The Hippocampus and Social Cognition

Anne C. Laurita and R. Nathan Spreng

Abstract The function of memory is not simply to recall the past but also to form and update models of our experiences that help us navigate the complexities of the social world. In the present chapter, we review behavioral, neuroimaging, and neuropsychological evidence that suggest an important role for memory—and the hippocampus—in social cognition.

Introduction

> "Lastly, she pictured to herself how this same little sister of hers would, in the after-time, be herself a grown woman; and how she would keep, through all her riper years, the simple and loving heart of her childhood: and how she would gather about her other little children, and make their eyes bright and eager with many a strange tale, perhaps even with the dream of Wonderland of long ago: and how she would feel with all their simple sorrows, and find a pleasure in all their simple joys, remembering her own child-life, and the happy summer days."
>
> —Lewis Carroll, Alice's Adventures in Wonderland

So ends Lewis Carroll's classic novel, with a nostalgic introspection by Alice's older sister. This passage illustrates how social cognition and memory intertwine to create a rich, social connectedness, infusing one's personal experience into reflections about the thoughts, aspirations and motivations of others. Just as Alice's sister draws from childhood memories to create her wistful vision of Alice's future, we too utilize our personal experiences to envision the inner worlds of those around us. Memory thus provides an essential footing from which we are able to reach out to and engage with our social environment.

Memory is not simply a static representation of the past. It is a surprisingly flexible account of our accumulated experience and knowledge—a record of our past measured in space, time and context. Functionally, we access, reconfigure and

A.C. Laurita • R. Nathan Spreng (✉)

Department of Human Development, Cornell University, Martha Van Rensselaer Hall, Ithaca, NY 14950, USA

e-mail: nathan.spreng@gmail.com

re-encode these representations as we rely on our memory to guide our present thoughts and actions and plan for our future. As memory plays a critical role in constructing our personal past, present and future, it is perhaps not surprising that memory also plays a crucial role in how we construct, interact with and predict the thoughts and actions of others. In this chapter, we explore this relationship between memory and social cognition. Specifically we discuss how hippocampal-mediated memory processes influence social functioning. We examine evidence from behavioral, neuroimaging, and neuropsychological studies that point to a strong bond between our ability to recollect and reconstruct our personal past and our capacity to imagine, infer and ultimately interact with the intentions of others. The hippocampal memory system is highly attuned to this kind of social information, for which relational binding is critical. Although there is insufficient evidence thus far to draw the conclusion that the hippocampus carries a special function for social cognition above and beyond what it does for memory, we examine recent evidence regarding how the hippocampus is recruited in social contexts.

We begin the chapter with a broad discussion of social cognition and memory. We next review the importance of the hippocampus in contextual and relational processing and explore its critical role in navigating physical and temporal contexts. Although consideration of a role for the hippocampus in social cognition is relatively novel, a growing body of evidence suggests that social cognition depends on the binding of discrete elements of social interaction. As binding is considered to be a central function of the hippocampus, and the medial temporal lobe memory system more broadly, this raises the intriguing possibility that social cognition may depend on the functioning of the hippocampal memory system and associated brain regions. We next suggest that this functional role of the hippocampal memory system be expanded to include navigating social contexts. We discuss experimental lesion, neuropsychological research and functional neuroimaging investigations that are providing increasingly convergent evidence pointing to an important role for the hippocampal memory system in social cognition. Increasingly, the neural basis of social cognition is associated with functionally connected brain networks. These networks are defined by correlated oscillations of activity in spatially-distributed brain regions observed during task or at rest. The default network, a set of brain regions implicated in mnemonic and associative processes, has been specifically implicated in the processing of socially-relevant information. As the hippocampus is a core node within this network, in the final section of the chapter we extend our review to studies of the default network and social cognition.

Memory and Social Cognition in Everyday Function

Social cognition, broadly defined, describes the way in which people understand themselves and other people. It encompasses the cognitive processes used to decode and encode the social world (Beer and Oschner 2006). These include perception of

self and others, the incorporation of social information into existing knowledge structures, and the selection of actions based on social cues. Here we focus on how social cognition involves the binding of basic social percepts and their integration into stored memory representations to guide future thoughts and behavior. In this respect we do not review early sensory processing or action planning, but rather focus on the constructive and binding aspects of social cognition in which hippocampal structures are likely to play a more direct role. As much of the research literature focuses on hippocampal functions, we restrict our discussion here to explicit encoding and retrieval processes.

In this first section we lay the conceptual foundation for the remainder of the chapter by suggesting four points of intersection between social cognition and memory in everyday life: perceiving interpersonal cues, constructing complex social representations, navigating social relations, and forming close personal bonds. Put another way, how does memory influence how we perceive, construct, interact and, ultimately connect with, our social world?

Perceiving Interpersonal Cues

At a fundamental level, social thinking requires the ability to perceive, disambiguate and ultimately categorize social stimuli. Some of these basic perceptual categories include living versus non-living, human versus non-human, friend versus enemy, and same versus other. The hippocampal memory system is critical for encoding and retrieval of these social percepts (Rubin et al. 2014). These memory processes are necessary to identify an acquaintance's face in a crowd or to differentiate your friend's from your sister's voice when answering a phone call. Accurately perceiving and recognizing social stimuli requires forming and accessing person cues, and developing a store of person-specific knowledge—both stable (such as personality traits) and transient (such as affective states). Through repeated exposure across multiple contexts, these cues form patterns and provide the basis of a more abstract sense of person identity (see Carlston and Smith 1996, for review). Explicit encoding and retrieval of person-specific knowledge and the formation of context-independent, person-schema depend on the hippocampal memory system (Eichenbaum and Cohen 2014; Ochsner et al. 2005). Other social perceptions, such as impression formation, are formed rapidly, often in a single exposure. These implicit associations occur outside of conscious awareness and are likely not dependent on the hippocampus (e.g. Freeman et al. 2014).

Constructing Complex Mental Representations

Across time, perceptions of personal identity are imbued with learned positive, negative, and neutral associations, linking stimuli and situational contexts with

specific social actors (Carlston and Smith 1996). Through repeated interactions, complex person-specific schema are formed including judgments of self-similarity and attributions of intent. Forming social relationships involves the development of complex mental representations, also known as "internal working models", of relationship partners (Bowlby 1969; Carlston 2010; Collins and Read 1994; Pietromonaco and Feldman Barrett 2000). Hippocampal memory systems play a critical role in forming these representations, weaving together past experiences and extracting stable patterns across time. Such mental representations consist of extensive interpersonal memories of figures in our social world that are integrated with affective associations (e.g., Zayas and Shoda 2005). These patterns of social expectation and behavior facilitate the development of long-lasting dyadic social relationships. In such close relationships, the utilization of an innate bonding system is also based upon the development of complex cognitive representations (Zayas and Shoda 2005; Zayas et al. 2002). These representations facilitate forward-modeling of behavior enabling individuals to predict the actions of others and guide their own actions in dynamic social contexts (Holmes 2002).

