Reviews

Episodic mindreading: Mentalizing guided by scene construction of imagined and remembered events

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ABSTRACT

Attributing mental states to other people fundamentally shapes how we bond, coordinate, and predict the actions of others. Perceiving a person’s facial expressions and body language in the present contribute to our ability to understand what they are thinking and feeling. Yet, people do not exist in a vacuum and individuals often think about people who are not directly in front of them. People inhabit remembered and imagined episodes, where the surrounding location and objects can guide attributions of their mental states. In this article, I propose the episodic mindreading hypothesis, arguing that the episodic representation of past and future events in which a target person is embedded will affect whether and how the target’s mind is read. The content and phenomenological quality of imagined and remembered episodes can alter what mental states are attributed to a target and the accessibility of those mental states. This hypothesis encourages researchers to think about mentalizing as neither dependent on nor completely exclusive from the episodic memory system. Instead, the episodic memory system can modulate and inform mindreading, and likely vice versa. The article reviews extant knowledge and highlights open questions for future research to explore with implications for healthy and impaired social cognition.

"If you describe a landscape, or a seascape, or a cityscape, always be sure to include a human figure somewhere in the scene. Why? Because readers are human beings, mostly interested in human beings.”

Vonnegut was right; readers (and pretty much everyone else for that matter) are mostly interested in other human beings, and especially in the contents of others’ minds. This preoccupation is a good thing, because it allows us to accomplish some of life’s central tasks: understanding, communicating, coordinating and commiserating with others.” Jamil Zaki quoting Kurt Vonnegut

A cornerstone of human cognition is our ability to understand other people’s minds. We readily detect minds and agents in pursuit of better understanding, predicting, and connecting with others (Epley, Waytz, & Cacioppo, 2007; Hampton, Bossaerts, & O’Doherty, 2008; Heider & Simmel, 1944; Johnson, Dziurawiec, Ellis, & Morton, 1991; Malle & Hodges, 2005; Tamir & Thornton, 2018; Waytz & Young, 2014; Wheatley, Kang, Parkinson, & Looser, 2012). When disruptions in brain regions and brain network connectivity that support perceiving and understanding others’ minds arise, such as those in autism spectrum disorder, psychopathy, and traumatic brain injury, the loss of effective and healthy social interaction is profound (Baron-Cohen, Leslie, & Frith, 1985; Bibby & McDonald, 2005; Gray, Jenkins, Heberlein, & Wegner, 2011; Marsh & Blair, 2008). How do we understand what someone else is thinking and feeling?

1. Minds are often embedded within imagined and remembered scenes

Researchers in psychology and neuroscience across social, affective, and developmental areas have made great progress demonstrating how we can deliberately and consciously infer others’ in-
tentions, thoughts, desires, and emotions (i.e., mentalizing\(^2\)) from the perceptual features of faces (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Looser & Wheatley, 2010; Saarala, Hlushchuk, & Williams, A. C. D. C., Schurmann, M., Kalso, E., & Hari, R., 2006), postures (Aviezer et al., 2008; Aviezer, Trope, & Todorov, 2012), and movement (Behne, Carpenter, & Tomasello, 2005; Castelli, Happé, Frith, & Frith, 2000; Gelman & Gottfried, 1996; Heider & Simmel, 1944; Luo & Baillargeon, 2005; Scholl & Tremoulet, 2000; Woodword, 1998). In everyday life, however, static faces and bodies do not appear in suspended isolation. They are surrounded by locations, objects, and other people that shape what the targets are thinking and feeling. When we try to anticipate or reflect on the mental states of a person that is not immediately in front of us, the target appears in our mind seamlessly integrated in a location with objects and other people comprising a multi-sensory experience that unfolds over time as a specific event or episode. Does the episodic content and detail within which a social interaction is embedded guide how we come to understand someone else’s thoughts and feelings? Is there a role for episodic simulation and episodic memory (i.e., imagining hypothetical and future events) and episodic memory (i.e., remembering past events) in enhancing our ability to peer inside the minds of others?

Here, I propose the episodic mindreading hypothesis, exploring the possibility that episodic simulation and episodic memory can interact with and inform our ability to understand the minds of other people embedded within these spatial-temporal representations. I begin by briefly outlining the episodic mindreading hypothesis. I then delineate the cognitive and neural processes supporting episodic simulation and episodic memory and distinguish them from those processes that support mentalizing. Next, I review evidence of episodic and mentalizing systems interacting, with particular emphasis on emerging evidence that manipulating episodic content can affect mentalizing during prosocial decision-making. Finally, I look beyond what is currently known, outlining future directions and discussing implications for healthy and impaired social cognition that arise from the hypothesis. Consider the following. What is the person in Fig. 1A thinking and feeling? Are they sleeping and snoring? Awake and in agony? Placing the face atop a body (Fig. 1B) provides a little more information but not much. Embedding the person in a specific location surrounded by objects and people, however, provides greater insight, revealing a player enraptured in thoughts of victory and excitement (Fig. 1C). The table tennis court, paddle, opponent, reactions from the crowd, and presence of a television camera inform our understanding of the player's mental states. Directly observing an event can affect what mental states a perceiver attributes to the target (e.g., Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; de Lange, Sparrok, Willems, Toni, & Bekkering, 2008; Gallese, 2007; Luo & Baillargeon, 2005; Onishi & Baillargeon, 2005; Rizzolatti & Craighero, 2004; Spunt, Sappute, & Lieberman, 2011; Wagner, Kelley, Hazby, & Heatherton, 2016; Wagner, Kelley, & Heatherton, 2011; Woodword, 1998; Zaki, Henning, Weber, & Ochsner, 2010). However, individuals often have to infer and predict mental states for targets that are not immediately present in the here and now: remembering past events and imagining hypothetical and future events, retrieving individual details of a face, body, and location, within these events.

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\(^1\) The photo depicts Jun Mizutani when he won a quarterfinal match for Japan over Singapore at the World Championships in 2012. Photo credit Jerome Adamstein at the Framework.

