Review Article

Cognitive Mapping Deficits in Schizophrenia: A Critical Overview

Anushree Bose[1,2], Sri Mahavir Agarwal[1,2], Sunil V. Kalmady[1,2], Ganesan Venkatasubramanian[1,2]

ABSTRACT

Hippocampal deficits are an established feature of schizophrenia and are complementary with recent evidences of marked allocentric processing deficits being reported in this disorder. By "Cognitive mapping" we intend to refer to the concepts from the seminal works of O'Keefe and Nadel (1978) that led to the development of cognitive map theory of hippocampal function. In this review, we summarize emerging evidences and issues that indicate that "Cognitive mapping deficits" form one of the important cognitive aberrations in schizophrenia. The importance has been placed upon hippocampally mediated allocentric processing deficits and their role in pathology of schizophrenia, for spatial/representational cognitive deficits and positive symptoms in particular. It is modestly summarized that emerging evidences point toward a web of spatial and cognitive representation errors concurrent with pronounced hippocampal dysfunction. In general, it can be stated that there are clear and consistent evidences that favor the cognitive mapping theory in explaining certain deficits of schizophrenia and for drawing out a possible and promising endophenotype/biomarkers. Further research in this regard demands attention.

Key words: *Allocentric, cognitive mapping, hallucinations, hippocampus, schizophrenia*

INTRODUCTION

Understanding the cognitive basis for schizophrenia has been challenging because it is characterized by a wide array of aberrations. One of the major difficulties in understanding the nature of deficits exhibited in schizophrenia emanates from the fact that sufficient research literature e.g., see[1] reflects that the deficits observed can be dissociable in terms of psychological and neural pathophysiology. Yet this pathophysiological dissociation does little in achieving an understanding of this disorder.[2] Nonetheless, it has been postulated that the wide-ranging pattern of cognitive aberrations in schizophrenia could potentially be narrowed down to a set of "core" deficits. The significant cross-task correlation[3] within the "context-sensitive" conditions of several cognitive tasks seem to support the theory that schizophrenia is characterized by "an impairment in using representations of context" to govern appropriate behavior.[4]

Access this article online	
Website: www.ijpm.info	**Quick Response Code**
DOI: 10.4103/0253-7176.127242	

Disparate lines of evidence suggest that a primary function of the hippocampus is to bind previously experienced item and context information to construct detailed item-in-context memories.[5,6] Hippocampal formation and medial temporal lobe (MTL) see[7] have been proposed to be critically involved in the pathogenesis of schizophrenia.[7,8] Hippocampus figures prominently in meta-analyses of brain

[1]Departments of Psychiatry, The Schizophrenia Clinic, [2]Translational Psychiatry Laboratory, Cognitive Neurobiology Division, Neurobiology Research Centre, National Institute of Mental Health & Neurosciences, Bengaluru, Karnataka, India

Address for correspondence: Dr. Ganesan Venkatasubramanian
Department of Psychiatry, National Institute of Mental Health & Neurosciences Bengaluru, Karnataka, India.
E-mail: venkat.nimhans@yahoo.com

abnormalities associated with schizophrenia[9-12] and pathophysiological theories of schizophrenia.[13-16] In this review, we focus our attention to the deficits in context representation with specific emphasis on egocentricity-allocentricity (which explains both visuospatial frame of reference[17,18] and social frame of reference),[19,20] their relation to the hippocampus and the resultant dysfunction that is manifested at several levels as features of schizophrenia.

Current models of visuospatial abilities (encompassing constructs like navigation, spatial learning and spatial memory) are explained by two perspectives of visual space: Allocentric (object or environment centered) reference and egocentric (self-centered or body-centered) reference. The visual space is thus delineated into egocentric and allocentric frames of references. Egocentrism is the ability to see the world from one's own perspective and allocentrism is the capacity to experience the world from a non-egocentric/environment or object-centered point of view. Observations from lesion studies and single unit recordings in animals and humans, as well as from functional imaging studies in humans e.g.,[21-25] have established the role of hippocampal and parahippocampal cortices in mediating allocentric abilities. Further, learning allocentric i.e., object – location associations has been particularly related to hippocampal function across species.[26-29] Hippocampal and parahippocampal activation occurs during the computation of spatial body positions, complex geometric scenes, or 3-dimensional (3D) navigation.[30,31] These evidences yield conclusive indications confirming the critical role for the hippocampus in cognitive mapping as discussed below.

The cognitive map theory was developed from the seminal works of O'Keefe and Nadel and was published in their book "Hippocampus as a cognitive map." As per this postulate, "hippocampus represents the environments, locations within those environments and their contents and thus mediates spatial memory processes and flexible navigation."[32] This model posits that, in humans, spatial maps are built in the right hippocampus whereas semantic maps are located in the left hippocampus. The former is responsible for encoding spatial relationships, while the latter provides semantic links and structure for comprehension and production of discourse. Evidences from the study of patients with amnesia support this theory.[33] Furthermore, one or both hippocampi integrate temporal information derived from the frontal lobes, this allows to timestamp each individual visit to a location and provides the basis for a spatio-temporal contextual or episodic memory system. Hippocampus also mediates "declarative memory"[34] and "flexible relational memory"[35] in humans and some animals. Most importantly, the cognitive map theory states that hippocampus specifically supports allocentric processing of space; while egocentric processing, the conceptual polar opposite of allocentric cognition, is supported by the parietal neocortex.[32] Conclusively, based on research evidences, the hippocampus has been hypothesized as essential to construction and storage of spatial information in the form of allocentric spatial cognitive maps;[36] declarative (explicit information) rather than procedural (implicit information) memory;[37] and disambiguation of the relations between stimuli that combine to form unique representations during the encoding and recall of information.[38-40] All of these hypotheses predict a spatial impairment after hippocampal damage.[41] This also implies that accurate mental representations are invariably dependent on adequate hippocampal function. In summary, this discussion implies hippocampal role in visual and spatial encoding, representation, recall, manipulation, memory and learning. In this article, attempting to expand on the original proposition of "The cognitive mapping theory" as proposed by O'Keefe and Nadel, we intend to summarize the observations to support the view that cognitive mapping deficits (hippocampal dysfunction and associated allocentric deficits) are among the critical contributors to schizophrenia disease process; more importantly, these deficits can be linked with certain important clinical manifestations of this disorder. To emphasize this, we have reviewed the contributions of the hippocampus and associated structures in this regard. Furthermore, we have illustrated the utility of allocentric and egocentric concepts (subsumed under the broader framework of our proposed cognitive mapping theory implicating hippocampal function) of understanding visuospatial and social frames of reference in explaining symptomatic expressions of schizophrenia by recent research findings.

COGNITIVE MAPPING DEFICITS IN SCHIZOPHRENIA

Studies that have evaluated egocentric/allocentric cognitive functions in schizophrenia are summarized in Table 1. Several paradigms are widely employed in the investigation of visuospatial representation (with specific focus on assessment of egocentricity-allocentricity) among both patients with schizophrenia and normal controls [Table 1]. In the following sections, we have attempted to relate these observations with the clinical manifestations of the schizophrenia.

Table 1: Studies that have evaluated egocentric/allocentric cognitive functions in schizophrenia*

Authors, year and article	Methodology	Results	Conclusions
Landgraf S, Amado I, Purkhart R, Ries J, Olié JP, van der Meer E. (2011). Visuo-spatial cognition in schizophrenia: Confirmation of a preference for local information processing. Schizophrenia Research 127; 163-170	Participants: 24 stabilized schizophrenia patients and 25 healthy, matched controls Mental mirroring task. Task difficulty was manipulated while stimulus surface structures were maintained unchanged. Information processing was assessed by recording eye movements	SZ were slower than C in the easiest condition but they made more errors than C in the more difficult conditions. SZ did not adapt their average fixation duration to task demands resulting in longer fixation duration in the easiest condition and shorter fixation duration in the most difficult condition compared to C	SZ patients employ local information processing even when it is maladaptive for task demands. That is, patients do not adapt their fixation duration to task demands implicating (i) a preference for scanning local stimuli features and (ii) information processing inflexibility. These features need to be taken into account when evaluating visuo-spatial cognitive performance in schizophrenia
Landgraf S, Krebs MO, Olié JP, Committeri G, van der Meer E, Berthoz A, Amado I. (2010). Real world referencing and schizophrenia: Are we experiencing the same reality? Neuropsychologia 48; 2922-2930	Participants: Schizophrenia patients, chronic=24 and normal controls=25 Virtual environment: Participants had to make a decision as to which of two trash cans was closest to themselves (viewer-centered, egocentric), to a ball (object-centered, unstable allocentric), or to a palace (landmark-centered, stable allocentric). Reaction time, error rate, learning rate and local task switch cost	In patients: Egocentric reaction time preserved; increased RT in both allocentric referencing conditions (stable and unstable) and overall increased error rate. Switch cost was diminished in patients when changing from the egocentric to the landmark-centered condition and elevated when changing from the landmark-centered to the egocentric condition	In schizophrenia patients adoption of an egocentric perspective is preserved; adopting an allocentric point of view and switching between egocentric and landmark-centered perspectives are impaired Perturbations in non-egocentric referencing and transferring efficiently between different referential systems might contribute to altered personal and social world comprehension in schizophrenia
Thakkar KN, Park S. (2010). Empathy, schizotypy and visuo-spatial transformations. Cogn Neuropsychiatry. 15(5): 477-500	Participants: Schizotypy patients=32 (16 women) Visuospatial perspective-taking task and mental letter rotation task RT and accuracy were analyzed in relation to dimensions of self-reported empathy, indexed using the interpersonal reactivity index and schizotypy, as measured by the schizotypal personality questionnaire	Greater cognitive and affective empathy associated with reduced negative schizotypy; In men, greater cognitive empathy associated with reduced positive schizotypy; improved accuracy for imagined self–other transformations in the perspective-taking task was associated with greater self-reported cognitive empathy in women and higher positive schizotypy across genders; faster mental letter rotation was associated with reduced cognitive empathy and increased negative schizotypy in women	The findings partially support the commonalities in visuospatial transformation ability, empathy and schizotypy and posit an interesting link between spatial manipulations of our internal representations and interactions with the physical world
Thakkar KN, Park S. (2010). Impaired passive maintenance and spared manipulation of internal representations in patients with schizophrenia. Schizophrenia Bulletin	Participants: Schizophrenia patients=520 and normal controls=519 Examining components of WM using a spatial DRT to measure maintenance processes and 2 mental rotation tasks (allocentric and egocentric) with no delay period or restriction on encoding time to measure manipulation processes	Consistent with previous findings, patients were impaired on the spatial DRT. However, patients performed equally well on the egocentric mental rotation task and were more accurate than controls on the allocentric mental rotation task as the required degree of rotation increased	These results indicated impaired maintenance and spared manipulation of representations in WM and suggest a pocket of cognitive function that might be enhanced in SZ
Girard TA, Christensen BK, Rizvi S. (2010). Visual-spatial episodic memory in schizophrenia: a multiple systems framework. Neuropsychology Vol. 24, No. 3, 368-378	Participants: Schizophrenia patients=30, healthy controls=30 Using the bin task, a human analog of rodent maze tasks, everyday objects were hidden in visually identical bins. Following a 1 min filled delay, participants were asked to identify both the object hidden and bin used on the basis of its spatial location. Three dimensions of visual-spatial memory were contrasted: (a) Memory for spatial locations versus memory for objects, (b) allocentric (viewpoint independent) versus egocentric (body-centered) spatial representations and (c) event (working) memory versus reference memory	Most pronounced was a differential deficit in memory for spatial locations under allocentric but not egocentric viewing conditions in the schizophrenia group relative to healthy controls. Similarly, schizophrenia-related spatial memory deficits were pronounced under demands for event memory but not reference memory	These results support a heuristic of preferential deficits in hippocampal-mediated forms of memory in schizophrenia. Moreover, the task provides a useful paradigm for translational research and the pattern of deficits suggests that persons with schizophrenia may benefit from mnemonic approaches favoring egocentric representations and consistency when interacting with our visual– spatial world