Navigating Social Relationships

As we discuss in more detail in the following section, the hippocampal memory system is critically involved in spatial processing (see Eichenbaum and Cohen 2014 for a review). This role has recently been extended to navigating social distances and social hierarchies (Tavares et al. 2015), insofar as the hippocampus binds various components of social information. From this perspective social cognition is considered analogous to navigating a social landscape with distance measured along two dimensions: power and social affiliation (Tavares et al. 2015). A parent, who possesses both high power status and high social-affiliation, would be close to their child in terms of social distance. In contrast, a friend who may be high in social affiliation but equivalent with respect to social power hierarchy would be considered more socially distant. As with mapping physical space, the hippocampus is important for charting and navigating the myriad social distances and hierarchies that make up our social milieu (Tavares et al. 2015; see also Kumaran et al. 2016). More specifically, hippocampal involvement in mapping social space hinges on representing others in multi-dimensional social spaces. Previously, others examining the neural basis of social distance found little evidence of hippocampal recruitment, when considering the tracking of only one dimension (Muscatell et al. 2012; Parkinson et al. 2014; Tamir and Mitchell 2011). Tavares et al. (2015) assert that the role of the hippocampus involves mapping the combination of social-dimensions rather than individual social-dimensions.

Social Bonding

Highly salient social memories comprise the mental representations we form of close others—children, parents, romantic partners (Pietromonaco and Feldman Barrett 2000). Romantic partner mental representations in particular promote the formation of stable, mutually-beneficial bonds with relationship partners. Within the context of pair-bonds, romantic partner mental representations have been further conceptualized as cognitive expansions of the self (Aron and Aron 1986). These partner representations have been demonstrated to play a role in subconscious pursuit of partner-specific interpersonal goals (Fitzsimons and Bargh 2003) and to inherently intertwine the cognitive and emotional contexts of both relationship partners (Zayas et al. 2002). Long-term declarative and relational memory, supported by the hippocampus, is crucial for forming and maintaining and accessing these 'other' representations, which form the basis of complex interpersonal bonds (Rubin et al. 2014). Moreover, these close-other representations can influence our perceptions, judgments and responses to others in our social world—a process known as social-cognitive transference (Anderson and Cole 1990; Günaydin et al. 2012).

Hippocampal Function and Social Cognition

The influence of hippocampally mediated memory processes on social cognition is an emerging area of inquiry. However, two well established accounts of hippocampal memory function: relational integration and constructive memory have provided a theoretical bridge between memory and social cognition. We review each of these theories in turn and discuss how they have been used to characterize this relationship. In the following sections, we draw from several different theoretical perspectives of hippocampal function in order to provide a comprehensive account of the potential role of the hippocampus in social cognition. However, for the purposes of this review, we remain agnostic with respect to the merit of these individual perspectives as theories of hippocampal functioning per se.

Relational Integration and Social Cognition: The Role of Spatial and Social Navigation

The role of the hippocampus in relational processing was first posited by O'Keefe and Nadel (1978), who proposed the cognitive mapping hypothesis of hippocampal functioning. This theory suggested that the hippocampal system forms mnemonic representations by linking stimuli to specific locations through a process of allocentric mapping of distance and direction of an object within its spatial

environment. Building from this earlier work, Eichenbaum et al. (1996) argued that the hippocampal memory system, conceptualized as a functional grouping of the hippocampus, medial temporal lobe, and cortical regions, was critically involved in relational processing as well as mapping stimuli to specific spatial contexts. The authors suggested that these representations were flexible and could be dynamically reconfigured to reflect changing contexts. Relational memory theory proposes that the hippocampus is responsible for computing an associative scaffold, linking items and events in "memory space" (Eichenbaum 2004; Eichenbaum et al. 1999). Others have hypothesized that memory space can include relational information beyond spatial location such as temporal, emotional or configural associations, implicating the hippocampal memory system in a range of complex cognitive processes that depend upon binding of relational information (e.g. Zeithamova et al. 2012). Next we review evidence that relational processing theory extends to the binding of social relationships—drawing a direct association between hippocampal memory and social cognition.

Social cognition is just one of several domains in which humans demonstrate active engagement with their environments, through dynamic representation, manipulation, and flexible updating to match action and context (Rubin et al. 2014). Hippocampal memory can be understood as a map, constructed from past experience, that guides our personal actions, as well as our interactions with the social world in the present and future (Rubin et al. 2014; Eichenbaum and Cohen 2014; Wang et al. 2015). In this respect, the hippocampal system performs a crucial role in constructing and navigating a much more complex memory space, one that includes an expansive map of personal and interpersonal experience (Eichenbaum and Cohen 2014). Indeed it has been suggested that the hippocampus builds a "currency" of spatially—or otherwise connected—scenes (Maguire and Mullally 2013). Furthermore, this conceptualization of hippocampal function overlaps significantly with the theory of constructive memory, discussed below.

More recently, research has suggested that social relations may occupy a significant portion of the human 'memory space', positioning the hippocampus as a hub for social navigation. In the social domain the hippocampal memory system would bind and dynamically reconfigure various elements of social relationships such as social distance and hierarchies, social bonds and transgressions. These relational scaffolds or schema are then accessed to guide behavior in social contexts (Zayas et al. 2002). Support for this idea was recently demonstrated in an fMRI investigation of hippocampal functioning and social relatedness (Tavares et al. 2015). In this study, social distance was manipulated along two primary dimensions: power (including competence, dominance, and hierarchy) and affiliation (including warmth, intimacy, trustworthiness, and love). Participants were presented with fictional characters in a virtual role-playing game. Hippocampal activity predicted changes in the interaction of self-reported affiliation and power between the participants and the fictional characters. Results were characterized in terms of vectors through social space along the two social-relationship dimensions (power-ranking and affiliation), with hippocampus activity associated with vector angles, and posterior cingulate cortex (PCC) associated with vector length—i.e. social

distance. This geometric representation of social distance is consistent with the relational theory of hippocampal function and represents an extension to the realm of social cognition (Eichenbaum and Cohen 2014; Tavares et al. 2015). Hippocampal activation during social navigation also correlated with individual differences in social skills. Greater activation was associated with reduced avoidance and neuroticism and increased conscientiousness, providing a further link between hippocampal function, social navigation and social capacity in the real world (Tavares et al. 2015). The authors also suggest that deficits in social cognition may be a direct consequence of hippocampal dysfunction. We discuss this further in the section on hippocampal amnesia below.

