTRACT

Attachment theory, developed by Mary Ainsworth and John Bowlby about seventy years ago, has become one of the most influential and comprehensive contemporary psychology theories. It predicts that early social interactions with significant others shape the emergence of distinct self- and other-representations, the latter affecting how we initiate and maintain social relationships across the lifespan. A person's attachment history will therefore associate with inter-individual differences in emotional and cognitive mechanisms sustaining representations, modeling, and understanding of others on the biological and brain level.

This review aims at summarizing the currently available social neuroscience data in healthy participants on how inter-individual differences in attachment associate with brain anatomy and activity across the lifespan, and to integrate these data into an extended and refined functional neuro-anatomical model of human attachment (*NAMA*). We first propose a new prototypical initial attachment pathway and its derivatives as a function of attachment security, avoidance, and anxiety. Based on these pathways, we suggest a neural attachment system composed of two emotional mentalization modules (aversion and approach) and two cognitive mentalization modules (emotion regulation and mental state representation) and provide evidence on their functionality depending on inter-individual differences in attachment. We subsequently expand this first-person social neuroscience account by also considering a second-person social neuroscience perspective comprising the concepts of bio-behavioral synchrony and particularly inter-brain coherence.

We hope that such extended and refined *NAMA* can inform attachment theory and ultimately help devising new prevention and intervention strategies for individuals and families at risk for attachment-related psychopathology.

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1. Introduction

1.1. *Attachment behavior: function, emergence, and inter-individual differences*

Attachment behavior constitutes a set of socially oriented functions conserved across mammalian species. Attachment theory proposes that all humans are equipped with an innate attachment system that enables strategic attachment behavior for eliciting the attention of, and support from, a caregiver when needed. To ensure that the proximity seeking signals of the child are readily perceived and acted upon, attachment theory furthermore suggests that the attachment system in children is complemented by a dedicated caregiving system in significant others (Ainsworth, Blehar, Waters, & Wall, 1978; Bowlby, 1969, 1980; Fraley, 2019; Fraley, Brumbaugh, & Marks, 2005; Mikulincer & Shaver, 2007; Mikulincer, Shaver, & Pereg, 2003).

The attachment system is primarily activated in times of need, danger, or distress, entailing a deviation from homeostasis. Such situations trigger the so-called primary attachment strategy, which initially consists in seeking physical proximity to the attachment figure and maintaining that physical proximity until the threat has passed. In so doing, the attachment system plays a vital role in the regulation of homeostasis through allostasis. Understood as the ongoing adjustment of one's internal milieu in terms of fundamental physiological processes as a response to environmental challenge, allostasis affects many aspects of infants' autonomous nervous system, such as temperature, heart rate, sleep, diet, etc. (Atzil, Gao, Fradkin, & Barrett, 2018; Beckes, Ijzerman, & Tops, 2015). More broadly speaking, the attachment relationship between a child and his/her caregiver(s) can therefore also be conceptualized as an open, socially dependent physiology and emotion regulation circuit (Canterberry & Gillath, 2012; Mikulincer et al., 2003).

When the primary attachment strategy of proximity seeking regularly results in successful homeostasis maintenance under distress, the individual develops an other-model that predicts feelings of security in attachment relationships. Understood as the "default state" of attachment-derived internal working models (IWMs; Mikulincer & Shaver, 2007), a caregivers' allostatic support is thought to not only be experienced as rewarding by the child per se, but also associated with additional rewarding qualities – because allostasis co-regulation is usually accompanied by the provision of nutrition, soothing, and comfort (Atzil et al., 2018). Furthermore, when proximity seeking under distress leads to the desired outcome of a feeling of safety and security, a positive self-model predicting the ability to elicit care from attachment figures when needed can be established (Mikulincer & Shaver, 2007). However, when supportive caregiving is absent or inconsistent, individuals will begin to employ so-called secondary attachment strategies that are associated with insecure attachment orientations: avoidance and anxiety. Attachment avoidance is characterized by an other-model predicting attachment figure absence and/or sustained stress (i.e., continuing deviation from homeostasis) despite interactions with close significant others. The avoidant self-model therefore is one of self-reliance; when they are unable to elicit support and allostasis co-regulation from the caregiver, individuals learn to soothe themselves through distancing from the source of stress and/or regulating emotions with denial, inhibition, or suppression. This pattern is also generally described as a *de-activation* of the attachment system. Conversely, anxious individuals employ a secondary strategy of hyper-proximity seeking to their attachment figure(s) on whom they are reliant for allostasis co-regulation. This may be indicative of an other-model that conceives of attachment figures as absolutely necessary for achieving felt-security – despite repeated experiences of rejection (hence also referred as to ambivalent attachment) –, and an according negative self-model of helplessness. Such a pattern is thought to emerge through inconsistent caregiving where social co-regulation occurs sporadically but unpredictably (i.e., through intermittent reinforcement) and is generally described as a *hyper-activation* of the attachment system (Mikulincer & Shaver, 2007).

Importantly, each attachment orientation – be it secure or insecure – is thought to have its own advantages and disadvantages at an individual level, because it emerges as a meaningful adaptation to the immediate social environment within which an individual grows up (Fonagy, 2001). Furthermore, as suggested by *Social Defense Theory*, the different attachment orientations may even reflect adaptive, complementary qualities on the level of social groups, particularly when it comes to responding to threat (Ein-Dor, 2014; Ein-Dor & Hirschberger, 2016; Ein-Dor, Mikulincer, Doron, & Shaver, 2010). Overall, these considerations bolster the notion that attachment insecurity should not be equated solely with negative attributes (Ein-Dor, 2014; Ein-Dor et al., 2010; Ein-Dor & Hirschberger, 2016).

Lastly, it should be noted here that a fourth category of attachment, called disorganized or unresolved, has been previously described as containing elements of both attachment avoidance and anxiety. Such attachment behavior is largely discussed in the literature surrounding attachment-related psychopathology, which is associated with a breakdown of organized attachment strategies comprising rapid, unstructured shifts between security, avoidance, and anxiety (Cyr, Euser, Bakermans-Kranenburg, & Van Ijzendoorn, 2010; Fearon, Bakermans-Kranenburg, van Ijzendoorn, Lapsley, & Roisman, 2010; Groh et al., 2014; Groh, Roisman, van Ijzendoorn, Bakermans-Kranenburg, & Fearon, 2012). As this review will mainly describe data from healthy participants and aims at dissociating the two insecure attachment orientations of avoidance and anxiety from each other in terms of their biological and brain substrates, it will predominantly focus on organized attachment.

1.2. *Towards a social neuroscience of human attachment*

Pioneered in the 1980s by John Cacioppo and Gary Berntson, social neuroscience emerged as a new combination of the until then independent fields of (social) psychology and neuroscience, with the specific aim of investigating the biological and brain basis of human social behavior using a multi-method and multi-modal experimental approach (Cacioppo &

Berntson, 1992; Cacioppo, Berntson, & Decety, 2010). Coinciding with the emergence of social neuroscience was the development of new neuroimaging techniques, in particular (functional) magnetic resonance imaging ([f]MRI) and positron emission tomography (PET), and more recently functional near-infrared spectroscopy (fNIRS). Furthermore, the use of already established methods, such as electroencephalography (EEG), was reconsidered and geared towards advancing our understanding of the neural basis of social interaction. Relying upon these techniques, it became possible to not only investigate the influence of inter-individual differences in attachment on emotion processing and social cognition on a behavioral and peripheral physiology level, but also on the level of the brain. Accordingly, since the early 2000s, the number of studies linking anatomical and functional brain measures with different means of classifying people into distinct attachment orientations has been steadily growing. At the same time, important advances were achieved on a biological level of investigation with the emerging possibility of genotyping and more recently analysis of epigenetic modification. The latter method is employed as a more direct means of assessing the interaction between nature and nurture to elucidate the role of genetic versus environmental influences on human behavior. Such approach appears particularly promising in the context of attachment because the emergence of inter-individual differences in attachment is nowadays understood to represent a prototypical nature by nurture interaction (Fonagy, 2001).

All above methods are nowadays referred to as “first-person social neuroscience” because they investigate the biological and neural correlates of human social behavior in single/isolated individuals. In the first remaining part of this review, studies using such first-person social neuroscience approach will be summarized and put into perspective by means of a functional neuro-anatomical model of human attachment (*NAMA*) – see also (Vrtička, 2017; Vrtička & Vuilleumier, 2012). The same methods, however, can also be employed in two (or more) individuals before, during, and/or after direct interaction with each other. The latter approach is also referred as to “second-person social neuroscience” (Schilbach et al., 2013). Within this context, a special focus is directed towards measuring brain activity in two (or more) interacting individuals and deriving a measure of inter-brain coherence by means of EEG and fNIRS hyperscanning. Although there is only very limited research directly associating such second-person social neuroscience data with inter-individual differences in attachment to date, the second part of this review will discuss the so far obtained results and highlight the future potential of second-person social neuroscience research related to attachment. Altogether, the aim of this review is to illustrate how social neuroscience – on both the first- and second-person level – may contribute to a better understanding of the underlying biological and brain basis of human attachment.

Please note that in our opinion, there is not enough coherent social neuroscience data available to date to allow for sophisticated meta-analyses. For example, an activation likelihood estimation (ALE) analysis of 12 peer-reviewed studies on associations between inter-individual differences in attachment and brain activity to emotional stimuli using fMRI was recently published (Ran & Zhang, 2018). However, the studies included in this ALE analysis used a wide variety of experimental designs and stimulus conditions such that a direct comparison of obtained results remains difficult and only yields limited interpretations. This review therefore aims at providing a conceptual overview of available data – from different modalities, including fMRI, PET, EEG, and fNIRS – and deriving a theoretical context from which future meta-analyses may be conducted once more coherent data from each modality becomes available.

2. The social neuroscience of human attachment

2.1. *General considerations*

During the past few decades, investigations of the biological and brain basis of human social behavior within the field of social neuroscience have revealed many interesting insights. We now have an extended comprehension of the most prominently involved neural circuits constituting the so-called “social brain” enabling us to understand others (Lieberman, 2007; Schacht & Vrtička, 2018; Vrtička, Bondolfi, Sander, & Vuilleumier, 2012; Vrtička, Sander, & Vuilleumier, 2011). Furthermore, there are well-elaborated theories on a possible distinction of interpersonal processes on the neurotransmitter/-peptide and neural networks level. These theories suggest a dissociation between fundamental interpersonal processes, such as the sex drive/lust, romantic love/attraction, and attachment – attachment here being mainly considered a non-sexual long-term bond ensuring offspring survival (Acevedo, Aron, Fisher, & Brown, 2012; Bartels & Zeki, 2004; Feldman, 2017; Fisher, 1998; Fisher, Aron, & Brown, 2006; Fisher, Aron, Mashek, Li, & Brown, 2002; Fletcher, Simpson, Campbell, & Overall, 2015; Hazan & Shaver, 1987; Xu et al., 2012). The above theories are complemented by accounts of brain circuits supporting social engagement behaviors versus defensive strategies of fight-or-flight (and freeze) (MacDonald & MacDonald, 2010; Porges, 2003), bio-behavioral bases of affiliation (tend and befriend) under stress (Taylor, 2006), and a fundamental push–pull between emotional versus cognitive information processing influenced by stress/arousal (Fonagy & Luyten, 2009). Furthermore, there are several theoretical accounts on the neurobiology of human attachment that support elaborated discussion of involved neurotransmitter/-peptide systems derived from animal models (Antonucci, Taurisano, Coppola, & Cassibba, 2018; Atzil et al., 2018; Feldman, 2017; Insel & Young, 2001; Laurita, Hazan, & Spreng, 2019). The most recent of these theoretical models also appreciate developments in the field regarding a transition from first-to second-person social neuroscience and the importance of bio-behavioral synchrony for human attachment behavior (Atzil et al., 2018; Feldman, 2017). Another related theory proposes that early experiences critically shape the structure and function of the brain through a *neuro-environmental loop* of plasticity, particularly the interaction of parental care and the developing amygdala-medial prefrontal cortex network that is at the core of human emotional functioning (Callaghan & Tottenham, 2016). Finally, there is a theoretical notion of human social interactions having an economical aspect by reducing the organism's and brain's energy expenditure, in the sense that being with others allows people to spend fewer resources on activities such as threat detection and emotion regulation (Gillath, Karantzas, & Fraley, 2016). Described in the context of *Social Baseline Theory* (Coan & Sbarra, 2015), being with others is associated with a baseline state of low energy consumption, and the expectation of low social support with an increased neural "baseline" activity as well as bodily readiness (e.g., higher fasting glucose level) to deal with potential stressors on one's own (Ein-Dor et al., 2015). None of the above theoretical accounts, however, explicitly consider inter-individual differences in relationship quality and particularly attachment across domains as suggested by attachment theory. Therefore, the aim of this review is to extend and refine our functional neuroanatomical model of human attachment (*NAMA)* that we proposed some years ago (Vrtička, 2017; Vrtička & Vuilleumier, 2012) and that is inspired by social neuroscience research emphasizing measures of inter-individual differences in attachment and their influence on brain anatomy and function.

In so doing, we first opt to describing a newly derived conceptual organization of the human attachment system by means of a prototypical initial attachment pathway as well as its derivatives linked to attachment security, avoidance, and anxiety on a first-person level. We suggest that the earliest activations of the attachment system in infancy and early childhood follow a prototypical initial pathway (Fig. 1a), and that repeated outcomes of this pathway will become represented in attachment-derived IWMs reflecting inter-individual differences in attachment security, avoidance, and anxiety over the course of months and years (Fig. 1b, c, d). At the same time, the time course of a single activation in the prototypical initial attachment pathway and its secure, avoidant, and anxious derivatives may occur over the course of minutes or hours. We subsequently associate the above-mentioned distinct interaction patterns with corresponding neurotransmitter/-peptide systems and brain circuits through *NAMA* on a first-person social neuroscience level (Figs. 2 and 3). Finally, a second-person social neuroscience account of human attachment is provided, particularly focusing on inter-brain coherence. An overall integration of above considerations by means of a discussion and a limitations and current remaining issues section conclude this review.

2.2. Prototypical attachment pathways

2.2.1. Prototypical initial attachment pathway

Attachment theory proposes that one of the central functions of attachment behavior is to alleviate distress by abolishing a present fear response through socially co-regulated allostasis (Atzil et al., 2018; Beckes et al., 2015; Canterberry & Gillath, 2012; Mikulincer, Birnbaum, Woddis, & Nachmias, 2000; Mikulincer et al., 2003; Mikulincer & Shaver, 2007). Accordingly, we suggest that activation of the prototypical initial attachment pathway begins when a threat in the external environment (or generated within the child) is present, and that the presence of this stressor triggers threat detection and an appropriate initial fear response. Such mechanism is likely maintained by means of a deviation from homeostasis and its neural representation as a relevant/salient signal requiring further action. As a core element of attachment theory, we propose that the fear response subsequently and automatically prompts the primary attachment strategy of proximity seeking, usually towards a caregiver. Importantly, we postulate that as long as the threat is present, the aim of proximity seeking is survival, and that the according and appropriate fear response – i.e., (negative) emotion up-regulation – will be present even after proximity to a caregiver is initially established. Given that proximity seeking is successful, the caregiver reacts appropriately and sensitively to the child's signals, and the source of threat is successfully removed, we suggest that social allostasis co-regulation in the child will occur in a next step. In so doing, we argue that social allostasis support will be experienced as rewarding by the child not only due to an abolishment of the fear response (leading to a return to physiological homeostasis), but also due to additional rewarding qualities from the caregiver such as the provision of nutrition, soothing, and comfort (Atzil et al., 2018). Consequently, due to their multifaceted rewarding properties, we propose that social interactions with the caregiver will be associated with a feeling of safety and security. Please note that the above only applies if the source of threat is successfully removed. If the caregiver tries to down-regulate the child's (appropriate) fear response while the threat is still present, this interaction will not be perceived as rewarding by the child. Finally, as the prototypical initial attachment pathway is repeatedly followed, we anticipate the emergence of IWMs of the self and others (either positive or negative), which reflect the individual's early attachment experiences sustained on this path (Fig. 1a).

2.2.2. Prototypical secure attachment pathway

Attachment theory suggests that if activation of the prototypical initial attachment pathway (Fig. 1a) routinely results in felt security, the individual develops a secure attachment orientation with IWMs characterized by positive models of both the self and others (Fig. 1b). Consequently, secure individuals continue to use *physical* proximity seeking as an attachment strategy. Furthermore, they develop the ability to self-regulate emotions through the activation of fight-or-flight/aversion reactions as well as the capacity to modulate emotional reactions through volitional control mechanisms when appropriate. The latter processes very likely rely upon the formation of stable emotion (self-)regulation neural circuits – and particularly a developing amygdala–medial prefrontal cortex network–through interactions with parental care (Callaghan & Tottenham, 2016). Such a process necessitates the mentalizing ability to discern when physical proximity seeking attempts are necessary, or alternately when pursuing self-regulation will be sufficient and efficient. To this end, we suggest that proximity seeking will also function with the help of mental representations of previous secure interactions (*mental* social approach/proximity seeking). We expect that initial self-regulation with the help of mental proximity seeking can still lead to co-regulation through physical proximity seeking at a later stage, as the IWMs predicts that the caregiver(s) will ultimately be available to provide that support. Because the child's IWMs of attachment reflect general caregiver availability, we additionally predict

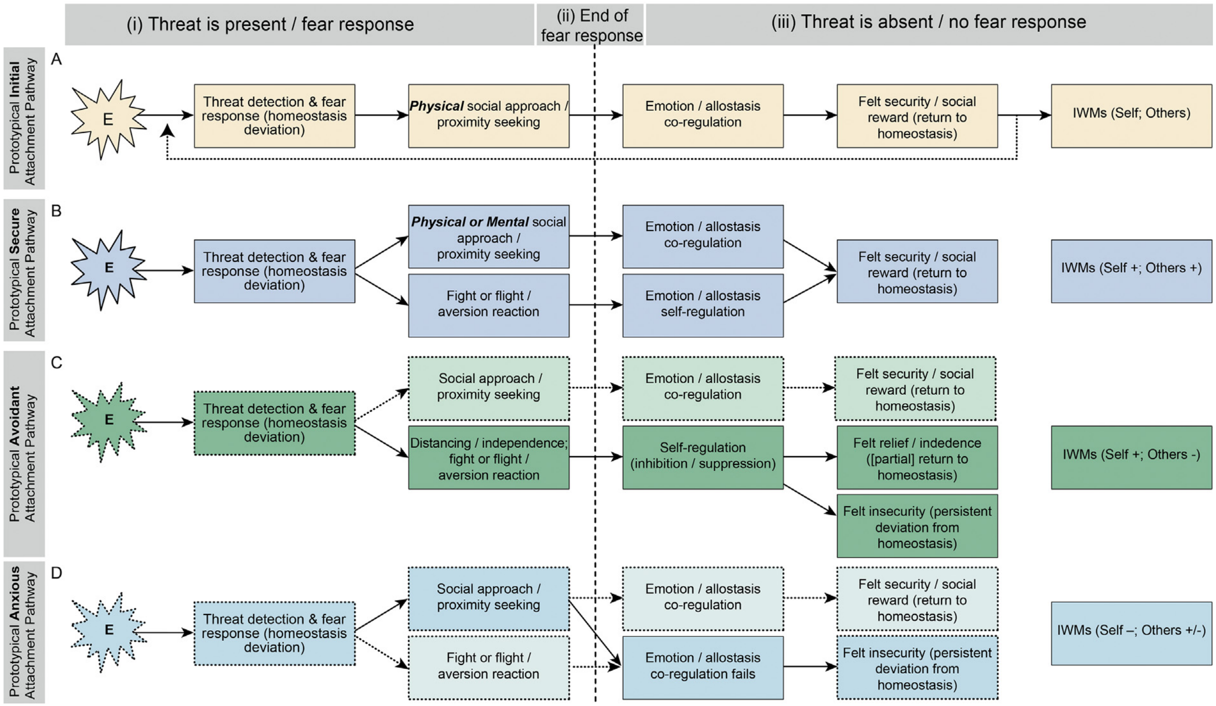


Fig. 1 – Prototypical attachment pathways. Illustration of our newly suggested prototypical attachment pathways inspired by attachment theory, with the initial pattern depicted in (a), and its derivatives corresponding to attachment security (b), avoidance (c), and anxiety (d) shown thereafter. The dashed arrow in (a) reflects the notion of many repetitions that lead to the emergence of internal working models (IWMs) of attachment. Dotted lines around boxes and dotted arrows in (c) and (d) indicate deviations from the initial/secure attachment pathway, and more transparent coloring of boxes points to a relative down-regulation of associated processes. Furthermore, we suggest that the prototypical pathways comprise three main phases following the initial event E that triggers attachment system activation and are characterized by the resulting fear response being (i) present, (ii) removed, and (iii) absent.

that mental representations of the caregiver(s) may in of themselves be soothing. In sum, secure individuals are able to use both co-regulation and self-regulation flexibly dependent on predictions made by the IWMs – and such flexibility is understood as the most advanced stage of emotion regulation (Canterberry & Gillath, 2012; Mikulincer et al., 2003; Mikulincer & Shaver, 2007).

