

Potential for the medial prefrontal cortex to link mentalizing and attachment schemas

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Abstract

Mentalizing—the process of thinking about others' and one's own thoughts and feelings—is ubiquitous and consequential. Traditionally, researchers have examined how the brain supports mentalizing. Here, we ask what content knowledge the brain relies on to mentalize. Based on converging evidence from developmental, cognitive, and social-affective neurosciences, we suggest that the socio-affective knowledge gained from early attachment relationships provide the basis for such content knowledge. Moreover, we suggest that this attachment relationship-generated schematized knowledge is represented in the medial prefrontal cortex (mPFC) and accessed during mentalizing. In this article, we (i) describe mPFC activity during early caregiving experiences to demonstrate its encoding of the affective meaning of parent-child interaction episodes; (ii) extrapolate from research on memory consolidation in the cognitive neurosciences to propose how regularities across parent-child interactions become abstracted into an attachment schema in the mPFC; (iii) discuss the functionality of mPFC-coordinated representations of attachment schemas for predicting the social world. Long recognized by attachment theory, our integrative perspective prompts researchers to neuroscientifically examine whether the social relationship with one's caregiver builds attachment knowledge that in turns forms the basis for mentalizing.

Keywords: mentalizing, attachment, development, schemas, prediction

One of the most remarkable characteristics of humans is our ability to think about others' thoughts and feelings. Whether collaborating with a team of colleagues at work or understanding our close others' most intimate vulnerabilities, we are always trying to make sense of the social world (Mildner and Tamir 2021). This process is formally known as mentalizing, and it is defined as the process of inferring other people's and one's own internal mental states, such as their beliefs, intentions, feelings, and traits. Mentalizing is important for building strong social relationships (Cacioppo et al. 2015, Sened et al. 2017, Baek et al. 2023) and improving our own emotional well-being (e.g. Schwarzer et al. 2021), to name only a handful of its benefits in everyday life.

Over the past few decades, social cognitive and affective neuroscientists have made important discoveries in delineating the neural bases of mentalizing. In particular, the medial prefrontal cortex (i.e. mPFC) has emerged as a central hub for mentalizing (Moran and Mitchell 2016; see Schurz et al. 2014, 2021 for a meta-analysis of other brain regions that support mentalizing). The mPFC has been posited to integrate lower-level/embodied representations from the primary sensorimotor cortex and anterior insula with higher-level conceptual representations in the prefrontal cortex, temporoparietal junction (TPJ), and temporal pole to make judgments about ourselves and others (e.g. Quesque and Brass 2019, Van Overwalle and Heleven 2021). In univariate contrasts, the mPFC is activated when we make mental state inferences about others

(Mitchell 2009), form impressions of others (e.g. Mende-Siedlecki et al. 2013), hold social information in working memory (Meyer and Collier 2020), and infer how others feel about us (Eisenberger et al. 2003). Additionally, computational approaches demonstrate that different aspects of mentalizing, such as whether someone is emotional, sly, or trying to connect, are represented by different subpopulations of neural responding in mPFC (Tamir et al. 2016, Saxe and Houlihan 2017, González and Chang 2021).

While investigation into the neural bases of mentalizing has identified the mPFC as centrally important for supporting the process of inferring the mental states of others and ourselves (Denny et al. 2012), a relatively underexplored question is what content knowledge does the brain draw from when we mentalize? Characterizing such content knowledge is important given that mentalizing is theorized as a predictive process that draws upon prior knowledge to make predictions about self and others in a social world (Kilner et al. 2007, Koster-Hale et al. 2013, Baker et al. 2017, Saxe and Houlihan 2017, Thornton and Tamir 2021). Past work has begun to describe how the mPFC draws upon content knowledge to make meaning in the world (Roy et al. 2012), including social knowledge. Examples of neural representations of social knowledge in mPFC include the personality of others (Wagner et al. 2012, Hassabis et al. 2014), how people are connected to one another in a social network (Parkinson et al. 2017), and the organizational dimensions of different types of social relationships (Cheng et al.

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2025). However, a developmental account of which social knowledge may be represented and when has been relatively absent. Given that development is hierarchical (Masten and Cicchetti 2010), where the structure and function of later-developing brain regions depend on the structure and function of earlier-developing brain regions (Tottenham and Sheridan 2009, Gabard-Durnam et al. 2016, Luo et al. 2024, Park et al. 2024, Gao 2025), it is crucial to examine the role of early experiences in constructing content knowledge relevant for mentalizing.

One strong candidate for understanding the type of content that informs mentalizing is the social-affective knowledge learned from early experiences with the caregiver—hereby termed attachment schemas (c.f. Tottenham 2020b, Vannucci et al. 2024, Tottenham and Vannucci 2025). The idea that early experiences with attachment figures inform how we come to make sense of ourselves and others later in life is not new; decades of developmental and social psychological behavioral research has demonstrated that people acquire a mental model of self and others (i.e. attachment schema) that explains the lasting impact of the quality of early caregiving experiences on later social functioning (Bowlby 1969, Ainsworth 1978, Sroufe 2005, Zayas et al. 2011, Fraley and Roisman 2015). Attachment schemas are largely non-declarative, causal-temporal knowledge structures that link a child's needs with whether that need is contingently met or unmet by the caregiver (Bowlby 1973, Bretherton 1991, Baldwin 1992, Pietromonaco and Barrett 2000, Waters and Waters 2006, Waters and Roisman 2019). Secure representations of attachment schemas reflect caregiving that is responsive, available and sensitive to a child's emotional needs while insecure representations of attachment schemas reflect caregiving that is insensitive, absent and/or inconsistent. Here, we suggest that the mPFC plays a large role in representing such developmentally-constructed attachment schemas, which form the content knowledge base for mentalizing.

Our hypothesis is motivated by the empirical neurobiological convergence of mentalizing in adulthood, schema representation, and sensitivity to caregiver cues during development. We performed a pseudo-conjunction analysis that identified a region of interest common to a mentalizing meta-analysis (Neurosynth), a schema meta-analysis (Gilboa and Marlatte 2017), and studies demonstrating sensitivity to parental cues ($x = 10$ to -10) (Ida Gobbini et al. 2004, Tottenham et al. 2012, Gee et al. 2014, Saxbe et al. 2015, Laurita et al. 2017, Rogers et al. 2022, Ulmer-Yaniv et al. 2022, Abramson et al. 2024, Bortolini et al. 2024). The mPFC region we focus on comprises the midline region encompassing the anterior cingulate cortex and extends rostrally and ventrally (BA10, 32, and 24; Fig. 1). This region has been variously referred to as ventromedial prefrontal cortex, ventral anterior cingulate cortex, and rostral medial prefrontal cortex. We use a broad and inclusive term 'medial prefrontal cortex' that can speak to developmental, cognitive, and socio-affective neuroscience fields—future research should determine if this terminology should be updated. This common neurobiology shared by mentalizing and schema representations in adulthood with regions sensitive to caregivers during development, motivates our proposal that mentalizing occurs through retrieval from early attachment schemas.

Importantly, we do not claim that the retrieval of attachment schemas during mentalizing may only recruit the mPFC. Mentalizing recruits a distributed brain network, such as the temporoparietal junction involved in representing beliefs about people (Saxe and Kanwisher 2013) and the temporal pole in social semantic scripts (Olson et al. 2007, Ross and Olson 2010). Attachment schemas too have been hypothesized to recruit circuits involved in affective learning and memory (ventral striatum, amygdala, hippocampus), and midcingulo-insular "salience" networks (Seeley 2019, Tottenham and Vannucci 2025). At the same time, we argue that the mPFC is especially well-positioned to orchestrate the instantiation of implicit, non-verbal schemas

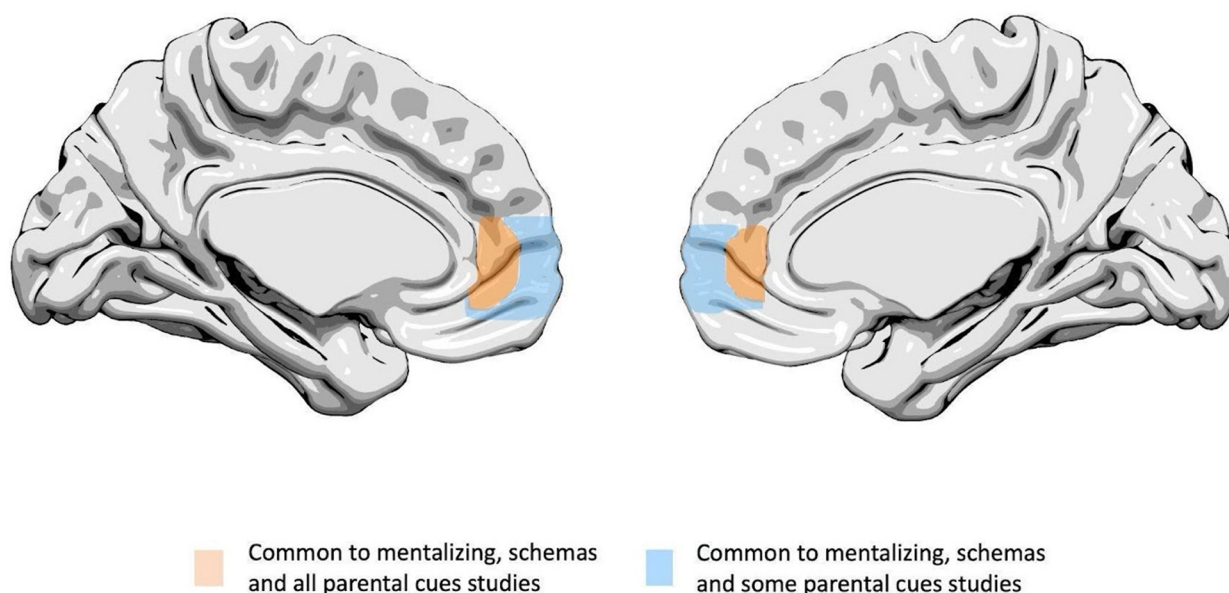


Figure 1. Pseudo conjunction analysis highlighting mPFC regions common to adult mentalizing meta-analysis (neurosynth), adult schema-mediated encoding meta-analysis (Gilboa & Marlatte 2017), and studies showing responsivity to parental cues during and across development (Ida Gobbini et al. 2004, Tottenham et al. 2012, Gee et al. 2014, Saxbe et al. 2015, Laurita et al. 2017, Rogers et al. 2022, Ulmer-Yaniv et al. 2022, Abramson et al. 2024, Bortolini et al. 2024). The orange region is present across the mentalizing meta-analysis, schema meta-analysis, and all parental cues studies. The blue region is present in the mentalizing meta-analysis, schema meta-analysis studies (e.g. Tomparry and Davachi 2017, Baldassano et al. 2017, Paulus et al. 2020), and some parental cues studies. X coordinates of this region span 10 to -10 (i.e. medial section of the prefrontal cortex). This region has also been variously referred to as vmPFC, ventral ACC, and rostral mPFC. All brain maps included in this analysis can be found on <https://osf.io/ms3re/>.