Constructive Memory and Social Cognition

Constructive memory theory (Schacter 2012) suggests that memories are not veridical presentations of the past but rather reconfigurations of related mnemonic features that are continuously re-shaped by retrieval and re-encoding processes. These same processes are posited to support the constructive nature of imagination, in which features of disparate prior experiences are re-integrated in novel ways such that new, imagined "experiences" can be creatively processed (Schacter 2012). Imagination, however, is not limited to the process of musing on personal pasts, presents, and futures; imagination also shares its inventive, additive nature with how we envision the experiences of other individuals in our social world. In this respect the constructive nature of memory supports social cognition, enabling us to predict social interactions and prepare adaptive responses. The concept of memory construal raises the possibility that how we represent our personal past will influence our actions and thoughts about others. In the next sections we briefly review how constructive memory shapes social cognition by influencing our self-perception, empathy towards others and group social behavior.

Self-Perception

Representations of the self have been conceptualized as a "cognitive filter", through which we see and understand others in our social world (Beer and Ochsner 2006). Individuals draw from remembered experiences and introspective thoughts to infer motivations and affective states of others (e.g. Meltzoff and Brooks 2001; Nickerson 1999). Constructed representations of the self can serve as reference points for characterizing and framing others in terms of similar personality traits or shared preferences. These notions of self serve to anchor perceptions of others' feelings and experiences (Epley et al. 2004). Moreover the influence of self-representation and memory on social cognition is likely reciprocal. There is a

deep history of cultural and developmental psychological theory arguing that self-concept is defined and enacted through social settings (e.g. Bem 1972; Sampson 1977; Vygotsky 1978; Markus and Cross 1990).

Empathy

The process of imagining the experiences of social others can facilitate empathy and prosocial behavior (Gaesser 2012). Vivid imagining has been associated with increased prosocial motivation and this relationship appears to be mediated by the hippocampal memory system. Memories of helping others that are recalled in greater detail and more coherently increase prosocial motivation (Gaesser and Schacter 2014). Individual differences in the capacity to vividly recollect past experiences have also been shown to modulate empathic responding (Ciaramelli et al. 2013).

Group Social Behavior

The hippocampal memory system also plays a role in group dynamics. Collective identity can be achieved through the merging of personal memory content (Brown et al. 2012, for review). Collective identity suggests that social group members can form shared memories through their social interactions (Bartlett 1932). This notion of a shared personal past may emerge from common childhood experiences, daily activities or major life experiences. These commonalities promote the construction of shared in-group schemata, leading to collective representations of a personal past. These shared schemata shape how group members remember their personal and group pasts, although group status (in/out) appears to moderate this effect (Lindner et al. 2012).

Thus far in the chapter we have provided a theoretical framework relating hippocampal memory system functioning to social cognition. Relational integration theory suggests that hippocampal-mediated memory processes are necessary to navigate social distance and complex social hierarchies. Constructive memory theory argues that how we retrieve, reconfigure and re-encode our past experiences can influence our imagined social future, influencing our sense of social proximity to the 'other', our capacity for prosocial behavior and our collective memory. Together these theories point to a critical role for memory in imagining our social future and successfully navigating our way there.

Mnemonic Contributions to Social Cognition

In this next section we review the experimental evidence linking hippocampal memory function and social cognition. We will begin with an evolutionary perspective, examining comparative psychological evidence. Next we will review

animal and human lesion studies. Experimental neuropsychology in animal models allows for direct, experimental manipulation of the neural regions involved in cognitive processes; however, this methodology is limited in its applicability to human models. Human neuropsychology—particularly, lesion studies—provides evidence for the cognitive and behavioral results of neural abnormalities in humans, but it is more difficult to ascribe cognitive processes to specific brain regions due to poorly-defined lesion boundaries. Finally, we review functional neuroimaging evidence. While these studies provide only correlational data, they enable more precise topographical mapping of cognitive processes in vivo. Further, by simultaneously recording data across the whole brain, functional neuroimaging enables network-level analysis, describing cognitive functions as emergent properties of spatially-distributed, yet functionally connected, brain regions. Here we review insights from each of these methodologies to characterize the role of the hippocampus and functionally-connected brain regions in social cognition.

Comparative Psychology

The capacity to successfully maneuver through our social world is fundamental to human survival. Basic social competency is thought to be fundamental for defining one's sense of self, surviving to mate and raise young and bolstering physical and mental health throughout the lifespan (e.g. Cohen 2004; House et al. 1988; Kiecolt-Glaser and Newton 2001; Vygotsky 1978). This social capacity to represent, reflect upon and anticipate the intentions of others differentiates the human species from our primate relatives (Tomasello 1999). Evolutionary theorists have proposed the "social brain hypothesis" to describe why humans have become comparatively more reliant upon social cognition for survival. This hypothesis suggests that throughout human evolution, an increasing number of social relationships and complexity of social hierarchies was associated with a rapid increase in brain size (Dunbar 1998; Humphrey 1976).

As humans gathered in tribal groupings, social capacity was needed to differentiate oneself from others and to represent, reflect upon and anticipate the intentions of those 'others' to optimize survival. This required tracking complex social dynamics including group sizes, inter-connectedness of members, and dominance hierarchies. Thus each incremental increase in group membership imposed exponentially greater mnemonic demands to encode these relationships and cognitive flexibility to update shifting relationships. According to social brain theorists, this rapid increase in cognitive load was an important factor in human cortical expansion. Evidence for such an association has been observed in non-human primates where affiliation with larger social groups is positively correlated with cortical volume (Dunbar 1998).

Experimental Neuropsychology

Although the enhanced capacity for social cognition in humans may reflect the "social brain hypothesis", other animal models can provide us with information about the specific recruitment of the hippocampus in social processing. In humans and non-human animals alike, the ability to remember different social individuals is essential for the formation of social relationships and groups. For example, social recognition in mice involves the capability to identify and recognize conspecifics. Social recognition in mice appears to be organized in a manner similar to that of other hippocampus-dependent memory capabilities; in one study, hippocampal lesions in mice disrupted social cognition after a 30-min delay (Kogan et al. 2000). Social processing has also been investigated using animal models of Alzheimer's Disease (AD). In one recent study, increasing the social demands by co-housing AD model mice with non-AD animals reversed memory deficits in the AD cohort (Hsiao et al. 2014). These memory gains were attributed to increases in brain-derived neurotrophic factor (BDNF) as well as hippocampal neurogenesis.

Hitti and Siegelbaum (2014) isolated the important role of the CA2 subfield of the hippocampus in social recognition. Using a novel transgenic adult mouse line, the authors reported that selective genetic inactivation of CA2 neurons resulted in the loss of social recognition; however, there was no observed change in other hippocampally-mediated behaviors. Other studies have demonstrated that lesions within CA2 selectively impair social recognition (Leser and Wagner 2015; Stevenson and Caldwell 2014), giving rise to the idea that this hippocampal subfield may be a 'social cognition' area.