In adulthood, whether secure individuals engage in proximity seeking may also depend on the severity and type of the stressor, and in the act of emotional self-regulation there is evidence that secure adults typically use constructive strategies via cognitive re-appraisal to dismantle the threat and ensuing negative thoughts (Mikulincer & Shaver, 2007; Vrtička et al., 2012).

2.2.3. *Prototypical avoidant attachment pathway*

When activation of the prototypical initial attachment pathway is routinely met by caregiver unavailability, sustained homeostasis deviation despite social proximity is thought to result in felt insecurity. Because such state likely even intensifies the initially experienced distress, the individual is thought to develop an avoidant attachment orientation. The according IWMs of avoidance are characterized by a negative other-model and a positive self-model to compensate the unavailability of others – also through defensive self-inflation (Canterberry & Gillath, 2012; Mikulincer et al., 2003; Mikulincer & Shaver, 2007).

Like in the prototypical initial attachment pathway (Fig. 1a), we propose that avoidant individuals may respond to threat through an appropriate fear response (Fig. 1c). However, as a deviation from the prototypical initial attachment pathway, we suggest that avoidant individuals' behavior will be characterized by a tendency to (passively/automatically and/or actively/consciously) evade circumstances where the attachment system is likely to be activated, which may limit the extent to which (external or internal) events can act as triggers of the attachment pathway. Accordingly, we propose that certain circumstances that usually trigger the prototypical initial attachment pathway – such as social exclusion/rejection or other signals that imply the absence of social co-regulation opportunities (see below) – will lead to a weaker fear response in avoidant individuals. We imply these patterns from IWMs predicting caregiver unavailability and thus the absence of social allostasis co-regulation based on attachment theory (Atzil et al., 2018). It should be noted, however, that we only expect the above pattern if the initial stressor can be successfully circumvented – through early detection and subsequent evasion – and/or it is only of a moderate intensity. Such early detection related to avoidance may in some cases entail initially increased vigilance toward situations where the attachment system may become activated as manifested by an early deployment of neural resources to process such information – corroborated, for example, by EEG data (see below). What is concerning the next step of the attachment pathway, we presume that in avoidant individuals, social approach/proximity seeking as a means of survival and to regulate the fear response when the threat has been removed will be less likely – again due to IWMs predicting caregiver unavailability. Instead, we suggest maintenance of social distancing (or social proximity without engagement) and a desire for independence, resulting in the preferential use of fight-or-flight aversive reactions. Consequently, in the subsequent step, we expect less emotion/allostasis co-regulation but more independent self-regulation – mainly through inhibition or emotion suppression (Vrtička et al., 2012) – and a resulting feeling of personal relief sustaining the desire for independence, rather than felt security associated with social reward. Please note that, according to attachment theory, we assume that self-regulation through inhibition or emotion suppression associated with avoidance will be only partially efficient in down-regulating the stress response and thus restoring homeostasis, or may fail entirely if the stressor is intense and/or cannot be averted. Thus, the outcome will constitute either a partial return to homeostasis, or persistent deviation from homeostasis entailing a chronically increased allostatic load, resulting in felt insecurity. This pattern accords with *Social Baseline Theory* (Coan & Sbarra, 2015) that predicts a heightened “default” state of brain activity and bodily readiness (i.e., fasting glucose level – Ein-Dor et al., 2015) in avoidant individuals regardless of the level of current threat due to the expectation of having to deal with stressors alone.

2.2.4. *Prototypical anxious attachment pathway*

Finally, when activation of proximity seeking under distress in the prototypical initial attachment pathway only leads to intermittent and unpredictable social emotion/allostasis co-regulation due to inconsistent caregiving, the individual is thought to typically develop an anxious attachment orientation. The according IWMs of anxiety are characterized by a negative self-model reflecting helplessness related to the inability to elicit care when needed, and an ambivalent other-model due to repeated rejection and a simultaneous wish for social co-regulation that has intermittently resulted in felt security (Canterberry & Gillath, 2012; Mikulincer et al., 2003; Mikulincer & Shaver, 2007).

Again, as in the prototypical initial attachment pathway (Fig. 1a), we propose that anxious individuals respond to threat through an initial fear response (Fig. 1d). However, in the case of attachment anxiety, we expect hyper-vigilance to signs of caregiver unavailability and thus a lower threshold for attachment pathway initiation as well as a more easily induced fear response. Such tendency may even lead to a fear response when no clear threat is present (i.e., when exposed to a neutral or ambivalent cue; see, for example, Yoon & Zinbarg, 2007). Please note that such a fear response should not be confounded with an emotional expression rather signaling anxiety in the context of risk assessment during the presence of an ambiguous threat – and having distinct facial features (eye darts and head swivels) (Perkins, Inchley-Mort, Pickering, Corr, & Burgess, 2012). Furthermore, we predict an intensification of social approach/proximity seeking under stress, as anxious individuals depend on social stress co-regulation and strongly wish for it due to intermittent successful social interactions entailing a return to homeostasis associated with felt security. The latter outcome, however, only occurs seldom because mostly, caregivers’ response to children’s proximity seeking attempts are insensitive or rejecting. Consequently, attachment anxiety often entails prolonged and intensified distress and felt insecurity due to persistent homeostasis deviation and thus increased allostatic load despite heightened social approach/proximity seeking attempts.

2.3. *A first-person social neuroscience functional neuro-anatomical model of human attachment (*NAMA*)*

In line with the above-described prototypical initial attachment pathway (Fig. 1a), we previously suggested a functional neuro-anatomical model of human attachment (*NAMA*) reflecting the associated core processes by means of most likely involved brain regions, and provide a list of involved neurotransmitter/-peptide systems (Fig. 2) – see also (Vrtička, 2017; Vrtička & Vuilleumier, 2012). Furthermore, we listed specific evidence from first-person social neuroscience investigations – pertaining to the derivatives of the prototypical initial attachment pathway – associated with secure, avoidant, and anxious attachment for each proposed core process, which is importantly extended and refined in this review (for a summary, see Fig. 3).

2.3.1. *The functional neuro-anatomical model of human attachment (*NAMA*)*

As described above, a prototypical attachment interaction “is one in which one person is threatened or distressed and seeks comfort and support from the other” (Mikulincer & Shaver, 2007) (p. 19). It has therefore been suggested that the human attachment system is made up of (at least) two different motivational components. On the one hand, a “prevention” component is described with the function of “inhibiting” behaviors associated with an increased probability of danger or injury in relation to threats or stressors. On the other hand, a “promotion” component is postulated with the function of maintaining an approach-oriented motivation to foster closeness to others and the attainment of felt security (Mikulincer & Shaver, 2007). Such a view is corroborated by the phylogenetic perspective of social engagement and attachment (Porges, 2003) that suggests a dynamic balance between social aversion tendencies maintained by more primitive survival-enhancing systems (especially sympathetic fight-or-flight circuits), and social approach tendencies that promote a sense of safety through close social interactions (MacDonald & MacDonald, 2010). Accordingly, information processing is thought to generally reflect a basic evaluation of safety versus danger, and to be intrinsically linked with behavioral tendencies to either approach or avoid a stimulus. These processes most likely occur rapidly and automatically (sometimes even unconsciously) in core social-affective stimulus appraisal brain networks (Lieberman, 2007). Within *NAMA*, we have therefore previously proposed that the human attachment system comprises an affective evaluation network made up of an aversion and an approach component that are in a dynamic balance (Fig. 2) – see also (Vrtička, 2017; Vrtička & Vuilleumier, 2012).

In line with our newly stated prototypical initial attachment pathway (Fig. 1a), attachment system activation is usually (albeit not exclusively) initiated by an event that triggers homeostasis deviation and a fear response. As described

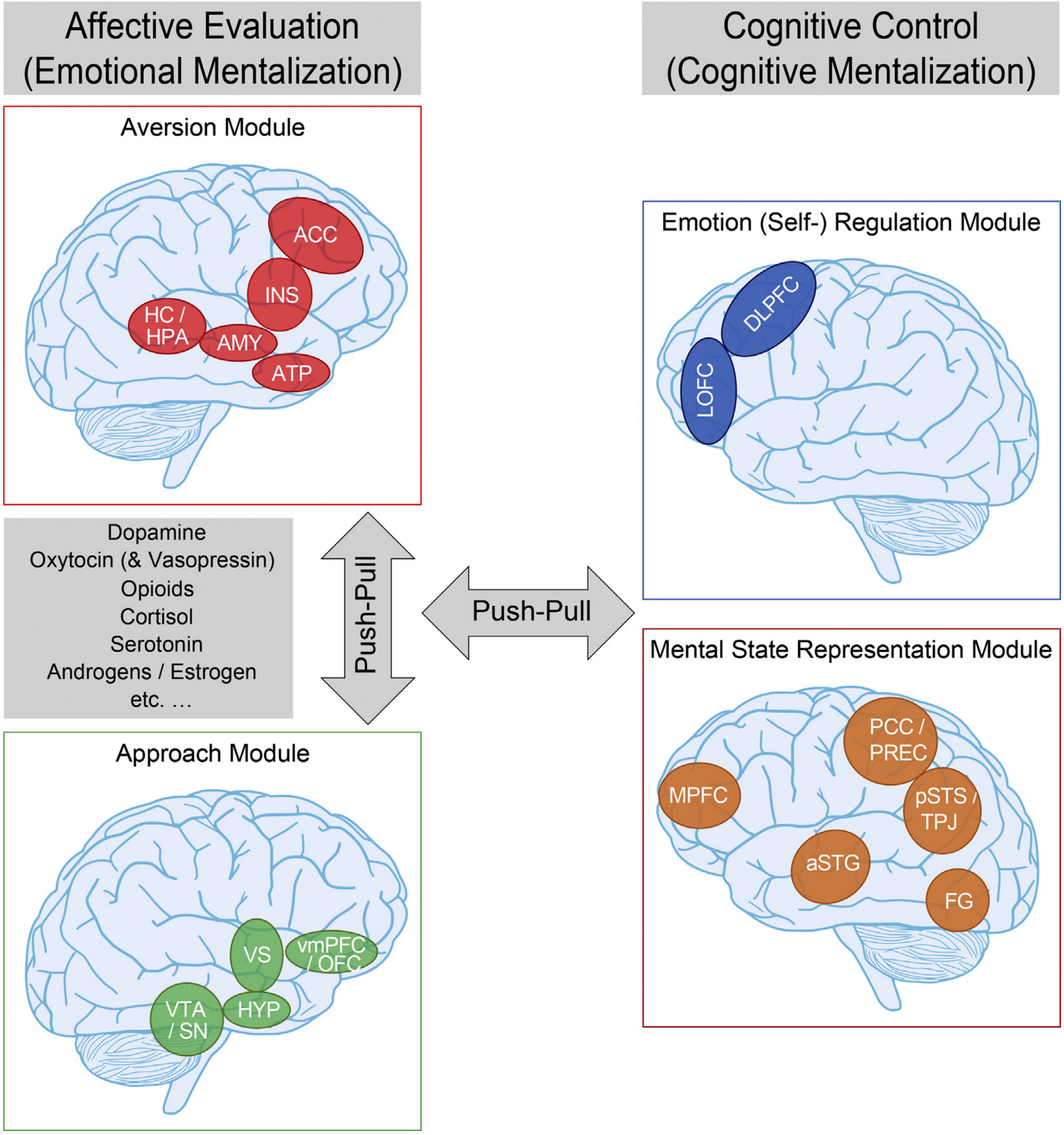


Fig. 2 – Functional neuro-anatomical model of human attachment (*NAMA*). We propose that the human attachment system is organized in two affective/emotional (left) versus cognitive (right) systems on the neural level, and that these systems can be further separated into two modules each (affective evaluation: aversion – red – and approach – green; cognitive control: emotion regulation – blue – and mental state representation – orange). We further suggest that the aversion and approach modules as part of the affective system, as well as the affective and cognitive systems are in a dynamic "push–pull" balance. Finally, we propose that neural activity within the affective system is mediated by (amongst others) dopamine, oxytocin (and vasopressin), endogenous opioids, cortisol, serotonin, androgens/estrogen, etc. Abbreviations: *aversion module* – ACC = anterior cingulate cortex, INS = insula, HC/HPA = hippocampus/HPA-axis, AMY = amygdala, ATP = anterior temporal pole; *approach module* – vmMPF/OFC = ventromedial prefrontal/orbitofrontal cortex, VS = ventral striatum, HYP = hypothalamus, VTA/SN = ventral tegmental area/substantia nigra; *emotion regulation module* – DLPFC = dorsolateral prefrontal cortex; LOFC = lateral orbitofrontal cortex; *mental state representation module* – MPFC = medial prefrontal cortex, PCC/PREC = posterior cingulate cortex/precuneus, pSTS/TPJ = posterior superior temporal sulcus/temporo-parietal junction, aSTG = anterior superior temporal gyrus, FG = fusiform gyrus. For more information, please refer to the main text. Adapted from Vrtička et al. (2012, 2017).

above, the fundamental function of such response is a prevention mechanism to enhance survival by inhibiting behaviors associated with an increased probability of danger or injury. Importantly, activation of the attachment system through such mechanism will likely occur not only through social- and attachment-related threats but also through non-social threats endangering bodily integrity or representing an immediate danger for survival more broadly speaking – as already acknowledged by Bowlby (Bowlby, 1969, 1980). On a neural level, we localize such function in the aversion module, a function that is nowadays also associated with heightened activity in a so-called extended saliency network typically associated with non-social negative affect, physical pain, stress, and fear. In addition, the saliency network is known to increase in activity during aversive social circumstances such as psychological pain related to social exclusion/rejection, social stress, social conflict, or sadness due to a social loss (Seeley et al., 2007; Vrtička, 2017; Vrtička & Vuilleumier, 2012). Prominent brain regions likely mediating such negative social- and non-social emotional processes include the amygdala, hippocampus [as important part of the negative feedback loop regulating the hypothalamic-pituitary-adrenal (HPA) axis], insula, anterior cingulate cortex, as well as anterior temporal pole (Eisenberger, Lieberman, & Williams, 2003; Engell, Haxby, & Todorov, 2007; Foley & Kirschbaum, 2010; Hayes, 2013; Kersting et al., 2009; Kim, Pellman, & Kim, 2015; Koban, Pourtois, Vocat, & Vuilleumier, 2010; Lamm, Decety, & Singer, 2011; Levesque et al., 2003). Within the prototypical initial attachment pathway and its derivatives, the aversion module likely has several implications and is activated at several instances, namely during: (i) threat detection and the initial fear response (comprising the neural representation of homeostasis deviation); (ii) the subsequent fight-or-flight response; (iii) social distancing as part of the avoidant response to maintain independence; and (iv) felt insecurity/persistent homeostasis deviation associated with the failure of social allostasis co-regulation despite proximity seeking (also sustaining psychological pain through social rejection). Consequently, in our view, the aversion module is involved in a series of stages related to threat, fear, and fight-or-flight responses that are parts of the same neurobiological system. Furthermore, in the context of caregiving, the aversion module will likely play a role in the detection of negative states in others requiring helpful assistance associated with empathy – the capacity to share and understand other people's emotions through vicariously experiencing their (negative) affective state (Vrtička, Favre, & Singer, 2017). Aversion module involvement in caregiving should, however, not last for too long or become the predominant emotional response to others' suffering, because it is an aversive and self-oriented emotional response often associated with withdrawal behavior motivated by the desire to protect oneself from prevalent negative emotional experiences. Such "negative consequence of empathy", also termed empathic or personal distress, will therefore preclude caregiving due to increased likelihood of activating the own attachment system (Canterberry & Gillath, 2012; Vrtička et al., 2017).