\(^2\) Here I will refer to this ability as mentalizing, but the term is often used interchangeably with theory of mind, mindreading, mental state reasoning, and is related to perspective taking and cognitive empathy. While mentalizing likely decomposes into more elemental component processes (Schaafsma et al., 2015; Schurz et al., 2014), mentalizing broadly refers to an ability to explicitly attribute and consider others’ mental states.

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\(^3\) Indeed, as is evident in robust work on mental time travel and mind wandering, people spend much of their cognitive life disengaged from current sensory input in order to remember the past and imagine the future (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Baird, Smallwood, & Schooler, 2011; Barsics, der Linden, & D’Argembeau, 2016; Kane et al., 2007; Killingsworth & Gilbert, 2010; McCormick, Rosenthal, Miller, & Maguire, 2018; Song & Wang, 2012; Stawarczyk, Majerus, Maj, Van der Linden, & D’Argembeau, 2011).
and integrating them into a coherent multi-sensory experience as a specific event (Fig. 1D).

2. The constructive episodic memory system: Remembering and imagining specific events

Before considering a relationship between episodic and mentalizing systems, it may be useful to first unpack key components of episodic representation and highlight recent theoretical developments in episodic memory research. A growing body of evidence has established a tight link between episodic memory and episodic simulation, suggesting that they draw on a shared cognitive-neural system in order to “replay” past events and “preplay” future events in one's mind (see Addis, 2020; Schacter et al., 2012; Schacter, Addis, & Szpunar, 2017 for review). Similar to episodic memory, episodic simulation involves consciously experiencing an unfolding sequence of details (e.g., people, objects) in a specific place with the component details stored in distributed modality-specific brain regions (e.g., Hassabis et al., 2014; Szpunar, St. Jacques, Robbins, Wig, & Schacter, 2013). The importance of relational processing in episodic retrieval (Schacter & Addis, 2007) and spatial processing are emphasized (Maguire & Mullally, 2013; Robin & Moscovitch, 2014), such that forming and maintaining a spatial context serves as a platform to which reinstated episodic details can be bound. Pattern completion enables the rapid associations between selected spatial locations, people, and objects into an experience that is specific in time and place, and pattern separation and related processes are needed to keep that experience distinct from other remembered and imagined events and prevent interference (Rolls, 2013; Yassa & Stark, 2011; Zheng et al., 2019).

Whereas episodic memory is inherently retrospective, episodic simulation is less anchored to a temporal direction. Episodic simulation often refers to imagining possible future events (Atance & O’Neill, 2001; Gilbert & Wilson, 2007; Jing, Madore, & Schacter, 2017; Seligman, Raillton, Baumeister, & Sripada, 2013; Szpunar, 2010; Szpunar, Spreng, & Schacter, 2014), but can contribute to imagining fictitious events (Hassabis, Kumaran, & Maguire, 2007; Summerfield, Hassabis, & Maguire, 2009, 2010) and imagining events set in the past that are alternative versions of previously experienced events (e.g., counterfactual events; De Brigard, Addis, Ford, Schacter, & Giovanelli, 2013; Van Hoeck et al., 2012).

Semantic knowledge provides schematic information for meaningfully structuring events (Bohm & Bernsten, 2011; D’Argembeau & Mathy, 2011; Irish, Addis, Hodges, & Piguet, 2012; Irish & Piguet, 2013; Irish & Piolino, 2016; Rathbone, Conway, & Moulin, 2011), and the episodic system is engaged to retrieve and relationally bind episodic details into a unified representation that unfolds through time in a coherent sequence forming a specific event or episode (Eichenbaum & Cohen, 2014; Konkel, Warren, Duff, Tranel, & Cohen, 2008). Continuing with the table tennis example, semantic knowledge of how a table tennis game is typically organized and played is activated, providing a conceptual framework of what could plausibly occur during a match. The episodic system would then be engaged to retrieve the details of players, paddles, table tennis court, crowd, and television camera (Fig. 1A-C), binding these details into a unified representation of an outstretched victorious player standing in front of table tennis court surrounded by a cheering crowd, television camera, and opponent (Fig. 1D). The actions and objects unfolding through time as a coherent spatial-temporal representation are experienced as a vivid mental movie—the player slamming the ping pong ball on the final point of the game, the opponent missing, the crowd rising and cheering—which makes the thoughts and feelings of the player more salient and less ambiguous. Presenting Fig. 1B along with semantic information “he won a game” may lead an individual to attribute some degree of accomplishment and positive arousal to the target; however, embedding the target in an episodic representation heightens the experience of the target's excitement and ecstasy.

Recent work has revealed that imagining and remembering specific events, beyond gradual learning mechanisms and semantic knowledge, can guide decision-making and behavior (Benoit, Gilbert, & Burgess, 2011; Duncan & Shohamy, 2016; Murty, FeldmanHall, Hunter, Phelps, & Davachi, 2016; Palombo, Keane, & Verfaellie, 2015; Schacter, 2012; Schacter, Benoit, & Szpunar, 2017; Wimmer & Buchel, 2016). Though it is not just what we imagine and remember that matters, but also how the events are subjectively experienced. A key feature shared by episodic simulation and episodic memory is the subjective feeling of experiencing those details as if they are happening in the present (i.e., a feeling of reliving or pre-experiencing) and how vividly they feel (e.g., how vividly is the imagery of the imagined or remembered scene experienced in your mind's eye: is the scene vivid as if you are there, or is the scene vague and distant?). The more vividly events are imagined and remembered, the more salient, likely and plausible they seem (Anderson, 1983; Carroll, 1978; D’Argembeau & Van der Linden, 2012; Gaesser & Schacter, 2014; Gary & Polaschek, 2000; Mazzoni & Memon, 2003; Szpunar & Schacter, 2013).