Human Neuropsychology: Hippocampal Amnesia and Social Cognition

Human neuropsychological studies have examined the role of memory in social cognition and the underlying hippocampal mechanisms for social cognitive processes. Much of the existing neuropsychological research focuses on how the loss of detailed memories and experiences from one's personal past—due to hippocampal lesions or damage—is correlated with social impairments. As we have discussed earlier hippocampal damage would be expected to disrupt relational processing or memory construal, leading to deficits in social cognition (Eichenbaum and Cohen 2014; Schacter 2012). In one recent study, patients with hippocampal damage showed impairments in episodic recall but preserved ability to generate coherent concepts of self (Kurczek et al. 2015). In contrast, those with medial prefrontal cortex (mPFC) damage were able to reconstruct detailed episodic events but were unable to integrate self concepts into the recollections (Kurczek et al. 2015). In a similar study, hippocampal and bilateral ventromedial PFC (vmPFC) patients were asked to make moral judgments about unfamiliar

individuals before and after learning about the individuals' behavior in previous moral situations. Interestingly, the hippocampal damage group showed the most amount of change (shift from good to bad or vice versa) in character judgments from pre-test to post-test. The vmPFC damage group demonstrated the least amount of change in moral character judgments. These findings suggest that the vmPFC is important for encoding affective context, whereas the hippocampus encodes situational context (Croft et al. 2010). Together, these studies suggest that the hippocampus is involved in social functioning but may interact with other brain regions to mediate social cognition in more real-world contexts. We will explore the role of functional brain networks further in the final section of the chapter.

As discussed in the constructive memory section above, the ability to use flexible cognition processes to imagine is closely linked with the social cognitive skills of theory of mind and mentalizing about the thoughts of others. Some research suggests that individuals need to be able to construct and process imagined scenes in order to represent the perspective of an 'other'. Several studies have documented deficits in the construction of imagined events following bilateral hippocampal damage (Andelman et al. 2010; Hassabis et al. 2007; Lee et al. 2012; Mullally et al. 2012; Race et al. 2011; Rosenbaum et al. 2009; Tulving 1985). Hassabis et al. (2007) tested a group of patients with hippocampal damage on an imagination-related cognitive task. These patients showed marked impairments in their abilities to create imagined, novel stories based on short verbal prompts. Furthermore, the imagined experiences lacked coherency with respect to the spatial or environmental setting, compared with healthy control subjects. The authors posited that this spatial fragmentation of imagined components was attributable to missing input from the hippocampal memory system. Within this group of patients, their lack of hippocampal function was most evident in the functional losses of the ability to bind together disparate aspects of experiences (real or imagined), a critical capacity for social cognition (see section "Constructing Complex Mental Representations"). Individuals may need to be able to construct and process imagined scenes in order to represent the perspective of an 'other', although this has not been tested directly. Further, it appears this relationship may be moderated by personal familiarity. While episodic scene reconstruction may be necessary to take the perspective of a familiar other, this does not appear to be the case for unknown others (Rabin and Rosenbaum 2012).

Hippocampal patients are also more likely to have poor social functioning in real-world contexts, with few strong social bonds and smaller social network size (Davidson et al. 2012; Warren et al. 2012). Patients reported making very few close friends and being less involved with neighborhood, religious, and community groups. Deficits in the ability to use hippocampal memory representations in the processes of encoding, updating or retrieving models of social others is a significant contributor in these patients' struggles to develop and maintain close social connections (Davidson et al. 2012).

Davidson et al. (2012) examined the close relationships of three amnesic individuals. The patients in this study showed less involvement in community groups than their demographically-matched control subjects. Two patients with adult-onset

hippocampal amnesia had made very few new friends since their injuries. In contrast, the third patient, with developmental amnesia, had fostered several close relationships over the time of the study. The authors concluded that social network size and social bonding is impaired in acquired hippocampal amnesia. However, Warren et al. (2012), demonstrated positive social outcomes in a case of severe hippocampal amnesia. These were attributed to the strength of the existing social networks (husband, extended family), which relieved the patient of many functional responsibilities, enabling her to focus on maintaining or expanding her social relationships. Additionally, Duff et al. (2008) reported on an amnesic patient who was successful in forming new close social relationships, despite her memory impairment. This stands as a second counterexample to the finding that those with hippocampal amnesia generally have great difficulty with everyday social tasks such as learning new names, consciously remembering sharing experiences with others, and updating mental representations of existing social relationships (for review, see Rubin et al. 2014). Clearly, more work is necessary to examine the social ramifications of amnesia. In healthy adults, the range of individual differences in memory ability predicts social network size (Stiller and Dunbar 2007), suggesting an augmenting function.

Hippocampal amnesia patients also demonstrate deficits in trait and state empathy (Beadle et al. 2013): to imagine the life events of unfamiliar others (Rabin and Rosenbaum 2012) and to make complex social judgments (Staniloiu et al. 2013). This last study provides an interesting perspective on social cognitive deficits in amnesia. They reported that their developmental amnesia patient was impaired on complex social judgment task but not on empathy or theory of mind tasks. The authors suggested that their findings implicated the hippocampus in more complex relational integration processes.

Duff and colleagues (2013b) studied several female patients with early stage AD and their interactions with familiar conversation partners. Somewhat surprisingly, the patients displayed significant learning on a cognitive task when paired with communication partners. The authors argued that the social interactions likely recruited neural resources outside of the medial temporal regions to support non-hippocampally-mediated learning (Duff et al. 2013b). These findings demonstrate how differences in social cognitive task demands relate to the recruitment of differential functional networks in the brain. The hippocampal memory system is not the only region involved in social processing, and this study raises important questions about the integration of various memory processes.

Functional Neuroimaging

The field of social cognitive neuroscience has undergone almost exponential growth over the last decade. In this section we limit our review to studies that specifically investigate the role of the hippocampal memory system in social

cognition. Specifically we review two common paradigms: (1) perception of self versus others and (2) recognition of social cues.

Perception of Self vs. Other

The hippocampus has been implicated in many processes which support differentiation of self versus other perceptions: recalling and reconstructing personal past events and imagining potential personal futures (e.g., Addis et al. 2007; Gaesser et al. 2013; Hassabis et al. 2007; Okuda et al. 2003; Race et al. 2011; Szpunar et al. 2007), scene construction (e.g., Hassabis and Maguire 2009; Mullally and Maguire 2014), creative thinking and imagination (Duff et al. 2013a). Other kinds of relational processes help to further differentiate amongst others without necessarily referencing the self: for example, combining information about the relationships between objects across time (e.g., Davachi 2006; Duff et al. 2007; Konkel and Cohen 2009; Ranganath 2010).

