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Self-projection and the brain

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When thinking about the future or the upcoming actions of another person, we mentally project ourselves into that alternative situation. Accumulating data suggest that envisioning the future (prospection), remembering the past, conceiving the viewpoint of others (theory of mind) and possibly some forms of navigation reflect the workings of the same core brain network. These abilities emerge at a similar age and share a common functional anatomy that includes frontal and medial temporal systems that are traditionally associated with planning, episodic memory and default (passive) cognitive states. We speculate that these abilities, most often studied as distinct, rely on a common set of processes by which past experiences are used adaptively to imagine perspectives and events beyond those that emerge from the immediate environment.

Introduction

A striking feature of mental life is the ability to consider alternatives to events in the immediate environment. We can shift our perspective from the present to vivid memories of our personal past, conceive what others are thinking and imagine ourselves in situations before they happen. We refer to the ability to shift perspective from the immediate present to alternative perspectives as self-projection. Self-projection has many uses and underlies the flexibility of human cognition and behavior; it equips us with abilities to make social inferences and anticipate the beliefs and actions of others.

Traditionally, the diverse abilities that depend on self-projection have been considered individually. For example, apart from a few important exceptions, which are discussed later, remembering the past has been studied without consideration of how these abilities relate to conceiving what others think and without reference to its adaptive value to cognition. Here, we explore the possibility that there is a shared brain network that supports diverse forms of self-projection, which includes thinking about the future (prospection), remembering the past, conceiving the viewpoint of others (theory of mind) and navigation. This network involves frontal and medial temporal–parietal lobe systems that are traditionally linked to planning and episodic memory. We hypothesize that, at its core, this network enables mental exploration of alternative perspectives based on our past experiences. The processes of the network are characterized by a personal, internal mode of mental simulation in contrast to perceptions that are driven primarily by the immediate external environment.

Our evidence for this network begins with the description of a prototypical ability that depends on self-projection – thinking about the future. We then consider the relationships among multiple forms of self-projection at functional and anatomical levels of analysis to show that, despite traditional separation, the multiple forms might arise from the workings of the same underlying brain network.

Prospection and related forms of self-projection

Prospection is the act of thinking about the future (Box 1). In this article, we discuss a specific variety of prospection that involves projecting oneself into the future – a form of episodic prospection that parallels episodic memory of the past [1,2]. Prospection is a natural place to begin because its purpose is intuitive: preparation for what might lie ahead requires a flexible system that can envision the future.

In using the term 'self-projection', the claim is made that prospection requires a shift of perception from the immediate environment to the alternative, imagined future environment, and that the imagined event is referenced to oneself. Self-reports suggest that prospection entails both first-person (field) perspectives and third-person (observer) views in which one sees oneself [3]. Prospection can involve conceptual content and affective states. Although difficult to establish, we assume that prospection is common and adaptive, and is used productively during decision making, navigation and social cognition.

Using this description, it is apparent that prospection shares similar processes with other cognitive acts that require projection of oneself from the immediate environment to alternative perspectives. For lack of a more suitable term, we refer to the mental construction of an imagined alternative perspective as a 'simulation'. Four well-studied cognitive abilities are candidates for using related forms of simulation: episodic memory, prospection, theory of mind and navigation (Table 1; Figure 1). All four forms rely on autobiographical information and are constructed as a perception of an alternative perspective or, in the case of theory of mind, is a simulation that considers another individual's perspective. Some studies suggest that these forms of self-projection emerge together at about the age of four years [4–6], which provides further evidence

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Box 1. History of prospection and the brain

Prospection is the act of thinking about the future and is the prototypical example of self-projection. The observation of planning deficits in patients who had frontal lobe lesions led to an understanding of the neural basis of prospection. In the mid-19th century, the case of Phineas Gage, a man whose frontal lobe was damaged during a bizarre accident with a tamping iron, revealed that 'there were structures in the human brain dedicated to the planning and execution of personally and socially suitable behavior' [71]. The discovery of neural activity patterns that maintain representations of past stimuli and anticipate future motor actions suggested candidate mechanisms for internal representations that support future-oriented behavior [8,16,19].

The contemporary concept of prospection, which is covered in this article, has emerged in diverse fields of psychology and neuroscience, including decision making, navigation, memory, social cognition and animal cognition. The name given to the concept has varied. Prospection and related concepts have been called 'episodic future thinking' [72], 'memory for the future' [73], 'pre-experiencing' [3], 'proscopic chronesthesia' [74], 'mental time travel' [17] and 'imagination' [32].