(Ghosh et al. 2014, Bovy et al. 2020, Sommer et al. 2022, Bein and Niv 2025) during mentalizing due to its representational capacities, position at the apex of multiple cognitive, sensory, and affective processing hierarchies, extensive connectivity patterns, and prolonged developmental time course (Damasio 1989, Creutzfeldt 1995, Tottenham 2020a). Moreover, phylogenetic evidence demonstrates that the mPFC is implicated in attachment circuitry across species (Landers and Sullivan 2012, Bienboire-Frosini et al. 2023), and humans' uniquely large medial prefrontal cortex (Holloway 1983, Semendeferi et al. 2001) is what enables the symbolic representation of attachment relationships (Hofer 1994, Selcuk et al. 2012, Ulmer-Yaniv et al. 2022, Zayas et al. 2025). Furthermore, although mPFC has evident connectivity with cortico-amygdala circuitry as early as infancy, mPFC connectivity with other regions associated with mentalizing takes a while to develop (Supekar et al. 2010), including connectivity between these regions during mentalizing (Richardson et al. 2018). This slow development with other mentalizing brain regions, paired with the observations that the mPFC responds to parental cues in infancy and is thought to be key to learning implicit, preverbal associations (Grossmann 2013, Raz and Saxe 2020), suggest that it may be particularly critical in the formation of the attachment schema knowledge drawn from during mentalizing, even later in development. Hence, the goal of this article is to discuss whether and why the mPFC is a central region involved in mentalizing via instantiation of attachment schemas. Brief mentions of other neural circuits such as the social brain network and cortico-subcortical circuitry are reviewed in service of demonstrating the important role of the mPFC.

To support our proposal that mentalizing occurs through the instantiation of attachment schemas, we situate their underlying neural processes within their full developmental learning trajectory. In the following sections, we integrate existing evidence across socio-affective, cognitive, and developmental neurosciences to hypothesize that mPFC representations of attachment schemas scaffold mentalizing over the course of development. We first describe mPFC activity during early caregiving experiences to demonstrate its encoding of the affective meaning of parent-child interaction episodes. Then, extrapolating from research on memory consolidation in the cognitive neurosciences, we propose how regularities across parent-child interactions become abstracted into an attachment schema in the mPFC. Finally, we discuss the functionality of attachment schemas for predicting the social world, where the interdependence of self-other representations in mPFC during mentalizing demonstrates many theoretical empirical parallels to attachment schemas.

Attachment learning in the developing mPFC during child-caregiver interaction episodes

Several lines of research suggests that the developing mPFC is sensitive to the quality of the child-caregiver relationship (Fig. 2A). First, the developing mPFC is phasically modulated by the presence or absence of the parent during development (Dehaene-Lambertz et al. 2010, Tottenham et al. 2012, Gee et al. 2014, Abramson et al. 2024). Second, mPFC development is altered in the long-term following caregiving-related early adversities, which involve major interruptions, separations, and/or dysfunctions in the parent-child relationship (e.g. abuse/neglect, caregiving switches; Kitayama et al. 2006, Mueller et al. 2010, Gorka et al. 2014, Van Harmelen et al. 2014, Morey et al. 2016, Teicher et al. 2016, Nikolaidis et al. 2022, Vannucci et al. 2023). Third, attachment security is linked to mPFC

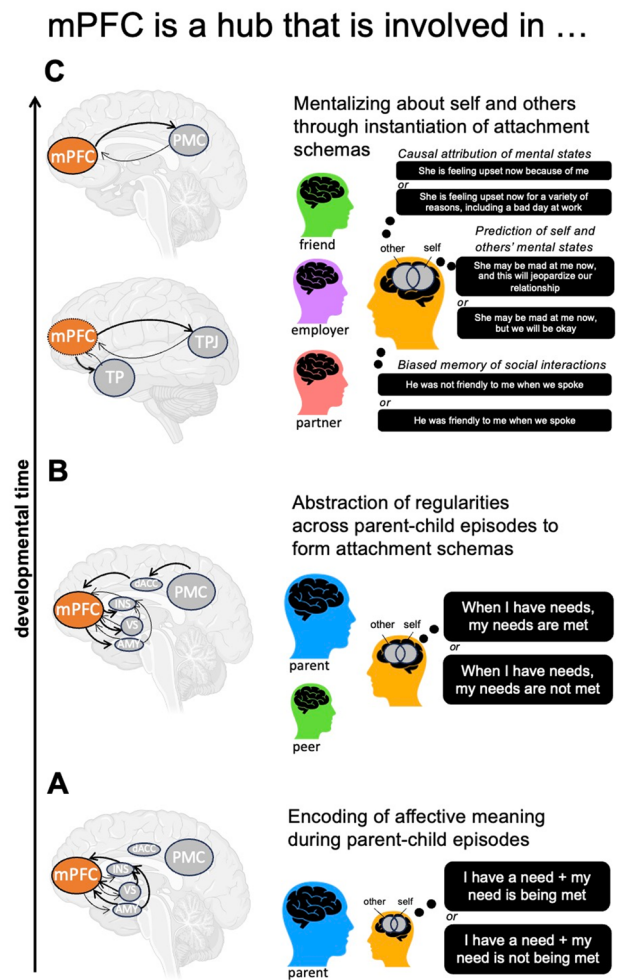


Figure 2. Mechanisms of whether and how mentalizing occurs through instantiation of developmentally-constructed attachment schemas. Although this information is likely non-verbal, we include language in thought bubbles to illustrate the content of the learned knowledge. (A) During parent-child interaction episodes in infancy, mPFC-cortico-subcortical circuitry, such as cortico-amygdala circuitry (implicated in stimulus-outcome learning; Tottenham 2020b) and cortico-striatal circuitry (implicated in action-outcome learning; Kotz et al. 2016), encodes affective meaning (i.e. I have a need + my need was (not) met). (B) As development progresses across infancy, childhood and adolescence, mPFC abstracts regularities across parent-child interactions via memory consolidation and replay to form attachment schemas (i.e. When I have needs, my needs are met). While modifications can occur following changes in attachment experiences (with peers or another caregiver), the early attachment relationship exerts an outsized influence on the content and structure of attachment schemas (i.e. reflected in the larger parent icon). (C) mPFC likely instantiates attachment schemas to enable socio-affective predictions that underlie mentalizing in adulthood, including but not limited to causal attribution of mental states, prediction of self and others' mental states, and biased memory recall of social interactions (Dykas and Cassidy 2011). This process is done in conjunction with the rest of the default mode network and brain regions implicated in social cognition, including temporoparietal junction, posterior cingulate cortex, and temporal pole for a variety of social targets. This hypothesis is motivated by a large body of evidence demonstrating other-in-relation-to-self representations, a key feature of attachment schemas during and across development. Bolded arrows in the figures indicate hypothesized directions of connectivity by different stages of development (see Tottenham and Vannucci 2025 for a full account of neural learning mechanisms). All regions listed are part of the cortico-midline "default-mode" network (Menon 2023), midcingulo-insular "salience" network (Seeley 2019), and/or the social-default mode network (Andrews-Hanna et al. 2010, Buckner and DiNicola 2019, Meyer 2019). mPFC = medial prefrontal cortex; PCC = posterior cingulate cortex; TPJ = temporoparietal junction; TP = temporal pole; AMY = amygdala; VS = ventral striatum; INS = insula; dACC = dorsal anterior cingulate cortex; PMc = posterior medial cortex (precuneus + posterior cingulate cortex).

development during childhood, be it in terms of structure, **function or connectivity patterns** (e.g. Gee et al. 2014, Choi et al. 2021). These findings suggest that during routine caregiving (or the lack thereof), infants and children learn to associate their needs (e.g. distress) and the affective outcomes of parental response (e.g. distress (non) relief; Callaghan and Tottenham 2016, Atzil et al. 2018). Of note, the developing mPFC coordinates with affective learning systems to support attachment learning and memory through stimulus-outcome associations (e.g. amygdala; Tottenham 2020b) and action-outcome associations (e.g. cortical-striatal circuitry, Kotz et al. 2016).

These instances of attachment learning are reminiscent of the formation of episodic memories. The cognitive neuroscience of learning and memory describes neural mechanisms (e.g. hippocampus, amygdala) that bind contextual and interoceptive features into meaningful events (e.g. who was present at a birthday party, where it was and what it felt like to be there; Tulving 2002, Ezzyat and Davachi 2011, Dolcos et al. 2017, DuBrow et al. 2024). This is akin to the binding of self+caregiver+affect information during attachment learning. The meaning learned from these early caregiving experiences persists into adulthood (Raposo et al. 2014), even though the developing brain undergoes significant reorganizations over time (e.g. synaptic pruning) and memories from early life are often not explicitly accessible to most adults (Bauer 2015). What neural mechanisms explain this effect? In the next section, we turn to the schematization of attachment learning into attachment schemas in the mPFC by drawing on memory consolidation principles. We also highlight the enduring impact of early caregiving experiences by briefly reviewing existing evidence on the relative stability and change of attachment schemas over development.