Brain regions recruited in self- and other- perception are distinctive (for review, see Beer and Ochsner 2006). Notions of the self become more semantic over time as experiences are relatedly accessed and re-encoded. However, judgments about non-close others are more dependent on episodic recollection (e.g. Klein et al. 1999; Klein et al. 1996), suggesting that the hippocampal memory system is implicated in 'other' more than 'self' perception. In a similar finding, Ochsner et al. (2005) looked at patterns of functional activation associated with reflecting on a close other individual's opinions about oneself or reflecting on one's own opinions of oneself. They reported that reflections on close others' judgments, but not those of the self, were associated with activation of the hippocampal memory system, suggesting that this system is engaged both by perception and judgment of the social 'other'. Yet, the existing literature on self and other referencing contains some inconsistencies; as mentioned earlier in this chapter, Kurczek et al. (2015) reported that hippocampal amnesia patients did not show a significant difference from healthy controls on a measure of self-referential processing. This raises the possibility that social-perception and social referencing may be discrete processes. While this question is beyond the scope of this review, it remains an important question for future research.

Rabin and Rosenbaum (2012) reported that the hippocampus is involved in theory of mind for familiar but not unfamiliar others. Perry et al. (2011) also demonstrated a differentiated role of the hippocampus based on the nature of other-oriented thought. In this study, subjects selected individuals who were similar versus dissimilar from themselves from a pool of varied protagonists. During scanning subjects were asked to imagine how themselves or their selected protagonists would feel in certain situations (for instance, losing a wallet). After scanning, subjects were led through interviews about their autobiographical memories. Specifically, the interviewers asked subjects if they remembered whether or not each event that had been presented in the scanning session had ever personally happened to them before. They further divided the subsequent data into

"remembered events" and "not remembered events". Results indicated that magnitude of the hippocampal activity was highest in the self condition, second highest in the similar other condition, and lowest in the dissimilar other condition. Additionally, there was a significant correlation between the self ratings and the similar-other ratings for "remembered events" but not for "not remembered events". This result demonstrates that personal episodic memory was recruited when subjects judged the protagonists' emotional states. The authors concluded that the hippocampus was involved in subjects' emotional judgments about the self and similar others.

Recognition of Social Cues

The ability to adapt our behavior based on dynamic social cues, such as changing facial expressions, relies heavily on working memory (Gobbini and Haxby 2007). We need to be able to distinguish between cognitive representations of different individuals' faces and those of different expressions from the same individual. Ross et al. (2013) examined neural activity in regions contributing to the processes of encoding, maintaining, and retrieving overlapping facial expression—here, two different affective expressions by the same or another individual. They utilized a match-to-sample task, contrasting conditions of overlap (two faces from the same individual, with different expressions) and non-overlap (two faces from different individuals, with different expressions). The authors found that, whereas lateral orbitofrontal cortex contributes to encoding and maintaining mental representations of overlapping stimuli, the hippocampus was engaged during retrieval. This suggests that retrieval of overlapping social percepts, as is likely required to differentiate facial expressions, is hippocampally dependent.

Taken together, the studies reviewed here provide converging evidence of mnemonic contributions to social cognition. From an evolutionary perspective, with increasing hippocampal volume linked to increasing social network size, to animal and human neuropsychological studies providing more causal evidence linking memory and social cognition and finally to functional neuroimaging studies providing a more precise topographical mapping of social cognition and hippocampal activation. These lines of evidence suggest a critical role for memory in navigating our complex and constantly shifting social milieu. In the final section of the chapter we will examine the contribution of memory to social cognition from a network neuroscience perspective. Specifically we will examine the role of the default network—a collection of brain regions functionally connected to the hippocampus that have been implicated in social cognition.

Social Cogntion and the Default Network

The recent discovery of a common functional anatomy for autobiographical memory (recalling personally experienced events) and theory of mind (inferring the mental states of others) suggested that memory and social cognitive processes share a common functional architecture that extends beyond the hippocampal memory system (Buckner and Carroll 2007; Spreng and Grady 2010; Rabin et al. 2010). This common functional architecture overlapped almost completely with a collection of functionally connected brain regions referred to as the default network (Spreng et al. 2009). Core brain areas within the default network include the medial temporal lobes, mPFC, lateral prefrontal cortex, lateral temporal cortices, PCC, and lateral parietal cortices (Addis et al. 2007; Buckner and Carroll 2007; Spreng et al. 2009). In this final section of the chapter we first describe how core nodes of the default network have been directly implicated in social processing. Then we review how default network and hippocampal memory systems interact with other brain regions and other functional networks during social cognition.

Default Network Brain Regions and Social Cognition

The default network has been implicated in processes including recollection and future thinking (Schacter 2012), autobiographical planning (Spreng et al. 2015) and mind-wandering (Fox et al. 2015). More recently the role of the default network has been associated with several aspects of social cognition. It has been implicated in the integration of personal and interpersonal information. Personal experiences are used to generate social conceptual knowledge, which in turn, leads to the development and implementation of strategic social behavior (Spreng 2013, for review; see also Spreng and Mar 2012). The integrity of vmPFC, a core node of the default network, predicts ability to retrieve impressions of others (Cassidy and Gutchess 2012). Attributional decisions and judgments of others' emotional states recruited areas of the default network, such as vmPFC, in a recent study (Haas et al. 2015). The default network also enables us to imagine the experiences of others. Hassabis et al. (2013) taught participants the personalities (based on the two dimensions of agreeableness and extraversion) of four characters. They then imagined their behavior across different situations. Results showed that activity in the mPFC reliably predicted which characters participants were imagining.

Furthermore, other core regions and subsystems of the default network have been specifically linked with social cognitive processes (for review, see Spreng and Andrews-Hanna 2015). Saxe (2010) found that activity in the right temporoparietal junction is associated with reflecting upon other individuals' beliefs. Inferior frontal and lateral temporal regions also show activation during social tasks, and have been specifically implicated in the semantic aspects of mentalizing (e.g., Binder and Desai 2011). Others still show that the PCC is active across a wide variety of self-

and other- related cognitive processes including self-referential processing, familiarity representation and theory of mind (Binder et al. 2009; Brewer et al. 2013; Qin and Northoff 2011; Spreng et al. 2009).

Default Network Functional Connectivity and Social Cognition

Throughout the chapter we have implicated the hippocampal memory system, a component of the default network, in social cognition. In the previous section we reviewed how specific nodes of the default network were implicated in various aspects of social cognition. Here we review how functional connectivity within the default network, and specifically between hippocampal memory systems and other default brain regions, supports social cognitive processing. Increased functional connectivity between hippocampal regions of interest and default network nodes indicates correlated neural activation that is associated with social-cognitive processes.