An idea that emerged at the same time as the concept of prospection is that prospection is spontaneously engaged when people are not otherwise performing directed behaviors [51]. In a paper published in 1985, Ingvar [73] anticipated many of the points we discuss here. For more on the concept of prospection and related forms of self-projection, see Refs [2,59,63,72,73,75]. Discussion from developmental and animal-cognition perspectives can be found in Moore and Lemmon [76] and Roberts [77].

of a common origin (see also Ref. [7]). In the next sections, we argue that these multiple forms of self-projection probably share a common brain network.

Brain mechanisms

Insight into the brain basis of prospection and related forms of self-projection comes primarily from human lesion and imaging studies. Neural evidence has so far lacked the necessary specificity to build a detailed model of the networks involved. Nonetheless, enough information has accumulated to create an initial framework. The network that supports self-projection involves frontal lobe systems that are traditionally associated with planning and medial temporal–parietal lobe systems that are associated with memory. Below, we describe evidence for the role of each system in self-projection and summarize recent human imaging data that directly link multiple forms of self-projection to a common core network.

Frontal lobe contributions to mental simulation

Deficits following frontal lobe lesions take many forms, depending on the regions affected and the extent of the lesion [8]. Among these deficits is an inability to plan and structure events in appropriate temporal sequences, which is relevant to the brain basis of self-projection. Despite these impairments, patients who have frontal lesions perform normally in well-established routines and can show high intellectual function, measured using intelligence tests [9]. However, when confronted with challenging situations and new environments, their inability to plan is apparent [10]. Behaviors are rigid; they move from one action to the next as if the completion of each step were its own goal rather than being motivated by a longer-term objective. For example, patients who have frontal lesions often fail to find alternative routes to solving tasks and substitute previously used actions for desired ones [11]. Patients' poor performance during neuropsychological tests underscores these qualitative descriptions. Deficits include the inability to order sequences temporally [12], plan actions on tasks that require foresight [13,14] and adjust behaviors flexibly as rules change [15].

Linking these deficits to some of the processes of self-projection, Mesulam noted that, along with its other functions, the prefrontal cortex might have a pivotal role in the ability to 'transpose the effective reference point [of perception] from self to other, from here to there, and from now to then' [8]. Fuster raised a similar idea that frontal lobe processes are fundamental to mental time travel, writing:

> 'Whereas faulty memory deprives the frontal patient of the ability to use experience of the recent past, faulty foresight deprives him or her of the ability to plan for the future. The two deficits are the mirror of each other: One reflects of a temporally reflective function, the other of a prospective one. These failing functions are two sides of the same coin, two mutually complementary aspects of temporal integration' [16].

Collectively, these neuropsychological findings suggest that the frontal cortex contributes to the ability to shift flexibly one's perspective beyond the immediate present. Tulving and colleagues [17] took this concept one step further and put forward a strong case for the frontal cortex being particularly important to the awareness of one's protracted existence across subjective time – what they referred to as 'autonoetic consciousness' [17,18]. However, it is difficult to know whether patients' deficits are specifically due to their inability to simulate models of the future and other alternative perspectives. The frontal cortex, among other brain regions, is characterized by

Table 1. Related forms of self-projection[a]

	Episodic memory	Navigation[b]	Theory of mind	Prospection
Orientation	Past	Present or future	Present or future	Future
Perceived as	True past event	Alternative location or personal viewpoint	Another person's viewpoint	Possible future event
Mode	Constructive	Constructive	Constructive	Constructive
Perceived accuracy	High	High	Medium	Low
Perspective	First person	First or third person	Other person	First or third person
Function(s)	Remembering	Way finding	Social cognition	Planning; social and cognitive problem solving

[a]Four related forms of self-projection are listed. These forms of self-projection are not completely independent abilities and could be organized in many ways.
[b]Navigation is perhaps the most tentative candidate for being related to the others. We include navigation because of shared functional properties and initial overlap in functional anatomy (e.g. Refs [69,70]).