3. The social nature of memory and imagination

Although people can remember and imagine events that do not include social interaction, they often do. Thought sampling procedures reveal that people’s spontaneous thoughts about the future and past frequently involve other people (Andrews-Hanna et al., 2013; D’Argembeau et al., 2014; D’Argembeau, Renaud, & Van der Linden, 2011; Mar, Mason, & Litvack, 2011); a telling content analysis of self-defining memories showed that 40% of memories were centered on social relationships (D’Argembeau et al., 2014). In addition to frequently remembering and imagining social interactions, people often exhibit better memory for social compared to non-social content (e.g., Meyer, Davachi, Ochsner, & Lieberman, 2019).

A recent meta-analysis (Benoit & Schacter, 2015) shows that both episodic memory and episodic simulation share a neural basis, including the medial temporal lobes, medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), lateral temporal cortex, and lateral parietal often referred to as the core or default network (Buckner, Andrews-Hanna, & Schacter, 2008; Raichle et al., 2001). Intriguingly, while some of the regions identified in this meta-analysis appear to be more selectively dedicated to episodic processes, other regions are also active during mentalizing possibly because imagined and remembered events so frequently include social interactions and inferring others’ mental states. Indeed, the mPFC, lateral temporal cortex, temporoparietal junction, temporal pole, mPFC, and PCC are so robustly engaged when explicitly considering others mental states (Ammodio & Frith, 2006; Saxe & Kanwisher, 2003; Zaki & Ochsner, 2012) that social neuroscientists have commonly referred to these regions as the mentalizing or theory of mind network (for meta-analyses see Bzdok et al., 2012; Schaalma, Pfaff, Spunt, & Adolphs, 2015; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Van Overwalle & Baetens, 2009). This recruitment of regions commonly associated with social cognition may be partially attributed to subjects incidentally imagining and remembering social interaction in these studies.

Reviewing the procedures for the individual studies used in a meta-analysis of episodic simulation and episodic memory (Benoit & Schacter, 2015) reveals that while imagining and remembering social interactions may not be an explicit component of the instructions, the examples provided by the researchers often involve social interactions such as imagining a marriage proposal (Addis, Roberts, & Schacter, 2009; Bellana, Liu, Diamond, Grady, & Moscovitch, 2017; Benoit & Schacter, 2015; Gilmore, Nelson, & McDermott, 2014; Irish et al., 2012; Rasmussen & Bernsten, 2013), but the underlying cognitive and neural hardware is remarkably similar.

4This is not to imply that there are no meaningful differences between episodic memory and episodic simulation (e.g., Addis et al., 2009; Bellana, Liu, Diamond, Grady, & Moscovitch, 2017; Benoit & Schacter, 2015; Gilmore, Nelson, & McDermott, 2014; Irish et al., 2012; Rasmussen & Bernsten, 2013), but the underlying cognitive and neural hardware is remarkably similar.
the default network that operate as subsystems, suggesting that episodic shows both shared and distinct processes supported by sets of regions in overlapping neural activity within the default network, particularly the hypothalamic content was an episode or others' mental states, as well as mentalizing content, regardless of whether shared component of shifting attention away from the immediate pre-sense environment and projecting oneself into a hypothetical situation—be it an alternative place or mind. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. The episodic mindreading hypothesis

While episodic memory and episodic simulation are not inherently social, previous work has demonstrated important contributions of episodic memory in social cognition (Laurita & Nathan Spreng, 2017; Montagrin, Salote, & Schiller, 2018; Rubin, Watson, Duff, & Cohen, 2014 for reviews). For example, researchers have considered the role of memory in social learning and forming shared experiences with others (Alea & Bluck, 2003; Bluck, Alea, Habermas, & Rubin, 2005; Coman, Brown, Koppel, & Hirst, 2009; Fivush, Haden, & Reese, 1996; Meyer, 1992; Pillemer, 1992; Rasmussen & Berntsen, 2013). Little attention, however, has been given to how imagining and remembering specific episodes involving social interactions can affect our ability to understand other people's minds.

The episodic mindreading hypothesis builds on previous work, bridging a new theoretical connection between episodic memory and social cognition. Specifically, the hypothesis posits the ability to remember and imagine specific episodes guides how targets' mental states within those episodes are perceived and, in some cases, what mental states are attributed. The details (e.g., location, objects, and agents) a target is retrieved with and bound to in an episode will constrain which mental states are assigned to the target. Furthermore, the extent to which episodic details are subjectively experienced will impact how strongly the mental states of a target are accessed. As an episode is more vividly experienced, the mental states of the target in that episode will become more accessible and more prominently considered.

5. Independent but interactive systems

5.1. Dissociable systems within the default network support episodic vs. mentalizing content

Early accounts emphasized a shared cognitive and neural basis supporting both episodic memory and mentalizing (Buckner & Carroll, 2007; Spreng, Mar, & Kim, 2009). These accounts emphasized both the shared component of shifting attention away from the immediate present and into alternative hypothetical content, regardless of whether the hypothetical content was an episode or others’ mental states, as well as overlapping neural activity within the default network, particularly the posterior cingulate and medial prefrontal cortex. However, growing evidence from functional connectivity and functional activity studies shows both shared and distinct processes supported by sets of regions in the default network that operate as subsystems, suggesting that episodic and mental state content are preferentially supported by distinct sets of regions in default network that operate as subsystems (Fig. 2) (Andrews-Hanna, Reiderl, Huang, & Buckner, 2010; Andrews-Hanna, Saxe, & Yarkoni, 2014; Andrews-Hanna, Smallwood, & Spreng, 2014; Braga & Buckner, 2017; Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Spreng & Grady, 2010; Tamir, Bricker, Dodell-Feder, & Mitchell, 2016).