   In a recent meta-analysis of functional neuroimaging studies of perspective-taking (Bzdok et al. 2013), ventral mPFC was robustly functionally connected with the hippocampal component of the default network. Functional connectivity between these regions was associated with reward-associations and evaluation-related processes. In contrast, dorsal mPFC showed greater functional connectivity to inferior frontal gyrus, temporal-parietal junction, and middle temporal gyrus regions. Functional connectivity within this aspect of the default network was associated with perspective-taking and episodic memory retrieval. These findings were convergent with a recent review which suggested that functional connectivity between the hippocampus and mPFC was important for future thinking and imagination (Buckner 2010). A study by Perry et al. (2011) also observed that the mPFC and the PCC are crucial for processing self-relevant information. The PCC plays an additional role in encoding information about others, while the hippocampus is engaged by internal mentation about oneself and differentiating self- from other-focused experiences. Specifically the hippocampus—in conjunction with the broader default network—served to mediate judgments of self versus others with respect to events in memory (Perry et al. 2011). These results highlight the importance of hippocampal interactions with other default network regions in mediating social cognition.

Conclusion

In this chapter we provided a broad overview of the research literature ascribing a role for the hippocampal memory system in social cognition. The hippocampus is highly attuned to social information, which is inherently composed of distinct components requiring relational binding. We suggest that social cognition is a form of mental processing that places high demands on the type of processing supported by the hippocampus. Currently however, there is insufficient evidence to suggest that the hippocampus plays a unique role for social cognition. We began the review by describing four areas in which memory and social cognition overlap in everyday functioning. Next we examined two theories of hippocampal memory, relational integration and constructive memory, and described how these memory theories readily extend to the domain of social cognition. In the third section we briefly surveyed the research literature investigating the association between memory and social cognition, reviewing results from evolutionary psychology, experimental and human neuropsychology, and functional neuroimaging. Finally we examined how the hippocampal memory system, working in concert with default network brain regions, was involved in social cognition.

Memory and social cognition are complex cognitive functions, each encompassing different processes and engaging numerous brain regions. That these complex functions interact or overlap at the level of the brain is perhaps not surprising. What is surprising is the extent of the overlap. Do they share a common psychological and neural architecture? Is social cognition simply a projection of personal memory and experience onto an external 'other'? Or might the social content engage different cognitive processes and brain regions? These remain active questions of research. Our ability to step outside ourselves, to appreciate, understand, predict and adapt to the thoughts, intentions and actions of others makes us truly human. Understanding how our store of experience and memory influences our perceptions of and engagement with the 'other' will only become more important in our increasingly interconnected world.

References

Addis DR, Wong AT, Schacter DL (2007) Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia 45(7):1363–1377

Andelman F, Hoofien D, Goldberg I, Aizenstein O, Neufeld MY (2010) Bilateral hippocampal lesion and a selective impairment of the ability for mental time travel. Neurocase 16 (5):426–435

Andersen SM, Cole SW (1990) "Do I know you?": The role of significant others in general social perception. J Pers Soc Psychol 59:384–399. doi:10.1037/0022-3514.59.3.384

Aron A, Aron EN (1986) Love and the expansion of self: understanding attraction and satisfaction. Hemisphere/Harper & Row, New York

Bartlett F (1932) Remembering: a study in experimental and social psychology. Cambridge University Press, New York

Beadle JN, Tranel D, Cohen NJ, Duff MC (2013) Empathy in hippocampal amnesia. Front Psychol 4:69. doi:10.3389/fpsyg.2013.00069

Beer JS, Ochsner KN (2006) Social cognition: a multi level analysis. Brain Res 1079(1):98–105

Bem DJ (1972) Constructing cross-situational consistencies in behavior: some thoughts on Alker's critique of Mischel. J Pers 40(1):17–26

Binder JR, Desai RH (2011) The neurobiology of semantic memory. Trends Cogn Sci 15:527–536

Binder JR, Desai RH, Graves WW, Conant LL (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cereb Cortex 19:2767–2796

Bowlby J (1969) Attachment and loss: attachment (vol. 1). Basic Books, New York

Brewer JA, Garrison KA, Whitfield-Gabrieli S (2013) What about the "self" is processed in the posterior cingulate cortex? Front Hum Neurosci 7:647

Brown AD, Kouri N, Hirst W (2012) Memory's malleability: its role in shaping collective memory and social identity. Front Psychol 3:257. doi:10.3389/fpsyg.2012.00257

Buckner RL (2010) The role of the hippocampus in prediction and imagination. Annu Rev Psychol 61:27–48

Buckner RL, Carroll DC (2007) Self-projection and the brain. Trends Cogn Sci 11:49–57. doi:10.1016/j.tics.2006.11.004

Bzdok D, Langner R, Schilbach L, Engemann DA, Laird AR, Fox PT, Eickhoff SB (2013) Segregation of the human medial prefrontal cortex in social cognition. Front Hum Neurosci 7:232

Carlston D (2010) Models of implicit and explicit mental representation. In: Gawronski B, Payne KB (eds) Handbook of implicit social cognition: measurement, theory, and applications. Guilford Press, New York, pp 38–61

Carlston DE, Smith ER (1996) Principles of mental representation. In: Higgins ET, Kruglanski AW (eds) Social psychology: handbook of basic principles. Guilford, New York, pp 184–210

Cassidy BS, Gutchess AH (2012) Structural variation within the amygdala and ventromedial prefrontal cortex predicts memory for impressions in older adults. Front Psychol 3:319. doi:10.3389/fpsyg.2012.00319

Ciaramelli E, Bernardi F, Moscovitch M (2013) Individualized theory of mind (iToM): when memory modulates empathy. Front Psychol 4:4. doi:10.3389/fpsyg.2013.00004

Cohen S (2004) Social relationships and health. Am Psychol 59(8):676

Collins NL, Read SJ (1994) Cognitive representations of adult attachment: the structure and function of working models. In: Bartholomew K, Perlman D (eds) Advances in personal relationships: vol. 5. Attachment processes in adulthood. Jessica Kingsley, London, pp 53–90

Croft KE, Duff MC, Kovach CK, Anderson SW, Adolphs R, Tranel D (2010) Detestable or marvelous? Neuroanatomical correlates of character judgments. Neuropsychologia 48 (6):1789–1801

Davachi L (2006) Item, context and relational episodic encoding in humans. Curr Opin Neurobiol 16(6):693–700

Davidson PS, Drouin H, Kwan D, Moscovitch M, Rosenbaum RS (2012) Memory as social glue: close interpersonal relationships in amnesic patients. Front Psychol 3:531. doi:10.3389/fpsyg.2012.00531

Duff MC, Hengst JA, Tranel D, Cohen NJ (2007) Talking across time: using reported speech as a communicative resource in amnesia. Aphasiology 21(6–8):702–716

Duff MC, Wszalek TW, Tranel D, Cohen NJ (2008) Successful life outcome and management of real-world memory demands despite profound anterograde amnesia. J Clin Exp Neuropsychol 30:931–945