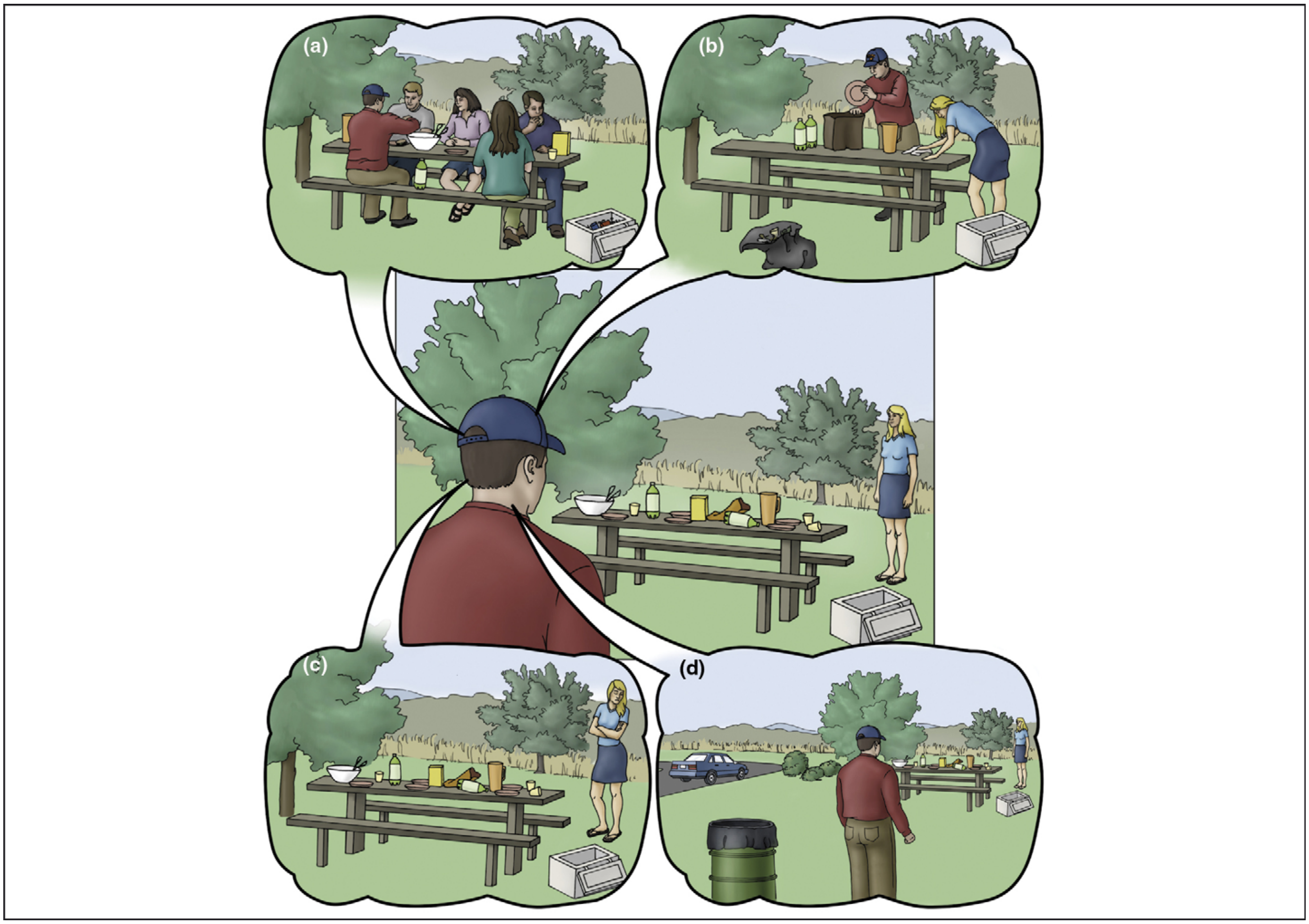

Figure 1. Forms of self-projection. Four forms of self-projection are illustrated to highlight their common reliance on a personal, mental simulation of another time, place or perspective. The scene being experienced is shown in the center and each alternative form of conceived perspective is in a thought bubble. Simulated perspectives include first-person and third-person views. **(a)** Remembering involves simulating the past, such as the picnic earlier. **(b)** Prospection involves simulating a possible future event, such as cleaning up the mess. **(c)** Theory of mind involves conceiving another person's perspective – in this instance, the mental state of the person about to be recruited to help clean. **(d)** Navigation – or topographic orientation – involves simulating another view or mapping the environment, such as a mental map of the world that surrounds the picnic area, including the location of the nearest trash bin. All these abilities depend on a shift from the present perspective to a simulated model of an alternative world. All use specific past instances from memory as constraints in forming the mental simulations. In this article, we provide evidence that these forms of self-projection might rely on a common brain network.

neurons that exhibit sustained activity patterns and, thus, provides a candidate mechanism for mental simulation [16,19]. In the next section, we suggest that a key contribution to the content of mental simulation comes from the medial temporal lobe memory system.