(*Continued*)

Table 1: (Continued)

Authors, year and article	Methodology	Results	Conclusions
Straube B, Green A, Chatterjee A, Kircher T. (2010). Encoding social interactions: The neural correlates of true and false memories. Journal of Cognitive Neuroscience X:Y, pp. 1-19	Participants: 18 healthy males; during fMRI data acquisition, participants watched video clips of an actor speaking and gesturing directly toward them (egocentric context) or toward an unseen third person (allocentric context). After scanning, a recognition task gauged participants' ability to recognize the sentences they had just seen and to recall the context in which the sentences had been spoken	No differences between the recognition of sentences spoken in egocentric and allocentric contexts. However, when participants were asked about the communication context ("Had the actor directly spoken to you"?), tended to believe falsely that the actor had directly spoken to them during allocentric conditions. Greater activity in the hippocampus was related to correct context memory, whereas the ventral ACC was activated for subsequent inaccurate context memory. For the interaction between encoding context and context memory, we observed increased activation for egocentric remembered items in the bilateral and medial frontal cortex, the BG and the left parietal and temporal lobe	Memories of social interactions are biased to be remembered egocentrically Self-referential encoding processes reflected in increased frontal activation and decreased hippocampal activation might be the basis of correct item but false context memory of social interactions
Villatte M, Monestès JL, McHugh L, Freixa i Baqué E, Loas G. (2010). Adopting the perspective of another in belief attribution: Contribution of relational frame theory to the understanding of impairments in schizophrenia. J. Behav. Ther. and Exp. Psychiat. 41 125-134	Participants: Non-clinical social anhedonia participants=30; schizophrenia patients=15 A task consisting of attributing a belief to another or to the self was employed	In comparison to two control groups, both experimental groups showed significant poorer performance when adopting the perspective of another	These results constitute important indications to target specific relational repertoires when attempting to remediate impairments in mental states attribution linked to schizophrenia
Folley BS, Astur R, Jagannathan K, Calhoun VD, Pearlson GD. (2010). Anomalous neural circuit function in schizophrenia during a VMWT. NeuroImage 49 (2010) 3373-3384	Participants: Schizophrenia patients=34 and normal controls=28 fMRI scanning during a block design VMWT using hidden and visible platform conditions. Independent components analysis was used to deconstruct neural contributions to hidden and visible platform conditions for patients and controls. We also examined performance variables, voxel-based morphometry and hippocampal subparcellation and regional bold variation	Patients exhibited impaired performance on the hidden and visible conditions of the task, related to negative symptom severity. While controls showed coupling between neural circuits, regional neuroanatomy and behavior, patients activated different task-related neural circuits, not associated with appropriate regional neuroanatomy. GLM analysis elucidated several comparable regions, with the exception of the hippocampus. Independent component analysis identified five neural circuits. Mesial temporal lobe regions, including the hippocampus, were consistently task-related across conditions and groups	Frontal, striatal and parietal circuits were recruited preferentially during the visible condition for patients, while frontal and temporal lobe regions were more saliently recruited by controls during the hidden platform condition. Gray matter concentrations and bold signal in hippocampal subregions were associated with task performance in controls but not patients Inefficient allocentric learning and memory in patients may be related to an inability to recruit appropriate task-dependent neural circuits
Weniger G, Irle E. (2008). Allocentric memory impaired and egocentric memory intact as assessed by virtual reality in recent-onset schizophrenia. schizophrenia research 101 (2008) 201-209	Participants: Schizophrenia patients=25 subjects with recent-onset; normal controls=25 Two virtual reality tasks affording the navigation and learning of a virtual park (allocentric memory) and a virtual maze (egocentric memory)	Schizophrenia subjects-significantly impaired in learning the virtual park (allocentric memory). However, schizophrenia subjects were as able as control subjects to learn the virtual maze. Stronger disorganized symptoms of schizophrenia subjects were significantly related to more errors on the virtual maze (egocentric memory)	Egocentric spatial learning adds to the many other implicit cognitive skills being largely preserved in schizophrenia. Possibly, the more global neural network supporting egocentric spatial learning is less affected than the declarative hippocampal memory system in early stages of schizophrenia and may offer opportunities for compensation in the presence of focal deficits

(*Continued*)

Table 1: (Continued)

Authors, year and article	Methodology	Results	Conclusions
Halari R, Mehrotra R, Sharma T, Ng V, Kumari V. (2006). Cognitive impairment but preservation of sexual dimorphism in cognitive abilities in chronic schizophrenia. Psychiatry Research 141, 129-139	Participants: Schizophrenia-Men (*n*=22) and women (*n*=21) and healthy controls men- (*n*=21) and women (*n*=21) The cognitive battery comprising tests of spatial (mental rotation, computerized version of the Benton judgment of line orientation) and verbal abilities (phonological and semantic fluency)	A series of multivariate analyses showed that the patient group performed worse than controls on all the cognitive tasks. Cognitive sexual dimorphism on all spatial tasks favoring men and verbal tasks favoring women remained. Within the patient sample, correlational data demonstrated that earlier age at onset of illness related to poorer spatial performance	Normal sexual dimorphism is undisturbed on both spatial and verbal tasks by the schizophrenia disease process
Sorkin A, Weinshall D, Modai I, Peled A. (2006). Improving the accuracy of the diagnosis of schizophrenia by means of virtual reality. Am J Psychiatry; 163:512-520	Participants: Schizophrenic patients=39 and healthy controls=21 Computerized navigation virtual maze task used to study sensory integration within working memory. The simulated journey consisted of a series of rooms, each of which included three doors. Each door was characterized by three features (color, shape and sound) and a single combination of features – the door-opening rule – was correct. Subjects had to learn the rule and use it. The participants were Subject performance profile: Error scores, response time, navigation ability and strategy	A classification procedure based on the subjects' performance profile correctly predicted 85% of the schizophrenic patients (and all of the comparison subjects). Several performance variables showed significant correlations with scores on a standard diagnostic measure (positive and negative syndrome scale), suggesting potential use of these measurements for the diagnosis of schizophrenia. On the other hand, the patients did not show unusual repetition of response despite stimulus cessation (called "perseveration" in classical studies of schizophrenia), which is a common symptom of the disease. This deficit appeared only when the subjects did not receive proper explanation of the task	The ability to study multimodal performance simultaneously by using virtual reality technology opens new possibilities for the diagnosis of schizophrenia with objective procedures
Hanlon FM, Weisend MP, Hamilton DA, Jones AP, Thoma RJ, Huang M, Martin K, Yeo RA, Miller GA, Cañive JM. (2006). Impairment on the hippocampal-dependent VMWT in schizophrenia. Schizophrenia Research 87; 67-80	Participants: 44 male subjects; Schizophrenia patients=22; normal controls=22 Two versions of the VMWT: A hippocampal-dependent hidden-platform version, relying on allocentric navigational abilities and a non-hippocampal-dependent visible-platform version, relying on cued-navigational abilities	Patients traveled further and took longer to find the hidden platform (the hippocampal dependent version that relies on allocentric navigational abilities) over training blocks and spent less time in the correct quadrant during a probe trial. There was no deficit in the visible-platform condition	These findings identify a behavioral impairment on a hippocampal-dependent task in schizophrenia and support using the MWT in testing animal models of schizophrenia
De Vignemont F, Zalla T, Posada A, Louvegnez A, Koenig O, Georgieff N, Franck N. (2006). Mental rotation in schizophrenia. Consciousness and Cognition 15; 295-309	Participants: Schizophrenia patients=13 (males=12; female=1) On antipsychotic medication; normal controls=13 Computerized administration of Birmingham Object Recognition Battery (6 tests) Clinical interview: SAPS and SANS	In schizophrenic patients, reaction time varied as a function of the angular disparity of the stimuli. They were significantly slower and less accurate. Interestingly, patients suffering from hallucinations made significantly more errors than non-hallucinatory patients	These latter results in terms of deficit of the forward model. We emphasized the necessity to distinguish different levels of action, more or less impaired in schizophrenia
Langdon R, Coltheart M. (2001). Visual perspective-taking and schizotypy: Evidence for a simulation-based account of mentalizing in normal adults. Cognition 82, 1-26	Participants: Normal controls=40; males-14; females=26 (psychology students, age 18-49 years) Visual perspective tasks: Item questions (asking locations of array-features) and appearance questions (asking how an array appears from another perspective) were presented with both viewer-rotation instructions (asking subjects to imagine moving themselves relative to an array) and array-rotation instructions (asking subjects to imagine rotating an array relative to their fixed viewpoint) Schizotypal personality questionnaire	Evidence of disturbed visual perspective-taking in normal adults with higher score on schizotypy and who are known to be relatively poor mentalizers High-schizotypal adults and low-schizotypal adults did not differ in their ability to judge item questions High-schizotypal adults performed more poorly than low-schizotypal adults in judging appearance questions under viewer-rotation instructions and performed better than low-schizotypal adults in judging appearance questions under array-rotation instructions	Poor mentalizing in normal adults is better understood as an impairment of perspective-taking (visual and/or cognitive) Introducing the concept of allocentric simulation to explain the functional basis of this perspective-taking impairment