Abstraction of attachment learning into attachment schemas in the mPFC during development

Cognitive neuroscience of learning and memory has demonstrated that the hippocampus is involved in the initial encoding of memories, but these memories are gradually transformed, abstracted, and generalized across multiple episodes in the temporal and prefrontal cortex over time (e.g. Ghosh and Gilboa 2014, Tompariy and Davachi 2017). In a similar manner, the development of attachment knowledge (i.e. When I have needs, my needs are met) may follow similar consolidation mechanisms with affective memories of parent-child episodes (i.e. I had a need during time X → my need was not met at time X; Tottenham and Vannucci 2025). Following principles of memory consolidation, we expect that memory reactivation (“replay”) within subcortical circuitry is responsible for initial attachment learning (Kaefer et al. 2022, Chen and Wilson 2023). Such replay subsequently drives the maturation of mPFC-cortical-subcortical connectivity (Gee et al. 2022, Tottenham and Vannucci 2025), where replay in the mPFC integrates overlapping representations into a general attachment schema (Cowan et al. 2021). Similarly, the mPFC has been posited as a hub that coordinates schema consolidation and instantiation in the cognitive neurosciences (Ghosh and Gilboa 2014, Tompariy and Davachi 2017; Fig. 2B).

The construction of attachment schemas in the mPFC occurs across a long developmental period: Infancy to adulthood spans at least 25 years, and mPFC development is especially protracted in humans relative to other precocial species (Cunningham et al. 2002, Curley et al. 2009, Pattwell et al. 2016, Tottenham 2020a). Here, caregivers play a privileged role in shaping attachment schemas:

infants form attachment to their caregivers regardless of its valence in order to meet their basic survival needs (e.g., Scott 1962, Moriceau and Sullivan 2006, McCormack et al. 2009, Tottenham et al. 2019). This suggests that emotional closeness to an individual is not the reason for the construction of attachment schemas early in life. However, the quality of early caregiving experiences do inform the content of attachment schemas. Indeed, children spend a long time with their caregivers before “leaving the nest” compared to other species, allowing for species-expected social sculpting of affective learning and abstraction of regularities in parent-child interaction for the construction of attachment schemas (Tottenham 2020b).

Although moderate stability of attachment schemas across time is expected (Waters and Roisman 2019), this luxuriously long development allows for modifications in attachment schemas through environmental adaptations. For example, attachment schemas are more likely to be modified in the face of drastic shifts in caregiving (Booth-LaForce et al. 2014, Waters et al. 2017, Raby and Dozier 2019, Khan et al. 2020, Nivison et al. 2021, Raby et al. 2021), such as adoption into homes with sensitive and responsive caregivers following early-caregiving adversities. During adolescence, the brain becomes increasingly tuned to peer influence (Blakemore 2008, Casey et al. 2008, Pfeifer et al. 2011, 2013, Somerville 2013), allowing for modifications in attachment schemas by caring friendships (Allen et al. 2004, Allen et al. 2018). A similar story is suggested by behavioral findings where previously insecurely-attached children become more securely attached with sensitive care from at least one person in their life later as adults (i.e. either a parent, peer, mentor, romantic partner; Fraley, 2019). Such modifications, should they occur, likely operate via mPFC-mediated processes of assimilation (i.e. new information aligns with existing attachment schema) or accommodation (i.e. new information contradicts existing attachment schema) (Piaget 1962, Euston et al. 2012, Takehara-Nishiuchi 2020, Tottenham and Vannucci 2025).

While modifications can occur, it is equally important to note that early caregiving experiences exert an outsized effect on the construction of attachment schemas (Fraley et al. 2013, Nivison et al. 2025). There are a few empirical neurobehavioral and theoretical reasons motivating this argument. First, the hierarchical nature of development would dictate that attachment schemas constructed from our earliest and most salient social relationship with the caregiver set the constraints for later development (Masten and Cicchetti 2010). Second, the function of schemas—as posited by both attachment theorists and cognitive neuroscientists—is to enable efficient processing of incoming information and habituation to one's environment (Bretherton 1991, Ghosh and Gilboa 2014); **therefore, if schemas were to change easily, individuals would be perennially confused and distressed navigating an orderless world.** Neurally, mPFC representations of schemas also exhibit slow changes over time (Baldassano et al. 2018). Third, schemas bias information processing to be schema-consistent (i.e. in attention, encoding, retrieval, consolidation; Vannucci et al. 2024), making schemas increasingly resistant to change over time (Lim et al. 2020). For example, adolescents with strong negative schemas of social interactions tend to recall more negative instances of social interactions (Johnston et al. 2023). This negative recall bias strengthens across development, and this effect is partially mediated by mPFC-striatal motivational learning (Jarcho et al. 2024). This effect is amplified for attachment schemas, whose implicit, non-verbal and non-declarative nature makes it difficult to easily modify (Bowlby 1969, 1973, 1980). Finally, even when attachment schemas are modified, early emotional memories are never completely

erased (Bisaz et al. 2021). Rather, their expression can be reinstated depending on context (Pattwell et al. 2011). Furthermore, behavioral evidence suggests that early life caregiving experiences explain unique variance in later life mentalizing behavior regardless of intervening social experiences in adolescence (Roisman and Fraley 2012, 2021), and differentiation of parental vs. peer cues persists in adolescence (Van Hoorn et al. 2018). Hence, while early experiences are not deterministic of future outcomes, they play a foundational role in constructing attachment schemas.

Thus far, we have established that attachment schemas are developmentally constructed in the mPFC with enduring sculpting by early caregiving experiences. If the function of schemas is to enable prediction, what kind of predictions are attachment schemas built for? In the following section, we show that attachment schemas are poised for social predictions in adulthood. We demonstrate this by reviewing mPFC activity recruited for mentalizing about both self and others and how attachment schemas may shape general social knowledge representation in the mPFC.

Instantiation of attachment schemas when mentalizing about self and others in the mPFC

The attachment schema foundationally constructed between the child and the caregiver becomes useful when mentalizing not only about the self and the caregiver, but also other social targets in adulthood, such as peers, romantic partners, co-workers, and strangers (Bowlby et al. 1992, Sroufe 2005). Consistent with such theoretical and behavioral evidence, the mPFC is reliably recruited when mentalizing about self and a variety of social targets. This finding is robust with different methodologies, from univariate activation, lesion studies, transcranial magnetic stimulation, and multivariate pattern analyses to electrocorticography studies for both spontaneous and intentional trait attributions (e.g. Wagner et al. 2012, Lieberman et al. 2019, Tan et al. 2022). While there is evidence for subfunctionalizations within the mPFC for mentalizing about self and other (e.g. Denny et al. 2012, Doré et al. 2015), there is also evidence of overlap (e.g. Wagner et al. 2012). The overlap in the mPFC for mentalizing about self and other is striking (Mitchell 2009, Lombardo et al. 2010, Lieberman et al. 2019), with some empirical reviews positing that the medial prefrontal cortex (i.e. Fig. 1) is a convergence zone that integrates knowledge about self, others and the environment (Krueger et al. 2009, Denny et al. 2012, Doré et al. 2015).

The neural overlap of self and other representations in the mPFC is consistent with a core feature of attachment schemas: others are represented in relation to the self (Aron et al. 1992, Pietromonaco and Barrett 2000, Andersen and Chen 2002; Fig. 2C). The ventral portion of the mPFC, an area consistently activated for self-referential thinking, is engaged during social cognition (Lieberman et al. 2019) and acquisition of abstract cognitive maps of social relationships (Park et al. 2020). Building on the logic that the mPFC maps relationships between people in one's network at a conceptual level, the mPFC may also map the topography of others through their relations with the self (Zerubavel et al. 2015). During development, knowledge about how others view the self are instantiated in the mPFC during self-appraisals (Pfeifer et al. 2009). Most compellingly, there is continuity in the representation of the parent-child attachment from infancy to adulthood (Ulmer-Yaniv et al. 2022) and mentalizing about mothers and self both resulted in similar activations within the mPFC even for adults (Vanderwal et al. 2008, Laurita et al. 2017). On the other hand, there is mixed evidence that closeness neurally modulates mentalizing in the

mPFC, with some studies suggesting that closeness leads to greater differentiation of mental states for close others relative to strangers (Krienen et al. 2010, Thornton et al. 2019a, Courtney and Meyer 2020) while other studies suggest no evidence for a moderating role of closeness (Laurita et al. 2017). This suggests that there is a unique influence of early caregiving relationships on mentalizing in adulthood regardless of closeness to the caregiver or other close social relationships later in life, thereby lending weight to the argument at the heart of attachment theory that representations of a caregiver's relations to self is central to representations of the self.

Conceptualizing the overlap in the mPFC as evidence for other-in-relation-to-self representations is complementary to existing work on mentalizing processes. Other-in-relation-to-self representations may be what support simulation theories (i.e. that we rely on self-knowledge when mentalizing about others; Tamir and Mitchell 2013), enable person and state specific models of social cognition (Thornton et al. 2019b), and update self-concepts when simulating others (Meyer 2019, Welker et al. 2024, Schneider et al. 2025).