The core subsystem (Fig. 2 gold), consisting of the posterior cingulate cortex and anterior MPFC extending into the angular gyrus, is extensively connected to all other regions across the default network and is thought to serve as a hub between subsystems (Andrews-Hanna, Reiderl, Sepulcre, Poulin, & Buckner, 2010; Andrews-Hanna et al., 2014). Whether remembering a past episode, imagining a future episode, or considering the mental states of another person, the core subsystem is pervasively recruited when individuals shift attention away from the immediate sensory environment and project themselves into a hypothetical situation—be it an alternative place or mind (Buckner, Andrews-Hanna, & Schacter, 2008; Spreng et al., 2009; Spreng & Grady, 2010; Tamir & Mitchell, 2011). The other two subsystems, however, are intrinsically more tightly connected within a subsystem than across subsystems and differentially associated in supporting episodic or mental state content (Andrews-Hanna, Reiderl, Sepulcre, et al., 2010; Braga & Buckner, 2017).

The dmPFC subsystem (Fig. 2 blue), comprised of the dMPFC, middle temporal gyrus, temporoparietal junction, and temporal pole, is robustly engaged when explicitly considering others mental states (Amodio & Frith, 2006; Saxe & Kanwisher, 2003; Zaki & Ochsner, 2012). Though these regions may not exclusively contribute to inferring others’ mental states, they are notably more active when making judgments of others’ mental states and dispositions compared to physical states or reflecting on oneself (Denny, Kober, Wager, & Ochsner, 2012). The dMPFC and the TPJ are particularly recognized for their contributions to a variety of social functions such as impression formation (Harris, Todorov, & Fiske, 2005; Mende-Siedlecki, Cai, & Todorov, 2013), prosocial behavior (Tusche, Böckler, Kanske, Trautwein, & Singer, 2016), norm enforcement (Baumgartner, Götte, Gügler, & Fehr, 2012), and moral judgment (Young, Cushman, Hauser, & Saxe, 2007; Young & Saxe, 2009).

Regions more selectively dedicated to episodic processes falling within the medial temporal lobe (MTL) subsystem (Fig. 2 red), comprised of the hippocampus, parahippocampus, retrosplenial cortex, posterior inferior parietal lobule, and sometimes vMPFC, are preferentially engaged during the generation of episodic content (i.e., generating an event that is specific in time and place). For example, constructing vivid mental imagery of scenes selectively accounted for a large portion of trial-by-trial variance in the MTL subsystem (Andrews-
Hanna, Reider, Sepulcre, et al., 2010). Functional connectivity within the MTL subsystem is associated with the degree of spontaneous thoughts about the past and future experiences (Andrews-Hanna, Reider, Huang, & Buckner, 2010). Amnestic patients with hippocampal damage are impaired at constructing atemporal imagined scenes (e.g., imagine lying on the beach) (Hassabis, Kumaran, Vann, & Maguire, 2007). Patients’ imagined scenes are not well integrated, consisting of fragmented images that lack spatial detail and coherence (see also Mullally, Intrabu, & Maguire, 2012).

Behavioral training in recollecting episodic details by guiding individuals to systematically recall details such as people, actions, and the surrounding environment (e.g., what people looked like, what they did, where they did it, how objects were arranged) increases activity in this network, including the hippocampus and posterior IPL (Madore, Szpunar, Addis, & Schacter, 2016), when people subsequently imagine future events. Moreover, the pattern and magnitude of activity in the MTL tracks with prospective spatial navigation (Brown et al., 2016; Javadi et al., 2017) and ratings of scene construction (Andrews-Hanna, Reider, Sepulcre, et al., 2010; Axelrod, Rees, & Bar, 2017; Palombo, Hayes, Peterson, Keane, & Verfaellie, 2018). For example, Palombo and colleagues (2018) found that activation in the MTL tracked with the extent to which participants reported imagining a scene (What did you picture? nothing/vague, objects only, whole scene). Indeed, greater MTL activity for high vs. low scene construction conditions was eliminated when scene ratings were included in the model (see Addis, Cheng, Roberts, & Schacter, 2011 for specific vs. general event framing of a similar paradigm).

Perhaps the most compelling evidence of dissociation comes from amnesic patients, who suffer severe deficits in remembering and imagining events (Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009; Tulving, 1985) however perform normally on a battery of standardized mentalizing tasks (e.g., the false belief, faux pas, and reading the mind in the eyes tasks). For example, patient K.C. with a well characterized, almost absolute, and selective impairment on episodic memory and imagination as a result of traumatic brain injury (Rosenbaum et al., 2009; Rosenbaum, Stuss, Levine, & Tulving, 2007) showed no impairment on mentalizing tasks compared to healthy controls. Patient H.C. with severely impaired episodic memory development due to early hippocampal damage performed indistinguishably from healthy controls on all mentalizing tasks that were measured (Rabin, Braverman, Gilboa, Stuss, & Rosenbaum, 2012). Similarly, earlier evidence from patients with Alzheimer’s disease, a population characterized by widespread brain damage throughout the default network including the medial temporal lobes, found that their performance was largely spared on all mentalizing tasks with the exception of one task that placed heavy demands on working memory capacity (Gregory et al., 2002). Thus, these neuropsychological studies suggest an intact episodic system may not be necessary to infer other people’s mental states in general.

Collectively, the data from these neuroimaging and patient studies provide evidence of dissociable systems preferentially associated with episodic and mental state content. In research that has directly examined both episodic and mentalizing tasks, the emphasis is typically on how self-generated thoughts supported by the default network are comprised of multiple cognitive processes, with less consideration of how these distinct cognitive processes could interact (Andrews-Hanna et al., 2014; Axelrod et al., 2017; Spreng & Grady, 2010). Yet, these findings of broad independence do not rule out the possibility that when people imagine and remember specific episodes, it influences how we infer the mental states of people within those specific episodes.