(*Continued*)

Table 1: (Continued)

Authors, year and article	Methodology	Results	Conclusions
Langdon R, Coltheart M, Ward PB, Catts SV. (2001). Visual and cognitive perspective-taking impairments in schizophrenia: A failure of allocentric simulation? Cognitive Neuropsychiatry, 6:4, 241-269	Participants: Schizophrenia patients-32 (2 inpatients and 30 out-patients) and healthy controls-24 mature-age psychology students Visual perspective tasks: Item questions (asking locations of array-features) and appearance questions (asking how an array appears from another perspective) were presented with both viewer-rotation instructions (asking subjects to imagine moving themselves relative to an array) and array-rotation instructions (asking subjects to imagine rotating an array relative to their fixed viewpoint) Clinical interview: SAPS and SANS	This study tested that prediction by investigating visual perspective-taking in patients and healthy controls, known to differ in mentalizing ability. Patients performed as well as controls on item questions (regardless of instruction) and appearance questions under array-rotation instructions, patients made more egocentric errors than controls judging appearance questions under viewer-rotation instructions	Evidences count against traditional theory-of-mind accounts and suggest instead that poor mentalizing in schizophrenia is better understood as an impairment of perspective-taking

RT – Reaction time; DRT – Delayed response task; WM – Working memory; VMWT – Virtual Morris water task; GLM - General linear model; SAPS – Scale for assessment of positive symptoms; SANS – Scale for assessment of negative symptoms; ACC – Anterior cingulate cortex; BG – Basal ganglia; *Summaries of the abstracts of these research publications

Deficits in source monitoring and clinical symptomatology

One crucial cognitive deficit in schizophrenia patients could be their inability to monitor their own actions[42,43] and differentiating between imagination and reality.[44,45] Several studies report a general impairment of action monitoring in schizophrenia patients.[42,43,46,47] Evidences suggest that errors of source memory, free recall and recognition are positively correlated with positive symptoms and inversely correlated with negative symptoms reflecting emotional and social deficits.[48] Additional support towards this paradigm for understanding the pathogenetic basis for hallucinations in schizophrenia comes from literature on “source monitoring,” which refers to the ability to remember the origin of information.[49] Positive symptoms such as hallucinations may thus be interpreted as a deficit of self-monitoring associated with a kind of over-activity of mental imagery: Patients’ inner life is particularly intense and vivid and the patients are unable to realize that their mental images come from themselves rather from the external world.[50,51] This function is impaired in patients with schizophrenia and underlies several positive[52,53] and negative symptoms see.[48] It has been proposed that episodic memory and source monitoring are closely interlinked so much so that brain structures implicated in the former (for the encoding process, storage and retrieval of memory trace) are also associated with the latter[54] vouching for a central role of the hippocampus in the entire process. Further, source monitoring has been shown to be associated with hippocampal activation (in storage of source memory,[55] correct retrieval of source information[56] and external source monitoring i.e., identifying and remembering external sources-persons from whom information is acquired).[57] The three-component model-the binding of the item and context model[58,59] – is in tune with these observations and this model postulates that different functions are performed by the sub-structures of the hippocampal system. The perirhinal cortex processes item information, the parahippocampal cortex processes context information and the hippocampus binds the item and the context. This has been partially supported by recent evidences. The perirhinal cortex is indeed related to the processing of status (i.e., familiar or novel) of item information and the hippocampus associated to the retrieval of the relationship between items and their sources. However, it is probable that the hippocampus plays roles in both the recognition processes.[57] Furthermore, recent evidences implicate sub-regions within MTL,[57] pre-frontal cortex (PFC) and posterior cortex in representing and/or processing source features see[60] for details. Taken together, these evidences indicate that source monitoring deficits are the outcome of a hippocampal dysfunction-binding failure between the item and its respective context. Further this deficit in source monitoring mediates positive and negative symptoms of schizophrenia.

Delusions and hallucinations

Perception[61] and memory[62] are substantially constructive and our perception and recollections are strongly influenced by our prior experiences and expectancies. Our memories are subject to experience-dependent biases[63] and are highly mutable by nature.[64,65] This can be explained by the discrepancy-attribution hypothesis.[66,67] Both true and false familiarities are experienced when a comparison between expectations and outcomes within a processing episode elicits a surprise or prediction error. This motivates the person to seek an explanation, attributing the surprise to some plausible source in the current environment or to similar features in the past.[68] This kind of processing errors seems to involve aberrant perceptions (representation of context and/or content of one's environment) and/or attributions (meta-representations) mediated by declarative memory system (semantic and episodic). These processes seem to explain reality alteration underlying positive symptoms of schizophrenia, such as hallucinations and delusions, which involve gross alterations in the experience of reality. It is also conceived that the drive to explain away odd experiences, in schizophrenia and related conditions, can result in delusion formation.[69,70] This then sculpts and vitiates future experiences and attributions.[71-73] Recent studies have demonstrated an association between illusory memories, perceptual aberrations and odd beliefs.[68] Structural abnormality in hippocampus (reduction in the dentate gyrus) has been reported to increase the prevalence of illusory pattern completion and reduce discrimination between present and past events as stored in memory.[16] Evidences indicate inappropriate engagement of the right PFC (pre-frontal cortex) in mediating false memory formation, odd perceptions and unusual beliefs by signaling inappropriate mismatches between expectancy and experience which engage new learning.[74] Such interactions among neural networks leads to the formation of novel associations, which may have adaptive advantages,[75,76] but in its extreme form, hyperactivity of such associations ultimately leads to psychotic symptoms.[68] Furthermore, role of the hippocampus in new learning and real time association formations hippocampal damage results in the inability to recall recent events; for models see;[77] the hippocampus as a possible mediator of accessing previously stored rigid scene information to permit its flexible engagement[78] and construction of mental images[79] lends it a more central role in mediating aberrant associations, which manifest as positive symptoms of delusions and hallucinations.

Deficits in context processing

The processing of stimuli in a spatiotemporal context is dependent on the hippocampus. The hippocampus is implicated in conjunctive coding of stimulus features.[80,81] This includes conjunctions between object identity and position[82-84] and temporal conjunctions.[85,86] Context processing deficits in schizophrenia are manifested as severe context insensitivity, associated with impairments in choosing subordinate over dominant responses based on context cues, high false alarm rates in object recognition and deficient retrieval of context information in source monitoring.[87] These deficits could be resulting from reduced connectivity in parahippocampal regions, leading to the formation of abnormal episodic representations, with poor binding of the object and spatial features and a predominance of object information, at the expense of spatial information. This bias causes the object cues to tend to override the context cues, which place only weak constraints on MTL processing. In addition, the poorly integrated entorhinal representations result in reduced retrieval during use of the paradigms that strongly draw on links between the different aspects of an episode, for instance source monitoring and free recall.[87,88] Further the reduced entorhinohippocampal connectivity leads to increased representational overlap in the system. This implies that some patterns are not stored in a distinctive episodic representation and cannot be retrieved at all. On the other hand, increased overlap enhances formation of so-called spurious attractors: Strong patterns-connected to many inputs and outputs. Such patterns may get inappropriately activated; especially in paradigms that enhance formation of overlapping representations through the presentation of similar stimuli (e.g., source monitoring).[87] It has been suggested that context processing and episodic memory share same underlying binding deficit.[87] Space and time allow us to determine "when and where" of our recent memories and are thus crucial to episodic memory formation. Recent study suggests hippocampal activation in both spatial and temporal order processing, at least in the context of navigation while parahippocampal and PFC, play largely distinct roles in spatial and temporal order processing, respectively.[89] Taken together, these evidences support the role of hippocampal system in binding deficits that lead to faulty context processing and construing of false memories or aberrant episodic memory snippets; signifying a deficiency probably explainable by cognitive mapping theory of hippocampal function.

Impairments of social cognition: False memory, empathy and theory of mind

Human relationships are contingent on the memories of social interactions. Nonverbal cues (such as gesture, body orientation and eye gaze) are essential in social situations: They allow an individual to recognize that he or she is being directly addressed e.g.,[90] and consequently define the egocentric or allocentric context in which communication occurs. The ability to recall if a past conversation occurred in an egocentric or allocentric context is undoubtedly important for maintaining interpersonal relationships and information about the neural processes responsible for encoding the context of a social communication are inadequate. Past research indicates that left inferior frontal, posterior temporal, premotor and hippocampal brain regions are involved in creating memories of speech and gesture communication.[91] False recognition is a phenomenon whereby people sometimes believe they recognize things that they have never actually encountered, for example, confusing a stranger with an old acquaintance. This often occurs in everyday situations. It has been reported that memories of social interactions are egocentrically biased. Further at the neural level, activations of specific cortical and hippocampal regions during encoding have been reflective of accurate and inaccurate recollections of social contextual information. Activity in the right hippocampus was associated with successful encoding of speech, gesture and their social context. This supports the hippocampal theories of relational associative memories.[92] Though these findings come from studies on healthy participants and specific studies probing false recognition or false contextual memories of social interactions have not been reported for schizophrenia patients; yet it is quite conceivable that pronounced allocentric deficits[93] together with hippocampal abnormalities could be contributing to the outstanding deficits in encoding social contexts and forming false memories of social interactions among schizophrenia patients.

A major aspect of "Empathy" involves adopting psychological perspective of another person and is related to the ability of taking another person's visuo-spatial perspective. Some studies have reported the role of visuospatial abilities in cognitive and affective empathy in schizotypy and schizophrenia patients.[94,95] Lower self-reported cognitive, but not affective, empathy has been reported in individuals diagnosed with schizophrenia[95] and impaired theory of mind has been extensively documented in patients with schizophrenia see[96] for review. These deficits co-occur in schizophrenia and are mediated through shared neural pathways; as in, there is evidence for parietal cortex and the temporoparietal junction being involved in both empathy and visuospatial processing.[97-99] Many studies have reported both reduced empathy[95,96,100,101] and subtle differences in spatial attention[102-106] and visuospatial transformation ability[107,108] in schizophrenia patients and among those found high in schizophrenia-like traits. These findings thus indicate that visuospatial representational deficits (in all probability involving hippocampal dysfunction) interfere with social representation and social perspective taking that are subsumed under empathy.