Additionally, mPFC representations of attachment schemas likely underpin the organization of social knowledge that has been deemed important for mentalizing. Recent computational advances in social neuroscience have organized social knowledge among three dimensions: mental states (e.g. hungry, upset), traits (e.g. conscientious, neurotic), and action layers (e.g. reaching for an object; Thornton and Tamir 2021). Furthermore, when the mPFC encodes the current mental state of any individual, the mPFC coordinates activity with the precuneus to automatically predict possible future mental states (Thornton et al. 2019a). These characteristics of social knowledge organization have developmental origins in attachment schemas as mediated by the mPFC. These attachment schemas are non-verbal, early-developing, and reflect other-in-relation-to-self survival. First, the fundamental capacity to represent people's behavior in terms of mental states emerges through caregivers' sensitive and contingent reflection of the child's mental states back to the child (e.g. Winnicott 1962, Fonagy and Luyten 2018). For instance, the developing mPFC is sensitive to parents' facial and verbal emotional cues during synchronous caregiving (Herba and Phillips 2004, Ulmer-Yaniv et al. 2022). Second, the causal-temporal structure of attachment schemas constrains the space of possible future mental states and how quickly such transitions can be (Dykas and Cassidy 2011). For example, an adult with an insecure attachment schema is quicker and more likely to attribute negative motives to others during social conflict relative to an adult with a secure attachment schema (Cassidy et al. 1996, Zimmermann 2004, Chris Fraley et al. 2006, Chris Fraley and Brumbaugh 2007). While no neuroscientific work has directly tested the influence of attachment schemas on mentalizing, emerging neural evidence suggests that mPFC-supported schemas shape predictions of emotion transitions in self and other (Thornton and Tamir 2017).

Taken together, the theoretical and empirical overlap of attachment schemas and mentalizing in the mPFC motivates asking whether mentalizing occurs through instantiation of attachment schemas. This idea is perhaps not surprising, given that the mPFC is a hub for conceptual systems, prospection, mentalizing, memory and the default-mode network (Spreng et al. 2009, Andrews-Hanna et al. 2010, Buckner and DiNicola 2019, Meyer 2019). Yet, given the survival value of early-life attachments and its consequences for the construction of attachment schemas, it is surprising that a developmentally-informed neuroscientific examination of whether and how attachment schemas influences mentalizing is relatively nascent. In our final section, we offer falsifiable hypotheses to test our theory and raise future questions to examine.

Future directions and conclusions

If early caregiving experiences shape attachment knowledge, which is drawn upon to mentalize, then **different attachment knowledge as represented in the mPFC will predict different inferences of other people's mental states, particularly in an ambiguous situation where multiple interpretations are possible** (Finn et al. 2018). For example, it may be possible to obtain a multivariate pattern in the mPFC that represents someone meeting vs. not meeting one's needs during early parent-child interactions and across development. These attachment schema classifiers could be applied to new data where participants with different attachment schemas will instantiate one type of classifier pattern over the other in an ambiguous social situation. These mPFC representations can be further linked to behavioral responses, such that more secure representations might predict stronger judgments of the self as agentic and worthy and stronger judgments of others as trustworthy and safe. Future research could additionally use inter- and intra-subject representational similarity analysis to link neural similarity within and between participants in the mPFC to behavioral similarities in attachment schemas (e.g. measured using semantic similarity with natural language processing). New methods that capture temporal contingencies in predictions about self and others in mPFC representations are also handy toolkits to capture the structure of attachment knowledge (e.g. Baldassano et al. 2017, Tomparry and Davachi 2017), the extent to which attachment schemas moderate the kinds of social information that are consolidated during rest (Meyer 2023) and event segmentation of social interactions (Zacks et al. 2007). Lastly, neural investigations on loneliness can inform theoretical and methodological approaches to studying neural representations of attachment schemas given that feelings of loneliness can be explained by similar socio-cognitive mechanisms that underlie attachment schemas (Mikulincer and Shaver 2013).

A few other questions remain regarding the neural coordination of attachment schemas and mentalizing. First, at the outset of this article, we noted that both mentalizing and attachment schemas recruit a distributed network (Schurz et al. 2014, 2021, Feldman 2017, Thornton and Tamir 2021, Tottenham and Vannucci 2025). Some candidate brain networks germane to the current investigation include the temporal poles (i.e. implicated in representing multimodal concepts: Rice et al. 2015, Binney et al. 2016), the temporoparietal junction (i.e. implicated in representing the beliefs of others: Saxe and Kanwisher 2013), the cortico-striatal circuitry (i.e. implicated in action-outcome learning: Kotz et al. 2016), the cortico-amygdala circuitry (i.e. implicated in stimulus-outcome learning: Tottenham 2020b), and the default mode network (i.e. Andrews-Hanna et al. 2010, Buckner and DiNicola 2019, Meyer 2019, Menon 2023). The consideration of how different networks in the brain coordinate with the mPFC to support attachment schema-supported social predictions will be crucial given that attachment schemas are embodied, context-dependent simulations (Barrett 2017, Atzil et al. 2018). Indeed, functional connectivity analyses can shed light on how the mPFC coordinates with cortico-subcortical systems and other regions of the social brain network to holistically elucidate neural mechanisms of attachment-schema-supported mentalizing (Li et al. 2014). Investigating how different neural networks coordinate with the mPFC across development will also be important in understanding how affective learning during early parent-child interactions become the neural substrate that enables mentalizing in adulthood.

Second, how can we best neurally examine the effect of attachment schema on mentalizing? Mentalizing is a heterogeneous

construct in social neuroscience, with a diversity of experimental tasks (i.e. trait judgements, false belief attribution, social animations) to study multiple types of processes (e.g. inferring others' emotions, reasoning about others' goals, processing of biological motion and agency), each of which can span rapid and automatic processes to effortful and conscious processes (Schaafsma et al. 2015). Here, we suggest experimental paradigms that best capture individuals' expectancies, social memory and affect—outcomes where decades of behavioral work have shown moderation effects of attachment schemas on mentalizing (c.f. Dykas and Cassidy 2011) – would be most productive. Theoretically-informed experimental paradigms will be crucial for understanding when and for whom attachment schema influences what types of mentalizing. For example, while attachment theory would predict that attachment schemas are instantiated during both emotional conversations with attachment figures and general social interactions with strangers (Bowlby 1969, Andersen and Chen 2002), empirical neural investigations can test if this is true and tease apart the underlying neural mechanisms.

Although many questions remain to be addressed, studying the neural basis of mentalizing has been the bread and butter of many social and affective neuroscientists. While mentalizing researchers have advanced our understanding of how we think about others' thoughts and feelings, we believe that we can deepen this inquiry by considering how content knowledge accumulated through interactions with attachment figures influences mentalizing processes. In particular, we propose that attachment schemas form the basis for mentalizing in the mPFC. Attachment theory has historically been studied largely by psychodynamic theorists, social psychologists, and developmental psychologists; here, we show that a neuroscientific operationalization of attachment in terms of semanticized attachment schema in the mPFC can help us understand the origins and content of mentalizing. Though the premise of this article is speculative, there is compelling converging evidence across different fields to warrant an empirical investigation. With the growing neurobiological understanding of socioaffective behavior and a broadening of methodological toolkits, the field is well-poised to address this timely question. Understanding the neural mechanisms of how attachment schemas influences mentalizing in the mPFC (and beyond) may help us understand the roots of normative and abnormal mentalizing behavior in everyday life and prompt evidence-based recommendations for building healthy social relationships for all.

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Author contributions

Zhouzhou He was involved in Conceptualization, Formal Analysis, Investigation, Writing—original draft and Writing—review & editing. Anna Vannucci was involved in Formal Analysis, Investigation, Writing—review & editing. Meghan L. Meyer was involved in Formal Analysis, Investigation, Writing—review & editing. Nim Tottenham was involved in Conceptualization, Formal Analysis, Investigation, Writing—original draft, and Writing—review & editing.

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Data availability

Brain maps can be found on <https://osf.io/ms3re/>.