Associated with the promotion aspect and a neuroception of safety entailing the function of maintaining an approach-oriented motivation to foster closeness to others and the attainment of felt security – particularly under distress – (Taylor, 2006), we propose that the approach module encodes (mutual) social interactions as innately rewarding and thus counteracting fear tendencies. Likely neural substrates for such function are reward-related, primarily dopaminergic areas including the ventral tegmental area, substantia nigra, ventral striatum, and ventromedial prefrontal/orbitofrontal cortex (Aron et al., 2005; Fletcher et al., 2015; Haber & Knutson, 2010; Kim et al., 2010, 2017; Minagawa-Kawai et al., 2009; Nitschke et al., 2004; Noriuchi, Kikuchi, & Senoo, 2008; Ranote et al., 2004; Strathearn, Fonagy, Amico, & Montague, 2009; Strathearn, Li, Fonagy, & Montague, 2008; Swain, Lorberbaum, Kose, & Strathearn, 2007; Xu et al., 2012). However, other neurotransmitter/-peptide systems, comprising oxytocin and vasopressin (originating from the pituitary/hypothalamus region), endogenous opioids, and serotonin, are also likely involved in the neuroception of safety, as these systems all show strong interconnections to, and anatomical overlap with the dopaminergic reward circuits (Feldman, 2017; Feldman, Monakhov, Pratt, & Ebstein, 2016; Insel & Young, 2001; Vrtička, 2017; Vrtička & Vuilleumier, 2012). As for the aversion component, it is, however, unlikely that the approach module is solely implicated during positive social- and attachment-related circumstances. Instead, several kinds of "social interactions with beloved ones (e.g., children, parents, partners), friends, or any "significant" (e.g., contextually relevant) other person with a cooperative relationship (e.g., joint task)" have been shown to be "associated with the experience of positive emotions and increased activity in the reward circuits" (Vrtička & Vuilleumier, 2012) (p. 6). Within the prototypical initial attachment pathway and its derivatives, the approach module is also likely involved at several instances with different implications, namely: (i) as an innate response to homeostasis deviation/stress reflecting an approach-oriented motivation to foster closeness to others; and (ii) as the rewarding neural representation of the return to homeostasis through social (co-)regulation usually associated with the provision of nutrition, soothing, and comfort (Atzil et al., 2018). Moreover, the approach module is likely implicated in caregiving associated with compassion, the emotion one experiences when feeling concern for another's suffering and the desire to enhance that individual's welfare (Vrtička et al., 2017).

In accordance with the above, it should be noted here that we see the approach and aversion modules as two rather independent – albeit complementary – neurobiological systems encoding positive versus negative social emotional states and not attachment security versus insecurity as two sides of the same system. In fact, as will be highlighted below, both modules can be influenced by inter-individual differences in attachment reflected in various hypo- and hyper-activation patterns as a function of security and insecurity (avoidance and anxiety), and – particularly in association with emotion (self)regulation – security is usually characterized by highest flexibility (Mikulincer et al., 2003).

Apart from the above-described affective evaluation network upholding rapid, automatic, and often unconscious appraisals of emotional information in terms of approach versus aversion behaviors, we previously suggested within *NAMA* that the human attachment system also comprises a cognitive control network (Vrtička, 2017; Vrtička & Vuilleumier, 2012). We postulate that this cognitive control network maintains conscious representations about others, as well as behavioral regulation and decision making and thus reflects top-down, intentional, and somewhat slower neural mechanisms (Lieberman, 2007). Once more, the neural computations as part of the cognitive control network are unlikely to be specific to attachment-related information but employed during social cognition more broadly.

One function that we attribute to the cognitive control network is the volitional control of emotions and social behaviors associated with emotion regulation, which we situate within an emotion (self-)regulation module. Such "cold" cognitive computations likely underlie several different kinds of regulatory mechanisms that are not necessarily exclusively linked to emotion regulation but cognitive control more generally, such as situation selection and modification (e.g., avoidance conditioning), attentional deployment (e.g., selective attention, distraction in association with working memory load), cognitive situation re-evaluation (e.g., re-appraisal), and response modulation (e.g., expressive suppression). These mechanisms are based on activity primarily in lateral ventral, middle, and dorsal prefrontal/orbitofrontal cortex, and have been repeatedly shown to down-regulate activity in brain areas associated with the aversion module and to entail reduction of subjective distress – main components of physiological regulation (Callaghan & Tottenham, 2016; Lieberman, 2007; Martin & Ochsner, 2016; Ochsner, Silvers, & Buhle, 2012; Reeck, Ames, & Ochsner, 2016). Importantly, in the context of attachment, implication of the cognitive control module in emotion regulation refers to emotion *self*-regulation, a process that is largely absent in infancy and early childhood where social co-regulation is the predominant means for physiological regulation/homeostasis maintenance. Furthermore, in association with caregiving, cognitive control appears important for sensitive responding to a child's needs whilst not becoming overwhelmed by personal/empathic distress and thus one's own negative emotions ((Atzil, Gao, Fradkin, & Barrett, 2018; Canterberry & Gillath, 2012; Shaver & Fraley, 2000; Vrtička, Favre, & Singer, 2017)).

Another function that we associate with the cognitive control network is the maintenance of representations of internally focused information about others through processes related to mentalizing/theory of mind (ToM) (Fonagy & Luyten, 2009; Frith & Frith, 2005; Lieberman, 2007), which we situate within a mental state representation module. Rational inferences about the mental states and intentions of others are fundamental parts of attachment-derived IWMs reflecting memories about previous interactions with significant others and resulting expectations/predictions about future social interactions. According to the literature, the mental state representation module should therefore most likely comprise cortical midline areas such as the medial orbitofrontal/prefrontal cortex, posterior cingulate cortex, and precuneus, as well as lateral temporal regions like the superior temporal sulcus, temporoparietal junction, anterior superior temporal gyrus, and fusiform gyrus (Kanske, 2018; Spreng & Grady, 2010; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005). In the context of attachment, we expect mental state representation to only gradually emerge through repeated interactions with significant others and to later generalize across different social relationships (Mikulincer & Shaver, 2007). What is concerning caregiving, mental state representation also appears vital for sensitive responding to a child's needs, particularly to contextualize his/her behavior and to appropriately infer the meaning behind the child's behavioral signals.

In our view, there is not only a dynamic balance between approach and aversion tendencies as part of the affective evaluation network. We suggest a similar "push–pull" mechanism to be present between affective evaluation and cognitive control. As already briefly explained above, affective evaluation is associated with the rather automatic, fast, bottom-up, implicit, and likely even unconscious processing of externally-focused (physical and visible) information about others (such as emotional expressions, actions, etc.), which are also closely related to mechanisms implicated in "emotional contagion" or "empathizing" (Baron-Cohen, 2009; Fonagy & Luyten, 2009; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). In turn, distinct top-down, slow, explicit, and voluntary levels of social and affective processing are thought to be preferentially involved in the representation of internally-focused information about others (such as mental states, intentions, etc.), and thus cognitive mentalization (Fonagy & Luyten, 2009; Lieberman, 2007). *NAMA* implies a dynamic balance between these affective and cognitive evaluation neural networks in terms of a "push–pull" mechanism, the latter being mediated by, amongst others, stress factors (Mayes, 2000, 2006). Besides stress, the level of urgency or novelty of a situation will also influence the "switch point" between different modes of processing, resulting in a shift towards activation of the emotional mentalization system. This shift would be accompanied by behavioral changes "from flexibility to automaticity, … that is from relatively slow executive functions … to faster and habitual behavior …" (Fonagy & Luyten, 2009) (p. 1367). From an evolutionary perspective, such shift between processing modes would normally be adaptive in threatening conditions, as it can promote immediate and automatic (reflexive) self-protective reactions. However, in interpersonal settings where cognitive mentalization is a prerequisite and danger neither vital nor immediate (Dunbar, 1998), a too strong or exclusive reliance on affective evaluation might represent an insufficient or suboptimal strategy – see also (Vrtička, 2017; Vrtička & Vuilleumier, 2012).

In that regard, it should be noted here that the dissociation between an affective evaluation versus a cognitive control network in terms of rapid, automatic, and often unconscious appraisals of emotional information versus top-down, intentional behavioral regulation and conscious representations of the self and others associated with attachment in *NAMA* is not to be understood as absolute. There is evidence that some aspects of the cognitive control network related to emotion regulation as well as mental state representation can also be triggered by and have an impact on social approach and aversion behavior without conscious awareness. Such mechanism has been nicely shown, for example, in the context of thought suppression (Gillath, Bunge, Shaver, Wendelken, & Mikulincer, 2005) and secure attachment priming (Canterberry & Gillath, 2013) (see also below).

Besides assuming that inter-individual differences in attachment may distinctly and independently influence the functioning of the two affective evaluation (i.e., aversion and approach) and cognitive control (i.e., emotion regulation and mental state representation) networks, one could also hypothesize that inter-individual differences in attachment system functioning can be seen as possible determinants of "switch point" shifts in the push–pull dynamic balance between affective evaluation and cognitive control (Fonagy & Luyten, 2009). Although the corresponding theory has been developed in association with borderline personality disorder, it can be regarded as more generally predicting that a shift of the "switch point" toward emotional mentalization coincides with a lower threshold of attachment system activation.

In the next sections of this review, we will provide specific refined and extended evidence from first-person social neuroscience investigations pertaining to the derivatives of the prototypical initial attachment pathway associated with attachment security, avoidance, and anxiety in relation to the four modules of *NAMA* (i.e., aversion, approach, emotion regulation, and mental state representation).

As stated previously, a main question will thereby be how the above-described inter-individual differences in attachment orientation reflected in underlying attachment-derived IWMs (i.e., de-activation *vs* hyper-activation) modulate emotion processing and social cognition in healthy participants, and therefore influence how we understand others.

Please note that this review considers several different approaches to measuring inter-individual differences of attachment. This comprises a range of self-report questionnaires as well as semi-structured narrative interviews and behavioral observations (see Table 1). Furthermore, social neuroscience data from adults, adolescents, as well as children, from both cross-sectional and longitudinal study designs are included (see Table 2). We are aware of the fact that the compatibility of questionnaire- and interview-based measures of attachment has been discussed (Roisman et al., 2007). Also, attachment is nowadays understood as being malleable – rather than, as initially thought, to a large extent predetermined by early relationships imprinting stable patterns across the life span (see e.g., Fraley, 2019). We nonetheless think that including various approaches to measuring inter-individual differences of attachment as well as biological and neuroimaging data from several age groups comprising children and adolescents is valuable for this review, as this approach allows the description of differences and commonalities in the observed patterns of results. For a discussion on potential issues regarding attachment orientation measurement and elaboration on comparability of data derived from different age groups and cross-sectional versus longitudinal study designs, please refer to the general discussion section at the end of this review.

We would furthermore like to indicate here that the so far employed social neuroscience paradigms (as summarized in the following sections) use a great variety of stimuli and experimental tasks. Quite often, the latter are not directly attachment-related per se as they investigate neural responses during, for example, regulation of emotions induced by social versus non-social images displaying strangers, or mothers seeing images of their own versus an unknown infant linked to caregiving. Crucially, however, all included studies contain an attachment measure that allows for deriving associations between biological and brain activation measures and inter-individual differences in attachment and thus the role of attachment in a range of social emotional processes that are relevant for interpersonal relationships.

Finally, we advise the reader that special emphasis will be directed towards resolved/organized attachment (secure, avoidant, anxious) in healthy participants. A short elaboration on the potential neural correlates of unresolved/disorganized attachment and putative associations between attachment and psychopathology can also be found in the general discussion section at the end of this review.

2.3.2. *First-Person Social Neuroimaging findings on inter-individual differences in attachment*

2.3.2.1. Secure versus insecure attachment. Several lines of social neuroscience research investigating brain processing of attachment-related information as a function of inter-individual differences in the context of secure versus insecure attachment are available to date.

A first line of research assesses neural processing of physical pain anticipation and/or delivery in association with the presence (*vs* absence) of a significant other who can provide active or passive social support under distress. In a pioneering investigation using fMRI (Coan, Schaefer, & Davidson, 2006), married female participants with secure-like relationship qualities – measured by means of marital quality ratings using the satisfaction subscale of the dyadic adjustment scale – were observed to show weaker insula activation during both the anticipation and experience of electrical shocks while holding their partner's (*vs* a stranger's) hand. Furthermore, higher marital quality predicted less threat-related neural activation in the right anterior insula, superior frontal gyrus, and hypothalamus during spousal, but not stranger, hand-holding. These findings imply weaker distress/aversion module reactivity and higher success of emotional support if the latter is provided directly/physically by a significant other, i.e., an attachment figure.

Using a similar experimental fMRI design (Eisenberger et al., 2011), female participants in long-term romantic relationships who received painful stimulation had less activity in dorsal anterior cingulate cortex and anterior insula as well as reduced subjective pain ratings while viewing pictures of their partner (*vs* control images of a stranger male or an object). Furthermore, there was increased activity in the ventromedial prefrontal cortex in response to partner pictures in association with longer relationship length and greater perceived partner support. Heightened ventromedial prefrontal cortex activity while viewing partner pictures was also linked to reduced pain ratings and reduced pain-related neural activity. Extending the findings by Coan et al. (2006), these data show that seeing an image of a significant other can already serve as a means of distress regulation – likely through secure-based mental representations as part of IWMs –, especially if the significant other is generally more supportive.

Altogether, these results imply that aversion module neural activity related to pain anticipation and/or processing can be diminished through attachment-related co-regulation by means of active (physical hand-holding) or passive (mental representation) partner presence, with one possible neural substrate of a “social safety signal” located in the ventromedial prefrontal cortex (part of the approach module – see below). Moreover, such co-regulation seems more effective when the relationship towards the regulating partner has secure attachment-like properties. One possible underlying biological mechanism of this pain/threat attenuation by social co-regulation may be related to opioid signaling, i.e., the release of endogenous opioids through social proximity under stress – for further reading, see the *Brain Opioid Theory of Social Attachment* (BOTSA) (Machin & Dunbar, 2011).

A second line of research is concerned with the possible neural substrates of secure attachment representations, most prominently investigated in the form of attachment security priming effects. In a first fMRI study of this kind (Canterberry & Gillath, 2013), participants were exposed to explicit and implicit security- and insecurity-related words. Findings revealed increased brain activation in a range of areas during security primes (as compared to neutral and insecurity primes), including approach, emotion regulation, and mental state representation modules. Such activation was interpreted as providing mental resources to be used for processing attachment-related information and improved coping.

In a subsequent fMRI study (Norman, Lawrence, Iles, Benattayallah, & Karl, 2015), participants were shown threatening words (in a linguistic dot-probe task) and faces with or without previous secure attachment priming while amygdala activity to verbal and emotional threat was measured. Findings revealed that participants who received secure attachment priming showed attenuated amygdala activation in both the emotional faces and dot-probe tasks. Furthermore, secure attachment priming seemed to work even in insecurely attached individuals (i.e., presence of trait attachment insecurity measured with the Relationships Structures questionnaire – ECR-RS); scores of trait attachment anxiety and avoidance were positively correlated with amygdala activation to threatening faces in the control group, but not in the attachment primed group.

Another study (Tang, Chen, Hu, & Liu, 2017) exposed participants to priming under two conditions: a secure priming condition using references to the partner, and a neutral priming condition using neutral references. After each priming event, participants saw positive or negative emotions displayed by unknown faces and had to rate these faces on valence. Behavioral analysis revealed that participants responded faster to positive emotional faces in the secure prime condition than in the neutral prime condition. Furthermore, several brain areas were more strongly activated during the secure as compared to the neutral prime, including precuneus/posterior cingulate cortex, anterior cingulate cortex, anterior temporal pole, orbitofrontal cortex, middle temporal cortex, and occipital gyrus. Additionally, activity in the occipital gyrus and precuneus during secure (*vs* neutral) primes was stronger in securely versus anxiously attached participants (as assessed by the Experiences in Close Relationships questionnaire revised – ECR-R). Secure priming also had a specific effect on brain activity in anxious (as compared to secure) participants, because it enhanced activity in the right middle temporal gyrus, bilateral middle frontal gyrus, and right anterior cingulate cortex to positive faces, but diminished activity in the right fusiform gyrus, right parahippocampal gyrus, and bilateral middle occipital and middle temporal gyri to negative faces.

One more fMRI study also employed a priming paradigm, but assessed performance during a semantic conceptual

Table 1 – Attachment/attachment-related measures used in the cited first- and second-person social neuroscience studies (sorted alphabetically).

Attachment Measure	Reference(s)
Adult Attachment Interview (AAI)	(George, Kaplan, & Main, 1985)
Adult Attachment Projective (AAP)	(George, West, & Pettem, 1999)
Adult Attachment Questionnaire (AAQ)	(Simpson, Rholes, & Phillips, 1996)
Adult Attachment Scale (AAS)	(Collins & Read, 1990)
Attachment Behavior Q-Sort (AQS)	(Waters, 1987)
Attachment Style Questionnaire (ASQ)	(Feeney & Noller, 2001)
Berkeley Adult Attachment Interview (BAAI)	(Goldberg, 1983)
Child attachment interview (CAI)	(Shmueli-Goetz, Target, Fonagy, & Datta, 2008)
Coding System for Mother–Child Interactions (CSMCI)	Healey, Gopin, Grossman, Campbell, and Halperin (2010)
Experiences in Close Relationships Questionnaire (Revised) (ECR/-R)	(Brennan, Clark, & Shaver, 1998; Fraley, Waller, & Brennan, 2000)
Experiences in Close Relationships Questionnaire Revised Child Version (ECR-RC)	Brenning et al. (2011)
Inclusion of the Other in the Self Scale (IOS)	(Aron, Aron, & Smollan, 1992)
Internal Working Model Scale (IWMS)	(Collins & Read, 1990; Hazan & Shaver, 1987)
Kerns Security Scale (KSS)	(Kerns, Aspelmeier, Gentzler, & Grabill, 2001)
Maternal Sensitivity/Maternal Behavior Q-Sort (MBQS)	(Pederson & Moran, 1995)
Parental Bonding Index (PBI)	(Parker, Tupling, & Brown, 1979)
Relationship Structures Questionnaire (ECR-RS)	(Fraley, Niedenthal, Marks, Brumbaugh, & Vicary, 2006)
Relationships Questionnaire (RQ)	(Bartholomew & Horowitz, 1991)
Relationships Scales Questionnaire (RSQ)	Griffin and Bartholomew (1994)
Revised Children’s Anxiety and Depression Scale - Parent report (RCADS-P)	(Chorpita, Moffitt, & Gray, 2005)
Separation Anxiety Test (SAT)	(Hansburg, 1972; Resnick, 1993)
Strange Situation Procedure (SSP)	(Ainsworth & Bell, 1970)

Table 2 – List of cited first- and second person social neuroscience studies including inter-individual differences in attachment/attachment-related measures (sorted alphabetically by first author name).