Theory of mind refers to the ability to attribute mental states like beliefs, intents, desires, knowledge, pretension, etc., to self and to others.[109] According to Langdon *et al*.[93] and Langdon and Coltheart[112], "theory of mind" impairments in mental states attribution in schizophrenia spectrum disorders are due to inefficient abilities to reconstruct another first-person experience (allocentric simulation). A study done by Langdon *et al*.[93,112] found that ability to take another person's perspective is impaired in schizophrenia patients. In relational frame theory terms, the ability to respond in accordance with the deictic frame of I-YOU would be impaired when additional relational responding is necessitated by the inclusion of the IF-THEN frame (i.e., "If I were you then I would believe that"). Several studies have demonstrated that schizophrenia patients perform less accurate than controls when required to reverse the frame of I-YOU (attribution of belief to another) and/or to respond in accordance with the frame of logical note (attribution of a false-belief).[110] These growing literature on mental states attribution in schizophrenia shows that patients with schizophrenia present a deficit in attributing false-belief.[96,111] It also supports the idea that these patients have an important disability of adopting another's point of view.[93] It has been shown that hippocampus mediates errors in construction of mental images[79] and may thus reflect inefficient abilities to reconstruct another first-person experience (allocentric simulation) underlying deficits of false-belief attribution.

Some studies have reported disturbed visuo-spatial perspective taking in normal adults with high scores on self-reported measures of schizotypy.[112] Since schizotypy refers to the personality traits that are related to symptoms of schizophrenia and imply a latent liability for the disorder,[94] such results are insightful. Those high on schizotypy are poor mentalizers, hence it is highly suggestive that poor mentalizing among normal adults may be better conceived as an impairment of perspective taking (visual and/or cognitive).[112]

Disorganization symptoms and excessive egocentricity processing in schizophrenia

Differential symptom picture of schizophrenia is associated with varying visuo-spatial performance profile among patients. Schizophrenia subjects with stronger disorganization symptoms have been found to perform poorly on egocentric processing tasks than their counterparts with lesser disorganization symptom.[94,113] Thakkar and Park[94] reported that greater accuracy on the perspective-taking task in the condition that required a self–other transformation was associated with increased positive syndrome schizotypy, suggesting that those individuals who tend to have anomalous cognitive and perceptual experiences are better at inhibiting their own perspective. Enhanced egocentric manipulations may be just as problematic as an inability to imagine another person's viewpoint and either way lead to reduced empathic understanding. This data when taken together with evidences supporting allocentric deficit hypothesis of schizophrenia[93] indicate that-in general, schizophrenia patients demonstrate allocentric deficits; but those with pronounced cognitive and perceptual processing deficits are further impaired on mental representation. They may demonstrate lesser deficits on allocentric perspective taking task, but their corresponding poorer performance on cognitive empathy indicates more deteriorated mental representations of complex (like social) environments.

SYNTHESIZING THE COGNITIVE MAPPING DEFICITS IN SCHIZOPHRENIA

Several studies have reported that allocentric processing is impaired, but egocentric processing is preserved among schizophrenia patients.[113,114] Allocentric simulation hypothesis posits that pathological referencing in schizophrenia results from the difficulty in adopting a world-centered – inter-subjective – reference frame. In reiterating this hypothesis, experimental data has shown intact reaction time (RT) and learning rate during egocentric referencing among patients with schizophrenia. Interestingly, this study further reported "a certain improvement in RT associated with task progression in the stable allocentric (landmark-centered) condition in patients; though the correlation between RT and set did not reach statistical significance."[114] This partially preserved stable allocentric (landmark-centered) task related RT improvement in patients could reflect the possibility that the egocentric and stable allocentric (landmark-centered) conditions reinforce structural representations of a stable body position or a stable environment respectively and are thus relatively preserved. The RT during unstable allocentric (object-centered) referencing that depends on the transient intrinsic nature of the object the ball always changes its position in the task used by[114] thus shows no improvement over time. This evidence seems to support the notion that "task-specific mechanisms prominently contribute to visuospatial cognitive dysfunctions in schizophrenia."[115] Further another recent study demonstrated that the posterior superior parietal cortex/precuneus play an important role in allocentric representation while the hippocampus and interactions between the hippocampus and these parietal areas, are important for flexible utilization of these representations[78] implicating a more central role of the hippocampus in mediating allocentric processing. However it should be noted that parietal neocortex has been implicated in egocentric processing. Egocentric and allocentric process have been found to demonstrate an enormous amount of overlap of underlying neural circuits.[116-119]

In their translational study, Girard *et al*.[121] examined allocentric and egocentric memory for spatial locations and recent event memory (EM) and reference memory (RM) among schizophrenia patients using the Virtual water morris task employed in animal models (rats). RM refers to information that is important and invariant across several problems, like general task rules and procedures, whereas recent EM refers to a flexible and dynamic memory for context-specific information unique to trials within task problems like in delayed-(non) matching tasks. Schizophrenia patients demonstrated pronounced allocentric memory deficits for spatial location and RM; and egocentric memory for spatial location and recent EM were relatively preserved. These findings were consistent with previous research studies.[113] Somewhat weaker but consistent differences reported between EM versus RM deficit in schizophrenia patients are that cognitive mapping theories of hippocampal function may be more relevant than EM-RM distinctions among humans.[120] The associative memory deficit in schizophrenia is also consistent with hippocampus mediated impairment. These findings bridge the gaps between animal models and human studies and also establish hippocampal dysfunction as central deficit of this pattern.[121]

In their study with a very large sample size, Thakkar and Park (2010)[94] reported impaired maintenance and spared manipulation of representations in working memory (WM). They found that mental manipulation of visual stimuli was spared in sample of patients and they observed a well-replicated impairment in passive maintenance of the location of stimuli. Further they reported that patients were more accurate than controls on the allocentric mental rotation at the largest degree of rotation, which placed the greatest demand on mental manipulation. The counterintuitive nature of this finding can be explained on several grounds. One potential reason behind this discrepancy is that tasks that purport to index WM manipulation ability do not isolate the component processes of WM.[94] Maintenance and manipulation are two interdependent but dissociable components of WM and thus it is possible to have one relatively preserved while the other is impaired as reported in these findings. The observation made here is novel and demands further investigation. This also suggests that a pocket of cognitive function might be enhanced in schizophrenia patients. Another possibility behind these observations could be-brain's compensatory mechanisms. Since the WM maintenance is impaired, the WM manipulation component could have been over exercised in everyday tasks and as a result of repeated usage, this feature could have led to a strengthened information processing pathway. As a result WM manipulation becomes enhanced among such patients. This finding favors our previously visited position on "a need for examining the task specific mechanisms that seem to make a prominent contribution to visuo-spatial cognitive dysfunction in schizophrenia."[115]

Several studies propose alternate explanation to these observed allocentric deficits. They propose that allocentric deficits might be the result of excessive egocentric referencing or inability inhibit one's own perspective; this proposition is in tandem with the disruption in visuo-spatial information processing and perception observed in patients with schizophrenia.[94,114,122-125] Recently allocentric processing deficits have been given more central concern. In these studies, it was demonstrated that perspective-taking difficulty (as reflected by performance deficits on theory of mind tasks with "indirect instructions") impairs insight in schizophrenia. Further Lysaker *et al*.[127] showed that reduced ability to organize and interpret ambiguous stimuli, to differentiate between self and other's perspectives and to formulate logical accounts of behavior and social exchange predicted poorer awareness of psychiatric symptoms among schizophrenia patients. They further suggested that replication of these results would indicate that in order to achieve awareness of their condition; patients with schizophrenia may need assistance with making sense of their environment and organizing their experience of the illness. These observations imply that, non-egocentric referencing, as a higher order cognitive function, is associated with decentration, functionality and disease outcome[126,127] and plays a crucial role in manifestation of schizophrenia.

Some useful evidence in this regard comes from "visuospatial perspective switch tasks." Schizophrenia patients demonstrate increased switch cost when switching from egocentric referencing to allocentric referencing but not vice-versa.[114] This finding is supported by research showing that switching towards a dominant (in case of schizophrenia patients'-egocentric) response requires greater effort than switching towards a less dominant (in case of schizophrenia patients'-allocentric) response.[128] The problem that patients with schizophrenia face is-undoing the inhibition for stimulus-response relation when switching egocentric to allocentric as the former is dominant in their case.[114] These findings suggest allocentric deficits as a stable feature of schizophrenia and give plausible explanations underneath these deficits.

In summary, recent evidences are expanding the scope of the cognitive mapping theory of hippocampal function. In their seminal work, O'Keefe and Nadel proposed role of hippocampus in encoding spatial relationship (right hippocampi), semantic maps (left hippocampi), integration of temporal information from frontal lobe and allocentric processing. We examined how emerging evidences point towards a broader role of hippocampus by indicating its role in source monitoring, false memories resulting for aberrant perception and attribution, contextual binding and social cognition (empathy and meta-representative abilities like Theory of mind). Furthermore, allocentric processing deficits have been found central to information processing in schizophrenia. Recent evidences indicate that circuitry for allocentric processing is not limited to hippocampal system. Both egocentric and allocentric processing share a remarkable overlap of neural circuitry e.g., regions of parietal lobe have been implicated in both egocentric[33] and allocentric processing).[78] Thus, these evidences merit a closer scrutiny and further investigations for concrete conclusions are drawn.

CRITIQUE ON COGNITIVE MAPPING THEORY FOR SCHIZOPHRENIA PATHOGENESIS

The critical limitation arise from the fact that current evidences indicate complementary roles of allocentric and egocentric representations of space depending on the number of locations/landmarks to be remembered and the size and familiarity of the environment.[129] Further egocentric and allocentric referencing have been found to closely interrelate on the behavioral and neuronal level. We have discussed evidences from studies of spatial WM in favor of our position, but WM being a constructive and compartmentalized concept, is yet to be studied in terms of its components to yield definitive conclusions. Further, discrepancies in RT while performing visuospatial perspective oriented tasks have raised some concerns about the nature of allocentric and egocentric processing (in relation to task complexity). We review these findings and discuss the challenge they posit to our proposition.

The egocentric and allocentric referencing are not entirely independent of each other. On the neural level, they share a fronto-parietal network with an overlap of up to 88%.[116-119] Egocentric tasks recruit posterior parietal and frontal premotor areas. In addition to these regions, allocentric processing also activates occipito-temporal and retrosplenial cortices. A study by Committeri *et al*.[116] contrasted cortical activity during viewer-centered, object-centered and landmark-centered referencing with a non-spatial condition. Egocentric referencing (viewer-centered) activated the dorsal stream and frontal areas. The unstable (object-centered) and stable (landmark-centered) allocentric conditions were associated with ventrolateral and medial occipito-temporal activation, respectively. Interestingly, the parahippocampal gyri were bilaterally activated exclusively in the landmark-centered condition, where subjects had to consider the surrounding's geometrical structure as a spatial reference. In fact, parahippocampal activity has been associated with contextual retrieval of extra-personal global structures from memory.[130,131] Further, the "two-system models" propose that transient "ego" and more sustained "allo" representations are processed in parallel, with preferential use of one system likely depending on self-motion, environmental structure and experience-dependent factors.[131] In addition, the multiple memory systems studied are relative versus mutually exclusive and may compete or support each other.[129,132,133] This data presents allocentric and egocentric processing as non-exclusive and dependent phenomena and complicates our claim of one being impaired and other preserved in patients with schizophrenia.