References

- Abramson L, Callaghan BL, Silvers JA et al. The effects of parental presence on amygdala and mPFC activation during fear conditioning: an exploratory study. *Dev Sci* 2024;**27**:e13505. <https://doi.org/10.1111/desc.13505>
- Ainsworth MDS. The Bowlby-Ainsworth attachment theory. *Behav Brain Sci* 1978;**1**:436–8. <https://doi.org/10.1017/S0140525X00075828>
- Allen JP, Grande L, Tan J et al. Parent and peer predictors of change in attachment security from adolescence to adulthood. *Child Dev* 2018;**89**:1120–32. <https://doi.org/10.1111/cdev.12840>
- Allen JP, McElhaney KB, Kuperminc GP et al. Stability and change in attachment security across adolescence. *Child Dev* 2004;**75**:1792–805. <https://doi.org/10.1111/j.1467-8624.2004.00817.x>
- Andersen SM, Chen S. The relational self: an interpersonal social-cognitive theory. *Psychol Rev* 2002;**109**:619–45. <https://doi.org/10.1037/0033-295X.109.4.619>
- Andrews-Hanna JR, Reidler JS, Sepulcre J et al. Functional-anatomic fractionation of the brain's default network. *Neuron* 2010;**65**:550–62. <https://doi.org/10.1016/j.neuron.2010.02.005>
- Aron A, Aron EN, Smollan D. Inclusion of other in the self scale and the structure of interpersonal closeness. *J Pers Soc Psychol* 1992;**63**:596–612. <https://doi.org/10.1037/0022-3514.63.4.596>
- Atzil S, Gao W, Fradkin I et al. Growing a social brain. *Nat Hum Behav* 2018;**2**:624–36. <https://doi.org/10.1038/s41562-018-0384-6>
- Baek EC, Hyon R, López K et al. Lonely individuals process the world in idiosyncratic ways. *Psychol Sci* 2023;**34**:683–95. <https://doi.org/10.1177/09567976221145316>
- Baker CL, Jara-Ettinger J, Saxe R et al. Rational quantitative attribution of beliefs, desires and percepts in human mentalizing. *Nat Hum Behav* 2017;**1**:0064. <https://doi.org/10.1038/s41562-017-0064>
- Baldassano C, Chen J, Zadbood A et al. Discovering event structure in continuous narrative perception and memory. *Neuron* 2017;**95**:709–21.e5. <https://doi.org/10.1016/j.neuron.2017.06.041>
- Baldassano C, Hasson U, Norman KA. Representation of real-world event schemas during narrative perception. *J Neurosci* 2018;**38**:9689–99. <https://doi.org/10.1523/JNEUROSCI.0251-18.2018>
- Baldwin MW. Relational schemas and the processing of social information. *Psychol Bull* 1992;**112**:461–84. <https://doi.org/10.1037/0033-2909.112.3.461>
- Barrett LF. The theory of constructed emotion: an active inference account of interoception and categorization. *Soc Cogn Affect Neurosci* 2017;**12**:1–23. <https://doi.org/10.1093/scan/nsw154>
- Bauer PJ. A complementary processes account of the development of childhood amnesia and a personal past. *Psychol Rev* 2015;**122**:204–31. <https://doi.org/10.1037/a0038939>
- Bein O, Niv Y. Schemas, reinforcement learning and the medial prefrontal cortex. *Nat Rev Neurosci* 2025;**26**:141–57. <https://doi.org/10.1038/s41583-024-00893-z>
- Bienboire-Frosini C, Marcet-Rius M, Orihuela A et al. Mother–Young bonding: neurobiological aspects and maternal biochemical signaling in altricial domesticated mammals. *Animals* 2023;**13**:532. <https://doi.org/10.3390/ani13030532>
- Binney RJ, Hoffman P, Lambon Ralph MA. Mapping the multiple graded contributions of the anterior temporal lobe representational hub to abstract and social concepts: evidence from distortion-corrected fMRI. *Cereb Cortex* 2016;**26**:4227–41. <https://doi.org/10.1093/cercor/bhw260>
- Bisaz R, Bessières B, Miranda JM et al. Recovery of memory from infantile amnesia is developmentally constrained. *Learn Mem* 2021;**28**:300–6.
- Blakemore S-J. The social brain in adolescence. *Nat Rev Neurosci* 2008;**9**:267–77. <https://doi.org/10.1038/nrn2353>
- Booth-LaForce C, Groh AM, Burchinal MR et al. V. CAREGIVING and contextual sources of continuity and change in attachment security from infancy to late adolescence. *Monogr Soc Res Child Dev* 2014;**79**:67–84. <https://doi.org/10.1111/mono.12114>
- Bortolini T, Laport MC, Latgé-Tovar S et al. The extended neural architecture of human attachment: an fMRI coordinate-based meta-analysis of affiliative studies. *Neurosci Biobehav Rev* 2024;**159**:105584. <https://doi.org/10.1016/j.neubiorev.2024.105584>
- Bovy L, Berkers RMWJ, Pottkämper JCM et al. Transcranial magnetic stimulation of the medial prefrontal cortex decreases emotional memory schemas. *Cereb Cortex* 2020;**30**:3608–16. <https://doi.org/10.1093/cercor/bhz329>
- Bowlby J. *Attachment and Loss* (No. 79). NY, New York: Basic Books, 1969.
- Bowlby J. Attachment and loss. In: *Separation: Anxiety and Anger*, Vol. 2. New York, NY: Basic Books, 1973.
- Bowlby J. Attachment and Loss. In: *Loss, Sadness and Depression*, Vol. 3. New York: Basic Books, 1980.
- Bowlby J, Ainsworth M, Bretherton I. The origins of attachment theory. *Dev Psychol* 1992;**28**:759–75.
- Bretherton I. Pouring new wine into old bottles: the social self as internal working model. In: Gunnar MR & Sroufe LA (eds.), *Self Processes and Development* (pp. 1–41). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc, 1991.
- Buckner RL, DiNicola LM. The brain's default network: updated anatomy, physiology and evolving insights. *Nat Rev Neurosci* 2019;**20**:593–608. <https://doi.org/10.1038/s41583-019-0212-7>
- Cacioppo S, Grippo AJ, London S et al. Loneliness: clinical import and interventions. *Perspect Psychol Sci* 2015;**10**:238–49. <https://doi.org/10.1177/1745691615570616>
- Callaghan BL, Tottenham N. The neuro-environmental loop of plasticity: a cross-species analysis of parental effects on emotion circuitry development following typical and adverse caregiving. *Neuropsychopharmacology* 2016;**41**:163–76. <https://doi.org/10.1038/npp.2015.204>
- Casey BJ, Getz S, Galvan A. The adolescent brain. *Dev Rev* 2008;**28**:62–77. <https://doi.org/10.1016/j.dr.2007.08.003>
- Cassidy J, Kirsh SJ, Scolton KL et al. Attachment and representations of peer relationships. *Dev Psychol* 1996;**32**:892–904. <https://doi.org/10.1037/0012-1649.32.5.892>
- Chen ZS, Wilson MA. How our understanding of memory replay evolves. *J Neurophysiol* 2023;**129**:552–80. <https://doi.org/10.1152/jn.00454.2022>
- Cheng X, Popal H, Wang H et al. The conceptual structure of human relationships across modern and historical cultures. *Nat Hum Behav* 2025;**9**:1162–75. <https://doi.org/10.1038/s41562-025-02122-8>
- Choi EJ, Taylor MJ, Vandewouw MM et al. Attachment security and striatal functional connectivity in typically developing children. *Dev Cogn Neurosci* 2021;**48**:100914. <https://doi.org/10.1016/j.dcn.2021.100914>

- Chris Fraley R, Brumbaugh CC. Adult attachment and preemptive defenses: converging evidence on the role of defensive exclusion at the level of encoding. *J Pers* 2007;**75**:1033–50. <https://doi.org/10.1111/j.1467-6494.2007.00465.x>
- Chris Fraley R, Niedenthal PM, Marks M et al. Adult attachment and the perception of emotional expressions: probing the hyperactivating strategies underlying anxious attachment. *J Pers* 2006;**74**:1163–90. <https://doi.org/10.1111/j.1467-6494.2006.00406.x>
- Courtney AL, Meyer ML. Self-Other representation in the social brain reflects social connection. *J Neurosci* 2020;**40**:5616–27. <https://doi.org/10.1523/JNEUROSCI.2826-19.2020>
- Cowan ET, Schapiro AC, Dunsmoor JE et al. Memory consolidation as an adaptive process. *Psychon Bull Rev* 2021;**28**:1796–810. <https://doi.org/10.3758/s13423-021-01978-x>
- Creutzfeldt OD. *Cortex cerebri: performance, structural and functional organisation of the cortex*. Oxford, England: Oxford University Press, 1995. <https://doi.org/10.1093/acprof:oso/9780198523246.001.0001>
- Cunningham MG, Bhattacharyya S, Benes FM. Amygdalo-cortical sprouting continues into early adulthood: implications for the development of normal and abnormal function during adolescence. *J Comp Neurol* 2002;**453**:116–30. <https://doi.org/10.1002/cne.10376>
- Curley JP, Davidson S, Bateson P et al. Social enrichment during post-natal development induces transgenerational effects on emotional and reproductive behavior in mice. *Front Behav Neurosci* 2009;**3**:25. <https://doi.org/10.3389/neuro.08.025.2009>
- Damasio AR. The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation* 1989;**1**:123–32. <https://doi.org/10.1162/neco.1989.1.1.123>
- Dehaene-Lambertz G, Montavont A, Jobert A et al. Language or music, mother or Mozart? Structural and environmental influences on infants' language networks. *Brain Lang* 2010;**114**:53–65. <https://doi.org/10.1016/j.bandl.2009.09.003>
- Denny BT, Kober H, Wager TD et al. A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *J Cogn Neurosci* 2012;**24**:1742–52. https://doi.org/10.1162/jocn_a_00233
- Dolcos F, Katsumi Y, Weymar M et al. Emerging directions in emotional episodic memory. *Front Psychol* 2017;**8**:1867. <https://doi.org/10.3389/fpsyg.2017.01867>
- Doré BP, Zerubavel N, Ochsner KN. Social cognitive neuroscience: a review of core systems. In: Mikulincer M et al. (eds), *APA Handbook of Personality and Social Psychology, Volume 1: Attitudes and Social Cognition*. Washington, DC: American Psychological Association, 2015, 693–720. <https://doi.org/10.1037/14341-022>
- DuBrow S, Sherman BE, Meager MR et al. Medial temporal lobe damage impairs temporal integration in episodic memory. *J Cogn Neurosci* 2024;**36**:2302–16. https://doi.org/10.1162/jocn_a_02222
- Dykas MJ, Cassidy J. Attachment and the processing of social information across the life span: theory and evidence. *Psychol Bull* 2011;**137**:19–46. <https://doi.org/10.1037/a0021367>
- Eisenberger NI, Lieberman MD, Williams KD. Does rejection hurt? An fMRI study of social exclusion. *Science* 2003;**302**:290–2. <https://doi.org/10.1126/science.1089134>
- Euston DR, Gruber AJ, McNaughton BL. The role of medial prefrontal cortex in memory and decision making. *Neuron* 2012;**76**:1057–70. <https://doi.org/10.1016/j.neuron.2012.12.002>
- Ezzyat Y, Davachi L. What constitutes an episode in episodic memory? *Psychol Sci* 2011;**22**:243–52. <https://doi.org/10.1177/0956797610393742>
- Feldman R. The neurobiology of human attachments. *Trends Cogn Sci* 2017;**21**:80–99. <https://doi.org/10.1016/j.tics.2016.11.007>
- Finn ES, Corlett PR, Chen G et al. Trait paranoia shapes inter-subject synchrony in brain activity during an ambiguous social narrative. *Nat Commun* 2018;**9**:2043. <https://doi.org/10.1038/s41467-018-04387-2>
- Fonagy P, Luyten P. Attachment, mentalizing, and the self. In: Livesley WJ, Larstone R (eds.), *Handbook of Personality Disorders: Theory, Research, and Treatment*. Vol 2, 2018, 123–40. New York, NY: The Guilford Press.
- Fraley RC. Attachment in adulthood: Recent developments, emerging debates, and future directions. *Annu Rev Psychol* 2019;**70**:401–22. <https://doi.org/10.1146/annurev-psych-010418-102813>
- Fraley RC, Gillath O, Deboeck PR. Do life events lead to enduring changes in adult attachment styles? A naturalistic longitudinal investigation. *J Pers Soc Psychol* 2021;**120**:1567–606. <https://doi.org/10.1037/pspi0000326>
- Fraley RC, Roisman GI. Do early caregiving experiences leave an enduring or transient mark on developmental adaptation? *Curr Opin Psychol* 2015;**1**:101–6. <https://doi.org/10.1016/j.copsyc.2014.11.007>
- Fraley RC, Roisman GI, Haltigan JD. The legacy of early experiences in development: Formalizing alternative models of how early experiences are carried forward over time. *Dev Psycho* 2013;**49**:109–26. <https://doi.org/10.1037/a0027852>
- Gabard-Durnam LJ, Gee DG, Goff B et al. Stimulus-elicited connectivity influences resting-state connectivity years later in human development: a prospective study. *J Neurosci* 2016;**36**:4771–84. <https://doi.org/10.1523/JNEUROSCI.0598-16.2016>
- Gao W. A hierarchical model of early brain functional network development. *Trends Cogn Sci* 2025;**S1364661325000804**. <https://doi.org/10.1016/j.tics.2025.04.001>
- Gee DG, Gabard-Durnam L, Telzer EH et al. Maternal buffering of human Amygdala-Prefrontal circuitry during childhood but not during adolescence. *Psychol Sci* 2014;**25**:2067–78. <https://doi.org/10.1177/0956797614550878>
- Gee DG, Hanson C, Caglar LR et al. Experimental evidence for a child-to-adolescent switch in human amygdala-prefrontal cortex communication: a cross-sectional pilot study. *Dev Sci* 2022;**25**:e13238. <https://doi.org/10.1111/desc.13238>
- Ghosh VE, Gilboa A. What is a memory schema? A historical perspective on current neuroscience literature. *Neuropsychologia* 2014;**53**:104–14. <https://doi.org/10.1016/j.neuropsychologia.2013.11.010>
- Ghosh VE, Moscovitch M, Melo Colella B et al. Schema representation in patients with ventromedial PFC lesions. *J Neurosci* 2014;**34**:12057–70. <https://doi.org/10.1523/JNEUROSCI.0740-14.2014>
- Gilboa A, Marlatte H. Neurobiology of schemas and schema-mediated memory. *Trends Cogn Sci* 2017;**21**:618–31. <https://doi.org/10.1016/j.tics.2017.04.013>
- González B, Chang LJ. Computational models of mentalizing. In: Gilead M and Ochsner KN (eds), *The Neural Basis of Mentalizing*. Cham, Switzerland: Springer International Publishing, 2021, 299–315. https://doi.org/10.1007/978-3-030-51890-5_15
- Gorka AX, Hanson JL, Radtke SR et al. Reduced hippocampal and medial prefrontal gray matter mediate the association between reported childhood maltreatment and trait anxiety in adulthood and predict sensitivity to future life stress. *Biol Mood Anxiety Disord* 2014;**4**:12. <https://doi.org/10.1186/2045-5380-4-12>
- Grossmann T. The role of medial prefrontal cortex in early social cognition. *Front Hum Neurosci* 2013;**7**. <https://doi.org/10.3389/fnhum.2013.00340>
- Hassabis D, Spreng RN, Rusu AA et al. Imagine all the people: how the brain creates and uses personality models to predict behavior. *Cereb Cortex* 2014;**24**:1979–87. <https://doi.org/10.1093/cercor/bht042>
- Herba C, Phillips M. Annotation: development of facial expression recognition from childhood to adolescence: behavioural and neurological perspectives. *J Child Psychol Psychiatry* 2004;**45**:1185–98. <https://doi.org/10.1111/j.1469-7610.2004.00316.x>
- Hofer MA. Early relationships as regulators of infant physiology and behavior. *Acta Paediatr Suppl* 1994;**397**:9–18. <https://doi.org/10.1111/j.1651-2227.1994.tb13260.x>