First-Person Social Neuroscience Data							
First Author	Year	Partici-pants	Topic	Stimuli/Study Design	Neuroima-ging Technique	Attachment Measure	Attachment comparisons
Acosta et al.	2018	Adults	Brain anatomy	Affective loss and attachment	MRI	Relationship Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety. Number of affective losses
Baskak et al.	in press	Adults	Theory of mind	Reading the Mind in the Eyes Test (RMET)	fNIRS (single person)	Relationship Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Benetti et al.	2010	Adults	Brain anatomy	Affective loss and attachment	MRI	Experiences in Close Relationships Questionnaire Revised (ECR-R)	Dimensional; avoidance *vs* anxiety. Number of affective losses
Bernier et al.	2019	Children	Brain anatomy	Longitudinal association between maternal sensitivity and child brain anatomy	MRI	Maternal sensitivity at child age 1	Dimensional; higher *vs* lower maternal sensitivity
Borchardt et al.	2018	Adults	EEG resting state	Resting-state EEG after attachment-related narratives	EEG	None	Categorical; secure, avoiding, and anxious narratives
Bosmans et al.	2018	Children and adolescents	*NR3C1* methylation	No stimuli	Epigenetics	Relationship Structures Questionnaire (ECR-RS)	Dimensional avoidance *vs* anxiety
Buchheim et al.	2006	Adults	Feasibility of assessing attachment narratives	Adult Attachment Projective (AAP)	fMRI	Adult Attachment Projective (AAP)	Categorical; mainly unresolved
Buchheim et al.	2008	Adults	BPD and attachment trauma	Adult Attachment Projective (AAP)	fMRI	Adult Attachment Projective (AAP)	Categorical; monadic *vs* dyadic AAP images
Buchheim et al.	2016	Adults	BPD and unresolved attachment	Adult Attachment Projective (AAP)	fMRI	Adult Attachment Projective (AAP)	Categorical; BPD patients *vs* controls & resolved *vs* unresolved attachment
Callaghan et al.	2019	Children/Adolescents	Maternal face processing	Images of the mother and an unknown female	fMRI	Subscale for separation anxiety from the RCADS-P; Kerns Security Scale	Dimensional; secure *vs* insecure
Canterberry & Gillath	2013	Adults	Security priming	Exposure to explicit and implicit security- and insecurity-related words	fMRI	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety. Categorical; security *vs* neutral priming
Choi et al.	2018	Children	Attachment security in children	Separation Anxiety Test (SAT)	fMRI	Separation Anxiety Test (SAT)	Categorical; secure *vs* insecure
Coan et al.	2006	Adults	Social emotion regulation under threat	Partner hand-holding during threat anticipation (electric shocks)	fMRI	No direct attachment measure; satisfaction subscale of the Dyadic Adjustment Ccale	Dimensional; lower *vs* higher marital quality

Debbane et al.	2017	Adolescents	Self- and other-representation	Attribution of positive and negative adjectives to the self or a close other (best same-sex friend)	fMRI	Relationships Questionnaire (RQ)	Dimensional; avoidance *vs* anxiety (self- *vs* other-model)
DeWall et al.	2012	Adults	Social exclusion	Cyberball paradigm	fMRI	Attachment Style Questionnaire (ASQ)	Dimensional; avoidant *vs* anxious
Donges et al.	2012	Adults	Emotion Processing	Masked sad and happy faces	fMRI	Relationships Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Ein-Dor et al.	2018	Adults	Epigenetic modification (OXTR, NR3C1)	No stimuli	Epigenetics	Derivate of the Adult Attachment Scale (AAS)	Dimensional avoidance *vs* anxiety
Eisenberger et al.	2011	Adults	Social emotion regulation under threat	Viewing images of an attachment figure (romantic partner) when receiving physical pain (electric shocks)	fMRI	No direct attachment measure; relationship length and perceived partner support	Dimensional; relationship length and perceived partner support
Fareri et al.	2012	Adults	Social network modulation of reward processing	Card guessing task with three partners (friend, confederate, computer)	fMRI	No direct attachment measure, but Inclusion of the Other in the Self Scale (IOS)	Dimensional; IOS closeness of friend
Fraedrich et al.	2010	Adults	Infant face processing	Positive, negative, and neutral infant faces	EEG	Adult Attachment Projective (AAP)	Categorical; secure *vs* Insecure
Galynker et al.	2012	Adults	Face processing	Images of the mother, a female friend, and female strangers	fMRI	Adult Attachment Interview (AAI) and Beck Depression Inventory	Categorical; mainly insecure
Gee et al.	2014	Children	Maternal face processing	Images of the mother and an unknown female	fMRI	Subscale for separation anxiety from the RCADS-P; Kerns Security Scale	Dimensional; secure *vs* insecure
Gillath et al.	2005	Adults	Emotion regulation	Suppression of negative relation-ship-related thoughts	fMRI	Experiences in Close Relationships (ECR)	Dimensional: avoidance *vs* anxiety
Groh et al.	2018	Adults	Infant face processing	Odball task with happy *vs* distressed infant faces	EEG	Attachment Script Assessment	Categorical; secure *vs* insecure
Haas et al.	2016	Adults	*OXT* methylation & brain activity	Emotional perspective-taking and emotion attribution	Epigenetics & fMRI	Attachment Style Questionnaire (ASQ)	Dimensional avoidance *vs* anxiety
Krahe at al.	2015	Adults	Partner support and pain	Laser-induced pain and presence *vs* absence of romantic partner as a passive form of social support	EEG	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety

(*continued on next page*)

Table 2 – (*continued*)

First-Person Social Neuroscience Data

First Author	Year	Partici-pants	Topic	Stimuli/Study Design	Neuroima-ging Technique	Attachment Measure	Attachment comparisons
Krahe at al.	2016	Adults	Partner support and pain	Laser-induced pain and dynamic touch by one's romantic partner as an active form of social support	EEG	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety
Krause et al.	2016	Adults	Functional connectivity	Seed-based functional connectivity after attachment-related narratives	fMRI	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety. Categorical; secure, avoiding, and anxious narratives
Krause et al.	2018	Adults	Functional connectivity	Seed-based functional connectivity after attachment-related narratives	fMRI	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety. Categorical; secure, avoiding, and anxious narratives
Kungl et al.	2017	Children	Facial familiarity processing	Passive viewing task presenting (foster) mother and stranger faces	EEG	Attachment Behavior Q-Sort (AQS)	Categorical; secure *vs* insecure. Categorical; foster children compared to control group
Labek et al.	2016	Adults	Appraisal of attachment scenes	Adult Attachment Projective Picture System (AAP)	fMRI	Adult Attachment Projective Picture System (AAP)	Categorical; AAP *vs* control images
Leblanc et al.	2017	Children	Brain anatomy	Longitudinal association between child attachment and adult brain structure	MRI	Attachment Behavior Q-Sort (AQS) at child age 15 months	Categorical; secure *vs* insecure
Lemche et al.	2006	Adults	Saliency processing	Semantic conceptual priming task	fMRI	Behavioral index of attachment security	Dimensional; security *vs* insecurity related to reaction times
Lenzi at al.	2013	Adults	Emotion observation and imitation	Infant facial expressions	fMRI	Adult Attachment Interview (AAI)	Categorical; secure *vs* avoidant/dismissive *vs* anxious/preoccupied
Leyh et al.	2016	Adults	Attention	Odball task with target letters; negative, positive, and neutral contexts from IAPS	EEG	Adult Attachment Interview (AAI)	Categorical; secure *vs* avoidant *vs* anxious
Leyh et al.	2016	Adults	Infant face processsing	Odball task with negative, positive, and neutral child faces	EEG	Adult Attachment Interview (AAI)	Categorical; secure *vs* insecure
Luijk et al.	2010	Infants	*FKBP5* methylation & SNP rs1360780	No stimuli	Epigenetics	Strange Situation Paradigm (SSP)	Categorical, focus on insecure-resistant

Lyons-Ruth et al.	2016	Adults	Brain anatomy	Longitudinal association between child disorganization and disrupted maternal communication and adult brain structure	MRI	Strange Situation Paradigm (SSP) at child age 18 months	Categorical; secure *vs* disorganized
Miller et al.	2019	Mother–Child Dyads	Inter-brain coherence	Neural synchrony during a cooperative (*vs* independent) reaction time task in association with child attachment to the mother	fNIRS hyperscanning	Experiences in Relationships questionnaire revised (ECR-R) and child version (ECR-RC)	Dimensional; avoidance and anxiety
Moutsiana et al.	2015	Adults	Brain anatomy	Longitudinal association between child attachment and adult brain structure	MRI	Strange Situation Paradigm (SSP) at child age 18 months	Categorical; insecure *vs* secure
Moutsiana et al.	2014	Infants and Adults	Emotion regulation	Longitudinal association between attachment orientation at age 18 months and brain activity 20 years later	fMRI	Stange Situation Procedure (SSP)	Categorical; secure *vs* avoidant *vs* anxious
Musser et al.	2012	Adults	Infant cry sounds	Brain activity to own *vs* unknown infant cry	fMRI	Maternal sensitivity at child age 18 months	Dimensional; lower *vs* higher maternal sensitivity
Nguyen et al.	in press	Mother–Child Dyads	Inter-brain coherence	Neural synchrony during a cooperative (*vs* independent) problem solving task in association with task-performance and behavioral reciprocity	fNIRS	Coding System for Mother–Child Interactions (CSMCI)	High *vs* low behavioral reciprocity (contingent responses resulting in a turn-taking quality of interactions as behavioral flow)
Nolte et al.	2013	Adults	Mentalization	Novel modification of the Reading the Mind in the Eyes Test (RMET-R)	fMRI	No specific attachment measure, but a general *vs* an attachment-related stress induction	Categorical; general *vs* attachment-related stress induction
Norman et al.	2015	Adults	Security priming	Effects of trait and primed attachment security on amygdala reactivity to threatening stimuli in an emotional faces and a linguistic dot-probe task	fMRI	Relationships Structures questionnaire (ECR-RS)	Dimensional; avoidance *vs* anxiety. Categorical; security *vs* neutral priming
Nummenmaa et al.	2014	Adults	Opioid receptor availability	No stimuli	PET	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety

(*continued on next page*)

Table 2 – (*continued*)

First-Person Social Neuroscience Data

First Author	Year	Partici-pants	Topic	Stimuli/Study Design	Neuroima-ging Technique	Attachment Measure	Attachment comparisons
Poore et al.	2012	Adults	Theory of mind, reward	Feedback either confirming or violating expectations about their partners' questionnaire responses	fMRI	Experiences in Close Relationships (ECR)	Dimensional; anxiety *vs* security
Quirin et al.	2010	Adults	Bain anatomy	No stiumuli	MRI	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety
Redlich et al.	2015	Adults	Brain function and structure related to attachment	Emotional face-matching task	fMRI & MRI	Relationship Scale Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Riem et al.	2012	Adults	Infant cry sounds	Infant cry *vs* scrambled cry sounds in women without children	fMRI	Berkeley Adult Attachment Interview	Categorical; mainly insecure
Rifkin-Graboi et al.	2015	Infants	Brain anatomy	Association between maternal sensitivity and child brain anatomy	MRI	Maternal sensitivity at child age 6 months	Dimensional; avoidance *vs* anxiety
Rigon et al.	2016	Adults	Brain anatomy and connectivity	No stimuli	MRI/DTI	Experiences in Close Relationships Questionnaire Revised (ECR-R)	Dimensional; avoidance *vs* anxiety
Schneider-Hassloff et al.	2015	Adults	Mentalization	Prisoners Dilemma Game	fMRI	Relationships Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Serra et al.	2015	Adults	Brain anatomy	White matter connectivity	DTI	Kerns Security Scale	Dimensional; secure *vs* insecure
Strathearn et al.	2009	Adults	Infant facial emotion processing	Happy, neutral, and sad own *vs* unknown infant faces	fMRI	Adult Attachment Interview (AAI)	Categorical; secure *vs* avoidant
Suslow et al.	2009	Adults	Emotion Processing	Masked sad and happy faces	fMRI	Relationships Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Takiguchi et al.	2015	Children and adolescents	Reward and reactive attachment disorder	Monetary reward task with high *vs* low reward conditions	fMRI	Internal Working Model Scale (IWMS)	Categorical; reactive attachment disorder *vs* typically developing. Dimensional; IWMS secure *vs* avoidant *vs* anxious
Tang et al.	2017	Adults	Security priming	Processing of emotional facial stimuli (aversive *vs* happy) after secure *vs* neutral priming	fMRI	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety. Categorical; security *vs* neutral priming
Thijssen et al.	2017	Children	Brain anatomy and connectivity	Longitudinal association between parental sensitivity and child brain anatomy and connectivity	(f)MRI	Parental sensitivity at child age 4 years	Dimensional; high *vs* low maternal sensitivity

van Ijzendoorn et al.	2010	Adults	*5HTTLPR* methylation	No stimuli	Epigenetics	Berkeley Adult Attachment Interview	Categorical; mainly unresolved/ disorganized
van Mulder et al.	2017	Infants	*FKBP5* methylation & SNP rs1360780	No stimuli	Epigenetics	Stange Situation Procedure (SSP)	Categorical
von Mohr et al.	2018	Adults	Partner support and pain	Laser-induced pain and dynamic touch by one's romantic partner as an active form of social support	EEG	Experiences in Close Relationships Revised (ECR-R)	Dimensional; avoidance *vs* anxiety
Vrtička et al.	2012	Adults	Emotion regulation	Natural viewing, re-appraisal, and suppression of social *vs* non-social, positive *vs* negative complex scenes	fMRI	Relationships Scales Questionnaire (RSQ)	Dimensional: avoidance *vs* anxiety
Vrtička et al.	2008	Adults	Social Feedback Processing	Emotional facial expressions (happy, angry) paired with words (won, lost)	fMRI	Adult Attachment Questionnaire (AAQ)	Dimensional; avoidance *vs* anxiety
Vrtička et al.	2014	Adolescents	Social Feedback Processing	Emotional facial expressions (happy, angry) paired with words (won, lost)	fMRI	Relationships Scales Questionnaire (RSQ)	Dimensional; avoidance *vs* anxiety
Warren et al.	2010	Adults	Cognitive Control	Emotion-word Stroop Task	fMRI	Adult Attachment Interview (AAI)	Categorical; mainly insecure
White et al.	2012	Children	Social exclusion	Cyberball paradigm	EEG	Child attachment interview	Categorical; mainly avoidance
Yaseen et al.	2016	Adults	Comparison of neural correlates of AAI *vs* RSQ	Partici-pants viewed their mothers in neutral-, valence-, and salience-rating conditions	fMRI	Adult Attachment Interview (AAI) and Relationships Scales Questionnaire (RSQ)	AAI *vs* RSQ
Zayas et al.	2009	Adults	Semantic processing of attachment-related cues	Priming with attachment-related contexts and subsequent presentation of rejection- or acceptance-related words	EEG	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety
Zhang et al.	2008	Adults	Face processing	Emotional and neutral faces	EEG	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety
Zilber et al.	2007	Adults	Image processing	Emotional and neutral IAPS images	EEG	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety
Zheng et al.	2015	Adults	Face processing	Emotional and neutral faces	EEG	Experiences in Close Relationships (ECR)	Dimensional; avoidance *vs* anxiety

priming task after a negative, stress inducing versus a neutral prime condition (Lemche et al., 2006). More specifically, before presentation of sentence statements describing self- or other-centered information that participants were asked to agree or disagree with by response, participants were exposed to subliminal sentence primes either containing nonsense information (neutral prime condition) or descriptions of unpleasant attachment experiences (stress prime condition). The mean reaction time difference between performance after the neutral versus the stress prime condition was associated with a greater level of attachment insecurity. Findings showed that levels of activity within bilateral amygdalae were highly positively correlated with attachment insecurity and autonomic response during the stress prime condition.

Taken together, these findings reveal an extended network of brain areas as parts of the approach, emotion regulation, and mental state representation modules of *NAMA* that come online as security primes are processed. They also indicate that security/insecurity primes influence subsequently processed positive and negative/threatening information – particularly by down-/up-regulating aversion module activity to negative information (in line with above-described effects of partner support on pain anticipation/processing). As Norman et al. (2015) state: "these findings support the potential use of attachment security-boosting methods as interventions and suggest a neural mechanism for the protective effect of social bonds" (p. 832).

A third line of research uses a range of experimental tasks, neuroimaging techniques, as well as attachment measures, and associates brain data (both functional and anatomical) with indices of inter-individual differences in secure versus insecure attachment – not further differentiating attachment insecurity into attachment avoidance versus anxiety.

Regarding functional brain data, several studies used fMRI in children and adults in association with the Adult Attachment Interview (AAI), Berkeley Attachment Interview, Adult Attachment Projective (AAP), and Separation Anxiety Test (SAT). Measures of attachment security versus insecurity were subsequently associated with brain activity during an emotion-Stroop task, face processing, infant cry listening, or fMRI versions of the AAP and SAT, respectively (Buchheim et al., 2006; Choi, Taylor, Hong, Kim, & Yi, 2018; Galynker et al., 2012; Riem, Bakermans-Kranenburg, van Ijzendoorn, Out, & Rombouts, 2012; Warren et al., 2010). Shortly summarized, these investigations found that: (i) insecure attachment involves a vulnerability to distraction by attachment-relevant emotional information, and greater requirement of cognitive control to attend to task-relevant non-emotional information; (ii) insecure attachment may to a certain degree neurally resemble depression (distinct but overlapping networks) when viewing images of the mother and a female friend; (iii) individuals with insecure attachment representations showed heightened amygdala activation when exposed to infant crying; (iv) attachment insecurity/disorganization was associated with increasing activation of medial temporal regions, including the amygdala and hippocampus, in the course of the AAP task; and (v) securely attached children showed greater activation in the frontal, limbic, and basal ganglia area, which included the dorsolateral prefrontal cortex, amygdala, cingulate cortex, and striatum, during the SAP. Although not entirely coherent, these data further bolster the impression that attachment security is predominantly associated with increased activity in the emotion regulation and mental state representation modules and concomitantly decreased activity in the aversion module.

Also assessing brain function but with means of EEG in children and adults, neural activation patterns were measured during different tasks involving face processing, and associated with attachment derived from the AAP, AAI, Attachment Behavior Q-Sort (AQS), and Attachment Script Assessment (Fraedrich, Lakatos, & Spangler, 2010; Groh & Haydon, 2018; Kungl, Bovenschen, & Spangler, 2017; Leyh, Heinisch, Behringer, Reiner, & Spangler, 2016; Leyh, Heinisch, Kungl, & Spangler, 2016). In so doing, most effects emerged for the ERP components N170 associated with face perception and P300 reflective of enhanced emotion processing. Regarding the N170, amplified amplitudes were observed for insecure (*vs* secure) mothers viewing infant faces – particularly if negative –, but dampened amplitudes for foster (*vs* control) children viewing foster mother and stranger faces, in all children when viewing stranger versus (foster) mother faces, as well as for insecurely (as compared to securely) attached children. This pattern was interpreted as indicative of altered saliency of face stimuli as a function of early adversity. Regarding the P300, secure (*vs* insecure) mothers were found to have an enlarged P300 amplitude to infant face stimuli – particularly if negative. This pattern was associated with a stronger attribution of relevance to emotional signals from children indicating the need for protective action. Interestingly, a heightened P3b response associated with greater allocation of cognitive resources was also reported in insecure (*vs* secure) mothers seeing their own infants' distressed (*vs* happy) facial expression and related to allocating disproportional attentional resources to processing their infants' distress. Such discrepancy may be partially explained by the P300 being thought of containing (at least) two subcomponents, the classic P300 being renamed P3b, and an additional P3a, with different underlying functions (Polich, 2007).