Duff MC, Kurczek J, Rubin R, Cohen NJ, Tranel D (2013a) Hippocampal amnesia disrupts creative thinking. Hippocampus 23(12):1143–1149

Duff MC, Gallegos D, Cohen NJ, Tranel D (2013b) Learning in Alzheimer's disease is facilitated by social interaction and common ground. J Comp Neurol 521(18):4356–4369

Dunbar R (1998) The social brain hypothesis. Evol Anthropol 6:178–190

Eichenbaum H (2004) Hippocampus: cognitive processes and neural representations that underlie declarative memory. Neuron 44(1):109–120

Eichenbaum H, Cohen NJ (2014) Can we reconcile the declarative memory and spatial navigation views on hippocampal function? Neuron 83(4):764–770

Eichenbaum H, Schoenbaum G, Young B, Bunsey M (1996) Functional organization of the hippocampal memory system. Proc Natl Acad Sci U S A 93(24):13500–13507

Eichenbaum H, Dudchenko P, Wood E, Shapiro M, Tanila H (1999) The hippocampus, memory, and place cells: is it spatial memory or a memory space? Neuron 23(2):209–226

Epley N, Keysar B, Van Boven L, Gilovich T (2004) Perspective taking as egocentric anchoring and adjustment. J Pers Soc Psychol 87(3):327

Fitzsimons GM, Bargh JA (2003) Thinking of you: nonconscious pursuit of interpersonal goals associated with relationship partners. J Pers Soc Psychol 84:148–164

Fox KCR, Spreng RN, Ellamil M, Andrews-Hanna JR, Christoff K (2015) The wandering brain: meta-analysis of functional neuroimaging studies of mind-wandering and related spontaneous thought processes. NeuroImage 111:611–621

Freeman JB, Stolier RM, Ingbretsen ZA, Hehman EA (2014) Amygdala responsivity to high-level social information from unseen faces. J Neurosci 34(32):10573–10581

Gaesser B (2012) Constructing memory, imagination, and empathy: a cognitive neuroscience perspective. Front Psychol 3:576. doi:10.3389/fpsyg.2012.00576

Gaesser B, Schacter DL (2014) Episodic simulation and episodic memory can increase intentions to help others. Proc Natl Acad Sci U S A 111(12):4415–4420

Gaesser B, Spreng RN, McLelland VC, Addis DR, Schacter DL (2013) Imagining the future: evidence for a hippocampal contribution to constructive processing. Hippocampus 23 (12):1150–1161

Gobbini MI, Haxby JV (2007) Neural systems for recognition of familiar faces. Neuropsychologia 45(1):32–41

Günaydin G, Zayas V, Selcuk E, Hazan C (2012) I like you but I don't know why: objective facial resemblance to significant others influences snap judgments. J Exp Soc Psychol 48:350–353

Haas BW, Anderson IW, Filkowski MM (2015) Interpersonal reactivity and the attribution of emotional reactions. Emotion 15(3):390

Hassabis D, Maguire EA (2009) The construction system of the brain. Philos Trans R Soc Lond B Biol Sci 364(1521):1263–1271

Hassabis D, Kumaran D, Maguire EA (2007) Using imagination to understand the neural basis of episodic memory. J Neurosci 27(52):14365–14374

Hassabis D, Spreng RN, Rusu AA, Robbins CA, Mar RA, Schacter DL (2013) Imagine all the people: how the brain creates and uses personality models to predict behavior. Cereb Cortex. doi:10.1093/cercor/bht042

Hitti FL, Siegelbaum SA (2014) The hippocampal CA2 region is essential for social memory. Nature 508(7494):88–92

Holmes JG (2002) Interpersonal expectations as the building blocks of social cognition: an interdependence theory perspective. Pers Relat 9:1–26

House JS, Landis KR, Umberson D (1988) Social relationships and health. Science 241:540–545. doi:10.1126/science.3399889

Hsiao YH, Hung HC, Chen SH, Gean PW (2014) Social interaction rescues memory deficit in an animal model of Alzheimer's disease by increasing BDNF-dependent hippocampal neurogenesis. J Neurosci 34(49):16207–16219

Humphrey NK (1976) The social function of intellect. Cambridge University Press, Cambridge

Kiecolt-Glaser JK, Newton TL (2001) Marriage and health: his and hers. Psychol Bull 127(4):472

Klein SB, Sherman JW, Loftus J (1996) The role of episodic and semantic memory in the development of trait self-knowledge. Soc Cogn 14(4):277–291

Klein SB, Chan RL, Loftus J (1999) Independence of episodic and semantic self-knowledge: the case from autism. Soc Cogn 17(4):413–436

Kogan JH, Frankland PW, Silva AJ (2000) Long-term memory underlying hippocampus-dependent social recognition in mice. Hippocampus 10(1):47–56

Konkel A, Cohen NJ (2009) Relational memory and the hippocampus: representations and methods. Front Neurosci 3(2):166

Kumaran D, Banino A, Blundell C, Hassabis D, Dayan P (2016) Computations underlying social hierarchy learning: distinct neural mechanisms for updating and representing self-relevant information. Neuron 92:1135–1147

Kurczek J, Wechsler E, Ahuja S, Jensen U, Cohen NJ, Tranel D, Duff M (2015) Differential contributions of hippocampus and medial prefrontal cortex to self-projection and self-referential processing. Neuropsychologia 73:116–126

Lee AC, Yeung LK, Barense MD (2012) The hippocampus and visual perception. Front Hum Neurosci 6:91

Leser N, Wagner S (2015) The effects of acute social isolation on long-term social recognition memory. Neurobiol Learn Mem 124:97–103

Lindner I, Schain C, Kopietz R, Echterhoff G (2012) When do we confuse self and other in action memory? Reduced false memories of self-performance after observing actions by an out-group vs. ingroup actor. Front Psychol 3:467. doi:10.3389/fpsyg.2012.00467

Maguire EA, Mullally SL (2013) The hippocampus: a manifesto for change. J Exp Psychol Gen 142(4):1180

Markus H, Cross S (1990) The interpersonal self. In: Pervin LA (ed) Handbook of personality: theory and research. Guilford Press, New York, pp 576–608

Meltzoff AN, Brooks R (2001) "Like me" as a building block for understanding other minds: bodily acts, attention, and intention. In: Malle BF, Moses LJ, Baldwin DA (eds) Intentions and intentionality: foundations of social cognition. MIT Press, Cambridge, MA, pp 171–191

Mullally SL, Maguire EA (2014) Learning to remember: the early ontogeny of episodic memory. Dev Cogn Neurosci 9:12–29

Mullally SL, Intraub H, Maguire EA (2012) Attenuated boundary extension produces a paradox-ical memory advantage in amnesic patients. Curr Biol 22(4):261–268