- Holloway RL. Human brain evolution: a search for units, models and synthesis. *Can J Anthropol* 1983;**3**:215–30.
- Ida Gobbin M, Leibenluft E, Santiago N et al. Social and emotional attachment in the neural representation of faces. *Neuroimage* 2004;**22**:1628–35. <https://doi.org/10.1016/j.neuroimage.2004.03.049>
- Jarcho J, Johnston C, Helion C et al. Remembering social threat: Frontal-Striatal mechanisms promote memory bias in socially anxious adolescents. *Biol Psychiatry* 2024;**95**:S43–4. <https://doi.org/10.1016/j.biopsych.2024.02.109>
- Johnston CR, Quarmley M, Nelson BD et al. Social feedback biases emerge during recall but not prediction and shift across the development of social anxiety. *Proc Natl Acad Sci USA* 2023;**120**:e2308593120. <https://doi.org/10.1073/pnas.2308593120>
- Kaefer K, Stella F, McNaughton BL et al. Replay, the default mode network and the cascaded memory systems model. *Nat Rev Neurosci* 2022;**23**:628–40. <https://doi.org/10.1038/s41583-022-00620-6>
- Khan F, Chong JY, Theisen JC et al. Development and change in attachment: a multiwave assessment of attachment and its correlates across childhood and adolescence. *J Pers Soc Psychol* 2020;**118**:1188–206. <https://doi.org/10.1037/pspi0000211>
- Kilner JM, Friston KJ, Frith CD. Predictive coding: an account of the mirror neuron system. *Cogn Process* 2007;**8**:159–66. <https://doi.org/10.1007/s10339-007-0170-2>
- Kitayama N, Quinn S, Bremner JD. Smaller volume of anterior cingulate cortex in abuse-related posttraumatic stress disorder. *J Affect Disord* 2006;**90**:171–4. <https://doi.org/10.1016/j.jad.2005.11.006>
- Koster-Hale J, Saxe R, Dungan J et al. Decoding moral judgments from neural representations of intentions. *Proc Natl Acad Sci USA* 2013;**110**:5648–53. <https://doi.org/10.1073/pnas.1207992110>
- Kotz SA, Brown RM, Schwartze M. Cortico-striatal circuits and the timing of action and perception. *Curr Opin Behav Sci* 2016;**8**:42–5. <https://doi.org/10.1016/j.cobeha.2016.01.010>
- Krienen FM, Tu P-C, Buckner RL. Clan mentality: evidence that the medial prefrontal cortex responds to close others. *J Neurosci* 2010;**30**:13906–15. <https://doi.org/10.1523/JNEUROSCI.2180-10.2010>
- Krueger F, Barbey AK, Grafman J. The medial prefrontal cortex mediates social event knowledge. *Trends Cogn Sci* 2009;**13**:103–9. <https://doi.org/10.1016/j.tics.2008.12.005>
- Landers MS, Sullivan RM. The development and neurobiology of infant attachment and fear. *Dev Neurosci* 2012;**34**:101–14. <https://doi.org/10.1159/000336732>
- Laurita AC, Hazan C, Spreng RN. Dissociable patterns of brain activity for mentalizing about known others: a role for attachment. *Soc Cogn Affect Neurosci* 2017;**12**:1072–82. <https://doi.org/10.1093/scan/nsx040>
- Li W, Mai X, Liu C. The default mode network and social understanding of others: what do brain connectivity studies tell us. *Front Hum Neurosci* 2014;**8**:74. <https://doi.org/10.3389/fnhum.2014.00074>
- Lieberman MD, Straccia MA, Meyer ML et al. Social, self, (situational), and affective processes in medial prefrontal cortex (MPFC): causal, multivariate, and reverse inference evidence. *Neurosci Biobehav Rev* 2019;**99**:311–28. <https://doi.org/10.1016/j.neubiorev.2018.12.021>
- Lim M, O'Grady C, Cane D et al. Threat prediction from schemas as a source of bias in pain perception. *J Neurosci* 2020;**40**:1538–48. <https://doi.org/10.1523/JNEUROSCI.2104-19.2019>
- Lombardo MV, Chakrabarti B, Bullmore ET, MRC AIMS Consortium, & Baron-Cohen, S. et al. Shared neural circuits for mentalizing about the self and others. *J Cogn Neurosci* 2010;**22**:1623–35. <https://doi.org/10.1162/jocn.2009.21287>
- Luo AC, Sydnor VJ, Pines A et al. Functional connectivity development along the sensorimotor-association axis enhances the cortical hierarchy. *Nat Commun* 2024;**15**:3511. <https://doi.org/10.1038/s41467-024-47748-w>
- Masten AS, Cicchetti D. Developmental cascades. *Dev Psychopathol* 2010;**22**:491–5. <https://doi.org/10.1017/S0954579410000222>
- McCormack K, Newman TK, Higley JD et al. Serotonin transporter gene variation, infant abuse, and responsiveness to stress in rhesus macaque mothers and infants. *Horm Behav* 2009;**55**:538–47. <https://doi.org/10.1016/j.yhbeh.2009.01.009>
- Mende-Siedlecki P, Said CP, Todorov A. The social evaluation of faces: a meta-analysis of functional neuroimaging studies. *Soc Cogn Affect Neurosci* 2013;**8**:285–99. <https://doi.org/10.1093/scan/nsr090>
- Menon V. 20 Years of the default mode network: a review and synthesis. *Neuron* 2023;**111**:2469–87. <https://doi.org/10.1016/j.neuron.2023.04.023>
- Meyer ML. Social by default: characterizing the social functions of the resting brain. *Curr Dir Psychol Sci* 2019;**28**:380–6. <https://doi.org/10.1177/0963721419857759>
- Meyer ML. Don't you forget about me: the importance of studying the brain basis of real-world interpersonal memory. *J Cogn Neurosci* 2023;**35**:149–57. https://doi.org/10.1162/jocn_a_01926
- Meyer ML, Collier E. Theory of minds: managing mental state inferences in working memory is associated with the dorsomedial subsystem of the default network and social integration. *Soc Cogn Affect Neurosci* 2020;**15**:63–73. <https://doi.org/10.1093/scan/nsaa022>
- Mikulincer M, Shaver PR. An attachment perspective on loneliness. In: Coplan RJ and Bowker JC (eds.), *The Handbook of Solitude*, 1st ed. 2013, 34–50. Hoboken, NJ: Wiley. <https://doi.org/10.1002/9781118427378.ch3>
- Mildner JN, Tamir DI. The people around you are inside your head: social context shapes spontaneous thought. *J Exp Psychol Gen* 2021;**150**:2375–86. <https://doi.org/10.1037/xge0001057>
- Mitchell JP. Inferences about mental states. *Philos Trans R Soc Lond B Biol Sci* 2009;**364**:1309–16. <https://doi.org/10.1098/rstb.2008.0318>
- Moran JM, Mitchell JP. Mentalizing. In: *Social Neuroscience*. Routledge: London, UK, 2016, 59–76.
- Morey RA, Haswell CC, Hooper SR et al. Amygdala, hippocampus, and ventral medial prefrontal cortex volumes differ in maltreated youth with and without chronic posttraumatic stress disorder. *Neuropsychopharmacology* 2016;**41**:791–801. <https://doi.org/10.1038/npp.2015.205>
- Moriceau S, Sullivan RM. Maternal presence serves as a switch between learning fear and attraction in infancy. *Nat Neurosci* 2006;**9**:1004–6. <https://doi.org/10.1038/nn1733>
- Mueller SC, Maheu FS, Dozier M et al. Early-life stress is associated with impairment in cognitive control in adolescence: an fMRI study. *Neuropsychologia* 2010;**48**:3037–44. <https://doi.org/10.1016/j.neuropsychologia.2010.06.013>
- Nikolaidis A, Heleniak C, Fields A et al. Heterogeneity in caregiving-related early adversity: creating stable dimensions and subtypes. *Dev Psychopathol* 2022;**34**:621–34. <https://doi.org/10.1017/S0954579421001668>
- Nivison MD, Filetti CR, Carlson EA et al. Agreement between retrospective and prospective assessments of childhood abuse revisited. *Dev Psychopathol* 2025;**37**:1190–9. <https://doi.org/10.1017/S0954579424001032>
- Nivison MD, Vandell DL, Booth-LaForce C et al. Convergent and discriminant validity of retrospective assessments of the quality of childhood parenting: prospective evidence from infancy to age 26 years. *Psychol Sci* 2021;**32**:721–34. <https://doi.org/10.1177/0956797620975775>
- Olson IR, Plotzker A, Ezzyat Y. The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain* 2007;**130**:1718–31. <https://doi.org/10.1093/brain/awm052>
- Park SA, Miller DS, Nili H et al. Map making: constructing, combining, and inferring on abstract cognitive maps. *Neuron* 2020;**107**:1226–38. <https://doi.org/10.1016/j.neuron.2020.06.030>