Collectively, these EEG findings start shedding light on more time-locked brain activation patterns associated with attachment security versus insecurity. However, they are still discrepant – due to strongly diverging experimental designs and participant populations –, and therefore in need of further extension and replication. More coherent patterns, however, appear to emerge when using comparisons between attachment avoidance and anxiety (see below).

Finally yet importantly, one study looked into associations between attachment derived from the Kerns Security Scale (KSS) and white matter connectivity using DTI (Serra et al., 2015). Findings revealed higher fractional anisotropy, an index of directionality of diffusion, related to attachment security in four left-hemisphere white matter association fibers (uncinate fasciculus, cingulum, superior longitudinal fasciculus, and inferior fronto-occipital fasciculus). These association fibers have previously been linked to communication between structures in the limbic system and to facilitate prefrontal, parietal, and temporal interactions, and thereby high-level cognitive functions. Attachment security may therefore be indicative of better emotion and social cognition (emotion regulation, mental state representation) integration, as the quality of the mother-infant relationship affects the construction of children's socio-emotional abilities and future adult relationships.

A fourth line of research is trying to establish longitudinal associations between attachment measured during infancy or childhood and brain morphology and/or activation in the same individuals at a later point in time using longitudinal experimental designs. Two investigations of this kind measured attachment by means of the Strange Situation Procedure (SSP) in children at age 18 months, and associated the outcomes with amygdala volumes when children became adults (Lyons-Ruth, Pechtel, Yoon, Anderson, & Teicher, 2016; Moutsiana et al., 2015). Both studies found smaller (left) amygdala volumes predicted by indices of attachment security at 18 months (i.e., no attachment insecurity or disorganization status in the SSP). Furthermore, in the first study, smaller amygdala volume was independent of maternal depression. In the second study, smaller amygdala volume did not correlate with later stressors, including childhood maltreatment and attachment disturbance in adolescence, but predicted less dissociation and weaker limbic irritability (i.e., paroxysmal somatic disturbances, brief hallucinatory events, visual phenomena, automatisms, and dissociative experiences) during adulthood. Another study (Leblanc, Degeilh, Daneault, Beauchamp, & Bernier, 2017) assessed child attachment with the Attachment Behavior Q-Sort (AQS) at child age 15 months and measured whole-brain gray matter volume when children were 10–11 years of age. Results indicated that children more securely attached to their mother in infancy had larger gray-matter volumes in the superior temporal sulcus and gyrus, temporo-parietal junction, and precentral gyrus in late childhood – all areas belonging to the mental state representation module of *NAMA*. The above results are consistent with research indicating accelerated limbic development and/or changes in connectivity of these areas to other brain regions in response to early social adversity. These findings suggest that "subtle, but important, variations in maternal care – as reflected in early measures of child attachment– influence neuroanatomical trajectories important to future cognitive and emotional functioning" (Rifkin-Graboi et al., 2015) (p. 1).

Finally, another line of research is not looking at the influence of early indications of (child) attachment on brain anatomy and function later on in life per se, but rather at parental (mainly maternal) sensitivity during early childhood as an indirect measure of parent-child attachment quality (Bernier et al., 2019; Thijssen et al., 2017). Within this context, sensitive parenting during early childhood is associated with prototypic secure-based caregiving and understood as predictive for the emergence of attachment security in children through intergenerational attachment transmission (Van Ijzendoorn, 1995; Verhage et al., 2016). Despite such differences in the employed measure of attachment security that is more closely associated with caregiving and caring more generally, the thereby obtained findings show considerable overlap with the above-described neural patterns. More precisely, more sensitive parenting seems to predict altered developmental trajectories of the amygdala and hippocampus as well as connectivity of these areas to emotion regulation and mental state representation nodes (Rifkin-Graboi et al., 2015).

Related to the above experimental approaches, there is evidence from cross-sectional as well as longitudinal fMRI studies that the parent-child relationship influences the maturing emotion neurobiology and particularly the developing amygdala-medial prefrontal cortex network involved in emotion (self-)regulation, as reflected by the notion of a *neuro-environmental loop* of plasticity (Callaghan & Tottenham, 2016). More concretely, in two studies that exposed children to images of their mother's versus an unknown female's face, differential amygdala reactivity and amygdala-prefrontal circuitry was observed to go along with affect-related regulation and measures of child-mother attachment security [subscale for separation anxiety from the Revised Children's Anxiety and Depression Scale – parent report (RCADS-P) and the KSS] (Callaghan et al., 2019; Gee et al., 2014). Furthermore, altered amygdala resting-state connectivity mediated the association between maternal aggressive behavior and the first onset of major depressive disorder in late adolescence (Callaghan et al., 2017).

Taken together, in *NAMA*, security appears to reflect increased emotion (self-)regulation module involvement/efficiency concordant with decreased aversion module activation. Another repeatedly appearing aspect of attachment security appears to be enhanced functioning of the mental state representation module entertaining the ability to cognitively infer the intentions and thoughts of others. Finally, approach module functioning seems improved as well, for example by the ventromedial prefrontal cortex figuring as a possible substrate for a neural signal of safety/security, and other reward-related brain areas under the influence of dopamine and oxytocin being more strongly activated in positive social contexts. As nicely summarized in a recent book chapter (Gillath et al., 2016), attachment security thus seems to "help a person to cope better with the threats that activate the attachment system" in various ways and already by merely priming people with information reflecting security, they can be brought "into a higher state of growth or flow" (p. 28).

2.3.2.2. AVOIDANT ATTACHMENT.

Regarding attachment avoidance, attachment theory and behavioral data point towards a general notion of de-activating strategies to minimize attachment system activation through inhibition/emotion suppression. At the same time, physiological data suggest increased stress during negative attachment-related situations that maybe related to a lack of social co-regulation of distress. The latter mechanism appears to be effective in securely (*vs* insecurely) attached individuals and mainly mediated by enhanced emotion regulation and/or mental state representation and concomitantly decreased aversion module activity (see above).

One prediction from attachment theory regarding avoidance associated with de-activating secondary attachment strategies is that in circumstances of stress, social co-regulation is expected as not readily available. Accordingly, in these contexts, aversion module activity should be decreased.

Such notion is corroborated by findings from one fMRI study that observed decreased aversion module activity (in the insula and dorsal anterior cingulate cortex) in young avoidant adults (assessed with the self-report Attachment Style Questionnaire – ASQ) during social exclusion/rejection induced by a cyberball virtual ball tossing paradigm (DeWall et al., 2012). Reduced anterior insula and dorsal anterior cingulate cortex activity in avoidant participants was interpreted as reflecting the reduced social need for closeness and weaker distress elicited by social rejection in these individuals.

In a similar EEG study during which 11- to 15-year-old children also played the cyberball game, no effects of avoidance were observed during social exclusion itself. However, differences in the N2 event-related potential were found during a newly added subsequent re-inclusion phase (White et al., 2012). More specifically, children classified as avoidant (compared to secure – assessed via the Child Attachment Interview) showed a greater increment in the N2 during re-inclusion, such effect being interpreted in association with stronger expectancy violation, i.e., continued expectations of rejection even after cessation of social exclusion. One aspect of de-activating strategies of avoidant individuals may therefore indeed be related to the prediction of their IWMs that significant others are unavailable and/or that experiences of social exclusion/rejection are more likely, so that such occurrences are entailing weaker aversion module activation.

Interestingly, however, in another EEG study comprising the administration of laser-induced pain to participants, higher avoidance (measured with the Experiences in Close Relationships Revised questionnaire – ECR-R) was indicative of stronger subjective pain ratings and enhanced neural processing of pain/its saliency (higher N2 and P2 amplitudes) when their partner was present (*vs* absent) (Krahe et al., 2015). The authors of this study refer to the general notion of attachment theory that avoidant individuals tend to hold negative perceptions of social support (Collins & Feeney, 2004), prefer dealing with threat on their own, and are less likely to turn to their support network when stressed (compared to secure or anxious individuals) (Ognibene & Collins, 1998; Wallace & Vaux, 1993). Accordingly, the unwanted presence of their partner may interfere with avoidant individuals' coping strategies, including their aim to "inhibit the experience of aversive emotional states and exclude these states from awareness" (Mikulincer et al., 2003) (p. 88).

In a follow-up EEG study (Krahe, Drabek, Paloyelis, & Fotopoulou, 2016), the same authors furthermore demonstrated that avoidant individuals exhibited increased N1 and N2 amplitudes when pleasant touch was administered to CT-containing skin of their arm, which was again associated with inter-individual differences in the expectation of social support, particularly regarding the unavailability of social resources to gate pain responses.

In a third follow-up study by the same authors (von Mohr, Krahe, Beck, & Fotopoulou, 2018), participants received laser-induced pain as well as social, active, affective (*vs* active but neutral) touch from their romantic partners according to the properties of a specific C-tactile afferent pathway. Affective touch from one's partner reduced subjective pain ratings and similarly attenuated brain activity measured by EEG both at earlier (N1) and later (N2–P2) stages of cortical processing. Here, however, adult attachment style (assessed by the ECR-R) did not affect N1 and N2–P2 components, but attachment anxiety had a moderating role on pain ratings.

Together, these social neuroscience data therefore suggest that de-activating strategies associated with avoidance may indeed preclude (too strong) aversion module activity during social exclusion/rejection due to the expectation of others as being unavailable for social co-regulation of distress. At the same time, aversion module activation may increase considerably – thereby exceeding a level of activation as compared to security and/or anxiety – if social support during distress is (unexpectedly) available, because this constellation interferes with avoidant individuals' usual self-oriented coping strategies.

The above brain data implies that attachment avoidance alters emotion self-regulation in contexts of social co-regulation availability, and therefore proposes that avoidant individuals' emotion self-regulation is functional if not interfered with socially. This pattern somewhat contradicts attachment theory that proposes generally less efficient emotion self-regulation for attachment avoidance (and anxiety). The question whether attachment avoidance entails a de-activation of aversion module activation indicative of more generally efficient emotion self-regulation – or other associated mechanisms – therefore is warranted.

Within this context, although not directly revealing activity overlapping with the aversion module, a first fMRI study found that masked sad faces induced weaker response in the somatosensory cortex (BA 3) in avoidant participants (assessed through the Relationships Scales Questionnaire – RSQ). Such finding was attributed to their habitual unwillingness to deal with partners' distress and needs for proximity (Suslow et al., 2009), possibly through a decreased propensity of emotional mirroring associated with empathy.

However, several other functional and anatomical studies point towards the opposite direction. For example, attachment avoidance (measured by means of the Relationships Structures questionnaire – ECR-RS) was found to positively correlate with amygdala activation to negative (fearful and angry) facial expressions in adults (Norman et al., 2015). Furthermore, increased insula activation was observed in avoidant mothers (classified by the AAI) seeing images of their own infants with sad/crying emotional facial expressions (Strathearn et al., 2009).

Available EEG data on emotion observation and imitation bolster such notion, as avoidant participants (classified by the AAI) showed a neural pattern consisting of hyper-activation of limbic and mirror areas possibly reflecting emotional dysregulation, and increased deactivation of fronto-medial areas likely related to the inhibition of attachment behaviors (Lenzi, Trentini, Tambelli, & Pantano, 2015).

Furthermore, attachment avoidance (measured by the ECR/-R) was related to lower structural integrity of the amygdala that was further associated with chronic hyperactivity (Rigon, Duff, & Voss, 2016), and to reduced hippocampus gray matter density that was related to reduced glucocorticoid/cortisol stress regulation capacity (Quirin, Gillath, Pruessner, & Eggert, 2010).

Similarly, in the study by Moutsiana et al. (2015) reported above, insecure attachment assessed through the SSP at child age 18 months was associated with larger bilateral amygdala volumes in young adults, with 87% of insecure individuals classified as avoidant. Such relation was interpreted to suggest that larger amygdalae may predispose individuals to elevated sensitivity to stress and/or symptoms of anxiety.

Moreover, changes in functional resting state connectivity were reported in adult participants after they listened to prototypical insecure-dismissive (i.e., avoidant) narratives (Krause et al., 2016, 2018). Generally speaking, it is thought that attachment-specific speech patterns and behavior may activate corresponding attachment-related schemas that can in turn alter the mental states of the listener in terms of a carry-over effect. Accordingly, the authors report in the first study that increased functional connectivity in the aversion network, including the dorsal anterior cingulate cortex and left anterior middle temporal gyrus, was specifically increased after exposure to avoidant narratives. Furthermore, increased dorsal anterior cingulate cortex seeded functional connectivity within the aversion network was positively related to participants' avoidant attachment style (measured with the Experiences in Close Relationships Revised questionnaire – ECR-R) and presence of a history of childhood trauma. In addition, after presentation of avoidant narratives in the second study, functional connectivity between the left caudate, bilateral temporo-parietal junction, and right dorsal posterior cingulum was reduced, compared to baseline. These findings suggest specific neural processing of prolonged negative mood-changes and schema activation induced by attachment-specific speech patterns. A follow-up resting-state EEG study (Borchardt et al., 2018) furthermore revealed that after listening to avoidant narratives, the decrease in duration of high vigilance stages was fastest compared to the other two conditions (secure and anxious narratives). The behavioral data supported the observation that especially the insecure narratives induced a tendency in the listener to affectively disengage from the narrative content.

Together, these data are indicative of heightened aversion module activity and altered aversion module structure in association with stress and its regulation in avoidant individuals – although the exact implication of amygdala and/or hippocampus atrophy versus hypertrophy remains to be elucidated.

Further evidence for increased susceptibility to attachment-related information – particularly if negative – associated with avoidance comes from fMRI studies directly investigating emotion self-regulation mechanisms.

In a fMRI task during which participants were asked to either think of negative attachment-related scenarios or to actively suppress such thoughts, avoidance (assessed by the Experiences in Close Relationships Questionnaire – ECR) was related to less deactivation in two brain regions (subcallosal cingulate cortex and lateral prefrontal cortex) during suppression. This finding was interpreted by the authors as suggesting that avoidant peoples' suppression was less complete or less efficient, in line with results from previous behavioral experiments (Gillath et al., 2005).

We built upon such initial observations and designed an fMRI study during which participants were shown complex scenes depicting social versus nonsocial and positive versus negative content (Vrtička et al., 2012), and instructed participants to either naturally view these images or to use cognitive re-appraisal versus (expressive) suppression as emotion regulation strategies. In participants scoring higher on avoidance (assessed with the RSQ), we observed activity suggesting heightened cognitive and emotional conflict (anterior cingulate cortex activation) in combination with increased regulatory inhibition (lateral and medial dorsal prefrontal cortex) during spontaneous viewing of social-emotional scenes. Furthermore, during re-appraisal, amygdala activation to negative social images only decreased for individuals scoring low on avoidance. Finally, during suppression, avoidance was associated with stronger neural responses to positive social images in the supplementary motor area and caudate, implying stronger regulatory efforts with the successful use of suppression.

On the one hand, these fMRI data suggest that avoidance is linked to preferential use of suppression as an emotion (self-) regulation strategy in both positive and negative social contexts, as previously suggested based on data from behavioral experiments and attachment theory in terms of de-activating strategies. On the other hand, these data demonstrate that for avoidant individuals, re-appraisal of negative social information may not work efficiently as an emotion self-regulation strategy. This relative inefficiency of re-appraisal is likely because re-appraisal as an antecedent-based regulation strategy requires the active engagement with an emerging emotion in order to change the latter – as opposed to suppression that is a response-based regulation strategy aimed at inhibiting an already present emotion.

Interestingly, another fMRI study relating attachment classification by means of the SSP at child age 18 months to brain activity 20 years later looked at neural responding during the regulation of positive affect, and particularly the up-regulation of positive emotions (Moutsiana et al., 2014). Findings revealed greater activation in prefrontal regions involved in cognitive control and reduced co-activation of the nucleus accumbens with the prefrontal cortex. This is consistent with relative inefficiency in the neural regulation of positive affect, specifically in association with avoidance (87% of insecure study participants). Congruent with, and extending our study (Vrtička et al., 2012), these data corroborate the notion that emotion regulation is altered in avoidant individuals also in positive (social) contexts, likely due to the fact that they usually try to minimize emotional responding through suppression.

Finally, within the context of emotion regulation, another study employing EEG looked at neural responses during face processing and found that emotional faces elicited a larger N170 face-processing related amplitude in avoidant participants (measured with the ECR) (Zheng, Zhang, & Zheng, 2015). This activation pattern was associated with stronger allocation of cognitive resources in avoidant individuals when encoding emotional faces at an early stage, a process that may contribute to the use of strategies to suppress the accessibility of previously encoded emotional information in recognition.

In sum, these findings pertaining to emotion regulation suggest the presence of two opposing mechanisms in association with avoidance. On the one hand, de-activating secondary attachment strategies characterizing avoidance appear to entail a relative insensitivity to negative social information signaling the unavailability of others for social co-regulation – like in contexts of social rejection/exclusion – thereby preventing (too strong) activation of the aversion module. On the other hand, avoidance seems to lead to increased sensitivity to negative social information associated with decreased capacity to regulate the thereby caused distress, manifested in increased aversion module activation as well as reduced amygdala and hippocampus structural integrity. At the same time, positive (social) emotion regulation also appears to be affected by avoidance, because positive emotions in a social context appear also to usually be suppressed. One possible mechanistic explanation may be that avoidant individuals have to rapidly evaluate incoming information regarding its attachment-related content to decide whether to process it further or to inhibit/suppress its implications. Such process seems to work for certain kind of information under certain circumstances, but not always and only if suppression can be subsequently employed. This pattern may help understanding why avoidant individuals tend to become highly emotional when their preferred regulation strategy of suppression fails or cannot be employed. Furthermore, the above pattern may be indicative of a higher default activation state of a fight-or-flight survival system. This interpretation would accord with *Social Baseline Theory* (Coan & Sbarra, 2015; Ein-Dor et al., 2015) and *Social Defense Theory* (Ein-Dor, 2014; Ein-Dor et al., 2010; Ein-Dor & Hirschberger, 2016) predicting that avoidant individuals do not expect social resources to be available and thus up-regulate their own defenses. Although non-adaptive in the presence of others, such avoidant strategy is appropriate and meaningful when others are constantly inaccessible, rejecting, or absent under distress.

Besides looking at attachment-related stress reactivity on a neural level, one can employ another indirect means of investigating potential HPA axis involvement with a novel first-person social neuroscience approach based on the assessment of epigenetic modification. Such approach builds upon the hypothesis that attachment, like many psychosocial outcomes, is the result of a gene by environment interaction (Fonagy, 2001)- a hypothesis inspired by seminal work in rodents" (Weaver et al., 2004).