5.2. Recruiting episodic memory when mentalizing

There is evidence that individuals will sometimes spontaneously draw on their own past experience when inferring the mental states of others, especially similar and close others. For example, brain activity for theory of mind judgments for targets with whom participants were personally familiar (e.g., family members or close friends) more closely resembles brain activity during an autobiographical memory task compared to theory of mind judgments for unfamiliar others across the default network, including structures in the MTL subsystem and hippocampus (Rabin & Rosenbaum, 2012). In a related study, participants explicitly reported spontaneously remembering events from their own past when making mental state judgments for themselves and others (Perry, Hendler, & Shamay-Tsoory, 2011). The researchers found increased activity in the hippocampus when including as a covariate participants’ reports of an autobiographical memory of the specific context the targets were depicted in (see also Rameson, Morelli, & Lieberman, 2012 for anecdotal reports of subjects spontaneously recalling past events from their own lives to “use as a template for understanding” the unfortunate circumstances of others during an empathy task). Together these results hint at the possibility that spontaneous recruited memories of our own past experiences may be recruited when mentalizing about others, however additional research is needed to demonstrate the reactivation of memories during mentalizing in real-time. Moreover, it is unclear in these studies whether episodic recruitment is causing changes in mentalizing.

5.3. Episodic representation can heighten mentalizing

Evidence of manipulating episodic simulation and memory influencing mentalizing comes from a series of recent studies on prosocial decision making. My collaborators and I have found that directing people to imagine and remember episodes of helping a person in need can increase prosocial intentions (i.e., willingness to help) in that situation compared to conditions that control for exposure to the person in need and conceptual priming of helping (Gaesser, DiBiase, & Kensinger, 2017; Gaesser, Dodds, & Schacter, 2017; Gaesser, Horn, & Young, 2015; Gaesser, Keeler, & Young, 2018; Gaesser & Schacter, 2014; Gaesser, Shimura, & Cikara, 2020; Sawczak, McAndrews, Gaesser, & Moscovitch, 2019). Imagining and remembering specific helping episodes increases willingness to help compared to visualizing the media website the story of need came from (e.g., blogs, twitter, and a newspaper) and discussion board comments recommending how the person in need could be helped. While the control conditions involve semantic retrieval and the generation of helping examples, the imagine and remember conditions alone required constructing temporally and contextually specific episodes (Gaesser, DiBiase, & Kensinger, 2017; Gaesser & Schacter, 2014).

As the scene imagery of the helping episode is more vividly experienced, it heightens the perceived plausibility and likelihood that one will help in that event. Most pertinent to the present article, episodic simulation also heightens mentalizing (Gaesser et al., 2018; Gaesser, DiBiase, & Kensinger, 2017). Specifically, episodic simulation increased the degree of self-reported perspective taking for the person in need (i.e., how much one adopted the thoughts and feelings of the person in need) compared to control conditions even though perspective taking was not explicitly required for the episodic helping task (i.e., imagine an event specific in time and place that involved helping the person in need). Moreover, manipulating the location of the imagined episode to strongly increase scene imagery also increased perspective taking (Fig. 3A; Gaesser et al., 2018). When scene imagery and perspective taking were entered into the same model for predicting willingness to help, we observed evidence of a multipath scene-by-mind perspective task. Together these results hint at the possibility that the connection between scenes and minds may be robust enough to overcome intergroup bias (Gaesser, Shimura, & Cikara, 2020)—and perhaps help to mitigate some of the antisocial effects of perspective taking backfiring when an individual is threatened by the mental perspective of an outgroup member (Saisenhath, Hodges,
We have begun to uncover the neural basis of this effect, finding that activity in the MTL subsystem (specifically the anatomically defined hippocampus and parahippocampus) and the RTPJ (independently defined using a theory of mind functional localizer) predicted willingness to help judgments, such that activity in the parahippocampus, hippocampus, and RTPJ regions was more strongly associated with willingness to help mediated by scene imagery and perspective-taking for the between-subjects level of analysis in Experiment 2 (person imagery was not a significant mediator). The model presents unstandardized regression coefficients and standard errors in parentheses adapted from Gaesser, Shimura, and Cikara (2020).

Converging evidence comes from patients with impaired episodic systems exhibiting concomitant deficits in mentalizing. Although earlier neuropsychological studies suggested a strong dissociation between episodic and mentalizing systems (Gregory et al., 2002; Rabin et al., 2012; Rosenbaum et al., 2009), more recent studies have revealed evidence of an interaction. For example, grey matter volume of the left hippocampus of individuals with temporal lobe epilepsy or lobectomy was associated with performance on social inference tasks such as detecting sarcasm and deceit (Cohn, St-Laurent, Barnett, & McAndrews, 2014). Three patients with hippocampal amnesia have been reported to have lower trait perspective taking (“cognitive empathy”) as well as emotional responsiveness and empathic concern (“affective empathy”) compared to healthy control participants (Beadle, Tranel, Cohen, & Duff, 2013). On the perspective taking subcomponent of the Interpersonal Reactivity Index (IRI) in particular, hippocampal patients were three standard deviations or more below healthy controls (Beadle et al., 2013). On the perspective taking subcomponent of the Interpersonal Reactivity Index (IRI) in particular, hippocampal patients were three standard deviations or more below healthy controls (Beadle et al., 2013). Similarly, patients with Alzheimer’s disease have been shown to exhibit deficits in trait perspective taking using the IRI (Dermody et al., 2016), and are impaired at identifying others’ emotional states.

It is worth noting that caregiver reports of patients with Alzheimer’s disease

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**Fig. 3.** (A) Imagining helping episodes located in a strong spatial context (Strong Spatial Context condition) increased perspective taking ratings compared to baseline control (No Helping condition) and imagining helping episodes located in a weak spatial context (Weak Spatial Context condition; Experiment 1, Gaesser et al., 2018). (B) Stimulating the RTPJ with TMS lowered ratings of perspective taking in the Control condition, but not in the Episodic condition. Error bars indicate standard error of the mean. (C) Multilevel mediation model on the relationship between task (Episodic Helping: EH vs. No Helping: NH) and willingness to help mediated by scene imagery and perspective-taking for the between-subjects level of analysis in Experiment 2 (person imagery was not a significant mediator). The model presents unstandardized regression coefficients and standard errors in parentheses adapted from Gaesser, Shimura, and Cikara (2020). **p < .10, *p < .05, **p < .01, ***p < .001.
relative to healthy elderly adults, when the others’ emotions are more ambiguous and variable (Fernandez-Duque, Hodges, Baird, & Black, 2010). Yet, given more global cognitive deficits in Alzheimer’s disease, these findings should not on their own be taken as strong evidence of a contribution of the episodic system to mentalizing, as deficits in mentalizing in Alzheimer’s disease may be attributable to impairment in working memory or executive function rather than episodic processes per se (Dermody et al., 2016; Fernandez-Duque et al., 2010; Zaitchik, Koff, Brownell, Winner, & Albert, 2006).