Finally, most of the current research has successfully explained positive symptoms of schizophrenia through deficits of source monitoring, meta-representation and context binding. Research evidences exploring the role of hippocampal pathology and allocentric deficits in relation to negative symptoms are too limited to indicate a conclusion.

SOME DIRECTIONS FOR FUTURE RESEARCH

There are some emerging issues that should be taken into consideration while interpreting current literature and these may play a crucial part in directing future research. One of them could be effects of medication. Studies on treatment naïve and treated patients are required to guide emerging findings and address discrepancies. Antipsychotics are expected to interfere with visuomotor learning; however the study by Weniger and Irle found no relationship between antipsychotic dosage and allocentric or egocentric task performance. Further clinical studies have shown that among schizophrenia patients, atypical antipsychotics have favorable effects on cognitive and motor functions.[134,135] Some studies have reported a protective effect of olanzapine on implicit but not explicit visual learning in schizophrenia subjects.[136,137] This could possibly give psychopharmacological explanation behind preserved egocentric abilities in schizophrenia patients. However, such findings, in absence of longitudinal studies reflecting on visuospatial abilities at different stages of the schizophrenia disease process, may at best be speculative and demand further investigation. Furthermore, in future, studies should also show whether preserved egocentric memory in recent-onset schizophrenia is a feature of the disease or rather reflects the beneficial properties of some or all atypical antipsychotic drugs.[113]

CONCLUSIONS

In this review, we have summarized studies supporting a consistent pattern of mapping deficits among patients with schizophrenia. These observations support the view that deficits in mental representations and mental constructions that are vital for cognitive mapping are among the critically impaired functions in schizophrenia. Visuospatial processing deficits and hippocampal abnormalities are robust and could possibly be a trait-marker for this disorder. A cognitive mapping viewpoint, drawn from these premises, can explain a wide range of deficits characterizing the schizophrenia disease process. Positive symptoms such as delusion, illusion and hallucinations in particular along with higher cognitive processes of empathy, false-belief attribution and other forms of meta-representation can be all explained by a single principle. Such theoretical unity facilitates comprehensive framework for conceptualizing the diversity of deficits expressed in schizophrenia disease process. In this light, unsurprisingly, research on visuospatial processing, meta-representation abilities and similar cognitive mapping constructs are catching momentum.

Although presented as intriguing, a lot remains to be desired from current research paradigms. Longitudinal studies with large sample size (to allow statistical rigor), differentiating between medicated and treatment naïve participants with positive and negative symptom picture over different phases would allow more clarity. Further, studies testing for allocentric deficits' specificity to schizophrenia are inadequate. Future researches need to focus on relatives of patients with schizophrenia and prodromal individuals; this will help determine if visuospatial impairments may serve as phenomenological markers for the disease. Future studies should also explore further possibilities of recruiting virtual reality paradigms in investigating allocentric and egocentric processing as they seem promising in providing-translational comparisons with animal models, 3D first person environment for simulating real-life like experimental contexts and are well tolerated by patients. Though research findings are not yet adequate in establishing schizophrenia as a disorder of cognitive mapping, this proposition may prove to be a comprehensive framework on further deliberation and deserves disciplined attention.

ACKNOWLEDGMENT

AB, SMA and SVK are supported by the welcome trust/DBT India Alliance. This work is supported by the Welcome Trust/DBT India Alliance Senior Fellowship Research Grant to GV (500236/Z/11/Z).

REFERENCES

1. Nuechterlein KH, Barch DM, Gold JM, Goldberg TE, Green

MF, Heaton RK. Identification of separable cognitive factors in schizophrenia. Schizophr Res 2004;72:29-39.
2. Barch DM, Ceaser A. Cognition in schizophrenia: Core psychological and neural mechanisms. Trends Cogn Sci 2012;16:27-34.
3. Cohen JD, Barch DM, Carter C, Servan-Schreiber D. Context-processing deficits in schizophrenia: Converging evidence from three theoretically motivated cognitive tasks. J Abnorm Psychol 1999;108:120-33.
4. Kuperberg G, Heckers S. Schizophrenia and cognitive function. Curr Opin Neurobiol 2000;10:205-10.
5. Brown AS. Prenatal infection as a risk factor for schizophrenia. Schizophr Bull 2006;32:200-2.
6. Ashdown H, Poole S, Boksa P, Luheshi GN. Interleukin-1 receptor antagonist as a modulator of gender differences in the febrile response to lipopolysaccharide in rats. Am J Physiol Regul Integr Comp Physiol 2007;292:R1667-74.
7. Harrison PJ. The hippocampus in schizophrenia: A review of the neuropathological evidence and its pathophysiological implications. Psychopharmacology (Berl) 2004;174:151-62.
8. Heckers S. Neuroimaging studies of the hippocampus in schizophrenia. Hippocampus 2001;11:520-8.
9. Nelson MD, Saykin AJ, Flashman LA, Riordan HJ. Hippocampal volume reduction in schizophrenia as assessed by magnetic resonance imaging: A meta-analytic study. Arch Gen Psychiatry 1998;55:433-40.
10. Vita A, De Peri L, Silenzi C, Dieci M. Brain morphology in first-episode schizophrenia: A meta-analysis of quantitative magnetic resonance imaging studies. Schizophr Res 2006;82:75-88.
11. Wright IC, Rabe-Hesketh S, Mellers J, Bullmore ET. Testing for laterality differences in regional brain volumes. Arch Gen Psychiatry 2000;57:511-2.
12. Goel RS, Verma NS, Mullan SA, Ashdown AC. Detection of filarial antigen and antibody in serum and hydrocele fluid of 100 patients of hydrocele. Int J Urol 2006;13:565-8.
13. Christensen BK, Bilder RM. Dual cytoarchitectonic trends: An evolutionary model of frontal lobe functioning and its application to psychopathology. Can J Psychiatry 2000;45:247-56.
14. Grace AA. Gating of information flow within the limbic system and the pathophysiology of schizophrenia. Brain Res Brain Res Rev 2000;31:330-41.
15. Ashdown H, Dumont Y, Ng M, Poole S, Boksa P, Luheshi GN. The role of cytokines in mediating effects of prenatal infection on the fetus: Implications for schizophrenia. Mol Psychiatry 2006;11:47-55.
16. Tamminga CA, Stan AD, Wagner AD. The hippocampal formation in schizophrenia. Am J Psychiatry 2010;167:1178-93.
17. Burgess N. Spatial cognition and the brain. Ann N Y Acad Sci 2008;1124:77-97.
18. Neggers SF, Van der Lubbe RH, Ramsey NF, Postma A. Interactions between ego- and allocentric neuronal representations of space. Neuroimage 2006;31:320-31.
19. de Vignemont F. Frames of reference in social cognition. Q J Exp Psychol (Hove) 2008;61:90-100.
20. Frith U, de Vignemont F. Egocentrism, allocentrism, and Asperger syndrome. Conscious Cogn 2005;14:719-38.
21. Aguirre GK, Detre JA, Alsop DC, D'Esposito M. The parahippocampus subserves topographical learning in man. Cereb Cortex 1996;6:823-9.
22. Aguirre GK, D'Esposito M. Environmental knowledge is subserved by separable dorsal/ventral neural areas. J Neurosci 1997;17:2512-8.
23. Burgess N, Maguire EA, Spiers HJ, O'Keefe J. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. Neuroimage 2001;14:439-53.
24. Epstein R, Graham KS, Downing PE. Viewpoint-specific scene representations in human parahippocampal cortex. Neuron 2003;37:865-76.
25. Maguire EA, Frackowiak RS, Frith CD. Recalling routes around london: Activation of the right hippocampus in taxi drivers. J Neurosci 1997;17:7103-10.
26. Crane J, Milner B. What went where? Impaired object-location learning in patients with right hippocampal lesions. Hippocampus 2005;15:216-31.
27. Gilbert PE, Kesner RP. Role of the rodent hippocampus in paired-associate learning involving associations between a stimulus and a spatial location. Behav Neurosci 2002;116:63-71.
28. Parkinson JK, Murray EA, Mishkin M. A selective mnemonic role for the hippocampus in monkeys: Memory for the location of objects. J Neurosci 1988;8:4159-67.
29. Rolls ET. A theory of hippocampal function in memory. Hippocampus 1996;6:601-20.
30. Berthoz A. The role of inhibition in the hierarchical gating of executed and imagined movements. Brain Res Cogn Brain Res 1996;3:101-13.
31. Berthoz A. Parietal and hippocampal contribution to topokinetic and topographic memory. Philos Trans R Soc Lond B Biol Sci 1997;352:1437-48.
32. Burgess N, Maguire EA, O'Keefe J. The human hippocampus and spatial and episodic memory. Neuron 2002;35:625-41.
33. O'Keefe J, Nadel L. Précis of O'Keefe & Nadel's the hippocampus as a cognitive map. Behav Brain Sci 1979;2:487-94.
34. Squire LR, Zola-Morgan S. The medial temporal lobe memory system. Science 1991;253:1380-6.
35. Cohen NJ, Eichenbaum H. Memory Amnesia and the Hippocampal System. Cambridge, MA: MIT Press; 1993.
36. O'Keefe J, Nadel L. The Hippocampus as a Cognitive Map. Great Britain: Oxford Clarendon Press; 1978.
37. Squire LR. Memory and Brain. New York: Oxford University Press; 1987.
38. Cohen NJ, Eichenbaum H. Memory Amnesia and the Hippocampal System. United States of America: Mit Press;1995.
39. Rudy JW, Sutherland RJ. Configural association theory and the hippocampal formation: An appraisal and reconfiguration. Hippocampus 1995;5:375-89.
40. Sutherland RJ, Rudy JW. Configurational association theory: The role of the hippocampal formation in learning, memory, and amnesia. Psychobiology 1989;17:129-44.
41. Hanlon FM, Weisend MP, Hamilton DA, Jones AP, Thoma RJ, Huang M, *et al*. Impairment on the hippocampal-dependent virtual Morris water task in schizophrenia. Schizophr Res 2006;87:67-80.
42. Frith CD. The Cognitive Neuropsychology of Schizophrenia. Hove: Herblaum; 1992.
43. Georgieff N, Jeannerod M. Beyond consciousness of external reality: A "who" system for consciousness of action and self-consciousness. Conscious Cogn 1998;7:465-77.
44. Bentall RP, Baker GA, Havers S. Reality monitoring and psychotic hallucinations. Br J Clin Psychol 1991;30 (Pt 3):213-22.
45. Brébion G, Amador X, David A, Malaspina D, Sharif Z, Gorman JM. Positive symptomatology and source-monitoring failure in schizophrenia – An analysis of symptom-specific effects. Psychiatry Res 2000;95:119-31.
46. Daprati E, Franck N, Georgieff N, Proust J, Pacherie E, Dalery J, *et al*. Looking for the agent: An investigation into consciousness of action and self-consciousness in schizophrenic patients. Cognition 1997;65:71-86.