In a first correlational study in humans (Ein-Dor, Verbeke, Mokry, & Vrtička, 2018), we assessed glucocorticoid receptor gene (*NR3C1*) promoter methylation in N = 109 adults classified on attachment by a measure derived from the Adult Attachment Scale (AAS). Our findings revealed selectively increased *NR3C1* promoter methylation in participants scoring high on avoidance (but not anxiety). These data provide preliminary evidence pointing toward less efficient HPA axis negative feedback loop regulation because the primary stress hormone cortisol binds at the *NR3C1* receptor thereby abolishing the stress response. This pattern likely entails altered emotion and stress regulation in avoidant individuals and attributes a potential modulating role to cortisol signaling. Another potential explanation of increased *NR3C1* methylation associated with avoidance may be generally increased physiological arousal due to anticipation of fewer social resources to deal with stress as described by *Social Baseline Theory* (Coan & Sbarra, 2015; Ein-Dor et al., 2015).

Finally, besides altered aversion module activation as such and in association with emotion self-regulation, attachment avoidance has been observed to be linked to brain activity as measured by EEG (ERP components N1, P1, and C1) in the context of attention, particularly to negative (and in some cases also neutral) emotional facial expressions. These effects were either described as aiming at devoting less attention to faces in general, or with the capacity to identifying social cues early and rapidly, both in association with deactivating strategies (Dan & Raz, 2012; Zhang, Li, & Zhou, 2008). Such data are indicative of attachment avoidance already influencing early regulatory mechanisms related to attention allocation to evade certain stimuli that may activate the attachment system in different ways.

Although attachment theory is mainly concerned with the influence of inter-individual differences of attachment on the processing of negative information – as the latter serve as main triggers of the attachment system and associated attachment pathway (see above) –, attachment also comprises an important positive, approach-related motivational component. The latter component is crucial for ensuring that proximity seeking is activated as a first response to homeostasis deviation/threat, and to encode social interactions that lead to a return to homeostasis and thus entail a felt sense of security as rewarding. In our framework, the above processes are summarized by activation of the approach module. The question of whether, and if yes how, avoidance and its associated de-activating strategies affect approach module functionality therefore appears warranted. Very interestingly, there is accumulating evidence from first-person social neuroscience investigations suggesting that avoidance involves blunted approach module activation.

In a first fMRI study (Vrtička, Andersson, Grandjean, Sander, & Vuilleumier, 2008), we observed decreased ventral striatum and ventral tegmental area activity as a function of increased avoidance scores (measured by the Adult Attachment Questionnaire – AAQ) when healthy adults received positive social feedback by means of happy facial expressions from unknown people paired with positive subjective performance feedback.

A second fMRI study published only one year later (Strathearn et al., 2009) confirmed our initial findings by showing that avoidant mothers (classified by the AAI) displayed decreased activity in the ventral striatum and medial orbitofrontal cortex when seeing images of their own smiling infants. Furthermore, activity in the hypothalamus during the baby face task was positively correlated with peripheral oxytocin levels during an independent mother-child interaction and was generally lower in avoidant mothers. Blunted approach module activity in association with avoidance therefore seems to be present in a more general positive social interaction context, as well as related to close social bonds in a caregiver-infant relationship, and such effect may be partially mediated by oxytocin.

One additional fMRI study provides further, albeit indirect support for decreased social reward-related brain activity within the approach module in relation to avoidance (Fareri, Niznikiewicz, Lee, & Delgado, 2012). Here, the authors assessed interpersonal closeness as measured with the “inclusion of the other in the self” (IOS) scale, and participants played a card guessing game for shared monetary outcomes with three partners: a friend, an unknown confederate, and a computer. Participants rated their excitement of winning money with each partner and provided scores on the IOS scale regarding their friend. Behavioral results revealed that the excitement of winning (and sharing the monetary reward) was highest for trials with the friend. The same pattern was observed in the ventral striatum and ventromedial orbitofrontal cortex as parts of the approach module, where activity was highest for winning trials with the friend. Furthermore, there was an intriguing association between IOS scores for the friend and ventral striatum activity during winning trials as a function of the three partner types. Whereas brain activity was consistently high during winning trials for participants scoring low on IOS, a computer < confederate < friend effect was present for participants scoring high on IOS. In other words, low interpersonal closeness seemed to have sustained or overemphasized non-social positive reward representation while decreasing sensitivity to social positive reward encoding in different social contexts – see also (Vrtička, 2012).

Finally, in an additional fMRI study examining the association between avoidance and brain responses to reward in children and adolescents, the authors used a gambling task with low versus high (*vs* no) monetary rewards, and assessed attachment using the Internal Working Model Scale (IWMS) questionnaire (Takiguchi et al., 2015). Furthermore, this study comprised a small group of individuals with reactive attachment disorder (RAD) and a control group. Consistent with the above findings, results revealed a negative association between avoidance and ventral striatum activity to rewarding stimuli (here: winning money). Furthermore, reduced activity in the caudate and nucleus accumbens – both part of the approach module – was observed during the high monetary reward condition in the RAD group compared with the control group. The latter finding suggests that modification of dopaminergic signaling localized to the striatum of children and adolescents may associate with RAD, which could lead towards potential future risks for psychopathology.

Apart from the one study by Strathearn et al. (2009) reporting a potential involvement of oxytocin in decreased reward-related activity associated with avoidance, the brain areas where an association between reduced activity and avoidance was found all seem to converge with the mesolimbic dopaminergic pathway and therefore imply the action of dopamine as primary neurotransmitter/-peptide. However, other neurotransmitter/-peptide systems may also play a role in approach module functionality.

Along these lines, one study using PET proposes the presence of a mechanism possibly mediated by endogenous opioids in relation to the approach module (Nummenmaa et al., 2015). In this study, a μ-opioid receptor (MOR) ligand was employed to assess MOR availability in association with attachment (measured with the ECR-R). Findings revealed a negative relation between avoidance and MOR availability in (among others) the dorsal striatum and orbitofrontal cortex. This finding could indicate a possible role of opioids in avoidance related to reward, because exogenous opioid agonists have been described to facilitate approach-oriented emotions (and inhibit avoidance-oriented emotions) more generally (Nummenmaa & Tuominen, 2018). There are several additional observations that suggest such proposed connection between the endogenous opioid system and avoidance. For example, a link between the minor allele (G) of the μ-opioid receptor polymorphism OPRM1 A118G, self-reported avoidance (using the RQ and ASQ), and the tendency to become engaged in affectionate relationships has been described (Troisi et al., 2011). Moreover, the abuse of heroin (but not drugs that do not influence the endogenous opioid system, such as ecstasy or cannabis) has been predominantly associated with (fearful-) avoidant attachment (employing the Family Attachment Interview) (Schindler, Thomasius, Petersen, & Sack, 2009). Also, more generally speaking, disruption of the endogenous opioid system by opiate addiction is known to be linked to antisocial behavior (Ross & Peselow, 2009). These findings further sustain a possible involvement of endogenous opioids in attachment as suggested by *BOTSA* (Machin & Dunbar, 2011), not only through effects on the aversion module in the context of pain and secure attachment more generally, but also on the approach module in association with avoidance in particular.

In the same study described above regarding the association between avoidance and *NR3C1* promoter methylation, we also assessed promoter methylation of the oxytocin receptor gene (*OXTR*) (Ein-Dor et al., 2018). We were interested in oxytocin signaling because, as suggested by the affiliative responses to stress model (Taylor, 2006), positive social relationships during both tend and befriend interactions in humans are thought to be neurally encoded in reward-related brain areas, and such neural encoding is likely to be associated with oxytocin (Feldman, 2017; Gordon et al., 2008; Kim et al., 2017; Li, Chen, Mascaro, Haroon, & Rilling, 2017; Strathearn et al., 2009; Wittfoth-Schardt et al., 2012). In addition, there is evidence that acute stress increases prosocial behavior (von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012). In line with the pattern observed for *NR3C1*, we also found a selective hyper-methylation of *OXTR* for avoidant (but not anxious) participants. These data further support the above mechanistic explanation of a physiological anticipation of, and actual lack of stress regulation through positive social contacts specifically related to avoidance. However, as this first study on *OXTR* (and *NR3C1*) methylation in association with attachment was purely correlational, and *OXTR* and *NR3C1* methylation did not correlate with each other as such, more research is needed to replicate and extend these findings. It should also be noted here that the role of oxytocin in interpersonal relationships is not solely positive (Beery, 2015; Nave, Camerer, & McCullough, 2015), and that oxytocin administration has been shown to actually have detrimental effects in insecurely attached participants and participants with borderline personality disorder (Bartz et al., 2010, 2011). Caution is therefore strongly advised.

So far, the above data show emerging associations between avoidance and brain activity linked to aversion, approach, as well as emotion regulation. What remains unclear to this point is whether avoidance may also be specifically implicated in mental state representation.

To our knowledge, there are only two first-person social neuroimaging investigations available to date that have specifically addressed this question. A first study used a Prisoners Dilemma Game (PDG) as an interactive mentalizing paradigm during fMRI scanning (Schneider-Hassloff, Straube, Nuscheler, Wemken, & Kircher, 2015). Results revealed increased activation in avoidant participants during the PDG task in the right amygdala, middle frontal gyrus, mid-cingulate cortex, superior parietal lobule, and bilateral inferior frontal gyrus. As such, avoidance did not primarily affect activity in our mental state representation module, but rather activity in the aversion module (amygdala, mid-cingulate cortex), and the emotion regulation module (middle and inferior frontal gyrus). The observed pattern was interpreted by the authors as suggesting that avoidance is associated with stronger engagement of cognitive mentalizing strategies and brain areas implicated in emotion regulation and cognitive control during mentalizing. This explanation dovetails with avoidance being characterized by the aim of down-regulating affect during social interaction through inhibitory and cognitive control processes, but concomitant rather high activity in the aversion module. Interestingly, an opposite pattern was observed for anxious individuals. In a second study, the authors used fNIRS to measure brain activity during the Reading the Mind from the Eyes Test (RMET) as a proxy for theory of mind (ToM) in late adolescence (Baskak et al., in press). Findings revealed overall higher activity during the ToM condition (relative to a control condition) in a secure versus an insecure group of participants (classified by means of the Relationship Scales Questionnaire – RSQ). Furthermore, higher activity was observed in channels corresponding to right superior temporal and adjacent parietal cortices in the secure relative to the insecure group during the ToM condition, those findings coinciding with data reported on secure attachment (see above). In turn, avoidance scores were negatively correlated with activity in channels that corresponded to right superior temporal cortex during ToM. The authors interpreted these data to suggest that attachment styles do have an effect on representation of ToM in terms of cortical activity in late adolescence. Particularly, avoidance may be represented by lower activity in the right superior temporal cortex during ToM, which could be related to weaker social need and habitual unwillingness for closeness.

It remains to be seen, however, how mental state representation is affected by avoidance (and anxiety) more generally, for example when using different experimental paradigms that involve different amounts of attachment relatedness and/or contexts of threat versus safety. One study has already probed such association by testing the influence of two personalized stress induction procedures – a general stress induction and an attachment-related stress induction – on the neural substrates of mentalization by means of a novel modification of the Reading the Mind in the Eyes Test (RMET-R) (Nolte et al., 2013). Although this study did not differentiate between avoidance and anxiety, findings disclosed that after stress exposure with the attachment-related stress induction, there was reduced mentalization-related activation in the left posterior superior temporal sulcus, left inferior frontal gyrus, and left temporoparietal junction. Moreover, the left middle frontal gyrus and left anterior insula showed greater functional connectivity to the left posterior STS. These findings were interpreted by the authors to indicate that attachment-related stress has a unique effect on the neural correlates of mentalization, namely by down-regulating activity in the mental state representation and emotion regulation modules. It would be very interesting to see whether this activation pattern may be different in avoidant versus anxious individuals, and what the implications of such dissociation may be.

A final issue related to avoidance and its associated IWMs concerns the fact that most so far available social neuroscience data was acquired in adults. Although initial attachment theory predicts (relative) stability of IWMs over the life span once established, more recent considerations point to malleability on both the short and long term (see the General Discussion section below). Data directly examining developmental processes in adolescents and children, however, is still very scarce.

In one fMRI study using the RSQ as attachment measure, we investigated social feedback processing in terms of the word-face task explained earlier in a population of 12-19 years old adolescents (Vrtička et al., 2014). In contrast to our data obtained in adults (Vrtička et al., 2008), data in adolescents did not reveal any specific associations between avoidance and reward-related activity during positive social feedback processing. Instead, avoidance was related to congruent versus incongruent social feedback processing more globally and suggested a shift towards the processing of congruent feedback with increasing avoidance scores in amygdala/hippocampus, caudate, ventral anterior cingulate cortex, and anterior insula. Most of the affected areas are included in the aversion module of our framework, whose function is also associated to saliency processing, i.e., the attribution of personal relevance to internal and external events (Seeley et al., 2007). Our data therefore point to a decrease in the attribution of self-relevance to incongruent social feedback, but an opposite tendency for congruent social feedback in relation to avoidance. In association with attachment theory, we interpreted these findings to suggest that one strategy avoidant adolescents may use to maintain their attachment system in a low activation state is to attribute less self-relevance to conflicting social information (i.e., incongruent social feedback), and to instead more readily process confirmatory social feedback, also on the emotional and visceral levels. Adolescence is a time where individuals increasingly turn to peers and adults outside of the immediate family context. To learn about the rules within these new social interactions, appropriate processing of information that signals potential conflict or disagreement (i.e., incongruent social feedback) appears particularly important. Interestingly, in the same study, we observed evidence for increased differential activity to incongruent social feedback in the ventral anterior cingulate cortex and anterior insula in older adolescents, and thus opposing findings related to avoidance. We therefore hypothesized that high avoidance during adolescence may preclude the usually observed “opening up” to social information in terms of social sensitivity, reflected by weaker brain responses to incongruent social feedback, and thus incur less mature processing of social feedback. However, more research, ideally employing longitudinal within-subject experimental designs, is needed to confirm and extend our argumentation.

2.3.2.3. Anxious attachment.

Attachment theory and behavioral data postulate a general notion of hyper-activating strategies in association with attachment anxiety. Such hyper-activation is thought to serve the function of enhancing attachment system activation to establish and maintain close social interaction, particularly to socially co-regulate emotions when in need. Physiological data furthermore indicate increased stress during negative attachment-related situations, which may be related to insufficient social co-regulation of distress (see above). However, physiological data cannot readily dissociate anxiety from avoidance, and it appears relevant to further describe how anxiety may functionally and anatomically relate to biological and neural mechanisms as investigated by means of social neuroscience paradigms.

One aspect of hyper-activating secondary attachment strategies in association with anxiety put forward by attachment theory is heightened sensitivity to information that may signal the unavailability of social co-regulation. This is due to the anxious other-model that conceives of attachment figures as absolutely necessary for achieving felt-security – despite repeated experiences of rejection. Linked to our attachment framework, one should thus expect increased aversion module activity indicative of increased negative attachment-related sensitivity.

Several functional and anatomical MRI investigations corroborate the assumption of increased aversion module activity in association with attachment anxiety. In our fMRI study on social feedback processing in adults (Vrtička et al., 2008), increased anxiety (measured by the AAQ) was positively correlated with (congruent) negative social feedback processing, i.e., losing in the task and seeing an angry facial expression. A similar pattern for anxiety (measured with the RSQ) was present in our fMRI study on social feedback processing in adolescents (Vrtička et al., 2014), which revealed increased activity in the amygdala/hippocampus as well as anterior insula and ventral anterior cingulate cortex for congruent negative social information. Please note that in our adolescent study, we interpreted such pattern of increased aversion module activation associated with anxiety as partially adaptive, because it is consistent with development over age (see also above). Similar findings of increased amygdala activation to negative emotional faces in anxious participants were present in two other fMRI studies (Norman et al., 2015; Redlich et al., 2015) assessing anxiety with the RSQ and ECR-RS, respectively. Furthermore, in the fMRI investigation measuring brain activity using the cyberball paradigm (DeWall et al., 2012), higher anxiety (acquired with the ASQ) was associated with heightened activity in the anterior insula and dorsal anterior cingulate cortex during social exclusion. Relatedly, a study using the PBI reported decreased hippocampus gray matter volume in mothers who reported lower perceived own maternal care (Kim et al., 2010), and the same brain area was found to have decreased gray matter volume as a function of anxiety scores measured by the ECR (Quirin et al., 2010). Attachment anxiety (assessed by the RSQ or ECR-R) was also found to be associated with increased gray matter volume in the amygdala, left insula, and in the pars opercularis of left inferior frontal gyrus, but decreased gray matter in the anterior temporal pole (Acosta, Jansen, Nuscheler, & Kircher, 2018; Benetti et al., 2010; Redlich et al., 2015).

Additional supportive evidence for heightened sensitivity to negative information in anxiously attached individuals is available from EEG studies probing neural responsivity in terms of semantic processing (N400 ERP component) and emotional saliency (LPP ERP component) to rejection-related words or negative pictures taken from the International Affective Picture System (IAPS) (Zayas, Shoda, Mischel, Osterhout, & Takahashi, 2009; Zilber, Goldstein, & Mikulincer, 2007). Both studies revealed patterns consistent with a stronger attribution of personal significance and/or perception of increased danger for the self of negative (social) information linked to attachment avoidance.

Overall, these findings on attachment anxiety appear to consistently point towards enhanced aversion module activation to negative attachment-related information and an associated increased attribution of saliency leading to a heightened arousal/stress response, also represented on the level of brain anatomy in regions associated with HPA axis functioning. Such data thus potentially reflect (at least one aspect of) hyper-activating secondary attachment strategies as part of anxious IWMs.

If attachment anxiety is related to enhanced aversion module activation in the context of attachment-related negativity/stress characteristic for hyper-activating strategies, can such pattern also be seen in association with functionality of the emotion (self-)regulation module?

In terms of specific associations between anxiety and emotion self-regulation, there is one study by Gillath et al. (2005) using the ECR as attachment measure involving a thinking versus stop thinking about negative attachment-related scenarios paradigm. Findings revealed that anxious participants showed increased activity in the anterior temporal pole, hippocampus, and dorsal anterior cingulate cortex when thinking about negative scenarios, but less activity in orbitofrontal cortex when suppressing these thoughts. Moreover, activity in the anterior temporal pole and the orbitofrontal cortex was inversely correlated. These data were taken to suggest that anxiety entails stronger activity in the aversion system during “normal” processing of negative attachment-related information and altered regulatory capacities to inhibit such processing during emotion regulation. No specific information, however, on the exact nature of the used emotion regulation strategy is available.

In our own fMRI study that we conducted some years later by measuring attachment with the RSQ (Vrtička et al., 2012), we only found evidence for increased amygdala activation when processing negative social images during natural viewing in association with anxiety, but no modification of activity during emotion regulation through either cognitive re-appraisal or (expressive) suppression. We interpreted such pattern as indicative for anxious people showing evidence for hyper-activating strategies when normally attending to negative social information (in accordance with what was discussed above), but that re-appraisal (and possibly also suppression) may be functional, if properly instructed.