Medial temporal–parietal lobe contributions

The medial temporal lobe, including the hippocampus and surrounding cortex, has a role in declarative memory, which includes episodic memory [20,21]. Damage to the medial temporal lobe often causes amnesia. A lesser-studied aspect of the amnesic syndrome is the inability to conceive the personal future. Talland [22], in his seminal description of amnesia in Korsakoff's syndrome, noted the loss of personal planning and self-reference. When he asked his patients about their future plans, they could only state generalities. Futhermore, H.M., whose brain damage following surgery for epilepsy left him densely amnesic [23], does not make predictions about future autobiographical events. When pushed to make a prediction, either he responds with an event from the distant past or he does not respond at all (S. Steinvorth and S. Corkin, personal communication). Patient K.C. shows a similar impairment [18].

An overlap between deficits of remembering and envisioning the future is revealed by patient D.B., who developed amnesia following anoxia [24]. In a systematic investigation, Klein and colleagues observed that D.B. either confabulated or did not know what he would be doing when questioned about his future. However, D.B. retained general knowledge of the future. For example, he remarked that a future issue that faced the environment was the 'threat that weather and rainfall patterns are going to change because of industrial pollution'. Thus, his deficit was not simply an absence of imagination or an inability to reason about the future. D.B. lacked the capacity to consider himself in the future as well as failing to remember his own past. Further study is needed to document fully whether amnesia is commonly associated with impairments in conceiving the personal future. The nature of the lesions that produce impairment also needs exploration, with particular attention to deficits following localized medial temporal lesions. Nonetheless, these initial observations are intriguing.

Recent neuroimaging data in participants with intact memory systems further suggest that medial temporal lobe structures that are associated with memory form a network that is important to self-projection, and that this network includes specific regions within the parietal lobe [25,26]. Studies of successful recollection have repeatedly shown activation of the hippocampal formation in combination with medial and lateral parietal lobe regions [27–29]. One hypothesis is that these cortical regions represent extended components of a medial temporal–parietal system that contributes to memory function. It is relevant, then, that the specific regions in the parietal cortex that are associated with memory overlap the regions that are active in other forms of self-projection, including theory-of-mind tasks (e.g. see Refs [30,31]; reviewed in Ref. [32]).

Moreover, if one examines hippocampal networks by placing a seed region in the hippocampal formation and mapping the correlated cortical regions, robust correlations are observed in parietal and frontal regions [33] that overlap the regions that are selectively activated during remembering, prospection and theory-of-mind tasks (Figure 2). Simulations of others' perspectives, and of ourselves in another time, might be built on specific past instances, as captured through medial temporal processing. We will return to this idea later.

Regulation of self-projection

Functions that shift the perspective from the immediate environment to another vantage point create an interesting challenge for the brain. We must keep track of these shifts, otherwise our perceptions would blur together. Decety and Grézes note that 'reality and imagination are not confused' [32]. A computational model of how such a process might be structured is far from being defined, but it will probably require a form of regulation by which perception of the current world is suppressed while simulation of possible alternatives are constructed, followed by a return to perception of the present. Povinelli considered this issue from a developmental perspective and noted that coordination of internal perspectives 'paves the way for the child to sustain not simply one current representation of the self but also to organize previous, current, and future representations under the temporally extended, metaconcept of "me"' [7].

We know little about the neural implementation of this process. However, separate lines of research converge to suggest that the frontopolar cortex and anterior midline frontal regions have an important role in regulating shifts in perspective. Beginning with the earliest neuroimaging studies of episodic memory, the frontopolar cortex, most often the right side, has been consistently activated when subjects engage epochs of remembering. This finding led to the suggestion that the frontopolar cortex has a role in retrieval mode – the special attentional state when one remembers the past (reviewed in Ref. [34]). Attributes of frontopolar activity are consistent with a role in high-level regulation and executive control. First, activity is sustained during periods of remembering [35,36]. Second, activity levels are often unaffected by the content of the memory, such as whether faces or words are accessed [37] or whether the retrieval event is successful [36].