Muscatell KA, Morelli SA, Falk EB, Way BM, Pfeifer JH, Galinsky AD et al (2012) Social status modulates neural activity in the mentalizing network. NeuroImage 60:1771–1777

Nickerson RS (1999) How we know—and sometimes misjudge—what others know: imputing one's own knowledge to others. Psychol Bull 125:737

O'keefe J, Nadel L (1978) The hippocampus as a cognitive map, vol 3. Clarendon Press, Oxford, pp. 483–484

Ochsner KN, Beer JS, Robertson ER, Cooper JC, Gabrieli JD, Kihsltrom JF, D'Esposito M (2005) The neural correlates of direct and reflected self-knowledge. NeuroImage 28(4):797–814

Okuda J, Fujii T, Ohtake H, Tsukiura T, Tanji K, Suzuki K, Yamadori A (2003) Thinking of the future and past: the roles of the frontal pole and the medial temporal lobes. NeuroImage 19 (4):1369–1380

Parkinson C, Liu S, Wheatley T (2014) A common cortical metric for spatial, temporal, and social distance. J Neurosci 34:1979–1987

Perry D, Hendler T, Shamay-Tsoory SG (2011) Projecting memories: the role of the hippocampus in emotional mentalizing. NeuroImage 54:1669–1676. doi:10.1016/j.neuroimage.2010.08.057

Pietromonaco PR, Feldman Barrett L (2000) The internal working models concept: what do we really know about the self in relation to others? Rev Gen Psychol 4:155–175. doi:10.1037/1089-2680.4.2.155

Qin P, Northoff G (2011) How is our self related to midline regions and the default-mode network? NeuroImage 57:1221–1233

Rabin JS, Rosenbaum RS (2012) Familiarity modulates the functional relationship between theory of mind and autobiographical memory. NeuroImage 62:520–529. doi:10.1016/j.neuroimage.2012.05.002

Rabin JS, Gilboa A, Stuss DT, Mar RA, Rosenbaum RS (2010) Common and unique neural correlates of autobiographical memory and theory of mind. J Cogn Neurosci 22:1095–1111. doi:10.1162/jocn.2009.21344

Race E, Keane MM, Verfaellie M (2011) Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. J Neurosci 31(28):10262–10269

Ranganath C (2010) A unified framework for the functional organization of the medial temporal lobes and the phenomenology of episodic memory. Hippocampus 20(11):1263–1290

Rosenbaum RS, Gilboa A, Levine B, Winocur G, Moscovitch M (2009) Amnesia as an impairment of detail generation and binding: evidence from personal, fictional, and semantic narratives in KC. Neuropsychologia 47(11):2181–2187

Ross RS, LoPresti ML, Schon K, Stern CE (2013) Role of the hippocampus and orbitofrontal cortex during the disambiguation of social cues in working memory. Cogn Affect Behav Neurosci 13(4):900–915

Rubin RD, Watson PD, Duff MC, Cohen NJ (2014) The role of the hippocampus in flexible cognition and social behavior. Front Hum Neurosci 8

Sampson EE (1977) Psychology and the American ideal. J Pers Soc Psychol 35(11):767

Saxe R (2010) The right temporo-parietal junction: a specific brain region for thinking about thoughts. In: Leslie A, German T (eds) Handbook of theory of mind. Erlbaum, Hillsdale, NJ, pp 1–35

Schacter DL (2012) Adaptive constructive processes and the future of memory. Am Psychol 67:603–613. doi:10.1037/a0029869

Spreng RN (2013) Examining the role of memory in social cognition. Front Psychol 4:437

Spreng RN, Andrews-Hanna JR (2015) The default network and social cognition. In: Toga AW (ed) Brain mapping: an encyclopedic reference. Academic Press, Elsevier, pp 165–169

Spreng RN, Grady C (2010) Patterns of brain activity supporting autobiographical memory, prospection and theory-of-mind and their relationship to the default mode network. J Cogn Neurosci 22:1112–1123. doi:10.1162/jocn.2009.21282

Spreng RN, Mar RA (2012) I remember you: a role for memory in social cognition and the functional neuroanatomy of their interaction. Brain Res 1428:43–50. doi:10.1016/j.brainres.2010.12.024

Spreng RN, Mar RA, Kim AS (2009) The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J Cogn Neurosci 21:489–510. doi:10.1162/jocn.2008.21029

Spreng RN, Gerlach KD, Turner GR, Schacter DL (2015) Autobiographical planning and the brain: activation and its modulation by qualitative features. J Cogn Neurosci. doi:10.1162/jocn_a_00846

Staniloiu A, Woermann F, Borsutzky S, Markowitsch HJ (2013) Social cognition in a case of amnesia with neurodevelopmental mechanisms. Front Psychol 4:342. doi:10.3389/fpsyg.2013.00342

Stevenson EL, Caldwell HK (2014) Lesions to the CA2 region of the hippocampus impair social memory in mice. Eur J Neurosci 40(9):3294–3301

Stiller J, Dunbar RI (2007) Perspective-taking and memory capacity predict social network size. Soc Networks 29:93–104

Szpunar KK, Watson JM, McDermott KB (2007) Neural substrates of envisioning the future. Proc Natl Acad Sci U S A 104(2):642–647

Tamir DI, Mitchell JP (2011) The default network distinguishes construals of proximal versus distal events. J Cogn Neurosci 23:2945–2955

Tavares RM, Mendelsohn A, Grossman Y, Williams CH, Shapiro M, Trope Y, Schiller D (2015) A map for social navigation in the human brain. Neuron 87(1):231–243

Tomasello M (1999) The human adaptation for culture. Annu Rev Anthropol 28:509–529

Tulving E (1985) Elements of episodic memory. Oxford University Press, London

Vygotsky L (1978) Interaction between learning and development. Read Dev Child 23(3):34–41

Wang JX, Cohen NJ, Voss JL (2015) Covert rapid action-memory simulation (CRAMS): a
    hypothesis of hippocampal–prefrontal interactions for adaptive behavior. Neurobiol Learn
    Mem 117:22–33
Warren DE, Duff MC, Magnotta V, Capizzano AA, Cassell MD, Tranel D (2012) Long-term
    neuropsychological, neuroanatomical, and life outcome in hippocampal amnesia. Clin
    Neuropsychol 26(2):335–369
Zayas V, Shoda Y (2005) Do automatic reactions elicited by thoughts of romantic partner, mother,
    and self relate to adult romantic attachment? Personal Soc Psychol Bull 31:1011–1025
Zayas V, Shoda Y, Ayduk ON (2002) Personality in context: an interpersonal systems perspective.
    J Pers 70:851–898
Zeithamova D, Dominick AL, Preston AR (2012) Hippocampal and ventral medial prefrontal
    activation during retrieval-mediated learning supports novel inference. Neuron 75(1):168–179