According with this notion is EEG data acquired during simultaneous noxious skin stimulation and the administration of affective touch (Krahe et al., 2016). When pleasant touch was administered to CT-containing skin of the arm, higher anxiety (measured with the ECR-R) predicted attenuated N1 and N2 amplitudes (in contrast to high avoidance – see above). This finding points to functionality of social co-regulation in anxious individuals, possibly in association with endogenous opioids. However, more data on emotion regulation related to attachment anxiety is clearly needed, ideally by using some of the previous experimental designs investigating social regulation of pain processing/threat anticipation that only dissociated secure(-like) from insecure(-like) attachment (Coan et al., 2006; Eisenberger et al., 2011).

What about approach module functionality and attachment anxiety? In terms of attachment theory and our suggested prototypical anxious attachment pathway (Fig. 1d), hyper-activating strategies associated with anxiety should enhance the tendency for proximity seeking under stress and sustain positive reward-related representations of successful social co-regulation experiences.

One fMRI study assessed brain activity as a function of attachment (measured by the RSQ) during the automatic processing of facial expressions (sad and happy faces masked by neutral faces) (Donges et al., 2012). Anxious adults were found to be automatically more responsive to positive approach-related facial expression in brain areas that are involved in the perception of facial emotion, facial mimicry, or the assessment of affective value and social distance – namely left inferior, middle, and medial prefrontal cortex, globus pallidus, claustrum, and right cerebellum. However, these areas only partially overlap with the approach module of *NAMA* (i.e., middle/medial prefrontal cortex).

Stronger evidence is available from another fMRI study (Poore et al., 2012) describing a link between attachment anxiety (using the ECR) and brain activity in the ventral striatum and ventromedial orbitofrontal cortex – although related to prediction–error activity in response to a social reward, and thus not social reward as such. The experiment consisted of a task during which participants' expectations for their romantic partners' positive regard of them were confirmed or violated, in either a positive or a negative direction. What emerged in the ventral striatum and ventromedial orbitofrontal cortex was a relation between anxiety and activity during the receipt of unexpected positive feedback. Furthermore, the authors report an inverse relation in the ventral striatum between brain activity to unexpected positive feedback and partner trust. These findings were discussed according to attachment theory in a sense that "attachment anxiety represents an uncertainty about relational outcomes and the extent to which partners reciprocate romantic sentiment" (p. 7). Put differently, while anxious participants fear rejection by their partners, they at the same time hope for closeness and care, motivations which likely manifest themselves by activation of the approach module during unexpected/strongly hoped for but deemed unlikely social confirmation. Approach module activation in anxious individuals may thus not only reflect the processing of positive (mutual) social outcomes, but other aspects of associated IWMs related to expectations of positive social interactions (i.e., other-model).

Regarding IWMs and specifically the other-model, it is also of interest to investigate mental state representation module functionality in the context of attachment anxiety. According to attachment theory, the latter should be ambivalent, as others are still seen as sources for protection and felt security and associated with a strong desire for and dependence on social co-regulation, but at the same time connoted with negative attributes due to repeated experiences of rejection.

To date, we are only aware of two fMRI studies specifically looking at mental state representation in association with attachment measures. The first study described previously (see section on mental state representation and avoidance) found increased activity associated with mentalization (during a prisoners dilemma game) as a function of anxiety in several brain areas, but these areas are not integral parts of the mental state representation network within *NAMA* (Schneider-Hassloff et al., 2015). In the second study (Debbane et al., 2017), we asked adolescent participants (ages 12 to 19) to attribute positive and negative trait adjectives to either themselves or their best (same-sex) friend, and measured inter-individual differences in attachment with the RQ. Our data showed that adjective attribution (i.e., mental state representation) was reliably associated with activity in an extended cognitive and emotional mentalizing network comprising cortical midline structures, lateral anterior and superior temporal cortex, as well as ventral striatum/caudate and amygdala/hippocampus. In a subsequent step, we assessed correlations between brain activity and RQ scores that were either reflecting positivity versus negativity of the attachment-derived self-model (i.e., more negative self-model = higher attachment anxiety), or positivity versus negativity of the other-model (i.e., more negative other-model = higher attachment avoidance) (Griffin & Bartholomew, 1994). We only found significant associations between brain activity and scores pertaining to the attachment-derived self-model reflecting attachment anxiety; the more negative the participants' self-model was (i.e., higher anxiety), the more activity we observed in the amygdala/hippocampus, anterior temporal pole anterior superior temporal gyrus, (pre)cuneus, dorsolateral prefrontal cortex, fusiform face area, and cerebellum during both positive and negative adjective self-attribution. Furthermore, higher anxiety was associated with less activity in the same brain areas during negative adjective attribution to the best friend. These findings suggest that thinking about the self and a close other may have entailed concomitant activation decreases and increases in both the affective evaluation (especially the aversion module) and cognitive control (emotion regulation and mental state representation modules) networks associated with anxiety. Interestingly, both positive and negative self-representations appeared to have been enhanced, while negative other-representations were reduced. Hyper-activating strategies underlying attachment anxiety could thus involve heightened sensitivity regarding self-representations more generally, but reduced representation of negative other-traits, especially if the other is one's best friend. It should be considered here, however, that these findings were derived from an adolescent population and involve adjective attribution to a close other. It therefore remains to be seen how these findings generalize across other populations, and whether they also hold for adjective attribution to different, closer versus more distant others. The above data also pertain to internally driven self- and other-representations and not to more complex mental state representation processes employed during the exposure to external social stimuli. Finally, the context within which adjective attribution was carried out in our study was relatively stress-free. In terms of the “push–pull” between cognitive and emotional mentalization, future investigations should also look at different degrees of stress that may affect the switch point, either as such or as a function of individual differences in attachment (Fonagy & Luyten, 2009).

As already discussed in the section on attachment avoidance (see above), social neuroscience research has recently begun to also examine the possible gene by environment interaction in association with attachment through epigenetics. Specifically related to attachment anxiety, however, the emerging patterns are inconclusive. The current review will therefore not discuss these epigenetic findings in detail. For further reading, please see (Bosmans, Young, & Hankin, 2018; Ein-Dor et al., 2018; Haas et al., 2016; Luijk et al., 2010; Mulder et al., 2017; van Ijzendoorn, Caspers, Bakermans-Kranenburg, Beach, & Philibert, 2010).

2.3.2.4. CONCLUSIONS AND PRACTICAL IMPLICATIONS.

As evident from the sections above, a growing number of studies employing first-person social neuroscience methods on the topic of human attachment are available in the literature. These studies, however, used a wide range of neuroimaging techniques, experimental paradigms, cross-sectional versus longitudinal study designs, as well as self-reports, behavioral observations, and semi-structured narrative procedures to assess inter-individual differences in attachment. Nonetheless – or even despite these considerable variations at several levels of investigation –, certain patterns pertaining to the suggested prototypical attachment pathways and the associated functional neuro-anatomical model of human attachment (*NAMA*) are emerging. A short summary of most consistent effects regarding attachment security, avoidance, and anxiety on the functioning of affective evaluation (approach and aversion) and cognitive control (emotion regulation and mental state representation) is provided Fig. 3.

In accordance with what was said before, there are several practical implications that emerge from the so far available findings.

First, it appears that secure-based attachment physical interactions as well as visual and mental representations of the latter can serve as potent regulators of pain, threat, and/or distress reactions maintained by the aversion module of *NAMA*. It has even been shown that secure-base priming can have such aversion-modulating effect in participants with elevated trait avoidance and anxiety. As Norman et al. (2015) state: “these findings support the potential use of attachment security-boosting methods as interventions and suggest a neural mechanism for the protective effect of social bonds” (p. 832). At the same time, there is growing evidence that particularly avoidance is associated with altered approach module functioning, which can preclude the beneficial effect of social bonds on pain and threat processing, or even exacerbate aversion module activity when social co-regulation is available. This pattern is likely due to the avoidant IWMs predicting unavailability of social resources for pain and distress co-regulation and the preferential use of self-regulatory emotion regulation strategies associated with inhibition and/or suppression. In the case of avoidance, it therefore appears relevant – also for attachment-informed therapeutic settings – to first re-instate a notion of reward experienced through social interactions and to re-build trust in the sense that significant others will be available when needed and that one has the efficiency and capacity to reliably elicit social co-regulation under distress.

Second, there seems to be first-person social neuroscience evidence that attachment insecurity in general, but avoidance in particular, is associated with altered emotion self-regulation capacity entailing HPA axis modification. This effect appears to again be partially driven by the preferential use of suppression and/or inhibition as emotion self-regulation strategy, which only seems to work to a certain degree and under certain circumstances. Specifically, when an antecedent-focused emotion regulation strategy like cognitive re-appraisal should be employed by avoidant individuals, this strategy was found to be less efficient in down-regulating aversion module activity when dealing with social negative information. Interestingly, no such effect was observed for anxiety, although natural emotion processing seems to be up-regulated in association with hyper-activating secondary attachment strategies. These first-person social neuroscience findings could thus also inform therapeutic settings where different emotion regulation strategies may be favored when treating individuals with difficulties associated with avoidance versus anxiety.

Third, there appears to be an indication that the first-person social neuroscience pattern related to avoidance is generally less adaptive than the pattern related to anxiety – as summarized above. In terms of prototypical attachment pathways, such finding seems related to the fact that for anxiety, proximity seeking under distress, social co-regulation of stress, and an associated positive representation of others (through rewarding experiences due to a return to homeostasis after social interaction) are still viable options, although not occurring very often/in a predictable manner. Conversely, for avoidance, involvement of the (social) approach part of the attachment pathway appears to be reduced from the start. As outlined in the first chapter, such activation pattern associated with the prototypical avoidant attachment pathway does represent a meaningful adaptation to an early environment where others are not readily available and are not contributing to stress co-regulation. Therefore, such avoidant strategy serves to “protect the self in intense personal relationships” and may “be necessary because the self, which is … the product of the other, forever remains vulnerable to social influence”. Nonetheless, the avoidant – as well as the anxious – strategy “signal a certain degree of weakness” (Fonagy, 2001) (p. 442). In terms of the “push–pull” notion of affective evaluation versus cognitive control (Fonagy & Luyten, 2009), attachment insecurity may predispose individuals to use more “rigid” strategies during social interactions, particularly under distress, making them less flexible and less receptive for learning new associations. In other words, a certain disadvantage is to be expected, maybe also associated with an elevated risk for developing interpersonal disturbances, when the adaptive strategies of avoidance and anxiety in specific unfavorable environments are internalized and generalized to other, not necessarily unfavorable circumstances. From the so far available social neuroscience data, it appears that avoidant individuals may be somewhat more vulnerable to

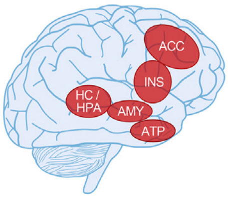
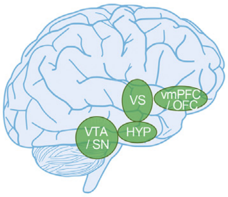
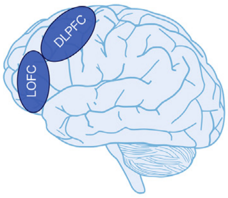
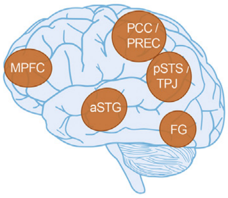
Module	Secure Attachment (balanced de- and hyper-activation)	Avoidant Attachment (de-activation)	Anxious Attachment (hyper-activation)
Aversion Module  	• Beneficial stress-reducing influence of secure-based social interactions, priming, and mental representations (anatomy, function, and connectivity) • Short- and long-term effects • Protective effect of readily available social (co-)regulation during stress & generally lower likelihood of early adversity ↓	• Lower activation during social exclusion due to expectation of rejection by others • Increased activation during negative social information processing when inhibition/suppression as emotion regulation strategy cannot be employed • Indication of long-term elevated stress / HPA axis modification • Limited efficiency of de-activating strategies ↑↓	• Higher activation during the processing of negative social information • Anatomical alteration pointing to long-term elevated stress / HPA axis modification • This pattern is consistent with hyper-activating strategies that increase the saliency of social cues pointing towards social rejection / the unavailability of others during stressful situations ↑
Approach Module  	• Activation generally reflecting positive motivational attributes towards, and affective representations of others – especially under conditions of threat and stress, i.e. when others are needed to (co-)regulate negative states • This pattern accords with a positive model of others characteristic for attachment security ↑	• Generally decreased approach module activation (both across close and more distant social contexts) • Role of oxytocin and/or endogenous opioids, apart from dopamine, in such processes • Pattern reflects negative other-model associated with attachment avoidance ↓	• Only limited evidence of altered approach module functionality • Some findings point to increased (automatic) processing of positive social cues, particularly when they occur unexpectedly, i.e. when social rejection is anticipated but does not occur • Patten agrees with a partially positive other-model / wish for closeness and care ↑
Emotion (Self-) Regulation Module  	• Emotion (self-)regulation appears functional and efficient (successful aversion module down-regulation through physical contact as well as by positive mental representation of significant others) • Indication of better connectivity between the emotion regulation and aversion modules • Mental state representation ↑	• Preferential use of inhibition / suppression when dealing with (social) emotions, both positive and negative • Emotion regulation appears ineffective when inhibition / suppression cannot be employed – e.g. cognitive re-appraisal fails in down-regulating aversion module activity during negative social information processing • Social (co-)regulation appears ineffective and may even exacerbate aversion module activity during stressful situations ↓	• Increased activation during natural processing of (social) negative information • No consistent indication of emotion down-regulation difficulties • Both cognitive re-appraisal and suppression / inhibition appear functional when properly instructed • Social (co-)regulation under stress also seems effective • Pattern points to dependence on external contribution towards emotion regulation associated with a negative self-model ↓
Mental State Representation Module  	seems to develop early • Predominantly positive represent-tations of others • More extensive (functional) connectivity with the other modules ↑	• Only very limited evidence • One study implies less mentalizing (RMET) • Possible tendency for hyper-mentalization due to the need for an early assessment of social situations so that inhibition / suppression can be employed if deemed necessary • More data is still needed ↓	• Only very limited evidence • One study in adolescents indicates both activation in- and decreases as a function of both mentalization content valence (positive versus negative) and focus (self versus close other) • More data is still needed ↓↑

Fig. 3 – Extended and refined summary of associations between approach, aversion, emotion regulation, and mental state representation module functionality and inter-individual differences in attachment security, avoidance, and anxiety, as disclosed by first-person social neuroscience data. Abbreviations: HPA = hypothalamus-pituitary adrenal; *aversion module* – ACC = anterior cingulate cortex, INS = insula, HC/HPA = hippocampus/HPA-axis, AMY = amygdala, ATP = anterior temporal pole; *approach module* – vmMPF/OFC = ventromedial prefrontal/orbitofrontal cortex, VS = ventral striatum, HYP = hypothalamus, VTA/SN = ventral tegmental area/substantia nigra; *emotion regulation module* – DLPFC = dorsolateral prefrontal cortex; LOFC = lateral orbitofrontal cortex; *mental state representation module* – MPFC = medial prefrontal cortex, PCC/PREC = posterior cingulate cortex/precuneus, pSTS/TPJ = posterior superior temporal sulcus/temporo-parietal junction, aSTG = anterior superior temporal gyrus, FG = fusiform gyrus.

psychopathology – although, for example, a preferential link between anxiety and borderline personality disorder (BPD) is evident (Fonagy & Luyten, 2009).

Overall, fundamental first-person social neuroscience research into the etiology of attachment security, avoidance, and anxiety certainly is warranted to better understand the associated alteration in affective (approach and aversion) as well as cognitive (emotion regulation and mental state representation) modules of *NAMA*. Furthermore, it may be interesting to look more closely into disorganized attachment that manifests both avoidant and anxious tendencies and to elucidate which modifications of module functionality may most strongly contribute to a breakdown of organized attachment strategies. Such first-person social neuroscience research on human attachment may not only disclose additional ways of promoting attachment security, but also inspire future prevention and intervention strategies for individuals and families at risk.

2.4. Second-person social neuroscience in the context of human attachment

The above data pertaining to associations between interindividual differences in attachment and brain anatomy and function from a first-person social neuroscience perspective provide important information on how human attachment may be most likely represented on the biological and brain level. One limitation of the underlying social neuroscience paradigms, however, is that they typically observe individuals in isolation. That is, participants view or hear social emotional stimuli when they are alone and thus not engaged in reciprocal interactions with other people. Such an approach appears suboptimal, as social emotional processing is "fundamentally different when we are in interaction with others rather than merely observing them" (Schilbach et al., 2013) (p. 393). The field of social neuroscience has therefore recently begun considering additional methods by which the neural substrates of social interaction can be observed: through the assessment of behavioral, biological, and brain processes in (at least) two people engaging in a direct interaction with each other. This represents a more ecologically valid approach for determining the biological and brain basis of processes enabling us to understanding others.

2.4.1. Social interaction, bio-behavioral synchrony, and attachment

What is needed for two (or more) individuals to successfully interact with each other? One central component that has recently been emphasized – also, or particularly, in association with attachment – is bio-behavioral synchrony. Bio-behavioral synchrony is defined as the coordination of biological processes and species-typical behaviors expressed during or immediately after social contact (Atzil, Hendler, & Feldman, 2014; Feldman, 2012a, 2012b, 2017). It is thought to be evident in (at least) four systems of the human organism: behavior, autonomic/physiological responses, endocrine responses, and brain activity. These four levels describe interpersonal attunement across many different modalities, comprising eye gaze, touch, and vocalizations, but also heart rate, hormone secretion (e.g., cortisol, oxytocin), and neural activation patterns. Furthermore, the degree of bio-behavioral synchrony is suggested to be highest in the closest social bonds between parents and their children, and to successively decrease as the degree of closeness decreases (Feldman, 2017).