It will likely not be the case that episodic processes will always engage mentalizing for a person embedded in the episode. Uncovering the dynamics of precisely when and under what circumstances episodic processes interact with mentalizing to enhance prosocial decision-making is a topic of ongoing investigation. At present, we have some evidence that the affective valence of the helping episode (whether the episode is emotionally positive or negative) may impact mentalizing. Specifically, the degree of self-reported perspective taking and the as-

### 6. An effect of episodic representation and mentalizing on social emotions

Throughout this article, we have focused on the contribution of episodic mechanisms to mentalizing (i.e., deliberately attributing and reasoning about mental states (e.g., thoughts, feelings, and beliefs) to others). Mentalizing is distinct from vicariously experiencing others’ emotions (affect-sharing, mirroring, empathy7) or otherwise having an emotional reaction to others (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Tusche et al., 2016; Zaki & Ochsner, 2012). However, mentalizing can affect one’s emotions. For example, deliberately considering the mental perspective of a suffering other can heighten prosocial concern and compassion for others’ welfare (Batson, 2011; Batson, Early, & Salvarani, 1997; Lamm, Batson, & Decety, 2007). And so, the question arises whether episodic representation can have downstream effects on socially-directed emotions by heightening mentalizing for a target within an episode. Initial evidence suggests the answer may be “yes” (Ciaramelli, Bernardi, & Moscovitch, 2013). Ciaramelli and colleagues investigated whether memories of others’ past experiences inform how one will think others’ will feel (mentalizing), and subsequently how one feels for them in the present. The researchers found that the amount of details recalled for a story of a person with domain-specific misfortunes (e.g., an unsuccessful love life, but successful work life) predicts how badly one thinks the person would feel, and how badly one feels for them, when the person experiences subsequent misfortunes related to that particular domain (e.g., a girlfriend forgets their anniversary). In other words, the better an individual was at remembering the details of other people’s past misfortunes, the worse an individual thinks the target will feel in similar circumstances and the worse an individual feels for them, facilitating mental state inferences to be tailored to fit unique social targets.8 This study suggests that episodic memory can shape the mental states we attribute to others and in turn our own emotional responses. Less is known about a possible

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7Empathy is a stretchy term. It has been used to capture multiple constructs

8One caveat in using these findings to support the episodic mind hypothesis is that the protocol used to code the amount of recalled detail in this study was fairly coarse, coding for overall amount of detail rather than parsing the content and type of detail such as memory for the person’s mental states vs. the surrounding environment and actions that inform those mental states. Thus, it is unclear if the memory-based personalizing of mentalizing was driven directly by recollections of the person’s mental states or by recollections of the surrounding episode per se.
influence of episodic mechanisms on emotional reactions to others without mentalizing.

Emotional and episodic content broadly dissociate and draw on distinct neural substrates (Feinstein, Duff, & Tranel, 2010; Guzmán-Vélez, Warren, Feinstein, Bruss, & Tranel, 2016). Yet these systems often interact with one another. For example, imagery can serve to amplify emotions (Amit & Greene, 2012; Holmes & Mathews, 2010; Lang, 1979; Libby & Eibach, 2011; Libby & Eibach, 2013). Moreover, the affective signal that arises from episodic memory (Wimmer & Buchel, 2016) and episodic simulation, in particular, is thought to serve an important functional role, enabling one to preview the subjective value of possible future outcomes and induce motivational incentives that guide decision-making (Bakkour et al., 2019; Benoît et al., 2011; Benoît, Szpunar, & Schacter, 2014; Bulley et al., 2019).

A growing body of studies have begun to investigate the link between memory and empathy for others' pain. Earlier work suggested that the hippocampus may be spontaneously recruited when thinking about others' social pain (e.g., others' suffering arising from social rejection, grief, or other psychological pain; Immordino-Yang & Singh, 2013 see also Pehrs, Zaki, Taruffi, Kuchinke, & Koelsch, 2018 for a context manipulation that may or may not have recruited episodic representation) and that sharing painful and similar experiences with other people increases trust, empathic concern, and cooperation (e.g., Bastian, Jetten, & Ferris, 2014; Hodges, Kiel, Kramer, Veach, & Villanueva, 2010). Newer developing research is emerging that directly investigates the reactivation of memory online during empathy for pain tasks, revealing that empathy for others' pain increases when people reported that they recalled a related autobiographical memory as well as its neural basis (Meconi et al., 2019; Wagner, Rütgen, & Lamm, 2019). For example, Wagner et al. provide some preliminary evidence that increased pattern similarity between first-hand pain experience and empathy for others' pain within the hippocampus, TPJ, retrosplenial cortex, and anterior insula. Intriguingly, the strength of coupling with the hippocampus scaled with self-report measures of perspective taking and to some extent empathic concern.