47. Franck N, Farrer C, Georgieff N, Marie-Cardine M, Daléry J, d'Amato T, *et al*. Defective recognition of one's own actions in patients with schizophrenia. Am J Psychiatry 2001;158:454-9.
48. Brébion G, Gorman JM, Amador X, Malaspina D, Sharif Z. Source monitoring impairments in schizophrenia: Characterisation and associations with positive and negative symptomatology. Psychiatry Res 2002;112:27-39.
49. Johnson MK, Hashtroudi S, Lindsay DS. Source monitoring. Psychol Bull 1993;114:3-28.
50. Bentall RP, Slade PD. Reality testing and auditory hallucinations: A signal detection analysis. Br J Clin Psychol 1985;24:159-69.
51. Horowitz MJ. A cognitive model of hallucinations. Am J Psychiatry 1975;132:789-95.
52. Bentall RP. The illusion of reality: A review and integration of psychological research on hallucinations. Psychol Bull 1990;107:82-95.
53. Frith C. Functional imaging and cognitive abnormalities. Lancet 1995;346:615-20.
54. Ferchiou A, Schürhoff F, Bulzacka E, Mahbouli M, Leboyer M, Szöke A. Source monitoring: General presentation and review of literature in schizophrenia. Encephale 2010;36:326-33.
55. Davachi L, Mitchell JP, Wagner AD. Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. Proc Natl Acad Sci U S A 2003;100:2157-62.
56. Cansino S, Maquet P, Dolan RJ, Rugg MD. Brain activity underlying encoding and retrieval of source memory. Cereb Cortex 2002;12:1048-56.
57. Mugikura S, Abe N, Suzuki M, Ueno A, Higano S, Takahashi S, *et al*. Hippocampal activation associated with successful external source monitoring. Neuropsychologia 2010;48:1543-50.
58. Diana RA, Yonelinas AP, Ranganath C. Imaging recollection and familiarity in the medial temporal lobe: A three-component model. Trends Cogn Sci 2007;11:379-86.
59. Eichenbaum H, Yonelinas AP, Ranganath C. The medial temporal lobe and recognition memory. Annu Rev Neurosci 2007;30:123-52.
60. Mitchell KJ, Johnson MK. Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? Psychol Bull 2009;135:638-77.
61. Helmholtz Hv, Kahl R, editors. The facts of perception. In: Selected Writings of Herman von Helmholtz. Connecticut: Weslyan University Press; 1878/1971.
62. Schacter DL, Norman KA, Koutstaal W. The cognitive neuroscience of constructive memory. Annu Rev Psychol 1998;49:289-318.
63. Bartlett FC. Remembering. A Study in Experimental and Social Psychology. Cambridge: Cambridge University Press; 1932.
64. Estes WK. Processes of memory loss, recovery, and distortion. Psychol Rev 1997;104:148-69.
65. Loftus EF, Palmer JC. Reconstruction of automobile destruction: An example of the interaction between language and memory. J Verbal Learn Verbal Behav 1974;13:585-9.
66. Whittlesea BW, Williams LD. Why do strangers feel familiar, but friends don't? A discrepancy-attribution account of feelings of familiarity. Acta Psychol (Amst) 1998;98:141-65.
67. Whittlesea BW. False memory and the discrepancy-attribution hypothesis: The prototype-familiarity illusion. J Exp Psychol Gen 2002;131:96-115.
68. Corlett PR, Simons JS, Pigott JS, Gardner JM, Murray GK, Krystal JH, *et al*. Illusions and delusions: Relating experimentally-induced false memories to anomalous experiences and ideas. Front Behav Neurosci 2009;3:53.
69. Maher BA. Delusional thinking and perceptual disorder. J Individ Psychol 1974;30:98-113.
70. Kapur S. Psychosis as a state of aberrant salience: A framework linking biology, phenomenology, and pharmacology in schizophrenia. Am J Psychiatry 2003;160:13-23.
71. Jaspers K. General Psychopathology. Manchester: Manchester University Press; 1963.
72. Pally R. The predicting brain: Unconscious repetition, conscious reflection and therapeutic change. Int J Psychoanal 2007;88(Pt 4):861-81.
73. Corlett PR, Murray GK, Honey GD, Aitken MR, Shanks DR, Robbins TW, *et al*. Disrupted prediction-error signal in psychosis: Evidence for an associative account of delusions. Brain 2007;130 (Pt 9):2387-400.
74. Corlett PR, Honey GD, Fletcher PC. From prediction error to psychosis: Ketamine as a pharmacological model of delusions. J Psychopharmacol 2007;21:238-52.
75. Stevens A, Price J. Prophets, Cults and Madness. London, Gerald Duckworth & Co. Ltd 2000.
76. Avila M, Thaker G, Adami H. Genetic epidemiology and schizophrenia: A study of reproductive fitness. Schizophr Res 2001;47:233-41.
77. Bird CM, Burgess N. The hippocampus and memory: Insights from spatial processing. Nat Rev Neurosci 2008;9:182-94.
78. Zhang H, Ekstrom A. Human neural systems underlying rigid and flexible forms of allocentric spatial representation. Hum Brain Mapp 2013;34:1070-87.
79. Recce M, Harris KD. Memory for places: A navigational model in support of Marr's theory of hippocampal function. Hippocampus 1996;6:735-48.
80. O'Reilly RC, Rudy JW. Conjunctive representations in learning and memory: Principles of cortical and hippocampal function. Psychol Rev 2001;108:311-45.
81. Norman KA, O'Reilly RC. Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. Psychol Rev 2003;110:611-46.
82. Bachevalier J, Nemanic S. Memory for spatial location and object-place associations are differently processed by the hippocampal formation, parahippocampal areas TH/TF and perirhinal cortex. Hippocampus 2008;18:64-80.
83. Rolls ET, Xiang J, Franco L. Object, space, and object-space representations in the primate hippocampus. J Neurophysiol 2005;94:833-44.
84. Suzuki WA, Miller EK, Desimone R. Object and place memory in the macaque entorhinal cortex. J Neurophysiol 1997;78:1062-81.
85. Lisman JE, Talamini LM, Raffone A. Recall of memory sequences by interaction of the dentate and CA3: A revised model of the phase precession. Neural Netw 2005;18:1191-201.
86. Ergorul C, Eichenbaum H. Essential role of the hippocampal formation in rapid learning of higher-order sequential associations. J Neurosci 2006;26:4111-7.
87. Talamini LM, Meeter M. Dominance of objects over context in a mediotemporal lobe model of schizophrenia. PLoS One 2009;4:e6505.
88. Talamini LM, Meeter M, Elvevåg B, Murre JM, Goldberg TE. Reduced parahippocampal connectivity produces schizophrenia-like memory deficits in simulated neural circuits with reduced parahippocampal connectivity. Arch Gen Psychiatry 2005;62:485-93.