Yet why does bio-behavioral synchrony emerge at the first place, and what is its role for human social interactions? According to a recent *Evolutionary Theory of Social Affiliation* (Atzil et al., 2018), bio-behavioral synchrony is a key feature of social species – including humans –, because in the latter, survival depends upon social bonds. More specifically, in social species, animals co-regulate one another's fundamental physiological processes to maintain homeostasis. As described in the introduction, if an environmental challenge leads to a deviation in homeostasis, allostatic regulation as an ongoing adjustment of an individual's internal milieu that is necessary for survival, growth and reproduction (Sterling, 2012) will occur. Social animals gradually learn to regulate their own and others' physiology through allostasis using social communication (Atzil & Barrett, 2017). For example, in humans, mothers regulate their infants' allostasis related to temperature, heart rate, sleep, and arousal (Beckes et al., 2015; Feldman, Eidelman, Sirota, & Weller, 2002; Feldman, Magori-Cohen, Galili, Singer, & Louzoun, 2011). It is at this point where attachment comes into play; the *Evolutionary Theory of Social Affiliation* (Atzil et al., 2018) suggests that a caregiver's allostatic support is not only rewarding by itself (Keramati & Gutkin, 2014), but that it is furthermore associated with the provision of nutrition, soothing, and comfort, thereby making social interactions a strong reinforcement. The origins of attachment and associated IWMs would thus likely lay in early allostasis co-regulation experiences and the thereby resulting predictions about the availability of others to serve as external allostasis co-regulators, as well as the own ability to call for external allostasis co-regulation when needed. In the words of Atzil et al. (2018): "We propose … that parental care is directed towards infant allostasis, and thus provides an optimal incentive for brain development and learning, as via allostasis the social dyad encourages the acquisition of new behaviors and concepts that are necessary for social affiliation." (p. 624).

Within this context of bio-behavioral synchrony and attachment, there is ample evidence for behavioral (e.g., eye gaze, vocalizations, affective expressions, touch, etc.), physiological (e.g., heart rate, breathing rate, etc.), and hormone secretion (e.g., oxytocin, cortisol, etc.) attunement within the parent-child and particularly mother-child bond, but also in later attachment relationships throughout life – see (Feldman, 2017). Furthermore, increased bio-behavioral synchrony between parents and their children at child age 3–4 months has been found to predict infants' attachment security, self-regulation, behavior adaptation, empathy, symbolic competence, and moral internalization across childhood and up to adolescence – see (Feldman, 2012b). Another line of research has illustrated that interpersonal synchrony by means of attuned movement increases prosocial behavior in children, a process likely indicative of very early development of altruistic behavior (Cirelli, Einarson, & Trainor, 2014; Cirelli, Wan, & Trainor, 2016; Rabinowitch & Meltzoff, 2017).

What remains less understood however, is brain-to-brain synchrony, or inter-brain coherence reflecting interpersonal attunement on the neural level, which has recently become a focus of second-person social neuroscience research. The general idea behind inter-brain coherence is that the independent neural oscillations of a sender and a receiver must become coupled so that information of any sort can flow between them (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). According to the phase reset model, such coupling occurs because ongoing oscillations in the receiver reset their phases to the incoming oscillations from the sender (Brandt, 1997). As a result, both the sender and receivers' brains entrain to the rhythm of the transmitted signal, providing a neural underpinning for interpersonal exchange and behavioral synchronization (Wilson & Wilson, 2005). Different patterns of inter-brain coherence are possible. The most prominent ones are dissociated into: (i) synchronization due to a common external signal (e.g., watching the same movie, listening to the same music, etc.); (ii) unidirectional synchronization from a follower to a leader; (iii) dynamic interaction where leader and follower have mutual influence on each other; and (iv) group interaction with multiple mutually interconnected and co-dependent individuals (Nummenmaa, Lahnakoski, & Glerean, 2018). For attachment-related research, unidirectional and dynamic/group interaction synchrony are most relevant, particularly during dyadic interaction tasks involving parents and their children or adults with differing relationships to each other. Due to technical restrictions, most prominent social neuroscience techniques used for such research are EEG and fNIRS.

What generally emerges from these investigations is that, when engaging in cooperative versus independent (or sometimes even competitive) tasks, inter-brain coherence appears to increase (Baker et al., 2016; Cheng, Li, & Hu, 2015; Cui, Bryant, & Reiss, 2012; Fishburn et al., 2018; Hu et al., 2018; Hu, Hu, Li, Pan, & Cheng, 2017; Leong et al., 2017; Liu et al., 2016, 2018; Miller et al., 2019; Pan, Cheng, Zhang, Li, & Hu, 2017; Pan, Novembre, Song, Li, & Hu, 2018; Quaresima & Ferrari, 2019; Reindl, Gerloff, Scharke, & Konrad, 2018; Wass et al., 2018). Furthermore, according to Feldman's (2017) considerations, inter-brain coherence seems to be generally higher in dyads that are closer to each other – e.g., in romantic couples versus pairs of strangers, or in children playing a game with their mothers versus unknown females (Kinreich, Djalovski, Kraus, Louzoun, & Feldman, 2017; Pan et al., 2017; Reindl et al., 2018). Moreover, a recent study reported that inter-brain coherence during handholding in romantic partners, one of whom received pain, was associated with pain reduction (Goldstein, Weissman-Fogel, Dumas, & Shamay-Tsoory, 2018). More precisely, using EEG and calculating inter-brain coherence in the alpha-mu band (8–12 Hz), handholding during pain administration increased coherence in a network that mainly involved the central regions of the pain target and the right hemisphere of the pain observer, and coherence in this network was found to correlate with analgesia magnitude and observer's empathic accuracy. In addition, particularly parent-infant inter-brain coherence may be indicative of emotion co-regulation, social learning through mutual eye gaze, attention, and communication (Leong et al., 2017; Wass et al., 2018). Finally, a recent study assessed inter-brain coherence in 12 senior high school students and their teacher during regular biology lessons using EEG by comparing retention of that lesson's content using different teaching styles (videos and lectures) (Bevilacqua et al., 2019). Findings revealed that students' inter-brain coherence and their content retention were higher for videos than lectures across the six classes. Furthermore, students who reported greater social closeness to the teacher showed higher inter-brain coherence with the teacher, but this was only the case for lectures, and students' retention of the class content correlated with student-teacher closeness, but not with inter-brain coherence. These findings imply that inter-brain coherence has a functional implication in social processes and pain analgesia, and that it may be modulated not only between categories of interpersonal closeness, but also within categories as function of inter-individual differences in relationship quality.

Broadly missing, however, are studies directly associating inter-brain coherence with measures of attachment.

In a first preliminary investigation, we recorded inter-brain coherence from $N = 28$ mother-child pairs (child age 8–12 years) using fNIRS hyperscanning while the pairs engaged in a cooperative [*vs* an independent (i.e., control condition)] button-press task (Miller et al., 2019). The goal during the cooperative phases was to press a keyboard-button as simultaneously after the appearance of a visual cue as possible and thus to attune one's behavior to one another. The control condition involved the same visual cue, but button-press responses were to be given independently of each other (no response contingency needed). We observed increased inter-brain coherence over right prefrontal and right temporal sites for cooperative versus independent game play – in line with previous accounts of these regions subserving roles related to social cognitive processing and mental state representation/theory of mind, particularly during direct social interaction, also within other hyperscanning paradigms (see Miller et al., 2019). Furthermore, we found sex-differences in this activation pattern, as inter-brain coherence was only altered by the cooperative versus independent tasks in mother-son but not mother–daughter pairs. Finally, we correlated inter-brain coherence increase during cooperation versus independent play with an attachment measure obtained from children reflecting their attachment towards their mother – the child version of the ECR-R – (Brenning, Soenens, Braet, & Bosmans, 2011). In an uncorrected analysis, we found that higher attachment avoidance towards the mother predicted less inter-brain coherence during cooperation in one right prefrontal brain region. This association, however, did not survive more stringent correction for multiple comparisons, and should thus be regarded with caution. Nonetheless, our finding agrees with de-activating strategies characterizing avoidant IWMs and less inter-personal attunement on the level of the brain when others are not readily perceived/expected as available during social exchange.

In another fNIRS hyperscanning study (Nguyen et al., 2020), we assessed inter-brain coherence in mother-child dyads (child age 5 years) during a cooperative versus independent problem-solving task consisting of a tangram puzzle game. In this task, mother-child pairs either had to work together (cooperation condition) or independently of each other (visually separated by a removable barrier; independent condition) to recreate puzzle templates. An additional resting state condition (relax with eyes closed) was included as a baseline control. Regions of interest (ROIs) were chosen to overlap with temporo-parietal areas involved in mental state representation/theory of mind as well as dorsolateral prefrontal areas important for attention and cognitive regulation (see Nguyen et al., 2020). Findings revealed that inter-brain coherence was significantly increased during the cooperation (as compared to both the independent and control) condition(s) across all ROIs, and that task-performance positively correlated with inter-brain coherence during cooperation. Inter-brain coherence therefore appeared functionally important to cooperatively perform better in the problem-solving task. Furthermore, we assessed behavioral reciprocity representing contingent responses resulting in a turn-taking quality of interactions as behavioral flow, and thus indicative of a high-quality (and thus secure-like) mother-child relationship coded from video recordings using the Coding System for Mother–Child Interactions (CSMCI). In so doing, we found that higher behavioral reciprocity associated with increased inter-brain coherence during cooperation. These findings further emphasize neural synchrony as a biomarker for parent-child interaction quality – albeit they cannot (yet) differentiate between attachment security versus insecurity and avoidance/anxiety.

We are currently extending our research into parent-infant inter-brain coherence using fNIRS hyperscanning by also testing father-child dyads and assessing potential differences in parent-boy and parent-girl dyads, as well as by including more specific (self-report and narrative) attachment measures in both parents and children. We will also try to elucidate potential links between inter-brain coherence and other aspects of bio-behavioral synchrony, for example peripheral physiology endocrinology, and behavior in both parent-child and adult–adult dyads.

Although the assessment of bio-behavioral synchrony appears particularly promising for attachment research, some challenges remain.

A first challenge concerns the functional implication of synchrony, particularly on a neural level. This comes from the fact that the most common current analysis methods to derive inter-brain coherence look for any kind of temporal contingency between two (or more) brain activity time courses – i.e., in-phase but also out-of-phase and opposite-in-phase patterns. Within this context, the important question remains whether more "synchrony" in terms of temporal contingency/coherence is always better. Particularly in regards to allostasis co-regulation within attachment relationships, for example, when a mother is soothing her crying child, it is intuitive to assume that maximal synchrony (i.e., the mother also starting to feel distressed and to cry) will not be most goal-conducive and that a temporary "desynchronization" may be more beneficial instead. Future investigations must therefore look at sequences of "synchronization" and "desynchronization". This cannot be achieved when only investigating inter-brain coherence during cooperative tasks (with expected higher coherence), but also situations where there is a certain level of distress that is supposed to activate the attachment system (because of a deviation from homeostasis and an associated need for allostasis co-regulation). It is likely that the degree of "desynchronization" and the time it takes to reach "resynchronization" will be indicative of the relationship quality and thus attachment.

A second, more general challenge concerns the integration of the different (i.e., behavioral, physiological, endocrine, and neural) measures of bio-behavioral synchrony, and likewise the different means of deriving inter-brain coherence by using EEG versus fNIRS. One difficulty may be the distinct time-courses (i.e., frequencies) of assessed signals. Usually, physiological and EEG methods have a much higher sampling rate than fNIRS, so that derivates of bio-behavioral synchrony cannot be directly integrated with each other. The same applies to endocrine measures, but in the opposite direction, because hormone secretion is usually assessed on a much longer time scale. Finally, behavioral indices may considerably vary in their temporal pattern as they can either be assessed over very short or prolonged time periods. To better understand the functional implication of inter-brain coherence, however, it appears essential to link it to the other bio-behavioral synchrony modalities. Such integrative approach will in turn help delineating the functional implication of synchrony, particularly in an attachment relationship context.

Overall, the investigation of bio-behavioral synchrony appears to represent a very promising future avenue in the context of social interactions more generally, and attachment in particular. Ideally, these second-person social neuroscience methods will be applied in closer combination with attachment measures, perhaps simultaneously with paradigms that are used to determine children's attachment classification (e.g., the SPP). In so doing, additional objective/third-person data could inform and extend information used for attachment classification. At the same time, a lot has yet to be learned about the functional implications of synchrony in biological and brain signals (i.e., is more synchrony always better, how do different levels of bio-behavioral synchrony relate to one another, etc.) and how such patterns may relate to attachment and interpersonal relationship quality more generally.

3. General discussion, limitations, and remaining issues

In this review, we provided an extension and refinement of *NAMA* based on a newly proposed prototypical initial attachment pathway and its derivatives relating to attachment security, avoidance, and anxiety. Furthermore, we extended first-person social neuroscience accounts by pointing towards newly emerging research using second-person social neuroscience methods such as EEG and particularly fNIRS hyperscanning. We hope that the above considerations may inform attachment theory and research, and provide a fruitful basis for future dialogue, also concerning prevention and intervention strategies for individuals and families at risk. In this dialogue, several issues should be considered that go beyond what has been previously discussed here. Some of these issues are briefly mentioned below.

As already described above, there is a wide variability of tests to derive inter-individual differences in attachment, employed (first- and second person) social neuroscience paradigms, measuring techniques, and considerations regarding participant age (i.e., cross-sectional *vs* longitudinal; children *vs* adolescents *vs* adults) in the so far available literature. Nonetheless, or even despite this variability at different levels of investigation, certain consistent patterns regarding attachment security, avoidance, and anxiety are starting to emerge.

At the same time, there remains the notion that different attachment instruments assess different underlying processes. This notion has been particularly expressed when comparing the adult attachment interview (AAI) to attachment self-report questionnaires in adults, which revealed that "developmental and social psychological measures of attachment security predict somewhat distinct – though theoretically anticipated – aspects of functioning in adult relationships" (Roisman et al., 2007). Consequently, when using different measures of attachment in social neuroscience research, somewhat divergent findings are to be expected. It therefore appears important to anticipate future studies that use more than one attachment measure in the same participant population to directly assess possible differences due to the attachment instruments employed. A first step in this direction has been taken by Yaseen and colleagues (Yaseen, Zhang, Muran, Winston, & Galynker, 2016), who administered both the adult attachment interview (AAI) and the Relationships Scales Questionnaire (RSQ) to 28 women who subsequently viewed their mothers in neutral-, valence-, and salience-rating conditions during fMRI scanning. Their findings revealed that the AAI was more strongly associated with activity related to interoceptive, 'core-self'-related processes, while the RSQ more readily captured activity linked to higher-order cognitions involved in attachment. The above said, it should be highlighted that the administration and analysis of narrative-based and behavioral (i.e., video ratings) attachment measures is considerably more complex and costly, particularly due to the requirement of trained, reliable raters. Furthermore, as narrative- and behavioral-based methods like the AAI are often conceived in a categorical way while self-report measures mostly derive dimensional scores, direct comparisons may be hampered. It nonetheless appears relevant to ensure comparability of social neuroscience findings derived by using different attachment measures, and to push forward a mutual dialogue between research groups with different traditions of assessing attachment in their participants.

Similarly, several aspects regarding the emergence, developmental change versus stability, and maintenance of inter-individual differences in attachment – also comprising the notion of age-related developmental shifts – were recently brought up (Fraley, 2019). For the present review, such considerations are relevant in the sense that associations of biological and brain patterns with certain attachment orientations, i.e., avoidance, should not be expected to be identical in different age groups, when using cross-sectional designs, or in the same aging individual assessed repeatedly using longitudinal designs. This notion, however, should not convey the message that social neuroscience investigations may only be performed in isolated age groups, i.e., adults, but rather that information from many different age groups is needed because the observed patterns are likely to differ as a function of participant age.

Furthermore, in this review, we focused on associations between brain anatomy and activity and inter-individual differences in attachment in healthy participants. We chose this approach to outline the functionality of the human attachment system from a more fundamental social neuroscience perspective. It is, however, well known that attachment insecurity may represent a risk factor for the development of psychopathology, particularly in relation to deficits associated with mentalization/mentalizing (Debbane et al., 2016; Fonagy & Luyten, 2009). One condition that is highlighted within this context is Borderline Personality Disorder (BPD) (Buchheim & Diamond, 2018; Levy, 2005), and social neuroscience investigations have examined possible links between attachment and BPD in the past (Buchheim et al., 2008, 2016). Along the same lines, researchers have begun to investigate possible neural substrates of unresolved/disorganized attachment that is usually characterized by the breakdown of organized (secure, avoidant, anxious) attachment strategies and often associated with early life adversity like loss through death, abuse, and/or threat of abandonment (Buchheim et al., 2006; Letourneau, Hart, & MacMaster, 2017). One prominent attachment measure employed for such investigations – mainly during fMRI scanning – is the Adult Attachment Projective (AAP), which consists of a series of black-and-white line drawings depicting one neutral and seven negative attachment-related scenes. More recently, the AAP has been extended by validated control images that enable a more detailed assessment in an fMRI environment (Labek, Viviani, Gizewski, Verius, & Buchheim, 2016). It will be important to continue this line of research by also using different attachment measurement methods to further elucidate possible associations between attachment insecurity and BPD, as well as to better classify the potential underlying neural processes related to attachment disorganization.

Finally, as evident from the included studies on the biological and brain substrates of human attachment, there is a clear bias towards women versus men and mothers versus fathers using first-person social neuroscience methods, and towards mother-child versus father-child dyads using second-person social neuroscience methods. Such bias is likely due to attachment theory initially emphasizing the importance of the mother for child development, a view that has only gradually started to change during the last decades (Bretherton, 2010). This development was likely influenced by societal transformations especially within western, educated, industrialized, rich, and democratic – in short WEIRD – cultures, where fathers became gradually more involved in childcare (Rohner & Veneziano, 2001). Recently, evidence has started accumulating that fathers also serve as attachment figures ((Abraham et al., 2014; Brown, Mangelsdorf, & Neff, 2012; Brown, Mangelsdorf, Shigeto, & Wong, 2018; Grossmann et al., 2002; Grossmann, Grossmann, Kindler, & Zimmermann, 2008; Lucassen et al., 2011)), and that the paternal brain may very much resemble the maternal brain from a fundamental neurobiological perspective (Feldman, Braun, & Champagne, 2019). Furthermore, the importance of the inter-parental relationship beyond mother- and father-child attachment was highlighted (Bretherton, 2010). In future first- and second-person social neuroscience investigations on human attachment, more efforts should therefore not only be directed towards investigating attachment in fathers and father-child dyads, but ideally also within the entire mother-child-father triad, and even beyond.

Taken together, it is evident that the social neuroscience of human attachment is still a quite recent field of investigation that needs further elaboration and extension. Such venture will necessitate a far-reaching and open dialogue between the two underlying disciplines of neuroscience and psychology, and require large-scale, longitudinal, and cross-cultural future investigations. Furthermore, as is currently happening in the field of social neuroscience, studies on the biological and brain basis of human attachment should increasingly embrace a second-person social neuroscience approach to examine interpersonal processes directly in two (or more) interacting individuals. The implications of thereby obtained results will not only advance our knowledge on the neurobiological underpinnings of understanding others, but also influence the emergence of new prevention and intervention strategies for individuals and families at risk, informing policymaking and ultimately society. Humans are born social, wired to connect to other minds (Cacioppo et al., 2010), and therefore strongly dependent upon constant, close, and healthy social bonds. Attachment theory, in combination with social neuroscience, can help us better understand the fundamental nature of the human species.

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