- Park S, Haak KV, Oldham S et al. A shifting role of thalamocortical connectivity in the emergence of cortical functional organization. *Nat Neurosci* 2024;**27**:1609–19. <https://doi.org/10.1038/s41593-024-01679-3>
- Parkinson C, Kleinbaum AM, Wheatley T. Spontaneous neural encoding of social network position. *Nat Hum Behav* 2017;**1**:0072. <https://doi.org/10.1038/s41562-017-0072>
- Pattwell SS, Bath KG, Casey BJ et al. Selective early-acquired fear memories undergo temporary suppression during adolescence. *Proc Natl Acad Sci USA* 2011;**108**:1182–7. <https://doi.org/10.1073/pnas.1012975108>
- Pattwell SS, Liston C, Jing D et al. Dynamic changes in neural circuitry during adolescence are associated with persistent attenuation of fear memories. *Nat Commun* 2016;**7**:11475. <https://doi.org/10.1038/ncomms11475>
- Paulus PC, Charest I, Benoit RG. Value shapes the structure of schematic representations in the medial prefrontal cortex. *bioRxiv*, 2020-08, 2020.
- Piaget J. The stages of the intellectual development of the child. *Bull Menninger Clin* 1962;**26**:120–8.
- Pfeifer JH, Kahn LE, Merchant JS et al. Longitudinal change in the neural bases of adolescent social self-evaluations: effects of age and pubertal development. *J Neurosci* 2013;**33**:7415–9. <https://doi.org/10.1523/JNEUROSCI.4074-12.2013>
- Pfeifer JH, Masten CL, Borofsky LA et al. Neural correlates of direct and reflected self-appraisals in adolescents and adults: when social perspective-taking informs self-perception. *Child Dev* 2009;**80**:1016–38. <https://doi.org/10.1111/j.1467-8624.2009.01314.x>
- Pfeifer JH, Masten CL, Moore WE et al. Entering adolescence: resistance to peer influence, risky behavior, and neural changes in emotion reactivity. *Neuron* 2011;**69**:1029–36. <https://doi.org/10.1016/j.neuron.2011.02.019>
- Pietromonaco PR, Barrett LF. The internal working models concept: What do we really know about the self in relation to others? *Review of General Psychology* 2000;**4**:155–75. <https://doi.org/10.1037/1089-2680.4.2.155>
- Quesque F, Brass M. The role of the temporoparietal junction in self-other distinction. *Brain Topogr* 2019;**32**:943–55. <https://doi.org/10.1007/s10548-019-00737-5>
- Raby KL, Dozier M. Attachment across the lifespan: Insights from adoptive families. *Curr Opin Psychol* 2019;**25**:81–5. <https://doi.org/10.1016/j.copsyc.2018.03.011>
- Raby KL, Waters TEA, Tabachnick AR et al. Increasing secure base script knowledge among parents with attachment and biobehavioral catch-up. *Dev Psychopathol* 2021;**33**:554–64. <https://doi.org/10.1017/S0954579420001765>
- Raposo SM, Mackenzie CS, Henriksen CA et al. Time does not heal all wounds: older adults who experienced childhood adversities have higher odds of mood, anxiety, and personality disorders. *Am J Geriatr Psychiatry* 2014;**22**:1241–50. <https://doi.org/10.1016/j.jagp.2013.04.009>
- Raz GAL, Saxe R. Learning in infancy is active, endogenously motivated, and depends on the prefrontal cortices. *Annu Rev Dev Psychol* 2020;**2**:247–68. <https://doi.org/10.1146/annurev-devpsych-121318-084841>
- Rice GE, Hoffman P, Lambon Ralph MA. Graded specialization within and between the anterior temporal lobes. *Ann NY Acad Sci* 2015;**1359**:84–97. <https://doi.org/10.1111/nyas.12951>
- Richardson H, Lisandrelli G, Riobueno-Naylor A et al. Development of the social brain from age three to twelve years. *Nat Commun* 2018;**9**:1027. <https://doi.org/10.1038/s41467-018-03399-2>
- Rogers CR, Chen X, Kwon S-J et al. The role of early attachment and parental presence in adolescent behavioral and neurobiological regulation. *Dev Cogn Neurosci* 2022;**53**:101046. <https://doi.org/10.1016/j.dcn.2021.101046>
- Roisman GI, Fraley RC. The legacy of early interpersonal experience. In: *Advances in Child Development and Behavior*, Vol. **42**. San Diego, CA: Elsevier, 2012, 79–112. <https://doi.org/10.1016/B978-0-12-394388-0.00003-4>
- Ross LA, Olson IR. Social cognition and the anterior temporal lobes. *Neuroimage* 2010;**49**:3452–62. <https://doi.org/10.1016/j.neuroimage.2009.11.012>
- Roy M, Shohamy D, Wager TD. Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends Cogn Sci* 2012;**16**:147–56. <https://doi.org/10.1016/j.tics.2012.01.005>
- Saxbe D, Del Piero L, Immordino-Yang MH et al. Neural correlates of adolescents' viewing of parents' and peers' emotions: associations with risk-taking behavior and risky peer affiliations. *Soc Neurosci* 2015;**10**:592–604. <https://doi.org/10.1080/17470919.2015.1022216>
- Saxe R, Houlihan SD. Formalizing emotion concepts within a Bayesian model of the theory of mind. *Curr Opin Psychol* 2017;**17**:15–21. <https://doi.org/10.1016/j.copsyc.2017.04.019>
- Saxe R, Kanwisher N. People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. In: *Social Neuroscience*. Hove, England: Psychology Press, 2013, 171–182.
- Schaafsma SM, Pfaff DW, Spunt RP et al. Deconstructing and reconstructing theory of mind. *Trends Cogn Sci* 2015;**19**:65–72. <https://doi.org/10.1016/j.tics.2014.11.007>
- Schneider MJ, Rubin-McGregor J, Elder J et al. Simulation requires activation of self-knowledge to change self-concept. *J Exp Psychol Gen* 2025;**154**:358–77. <https://doi.org/10.1037/xge0001663>
- Schurz M, Radua J, Aichhorn M et al. Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 2014;**42**:9–34. <https://doi.org/10.1016/j.neubiorev.2014.01.009>
- Schurz M, Radua J, Tholen MG et al. Toward a hierarchical model of social cognition: a neuroimaging meta-analysis and integrative review of empathy and theory of mind. *Psychol Bull* 2021;**147**:293–327. <https://doi.org/10.1037/bul0000303>
- Schwarzer N-H, Nolte T, Fonagy P et al. Mentalizing and emotion regulation: evidence from a nonclinical sample. *Int Forum Psychoanal* 2021;**30**:34–45. <https://doi.org/10.1080/0803706X.2021.1873418>
- Scott JP. Critical periods in behavioral development: critical periods determine the direction of social, intellectual, and emotional development. *Science* 1962;**138**:949–58. <https://doi.org/10.1126/science.138.3544.949>
- Seeley WW. The salience network: A neural system for perceiving and responding to homeostatic demands. *J Neurosci* 2019;**39**:9878–82. <https://doi.org/10.1523/JNEUROSCI.1138-17.2019>
- Selcuk E, Zayas V, Günaydin G et al. Mental representations of attachment figures facilitate recovery following upsetting autobiographical memory recall. *J Pers Soc Psychol* 2012;**103**:362–78. <https://doi.org/10.1037/a0028125>
- Semendeferi K, Armstrong E, Schleicher A et al. Prefrontal cortex in humans and apes: a comparative study of area 10. *Am J Phys Anthropol* 2001;**114**:224–41.
- Sened H, Lavidor M, Lazarus G et al. Empathic accuracy and relationship satisfaction: a meta-analytic review. *J Fam Psychol* 2017;**31**:742–52. <https://doi.org/10.1037/fam0000320>
- Somerville LH. The teenage brain. *Curr Dir Psychol Sci* 2013;**22**:121–7. <https://doi.org/10.1177/0963721413476512>
- Sommer T, Hennies N, Lewis PA et al. The assimilation of novel information into schemata and its efficient consolidation. *J Neurosci* 2022;**42**:5916–29. <https://doi.org/10.1523/JNEUROSCI.2373-21.2022>
- Spreng RN, Mar RA, Kim ASN. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J Cogn Neurosci* 2009;**21**:489–510. <https://doi.org/10.1162/jocn.2008.21029>