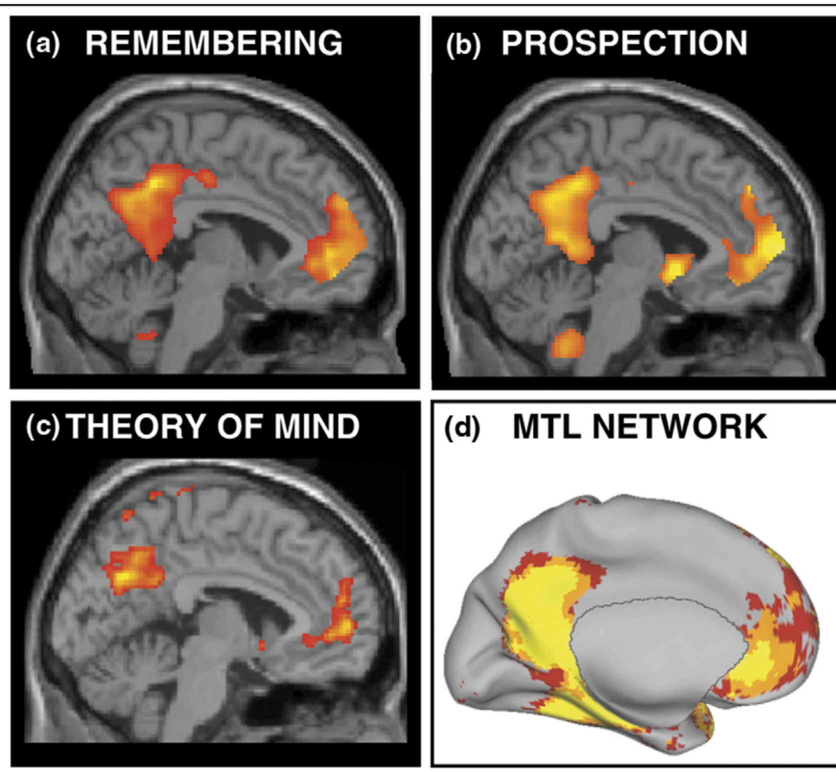

Figure 2. Brain activation during three forms of self-projection. Each image displays the midline of the left hemisphere with brighter colors, indicating regions of increased activation. There is a remarkable correspondence in activation during remembering **(a)**, prospection **(b)** and theory-of-mind **(c)** tasks. Convergence also extends to lateral parietal regions (not shown), located within the inferior parietal lobule near the temporo–parietal junction. Within-subject studies are required to determine the extent of the overlap. Data in (a) and (b) adapted from Ref. [46]. Data in (c) provided by Rebecca Saxe, based on Ref. [30]. **(d)** Cortical regions that functionally correlated with the medial temporal lobe (MTL). Note that the MTL network overlaps the regions that are recruited during the multiple forms of self-projection. (d) adapted from Ref. [33].

Frontopolar activity is not selective to remembering. Outside of the memory domain, Grafman and colleagues [38] demonstrated that the frontopolar cortex is recruited when tasks require consideration of a main goal at the same time as processing sub-goals. This observation has been replicated and extended (e.g. Refs [39,40]). A direct comparison of episodic retrieval and tasks that require sub-goal processing suggests anatomic overlap for certain frontopolar regions [41].

A final set of findings suggests that the frontopolar cortex contributes to theory of mind. Gallagher and Frith [42] reviewed evidence from tasks that were designed explicitly to capture participants' mental states in the act of simulating another person's perspective [43,44]. They suggest that the paracingulate cortex, the anteriormost portion of the frontal midline, is recruited in executive components of simulating others' perspectives. This region is contiguous but distinct from those reported above in studies of episodic remembering. Furthermore, after considering alternative accounts, Gallagher and Frith conclude that this region helps to 'determine [another's] mental state, such as a belief, that is decoupled from reality, and to handle simultaneously these two perspectives on the world' [42].

There are two important points to take from Gallagher and Frith's analysis in the context of the studies mentioned earlier. First, we are far from understanding the specific relevant anatomy for prospection and related forms of self-projection. A particularly unclear aspect is the relationship between midline frontal and frontopolar regions that typically extend laterally to the midline. Second, despite these ambiguities, there is general agreement that a set of contiguous regions in the anteriormost portions of the frontal lobe are concerned with regulating shifts between perspectives.

Convergence of prospection, remembering and theory of mind

Evidence that multiple forms of self-projection depend on a shared brain network comes from human imaging studies. Several studies have specifically explored future thinking in direct contrast to remembering [45–47]. Each study included a series of cues to think about a past or planned event. Under these conditions, participants constructed elaborate plans for the future that were autobiographical and detailed. For example, one woman described a future event cued by the word 'dress' [46]:

> 'My sister will be finishing…her undergraduate education, I imagine some neat place…it would be a very nice spring day and my mom and my dad will be there. And I can see myself sitting in some kind of sundress, like yellow, and under some trees…'