Recent work on episodic simulation has revealed that upregulating episodic simulation ability can be used to amplify affective empathy for others suffering (Vollberg, Gaesser, & Cikara, 2019). Training subjects to generate more episodic detail for a set of neutral scene using the episodic specificity induction task (e.g., practicing generating episodic details for everyday activities in a kitchen such as food prep and eating; Madore, Gaesser, & Schacter, 2014), unrelated to situations and content of an empathy judgment task, subsequently increased empathy for others including in-group as well as out-group members. People felt worse for others the more they spontaneously generated episodic details surrounding other’s suffering. Dovetailing with these findings is work on patients with compromised episodic simulation ability and medial temporal lobe functioning showing differences in emotions directed at benefiting the welfare of a person in need (i.e., prosocial and empathic concern) (Sawczak et al., 2019) (closely related to compassion, DeSteno, 2015; Goetz, Keltner, & Simon-Thomas, 2010; Stellar, Cohen, Oveis, & Keltner, 2015) compared to healthy adults. Critically, whereas manipulating episodic simulation increased empathic concern in healthy adults, this manipulation had no effect on empathic concern individuals who have compromised medial temporal lobe functioning, such as patients who have undergone resection of medial temporal lobe tissue as treatment for epilepsy (Sawczak et al., 2019). Currently unknown at present, however, is the precise neural computations underlying how episodic simulations of social interactions amplify empathy and their potential contributions to other socially-relevant emotions (Vollberg & Cikara, 2018).

7. Open questions and future directions

Reading other people’s minds is crucial for successfully navigating social interaction. Here I have put forth the episodic mindreading hypothesis, arguing that the episodic representation within which a person is embedded will also guide how we read their mind. The content and phenomenological quality of imagined and remembered episodes can alter what mental states we attribute to a target and the accessibility of these mental states. Although the episodic mindreading hypothesis helps account for an emerging body of evidence, future research is needed to build on and sharpen the concepts proposed here. Below, I highlight new questions that emerge as consequences of this hypothesis as well as gaps in our extant knowledge that will be exciting avenues to explore.

7.1. Contributions of episodic and semantic memory

One issue to consider is the role of semantic memory in supporting the interaction between episodes and minds. Episodic memory and semantic memory are interdependent (Binder & Desai, 2011; Greenberg & Verfaellie, 2010; Tulving, 1972), with semantic memory providing schematic information for structuring events (Bohn & Berntsen, 2011; D’Argembeau & Mathy, 2011; Irish et al., 2012; Irish & Piolino, 2016; Rathbone et al., 2011). How does semantic memory contribute to the relationship between episodes and mentalizing? One possibility is that intact autobiographical and general semantic memory may be necessary for forming coherent and meaningful episodes that effectively inform mentalizing. While there may be situations in which semantic knowledge alone is sufficient to successfully mentalize (e.g., knowing that a person will in general feel hurt after a romantic breakup), the vividness of episodic details increases considerations of the target’s thoughts and feelings (Gaesser, DiBiasi, & Kensinger, 2017; Gaesser et al., 2018 Gaesser et al., 2019), as well as customizing mentalizing for a specific individual in a particular situation (Garamelli et al., 2013). Previous work suggests that familiarity with the target of mentalizing may differentially recruit episodic vs. semantic memory systems. Specifically, Rabin and Rosenbaum (2012) have suggested we are more likely to rely on the episodic system to understand others’ minds when we personally know others and share past experiences with them. That is not to say that the episodic system cannot be deployed to simulate social interactions with strangers, but it may be more readily engaged when the target is familiar.

A related question is whether the episodic system contributes to understanding others’ minds through its role in the formation of semanticallyized knowledge in addition to the construction of specific episodes? Recent work in the memory literature has begun to reveal the circuitry within the medial temporal lobes and connectivity to neocortical regions that enables the extraction of semantic knowledge across reoccurring and overlapping experiences (Ferreira, Charest, & Wimber, 2019; Schapiro, Turk-Browne, Botvinick, & Norman, 2017; Schlichting, Mumford, & Preston, 2015; Tompary & Davachi, 2017). In this way, the episodic system may enable the extraction of regularities in the environment between particular mental states and surrounding details (i.e., constellation of locations, objects, people, and actions) and inform generalized knowledge about the likelihood of an individual experiencing particular mental states when bound to particular constellations of details and types of situations.

Adjacent to considerations of episodic and semantic processes is the association between episodic and narrative processing. In addition to the research mentioned earlier—on how directly observing perceptual features of faces, postures, movement, and events can affect what mental states a perceivers attributes to the target—a number of paradigms have elicited mentalizing and theory of mind through fictional stories or narratives (Baron-Cohen et al., 1985; Bruneau, Cikara, & Saxe, 2015; Fletcher et al., 1995; Gallagher et al., 2000; H. Wimmer & Perner, 1983; Young et al., 2007). Though mentalizing about narratives may rely on overlapping processes with episodic memory and simulation to some extent (Chow et al., 2014; Mar, 2011), clearly not all mentalizing narrative tasks will draw on episodic content to be successful. A recent study examining the contribution of default network
subsystems to reading and social cognition found that reading stories containing a person or a person's mental states preferentially recruited the dmPFC subsystem and not the MTL subsystem. Instead activity in the MTL subsystem was preferentially associated with whether the stories contained vivid imagery. Individual differences in the degree of dmPFC recruitment (but not MTL recruitment) when reading these stories predicted the extent to which others' intentions (i.e., intentional vs. accidental harm) affected moral judgments of punishment on an independent task (Tamir et al., 2016). Intriguingly, there was a trending (social vs. non-social x vivid vs. abstract) interaction of activity in the hippocampus hinting at a potential relationship between episodes and minds in fictional stories. Future work, however, will be needed to tease apart the relationship between episodic, semantic, and narrative processing to mentalizing.

7.2. Bi-directional interaction

The episodic mindreading hypothesis posits that episodic representation can interact with our ability to understand other people's minds embedded within those representations. Extant evidence suggests the content and phenomenological quality of imagined and remembered episodes can guide the perception and attribution of others' mental states. A natural question to ask is whether the arrow of causality goes the other direction: from mind to episode. Can manipulating the mental states attributed to others affect how we imagine and remember the surrounding episodes? The answer may well be yes, but we do not really know whether this is the case and in what ways episodes can be affected by the mental states of others within the episodes (see Hassabis et al., 2014 for related discussions on personality traits). Another avenue to pursue is to gain a better understanding of how episodes and minds spontaneously interact with one another during rest state when no experimental task is provided and subjects are free to self-generate thought in an unconstrained manner. While extensive research has demonstrated that both systems are robustly co-activated and are likely interacting during rest (e.g., Andrews-Hanna et al., 2014), little work has investigated the functional consequences of an interaction between systems during rest. Recent work has shown that connectivity between the hippocampus and the mPFC and between the mPFC and the TPJ during rest following encoding of social information are critical to consolidating memories of people and associated social roles and traits (Meyer et al., 2019). A similar interaction during rest may also hold true for consolidating memories that contain others' mental states.