- Sroufe LA. Attachment and development: a prospective, longitudinal study from birth to adulthood. *Attach Hum Dev* 2005;**7**:349–67. <https://doi.org/10.1080/14616730500365928>
- Supekar K, Uddin LQ, Prater K et al. Development of functional and structural connectivity within the default mode network in young children. *Neuroimage* 2010;**52**:290–301. <https://doi.org/10.1016/j.neuroimage.2010.04.009>
- Takehara-Nishiuchi K. Prefrontal–hippocampal interaction during the encoding of new memories. *Brain Neurosci Adv* 2020;**4**: 2398212820925580. <https://doi.org/10.1177/2398212820925580>
- Tamir DI, Mitchell JP. Anchoring and adjustment during social inferences. *J Exp Psychol Gen* 2013;**142**:151–62. <https://doi.org/10.1037/a0028232>
- Tamir DI, Thornton MA, Contreras JM et al. Neural evidence that three dimensions organize mental state representation: rationality, social impact, and valence. *Proc Natl Acad Sci USA* 2016;**113**:194–9. <https://doi.org/10.1073/pnas.1511905112>
- Tan KM, Daitch AL, Pinheiro-Chagas P et al. Electroencephalographic evidence of a common neurocognitive sequence for mentalizing about the self and others. *Nat Commun* 2022;**13**:1919. <https://doi.org/10.1038/s41467-022-29510-2>
- Teicher MH, Samson JA, Anderson CM et al. The effects of childhood maltreatment on brain structure, function and connectivity. *Nat Rev Neurosci* 2016;**17**:652–66. <https://doi.org/10.1038/nrn.2016.111>
- Thornton MA, Tamir DI. Mental models accurately predict emotion transitions. *Proc Natl Acad Sci USA* 2017;**114**:5982–7. <https://doi.org/10.1073/pnas.1616056114>
- Thornton MA, Tamir DI. The organization of social knowledge is tuned for prediction. In: Gilead M and Ochsner KN (eds.), *The Neural Basis of Mentalizing*. Cham, Switzerland: Springer International Publishing, 2021, 283–297. https://doi.org/10.1007/978-3-030-51890-5_14
- Thornton MA, Weaverdyck ME, Mildner JN et al. People represent their own mental states more distinctly than those of others. *Nat Commun* 2019a;**10**:2117. <https://doi.org/10.1038/s41467-019-10083-6>
- Thornton MA, Weaverdyck ME, Tamir DI. The brain represents people as the mental states they habitually experience. *Nat Commun* 2019b;**10**:2291. <https://doi.org/10.1038/s41467-019-10309-7>
- Tompary A, Davachi L. Consolidation promotes the emergence of representational overlap in the hippocampus and medial prefrontal cortex. *Neuron* 2017;**96**:228–41.e5. <https://doi.org/10.1016/j.neuron.2017.09.005>
- Tottenham N, Sheridan MA. A review of adversity, the amygdala and the hippocampus: a consideration of developmental timing. *Front Hum Neurosci* 2009;**3**:68. <https://doi.org/10.3389/fnhum.2009.0068.2009>
- Tottenham N. Early adversity and the neonatal human brain. *Biol Psychiatry* 2020a;**87**:350–8. <https://doi.org/10.1016/j.biopsych.2019.06.018>
- Tottenham N. Neural meaning making, prediction, and prefrontal–subcortical development following early adverse caregiving. *Dev Psychopathol* 2020b;**32**:1563–78. <https://doi.org/10.1017/S0954579420001169>
- Tottenham N, Shapiro M, Flannery J et al. Parental presence switches avoidance to attraction learning in children. *Nat Hum Behav* 2019;**3**:1070–7. <https://doi.org/10.1038/s41562-019-0656-9>
- Tottenham N, Shapiro M, Telzer EH et al. Amygdala response to mother. *Dev Sci* 2012;**15**:307–19. <https://doi.org/10.1111/j.1467-7687.2011.01128.x>
- Tottenham N, Vannucci A. Attachment as prediction: insights from cognitive and developmental neuroscience. *Curr Dir Psychol Sci* 2025;**34**:195–206. <https://doi.org/10.1177/09637214251313714>
- Tulving E. Episodic memory: from mind to brain. *Annu Rev Psychol* 2002;**53**:1–25. <https://doi.org/10.1146/annurev.psych.53.100901.135114>
- Ulmer-Yaniv A, Waidergoren S, Shaked A et al. Neural representation of the parent–child attachment from infancy to adulthood. *Soc Cogn Affect Neurosci* 2022;**17**:609–24. <https://doi.org/10.1093/scan/nsab132>
- Van Harmelen A-L, Hauber K, Gunther Moor B et al. Childhood emotional maltreatment severity is associated with dorsal medial prefrontal cortex responsivity to social exclusion in young adults. *PLoS One* 2014;**9**:e85107. <https://doi.org/10.1371/journal.pone.0085107>
- Van Hoorn J, McCormick EM, Rogers CR et al. Differential effects of parent and peer presence on neural correlates of risk taking in adolescence. *Soc Cogn Affect Neurosci* 2018;**13**:945–55. <https://doi.org/10.1093/scan/nsy071>
- Van Overwalle F, Heleven E. The neural basis and representation of social attributions. In: Gilead M & Ochsner KN (eds.), *The Neural Basis of Mentalizing*. Cham, Switzerland: Springer International Publishing, 2021, 385–408. https://doi.org/10.1007/978-3-030-51890-5_19
- Vanderwal T, Hunyadi E, Grupe DW et al. Self, mother and abstract other: an fMRI study of reflective social processing. *Neuroimage* 2008;**41**:1437–46. <https://doi.org/10.1016/j.neuroimage.2008.03.058>
- Vannucci A, Fields A, Bloom PA et al. Probing the content of affective semantic memory following caregiving-related early adversity. *Dev Sci* 2024;**27**:e13518. <https://doi.org/10.1111/desc.13518>
- Vannucci A, Fields A, Hansen E et al. Interpersonal early adversity demonstrates dissimilarity from early socioeconomic disadvantage in the course of human brain development: a meta-analysis. *Neurosci Biobehav Rev* 2023;**150**:105210. <https://doi.org/10.1016/j.neubiorev.2023.105210>
- Wagner DD, Haxby JV, Heatherton TF. The representation of self and person knowledge in the medial prefrontal cortex. *Wiley Interdiscip Rev Cogn Sci* 2012;**3**:451–70. <https://doi.org/10.1002/wcs.1183>
- Waters HS, Waters E. The attachment working models concept: among other things, we build script-like representations of secure base experiences. *Attach Hum Dev* 2006;**8**:185–97. <https://doi.org/10.1080/14616730600856016>
- Waters TEA, Ruiz SK, Roisman GI. Origins of secure base script knowledge and the developmental construction of attachment representations. *Child Dev* 2017;**88**:198–209. <https://doi.org/10.1111/cdev.12571>
- Waters TE, Roisman GI. The secure base script concept: an overview. *Curr Opin Psychol* 2019;**25**:162–6. <https://doi.org/10.1016/j.copsyc.2018.08.002>
- Welker C, Wheatley T, Cason G et al. Self-views converge during enjoyable conversations. *Proc Natl Acad Sci USA* 2024;**121**:e2321652121. <https://doi.org/10.1073/pnas.2321652121>
- Winnicott DW. The theory of the parent–infant relationship: further remarks. *Int J Psychoanal* 1962;**43**:238.
- Zacks JM, Speer NK, Swallow KM et al. Event perception: a mind–brain perspective. *Psychol Bull* 2007;**133**:273–93. <https://doi.org/10.1037/0033-2909.133.2.273>
- Zayas V, Mischel W, Shoda Y et al. Roots of adult attachment: maternal caregiving at 18 months predicts adult peer and partner attachment. *Soc Psychol Personal Sci* 2011;**2**:289–97. <https://doi.org/10.1177/1948550610389822>
- Zayas V, Urganci B, Strycharz S. Out of sight but in mind: Experimentally activating partner representations in daily life buffers against common stressors. *Emotion* 2025;**25**:430–42. <https://doi.org/10.1037/emo0001419>
- Zerubavel N, Bearman PS, Weber J et al. Neural mechanisms tracking popularity in real-world social networks. *Proc Natl Acad Sci USA* 2015;**112**:15072–7. <https://doi.org/10.1073/pnas.1511477112>
- Zimmermann P. Attachment representations and characteristics of friendship relations during adolescence. *J Exp Child Psychol* 2004;**88**:83–101. <https://doi.org/10.1016/j.jecp.2004.02.002>