Results suggest that episodic remembering and envisioning the future share a common network. Figure 2 illustrates this correspondence using data from Ref. [46]. Consistent with expectations from neuropsychological findings, the shared network included prefrontal and frontopolar regions along the midline and posterior parietal regions (extending into retrosplenial cortex and precuneus, and lateral regions within the inferior parietal lobule) and the medial temporal lobe. This specific network is intriguing in the context of prior neuroimaging studies of related functions. First, the network includes posterior cortical regions that are commonly activated by retrieval tasks, as noted earlier, including tests of remembering based on Tulving's remember/know paradigm (e.g. reviewed in Ref. [26]). These posterior cortical regions are likely to be components of the same medial temporal–parietal lobe network (Figure 2). Second, also prominently activated are midline frontal regions that emerge in this network and in studies of self-referential and social decisions [48–50]. Autobiographical memory tasks, which simultaneously include both memory demands and strong self-referential components, robustly activate both the medial temporal–parietal and the frontal components of the network [51–55].

In a study of theory of mind, Saxe and Kanwisher [30] provide further evidence that the core network generalizes beyond traditional memory tasks (see also Ref. [31]). Individuals answered questions about stories that required participants to conceive a reality that was different from the current state of the world. In one condition, the conceived state was a belief held by a person; in the other condition, the conceived state was an image held by an inanimate object (e.g. a camera). The two conditions were matched on complexity and the approximate time taken to understand the stories. Conceiving the beliefs of another person strongly activated the network shared by prospection and remembering (Figure 2); the control condition did not. Thus, imagining one's own future or the perspective of another person recruits the same core network, whereas other forms of imagination fail to activate this network.

In the realm of moral judgments, Greene and colleagues examined brain networks that were more active when individuals considered moral decisions that involved personal interactions than those that involved impersonal interactions [56] (see also Ref. [57]). They found that moral judgments that involved personal interactions recruited a network similar to that illustrated in Figure 2 (also see Figure 2 in Ref. [56]).

What does this selective generalization mean? The combined observations suggest that the core network that supports remembering, prospection, theory of mind and related tasks is not shared by all tasks that require complex problem solving or imagination. Rather, the network seems to be specialized for, and actively engaged by, mental acts that require the projection of oneself into another time, place or perspective. Prospection and related forms of self-projection might enable mental simulations that involve the interactions of people, who have intentions and autonomous mental states, by projecting our own mental states into different vantage points, in an analogous manner to how one projects oneself into the past and future. See Box 2 for a discussion of the default mode in relation to self-projection.

Proto-forms of experience projection in animals

Prospection and related forms of experience projection have received thoughtful consideration regarding the degree to which non-human animals possess them (e.g. Refs [58,59]; see also Refs [2,60]). Some have argued that experience

Box 2. The default mode and its relationship to self-projection

A long-recognized but puzzling aspect of brain function is that as one goes from a restful state to an active, engaged cognitive state, such as when solving a difficult mental arithmetic problem, the total cerebral mean blood flow and oxygen uptake in the brain remain constant [78]. That is, in terms of brain physiology, similar energy is devoted to undirected brain processes as it is to brain processes when an individual is engaged in a directed task. This finding implies that extensive brain activity of some form persists in the absence of immediate task goals.

Analyses based on positron emission tomography (PET) have confirmed that a highly stereotypic pattern of increased brain activity is adopted during passive task states compared with many forms of active task state [79]. Figure I shows this pattern from a combined analysis of nine separate PET studies; the pattern has been replicated across numerous PET and functional magnetic resonance imaging (fMRI) studies. The network prominently includes frontal regions along the midline, a network of lateral and medial parietal regions, and medial temporal lobe structures. The consistency of this activity pattern in undirected task states, in addition to its metabolic properties, led Marcus Raichle and colleagues to label it the 'default mode' [80].

The default network is remarkably similar to that adopted during directed abilities that depend on self-projection, including remembering and prospection. This convergence raises the possibility that default modes of cognition are characterized by a shift from perceiving the external world to internal modes of cognition that simulate worlds that are separate from the one being directly experienced.