7.3. New ways of looking at social problem-solving

The specificity of episodic representation has been shown to facilitate social problem-solving. Specifically, impairments in episodic detail have been associated with diminished performance on tasks that involve solving hypothetical social dilemmas (i.e., means-end problem solving) in temporal lobe epilepsy and mild cognitive impairment patients. Such that, these patient populations generate fewer solutions compared to healthy control groups (Sheldon et al., 2015; Sheldon, McAndrews, & Moscovitch, 2011). Moreover, manipulating the specificity and detail of episodic retrieval on an unrelated set of events improves social problem-solving performance, boosting the number of solutions generated by healthy younger and older adults (Madore & Schacter, 2014). This effect on social problem-solving performance is attributed to changes in episodic retrieval and construction (Schacter & Madore, 2016). In light of the episodic mindreading hypothesis, perhaps part of the facilitating effect of episodic specificity on social problem solving is being driven by effects of increased episodic detail augmenting mentalizing that researchers previously did not know to look for. Interestingly, recent work has shown similar effects of manipulating specificity on a future-self problem solving task for worrisome future events unique to an individual (Jing, Madore, & Schacter, 2016). Perhaps episodic simulation not only increases problem solving...
via heightened perspective taking of others, but also heightens problem solving via perspective taking of a future self.

7.4. Seeing minds as analogous to objects

Finally, an influence of episodic content on mentalizing can be viewed, in some respects, as analogous to how surrounding locations and items in the immediate sensory environment can guide the perception of objects. Contextual associative processing of the surrounding visual scene makes object recognition more efficient, increasing the speed and accuracy of identifying objects within the scene (Bar, 2004, 2007). For example, researchers have examined object recognition performance while viewing a jumbled collection of pictures that would together otherwise depict a coherent scene as it would naturally occur. Rearranging the pictures into disjointed configurations in which individual objects remain intact but background information is jumbled hinders the identification of briefly presented objects—even for highly familiar objects (e.g., identifying a bicycle) (Biederman, 1972). Moreover, ambiguous objects that are difficult to identify based on their intrinsic physical properties (is that a drill or a hair dryer?) can be resolved by presenting ambiguous objects in a specific location (placing it on a workbench vs. bathroom sink) (Bar, 2004). Are there similar situations when scene and episodic representation aid in resolving ambiguous mental states under conditions of uncertainty (e.g., Jenkins & Mitchell, 2010)? Can episodic mechanisms increase the accuracy and efficiency of mental state attribution by facilitating mentalizing of the target (Fig. 5)? While we await future research to fully address these questions, work on emotion perception suggests that embedding targets in specific locations will shape the mental states we will attribute to questions, work on emotion perception suggests that embedding targets in specific locations will shape the mental states we will attribute to targets (Fig. 5)? While we await future research to fully address these questions, work on emotion perception suggests that embedding targets in specific locations will shape the mental states we will attribute to targets (Fig. 5). What's more, patients may be able to rely on global judgments and schemas about other people's overall feelings. It seems more likely mentalizing in specific situations will not benefit from being able to imagine and remember episodes of those particular situations and help to resolve ambiguous mental states (Fernandez-Duque et al., 2010). This pattern may be similar to the benefits of episodic representation to temporal discounting, in which amnesic patients exhibit similar temporal discounting to healthy controls in neutral control tasks but do not benefit from making more farsighted decisions (i.e., attenuated discounting) after imagining specific future events (Kwan et al., 2012; Palombo et al., 2015). Future research will be needed to test these ideas while being careful to isolate episodic contributions to mentalizing from declines in working memory or executive function that can often present in these patient populations.

Perhaps equally important is investigating whether interventions targeting episodic mechanisms can be used to improve deficits in social cognition and behavior in patient populations with impairments in mentalizing (e.g., autism spectrum disorder). The episodic mindreading hypothesis proposed in this article predicts that individuals with impairments in mentalizing but a healthy episodic system may show heightened mentalizing by imagining and remembering episodes, though this increase may be partially dependent on the extent of residual mentalizing ability. For example, someone with zero mentalizing ability is unlikely to exhibit any benefit from episodic simulation and memory. The current work invites future investigations of the relationship between episodic mechanisms and mentalizing deficits that we previously did not know to look for, while also generating novel predictions about increased episodic detail and vividness to heighten healthy individual's ability infer the minds of others. It seems we may come to better understand, coordinate, and commiserate with others, in part, because we can imagine and remember the episodes that surround their minds.

8. Conclusion

Vonnegut and Zaki were right: people are mostly interested in other people—especially in understanding the contents of other people's minds. Unless you are buzzed re-creating still lifes at a paint and sip, a scene devoid of people may not be particularly interesting. Yet, a scene, and the episodic system that supports its construction, is not consequential to understanding other people and the contents of their minds. Here, I have proposed that the content and quality of how the scene is depicted—be it a landscape, seascape, or table-tenniscape—matters when it comes to perceiving and inferring mental states. Researchers in social cognition and neuroscience, in emphasizing the importance of person perception and categorization, may have overlooked the importance of the surrounding episode in guiding our ability to peer into the minds of others. Future work on episodes and minds is fertile intellectual ground for exploration with potentially broad implications for better understanding mentalizing in healthy individuals and illuminating deficits in clinical populations. The time is ripe to investigate the importance of the episodes that people, and their minds, are often embedded in.

References


9 Paint and sip refers to a group art class lesson during which the people drink wine and other alcoholic beverages as they paint. Whether this activity disinhibits latent creative talent or merely disinhibits aesthetic taste and judgment is a matter of ongoing debate.
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