89. Ekstrom AD, Copara MS, Isham EA, Wang WC, Yonelinas AP. Dissociable networks involved in spatial and temporal order source retrieval. Neuroimage 2011;56:1803-13.
90. Özyürek A. Do speakers design their cospeech gestures for their addressees? The effects of addressee location on representational gestures. J Mem Lang 2002;46:688-704.
91. Straube B, Green A, Weis S, Chatterjee A, Kircher T. Memory effects of speech and gesture binding: Cortical and hippocampal activation in relation to subsequent memory performance. J Cogn Neurosci 2009;21:821-36.
92. Straube B, Green A, Chatterjee A, Kircher T. Encoding social interactions: The neural correlates of true and false memories. J Cogn Neurosci 2011;23:306-24.
93. Langdon R, Coltheart M, Ward PB, Catts SV. Visual and cognitive perspective-taking impairments in schizophrenia: A failure of allocentric simulation?. Cognitive Neuropsychiatry. 2001;6:241-69.
94. Thakkar KN, Park S. Empathy, schizotypy, and visuospatial transformations. Cogn Neuropsychiatry 2010;15:477-500.
95. Montag C, Heinz A, Kunz D, Gallinat J. Self-reported empathic abilities in schizophrenia. Schizophr Res 2007;92:85-9.
96. Brüne M. "Theory of mind" in schizophrenia: A review of the literature. Schizophr Bull 2005;31:21-42.
97. Decety J, Lamm C. The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to meta-cognition. Neuroscientist 2007;13:580-93.
98. Iacoboni M, Dapretto M. The mirror neuron system and the consequences of its dysfunction. Nat Rev Neurosci 2006;7:942-51.
99. Marshall JC, Fink GR. Spatial cognition: Where we were and where we are. Neuroimage 2001;14:S2-7.
100. Dinn WM, Harris CL, Aycicegi A, Greene P, Andover MS. Positive and negative schizotypy in a student sample: Neurocognitive and clinical correlates. Schizophr Res 2002;56:171-85.
101. Henry JD, Bailey PE, Rendell PG. Empathy, social functioning and schizotypy. Psychiatry Res 2008;160:15-22.
102. Bracha HS, Livingston RL, Clothier J, Linington BB, Karson CN. Correlation of severity of psychiatric patients' delusions with right hemispatial inattention (left-turning behavior). Am J Psychiatry 1993;150:330-2.
103. Brugger P, Graves RE. Right hemispatial inattention and magical ideation. Eur Arch Psychiatry Clin Neurosci 1997;247:55-7.
104. Mohr C, Bracha HS, Brugger P. Magical ideation modulates spatial behavior. J Neuropsychiatry Clin Neurosci 2003;15:168-74.
105. Mohr C, Landis T, Bracha HS, Fathi M, Brugger P. Levodopa reverses gait asymmetries related to anhedonia and magical ideation. Eur Arch Psychiatry Clin Neurosci 2005;255:33-9.
106. Taylor KI, Zäch P, Brugger P. Why is magical ideation related to leftward deviation on an implicit line bisection task? Cortex 2002;38:247-52.
107. Langdon R, Coltheart M. Mentalising, schizotypy, and schizophrenia. Cognition 1999;71:43-71.
108. Mohr C, Blanke O, Brugger P. Perceptual aberrations impair mental own-body transformations. Behav Neurosci 2006;120:528-34.
109. Premack D, Woodruff G. Does the chimpanzee have a theory of mind? Behav Brain Sci 1978;1:515-26.
110. Villatte M, Monestès JL, McHugh L, Freixa i Baqué E, Loas G. Adopting the perspective of another in belief attribution: Contribution of Relational Frame Theory to the understanding of impairments in schizophrenia. J Behav Ther Exp Psychiatry 2010;41:125-34.
111. Sprong M, Schothorst P, Vos E, Hox J, van Engeland H. Theory of mind in schizophrenia: Meta-analysis. Br J Psychiatry 2007;191:5-13.
112. Langdon R, Coltheart M. Visual perspective-taking and schizotypy: Evidence for a simulation-based account of mentalizing in normal adults. Cognition 2001;82:1-26.
113. Weniger G, Irle E. Allocentric memory impaired and egocentric memory intact as assessed by virtual reality in recent-onset schizophrenia. Schizophr Res 2008;101:201-9.
114. Landgraf S, Krebs MO, Olié JP, Committeri G, van der Meer E, Berthoz A, *et al*. Real world referencing and schizophrenia: Are we experiencing the same reality? Neuropsychologia 2010;48:2922-30.
115. Landgraf S, Amado I, Purkhart R, Ries J, Olié JP, van der Meer E. Visuo-spatial cognition in schizophrenia: Confirmation of a preference for local information processing. Schizophr Res 2011;127:163-70.
116. Committeri G, Galati G, Paradis AL, Pizzamiglio L, Berthoz A, LeBihan D. Reference frames for spatial cognition: Different brain areas are involved in viewer-, object-, and landmark-centered judgments about object location. J Cogn Neurosci 2004;16:1517-35.
117. Galati G, Lobel E, Vallar G, Berthoz A, Pizzamiglio L, Le Bihan D. The neural basis of egocentric and allocentric coding of space in humans: A functional magnetic resonance study. Exp Brain Res 2000;133:156-64.
118. Galati G, Pelle G, Berthoz A, Committeri G. Multiple reference frames used by the human brain for spatial perception and memory. Exp Brain Res 2010;206:109-20.
119. Schmidt D, Krause BJ, Weiss PH, Fink GR, Shah NJ, Amorim MA, *et al*. Visuospatial working memory and changes of the point of view in 3D space. Neuroimage 2007;36:955-68.
120. Abrahams S, Pickering A, Polkey CE, Morris RG. Spatial memory deficits in patients with unilateral damage to the right hippocampal formation. Neuropsychologia 1997;35:11-24.
121. Girard TA, Christensen BK, Rizvi S. Visual-spatial episodic memory in schizophrenia: A multiple systems framework. Neuropsychology 2010;24:368-78.
122. Cannon TD, Huttunen MO, Lonnqvist J, Tuulio-Henriksson A, Pirkola T, Glahn D, *et al*. The inheritance of neuropsychological dysfunction in twins discordant for schizophrenia. Am J Hum Genet 2000;67:369-82.
123. Keefe RS, Roitman SE, Harvey PD, Blum CS, DuPre RL, Prieto DM, *et al*. A pen-and-paper human analogue of a monkey prefrontal cortex activation task: Spatial working memory in patients with schizophrenia. Schizophr Res 1995;17:25-33.
124. Landgraf S, Amado I, Bourdel MC, Leonardi S, Krebs MO. Memory-guided saccade abnormalities in schizophrenic patients and their healthy, full biological siblings. Psychol Med 2008;38:861-70.
125. Park S, Holzman PS. Schizophrenics show spatial working memory deficits. Arch Gen Psychiatry 1992;49:975-82.
126. Langdon R, Ward P. Taking the perspective of the other contributes to awareness of illness in schizophrenia. Schizophr Bull 2009;35:1003-11.
127. Lysaker PH, Daroyanni P, Ringer JM, Beattie NL, Strasburger AM, Davis LW. Associations of awareness of illness in schizophrenia spectrum disorder with social cognition and cognitive perceptual organization. J Nerv Ment Dis 2007;195:618-21.
128. Davidson MC, Amso D, Anderson LC, Diamond A. Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. Neuropsychologia

2006;44:2037-78.
129. Burgess N. Spatial memory: How egocentric and allocentric combine. Trends Cogn Sci 2006;10:551-7.
130. Aminoff E, Gronau N, Bar M. The parahippocampal cortex mediates spatial and nonspatial associations. Cereb Cortex 2007;17:1493-503.
131. Bar M, Aminoff E, Schacter DL. Scenes unseen: The parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. J Neurosci 2008;28:8539-44.
132. Burgess N, Jeffery KJ, O'Keefe J. The Hippocampal and Parietal Foundations of Spatial Cognition. New York: Oxford University Press; 1999.
133. Poldrack RA, Packard MG. Competition among multiple memory systems: Converging evidence from animal and human brain studies. Neuropsychologia 2003;41:245-51.
134. Kern RS, Green MF, Marshall BD Jr, Wirshing WC, Wirshing D, McGurk S, *et al*. Risperidone vs. haloperidol on reaction time, manual dexterity, and motor learning in treatment-resistant schizophrenia patients. Biol Psychiatry 1998;44:726-32.
135. Meltzer HY, McGurk SR. The effects of clozapine, risperidone, and olanzapine on cognitive function in schizophrenia. Schizophr Bull 1999;25:233-55.
136. Paquet F, Soucy JP, Stip E, Lévesque M, Elie A, Bédard MA. Comparison between olanzapine and haloperidol on procedural learning and the relationship with striatal D2 receptor occupancy in schizophrenia. J Neuropsychiatry Clin Neurosci 2004;16:47-56.
137. Stevens A, Schwarz J, Schwarz B, Ruf I, Kolter T, Czekalla J. Implicit and explicit learning in schizophrenics treated with olanzapine and with classic neuroleptics. Psychopharmacology (Berl) 2002;160:299-306.

How to cite this article: Bose A, Agarwal SM, Kalmady SV, Venkatasubramanian G. Cognitive mapping deficits in schizophrenia: A critical overview. Indian J Psychol Med 2014;36:9-26.

Source of Support: Nil, **Conflict of Interest:** None.

Supplementary Table 1: Experimental paradigms of investigating mental representation

Task name and the study	Description of task	Administration
Pattern recognition task Landgraf *et al*. (2011)	Each item consisted of one pair of the same chess-board-like pattern. The two patterns could be in a specific mirroring relation resulting in four difficulty levels: Identical, vertically mirrored, horizontally mirrored and diagonally mirrored. Participants completed four blocks with 12 pattern pairs each. At the beginning of each block, participants were given the condition to be recognized in the block. The first block was always the identity condition. The three other block conditions were randomized between participants. There were six targets and six distracters in each block, whose order was pseudo-randomized. Targets were pattern pairs that showed the instructed block condition. If recognized, participants had to press the left mouse button. Distracters were pattern pairs that did not show the instructed block condition (only one of the three other relations was possible). For distracters, participants had to press the right mouse button. Because six different patterns were used, each pattern was shown twice in each block – once as a target and once as a distracter. Each trial in a block consisted of four phases. A fixation cross was presented for 1000 ms. Then the pattern pair was presented. Concurrently with the response (time limit 15 s), the pattern pair disappeared and was instantaneously followed by a mask for 2000 ms. The mask consisted of two neutral patterns with the same luminance as the test patterns. A smiley figure appeared indicating to continue with the next trial on a self-paced basis	Participants were instructed to answer as fast and as accurately as possible. Completion of the task took about 10 min
Letter rotation task Thakkar and Park, 2010	The experiment consisted of 320 total trials, divided into four blocks, which consisted of four repetitions of each stimulus type in a randomized order. Trials in which the subject did not respond within the 10 s time-out period were excluded from further analysis One of five letters (B, K, F, R, or G) was presented in either mirror or normal orientation at one of eight different angular orientations, ranging from 22.5° to 337.5° clockwise, from the upright position, in 45° steps. Participants were asked to indicate whether the letter was presented in normal or mirror orientation by pressing a key labeled "N" or "M" with their left or right index finger. Response key mappings were counterbalanced across participants so that for half of the subjects normal orientation was indicated with the left index finger and mirror orientation was indicated with the right index finger; for the other half of the subjects, response key mappings were reversed. Stimulus presentation and response collection were controlled by Matlab (Brainard, 1997)	Stimuli extended 6° of visual angle horizontally and vertically and were presented in the center of the computer screen until a response was made or after a 10 s time-out period. A black fixation cross was presented during the 1000 ms inter-trial interval before the next trial could begin

(*Continued*)

Supplementary Table 1: (Continued)