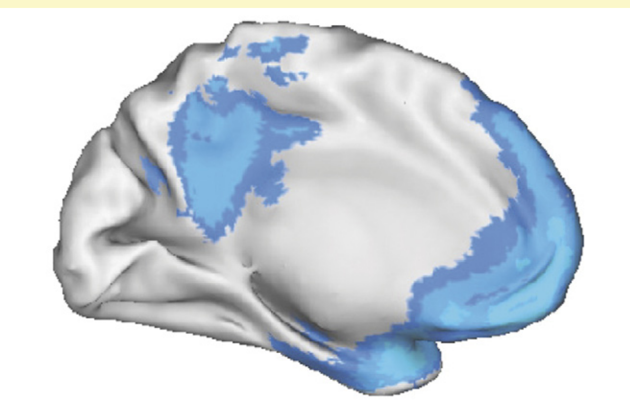

Figure I. The brain activity pattern associated with the default mode. The network of regions illustrates those brain regions that are most active when people passively think to themselves, as compared with a range of active tasks that demand external attention and decision processes. Note the remarkable similarity between the default regions and those engaged during self-projection and also the similarity to those regions that are functionally correlated with the medial temporal lobe memory system, as shown in Figure 2. Adapted from Ref. [79].

projection is a uniquely human ability and others have argued that prospection-like abilities exist in other animals. Three conclusions emerge from the literature. First, certain bird species have adapted to overcome similar challenges that self-projection might have evolved to address in humans, presumably through convergent evolution [59,61,62]. Second, self-projection in humans is more developed than in other animals, perhaps with qualitative differences that emerge from our self-awareness [58,63]. Finally, other animals exhibit behavioral and neural patterns that might represent proto-forms of self-projection. These proto-forms provide opportunities for mechanistic study.

Of all known parallels of self-projection, the most remarkable is that of certain caching birds [59]. Scrub jays cache food across numerous locations. On their return, they recover food from the specific locations, prioritizing perishable foods that are still edible [61]. To protect their cache, scrub jays preferentially select storage locations that are out of sight of pilfering birds [62]. Moreover, if the scrub jays have experience of pilfering the food of others, they will recache their own food if another bird was present when they first stored the food, as if to protect it from future theft [62].

In many ways, scrub jay behavior is reminiscent of human abilities, including the likely presence of a form of experience projection. It is difficult to know whether the birds use similar processes to those of humans when they perform these behaviors, but we suspect that they do not. Brain anatomy in birds is sufficiently different from higher mammals, including the absence of the six-layer cortex, so it is likely that the neural implementation is different [59]. Our common ancestor to birds is distant, and few species exhibit complex behaviors that suggest experience projection; therefore, the simplest conclusion is that these abilities in scrub jays evolved in parallel with similar human abilities. Parallel evolution of behaviors in scrub jays demonstrates the power of natural selection for shaping adaptive future-oriented behaviors.

Prospection-like abilities exist to varying degrees in great apes. Given their close evolutionary lineage to humans, abilities in primates are more likely to be proto-forms of human abilities, so they might reflect common ancestral capacities rather than convergent evolution such as that seen in scrub jays. Great apes use tools and delay gratification in ways that anticipate future events [63]. Chimpanzees and orangutans will select and save a suitable tool for use many hours later [64]. However, it has been difficult to establish whether great apes have planning capacity that is similar to humans. For this reason, many have argued that abilities that depend on self-projection in its fullest form are uniquely human.

Proto-forms of self-projection provide opportunities to test how these abilities can be implemented in mammalian neural systems. Rodents are of particular interest because of their amenability to multi-unit recording and genetic manipulations, but do they have proto-forms of self-projection? We believe they do. In their classic study of latent learning, Tolman and Gleitman [65] allowed rats to explore a T-maze (discussed in Ref. [66]; Figure 3). Across sequential trials, the rats were forced to forage for food in both arms of the maze. The rats were then removed and placed in one arm of the maze where they received a series of foot shocks. When placed back in the T-maze, 88% of the rats chose the safe arm of the maze.

How did the rats make this decision? The rats were never shocked during their initial exploration when they made navigation decisions. Yet, when faced with a decision following the off-site experience, they moved away from the unsafe corner. One possibility is that the rats, in some form, preplay activity sequences for left and right turns before making the actions. After the rats experience the shocks, the preplay might be sufficient to elicit an aversive neural activity correlate and sway the decision. Thus, although proto-forms of prospection in rodents almost certainly lack central aspects of human abilities, including

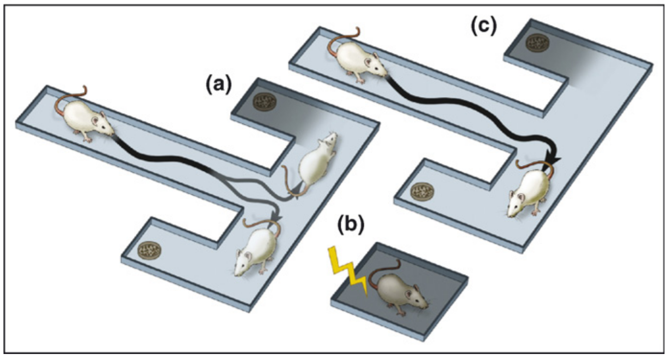

Figure 3. Candidate proto-forms of prospection in rats. Tolman and Gleitman's famous behavioral experiment on latent learning using a T-maze [65]. The maze contained two arms: for illustration, the end chamber of one arm is darkened and the end chamber of the other arm is light. **(a)** Initially, the rat explores all parts of the T-maze. **(b)** The rat is removed and placed in the darkened chamber where it experiences a series of shocks. **(c)** When placed back in the T-maze, the rat chooses the safe path. The rat probably represents the decision choice, in some manner, in advance of the action, which raises the possibility of a proto-form of experience projection.

simulation of oneself in the future, their abilities might depend on complex neural sequences that represent the past and future (see Ref. [67]). Further work is required to understand how such representations in rodents form and how they are combined with signals from affective and reward systems to control decision making.

Conclusions and future directions

In this article, we have considered the speculative possibility that a core brain network supports multiple forms of self-projection. Thinking about the future, episodic remembering, conceiving the perspective of others (theory of mind) and navigation engage this network, which suggests that they share similar reliance on internal modes of cognition and on brain systems that enable perception of alternative vantage points. Perhaps these abilities, traditionally considered as distinct, are best understood as part of a larger class of function that enables flexible forms of self-projection. By this view, self-projection relies closely on memory systems because past experience serves as the foundation on which alternative perspectives and conceived futures are built.

Future research can expand beyond the present concepts, which are admittedly vague, by exploring the nature of the processing differences between situations that are solved using the core network (Figure 2) and those that are not. Are situations that are associated with increased activity based on simulated first-person perspectives? Do the situations always have emotional content? Do they always have social content? Do the common attributes involve a shift in spatial perspective? Or are conceptual shifts in perspective that are devoid of specific visual or spatial content sufficient? See Box 3 for Questions and future directions.

Perhaps the most important implication of this review of the literature is the suggestion of how a common brain network can flexibly provide adaptive function across several seemingly distinct domains. The network described here is tied to the medial temporal lobe system, which is traditionally considered almost exclusively in the context of remembering the past. We suspect the adaptive value of episodic memory is not solely in its ability to afford mental reconstruction of the past but rather in its contribution to building mental models – simulations – of what might happen next or other perspectives on the immediate environment, such as what others are thinking (see Ref. [63]). As Schacter and Addis note in an upcoming review [68], this explanation helps us to understand why memory is constructive and why it is prone to errors and alterations. Perhaps a feature of the core network that is involved in self-projection is its flexibility in simulating multiple alternatives that only approximate real situations. The flexibility of the core network might be its adaptive function, rather than the accuracy of the network to represent specific and exact configurations of past events. That is, we remember the past to envision the future.

Box 3. Questions and future directions

- The concepts of 'self-projection' and 'simulation' as used here are vague and likely to be controversial. The use of these terms does not reflect a lack of precision but rather ignorance of more suitable terms to describe the putative processing functions of the core network (Figure 2). An important direction for future research will be to acquire more data to improve our understanding of the processing attributes of the core network and the computations performed.
- Lesion studies and other forms of clinical data that relate medial temporal lobe contributions to self-projection are meager. Our central hypothesis is that self-projection depends on memory systems to guide plausible mental simulations. Can deficits in self-projection in amnesic patients who have well-characterized (focal) lesions be systematically documented? Do patient groups such as those who have Alzheimer's disease show deficits consistent with impairment of self-projection?
- Experimental paradigms used to study self-projection, particularly prospection, are challenging. Accessible paradigms for studying prospection and other forms of self-projection need to be developed. Methods that can probe the content of thought, perhaps based on human imaging, could provide solutions. Also promising are methods based on virtual-reality environments, where experimenters can systematically manipulate the subject's opportunities to draw on past experiences and to predict upcoming situations.
- The overlap between the network that is actively used in tasks that require self-projection and regions that are active in passive task states – the 'default mode' – is striking. An intriguing area for further study is to explore the degree to which this overlap reflects a tendency to construct spontaneously mental simulations when not otherwise engaged in demanding external tasks. Similarly, the study of the default mode might provide an insight into processes that are engaged during self-projection.
- Many tasks can be approached in multiple ways, but what kinds of problems, if any, can only be solved using self-projection? The answer to this question is particularly important because it would help us to understand what functional adaptations have arisen uniquely as a consequence of prospection and other forms of self-projection. Our abilities to plan, make social and moral judgments, and consider complex organizational structures are all candidates.

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