Task name and the study	Description of task	Administration
A block fMRI design VMWT composed of visible and hidden conditions Folley *et al*. (2010)	Subjects viewed a screen from the perspective of being placed in a pool of water within a surrounding room. Subjects maneuvered around the environment using a joystick until they found the platform. In hidden condition, furniture and objects were at fixed locations along the walls. In visible condition, a cylindrical wall masked these cues. In both, four equidistantly spaced yellow balls hovered over the water surface as reference points to possible platform locations, with one being placed in the center of each of the four quadrants. The platform lay beneath one of these. In visible condition, the platform could be easily seen between one ball and the water surface and the platform was in the same location during each trial. In hidden, the platform was "hidden" beneath the surface of the water at the same ball location throughout the experiment. The platform was located identically in the hidden and visible trials, however in visible there was a brick wall raised between the pool and the distal cues so that subjects were unaware that the locations were the same across trial types. For each trial, subjects began from a pseudo-randomly determined North, South, East or West location, navigating the pool using a joystick. On successfully finding the platform, "congratulations!" appeared on the screen. Each condition used a fixed time length, so that successful attempts resulted in additional platform searching trials until the subject ran out of time. During unsuccessful attempts, time spent during that condition would end and the subject would be advanced to the next condition according to the block design timing. Subjects completed two runs (7 min 13 s each) of six visible (31 s each) and five hidden (38 s each) conditions. A 3 s "hidden" or "visible" instruction screen preceded each condition and appeared on the bottom of trial screens	Before fMRI testing, subjects practiced 16 hidden, 1 probe (where subjects navigated to a proposed platform when it was actually extracted from the pool) and 4 visible trials. Subjects who could not successfully complete the task following these trials were not permitted to continue with the fMRI task. Data from the practice trials, including the probe trials, were not collected and are unavailable for analysis
The bin task Girard, Rizvi and Christensen; 2010 The perspective taking task/ person rotation task Thakkar and Park, 2010	This task comprises nine visually identical bins (10 cm height, 9 cm diameter) with detachable lids affixed in a circular formation (19 cm apart along the arc) on a large, square, black board (6,400 cm^2). The board covered the top of a table that was surrounded by four identical chairs, one on each side, in a room with various environmental features (i.e., artwork, computers, desks, shelves, etc.) Test sheets for the cancellation task presented participants with an array (17 rows and 15 columns) of 11 randomly ordered geometric shapes (e.g., triangle, half-moon); each shape served once as a target to be crossed out across repetitions of this task A photograph of an individual with his or her arms out to the side faced either toward or away from the participant and was presented in one of six different angular orientations, ranging from 67.5° to 292.5° clockwise, from the upright position, in 45° steps . There were four possible stimulus figures, two women and two men. Either the right or the left hand was marked by a red circle. Participants were asked to imagine themselves in the position of the figure on the screen and indicate whether the circled hand would be their right or left hand by pressing a key labeled "L" and "R" with the left and right index finger, respectively. Subjects were instructed to respond as quickly and accurately as possible. A left judgment was indicated by pressing a key with the index finger of their left hand and a right judgment was indicated by pressing a key with the index finger of their right hand. Stimulus presentation and response collection were controlled by Matlab (Brainard, 1997)	The positions of the object figures were counterbalanced across the nine pages Stimuli extended 12° of visual angle horizontally and vertically and were presented in the center of the computer screen until a response was made or after a 10 s time-out period. A black fixation cross was presented during the 1000 ms inter-trial interval before the next trial could begin. The experiment consisted of 384 total trials, divided into four blocks, which consisted of eight repetitions of each stimulus type in a randomized order. Trials in which the subject did not respond within the 10 s time-out period were excluded from further analysis
False-belief attribution task Villatte *et al*. (2010)	The experiment consisted of one block of 48 true-false trials that were divided in four categories, according to two types of attribution (self and other) crossed with two types of belief (true and false). Thus, among trials of self-attribution, there were twelve trials for true-beliefs and twelve trials for false-beliefs. There was the same ratio of true- and false-beliefs for trials of attribution to other and there were an equal number of true and false statements. Three objects sets appeared in the statements: A Smarties box and pencils; a farina box and cacao; a cacao box and farina Instructions: "You will see appear on the screen the first part of a statement. Once you have read the first part, you must press the key "enter" in order for the end of the statement to appear. Then your job will be to press 1 if the whole statement is true and 2 if it is false. In the different statements that you will read, "You" refers always to you and "I" to anyone else who would be talking to you" Both accuracy rates and response times were recorded (with longer response latencies predicted to reflect poorer performance). Response latencies were recorded as follows: Once the participant had read the first part of the statement (example: "If I put the pencils in the Smarties box and you are here, you would think the Smarties box contains"), s/he had to press the key "enter." Then, the end of the statement and the two allowable responses appeared on screen (example: "Pencils" true/false). Response latencies were recorded between the participant pressing "enter" after having read the first part of the statement and his/her response by pressing one of the two activated keys (response latencies that exceeded two SD's above the mean were removed from the statistical analyses	An E-Prime (version 1.1) program was compiled in order to present the task to the participants on a personal computer with a 660 MHz processor, a 15 inch color monitor and a numeric pad. All trials in the program were presented in French (black letters, font 26). All trials were presented randomly and no feedback was given after the participant's response. In this task, it is important for the participant to understand that "You" and "I" represent the perspective of the participant and the perspective of anyone who would be talking to the participant, respectively. To ensure that all participants responded in the same way, after the session, each of the participants was asked if "I" corresponded to him/her or to anyone else (and the same question for "You"). Anyone who did not respond correctly to these two questions was excluded from the analyses

(*Continued*)

Supplementary Table 1: (Continued)

Task name and the study	Description of task	Administration
Virtual park and virtual maze Weniger and Irle, 2006	The environments were three-dimensional, fully colored and textured and presented a first-person view. Subjects controlled their movements with a joystick. There were two virtual reality tasks (virtual park, virtual maze) each replicated five times. The order of the tasks was alternated between subjects The virtual park environment comprised 9 points of two-way intersection and 11 cul-de-sacs. Each cul-de-sac contained a pot, but only one pot contained money. Subjects were instructed to find the shortest way to the pot with money in it. Landmarks (house, garden, car, tree, lake, river, bridge, playground, mountain, etc.) were spread throughout the environment, allowing subjects to learn routes based solely on these landmarks The virtual maze environment comprised 6 points of two-way intersection and 7 cul-de-sacs containing pots, from which one contained money. The maze consisted of brick walls, a similarly colored floor and a blue sky. All intersections appeared identical when approached from different directions. As the maze did not include any landmarks, egocentric navigation strategies were necessary to solve the task. In each trial of the virtual park and the virtual maze, subjects started at the same location and then had to find the target that remained in the same location across trials	In a semi-darkened room, participants sat 60 cm in front of a 19 in. Computer screen. Stimuli were presented via the software Presentation 9.10 (Neurobehavioral Systems Inc.). Task order was: Reference changing, working memory span, spatial incompatibility task. Reference changing task (Committeri *et al*., 2004): Participants were familiarized with the task by a 25 s video depicting the virtual environment, verbal explanations by the experimenter and a short practice session
Spatial incompatibility task Davidson *et al*., 2006	Two cartoon images (red heart, red flower) were presented either on the left or right side of the computer screen. Response buttons were the same as in the working memory span task. Seeing a red heart, participants had to push the button that was on the same side as the heart. Seeing a red flower, they had to push the button opposite to the flower. Hearts and flowers were presented pseudo-randomly	After a short familiarization phase, 33 test items were presented. Participants had to respond as quickly and as accurately as possible. The task lasted 3 min
Working memory task Davidson *et al*., 2006	Participants had to press one of two keyboard buttons (‘1’=left button; ‘0’=right button) in response to images presented on the screen In the first condition, participants had to memorize two abstract images. These two images were pseudo-randomly presented in two experimental blocks with 20 image presentations each. Participants had to press the right button when seeing one image and the left button when seeing the other image In the second condition, participants had to memorize six abstract images; three for the right and three for the left button. Again, two blocks were presented. Each block consisted of 24 pseudorandom image presentations with each of the six images appearing 4 times. Participants had to respond as quickly and as accurately as possible. The task lasted 5 min	
Mental rotation task De Vignemont *et al*. (2006)	The stimuli were presented on a Macintosh Powerbook G3 computer. Their size was approximately 7 cm on the computer screen and they were drawn in grey levels on a white background. The subjects were seated 50 cm from the screen. Response time and errors were recorded by the computer. There were three conditions, with three types of stimuli: Hands, gloves and letters/numbers Hands: The hand stimuli were adapted from those developed by Parsons (1994). They consisted of drawings of a left and a right hand viewed from four perspectives, two in 2D (palm, back) and two in 3D (fist, grasp). Subjects had to decide whether the stimulus displayed on the screen was a right or a left hand. They were asked to respond as fast and accurately as possible, by pressing a key labeled “left” or “right” on the computer keyboard with the left and right index, respectively. Gloves: The glove stimuli were obtained by subtly altering the hand stimuli. The instruction was to imagine that one puts one’s own hand in the glove and to decide whether it was a right or a left hand. As in the hand condition, subjects were asked to respond as fast and accurately as possible by pressing a key labeled “left” or “right” on the computer keyboard with the left and right index, respectively Letters/numbers: The stimuli consisted of capital letters (F or R) and Arabic digits (5 or 7) written in Times New Roman. They were presented either in mirror or in normal orientation. Subjects were instructed to determine whether the stimulus that appeared on the screen was written in a normal way or in mirror. They were asked to respond as fast and accurately as possible by pressing a key labeled “mirror” or “normal” on the computer keyboard with the left and right index finger, respectively. For each condition, the drawing was presented in eight different angular orientations, ranging from 0 to 315 clockwise, from the normal upright, in 45 steps, which resulted in a total number of 64 stimuli. Each of the 64 stimuli repeated three times for a total of 192 trials. The 192 trials were organized in six blocks of 32 trials, with an equal number of stimuli of each type and orientation Blocks were constructed with the constraint that a left or a right hand/gloves (and a mirror or a normal letter/number) never appeared more than twice in a row and that the same orientation never appeared twice in a row	Four practice trials were given at the beginning with stimulus orientations that have never been used. In the training session feedback was given. The subject was then given the possibility of verifying her/his production and querying for further information. The examiner accurately verified that the subjects would understand and maintain the instructions in the course of the experiment by recalling them the instructions and by asking them to repeat them. Each trial began with a fixation point that lasted for 1000 ms. Then the screen turned white for 100 ms and the stimulus appeared and remained on the screen until the subject’s response. Then the screen turned white again for approximately 1000 ms and the fixation point appeared again to announce the next trial. No feedback was given to the subjects. Subjects were instructed to make no movement when processing the stimuli. All the subjects carried out the three conditions in a random order, at three different times

(*Continued*)

Supplementary Table 1: (Continued)

Task name and the study	Description of task	Administration
VMWT (escaping water flush) Hanlon *et al*. (2006)	Task procedures were those of Hamilton *et al*. (2003). Subjects were tested on two versions of the task. In both versions, navigation to a goal (platform) was measured with a computerized (virtual) version of the MWT. The subject navigates in a virtual environment consisting of a room with a square floor-plan and a circular pool in the center. All four walls of the room are identical in appearance except for a different landmark flush with the wall to use as spatial cues (four landmarks in total). The landmarks are placed off-center vertically by a fixed amount and placed off-center horizontally so that a subject could not find the platform by taking a straight trajectory from any starting location toward a landmark. The field of view is 48°, which allows participants to view one or two cues simultaneously on the display. The surface of the pool consists of an opaque, blue pattern that is patterned (tiled) through anti-aliasing of the original images to reduce (if not eliminate) any grid-like pattern that could be detected by the subject. The pool contains a square platform, 1.75% of the pool area. For analysis the pool's area was divided into four quadrants. In the first version of this task the subject was to learn to virtually swim to the hidden platform to escape from the water. The subjects escaped from the water as quickly as they could by finding the hidden platform that was under the surface of the water. The hidden location was in a fixed position over trials. Each participant received 24 training trials in six blocks of four trials, with each of four different starting locations occurring six times. Starting positions were chosen according to a pseudorandom sequence. If the platform was found within 60 s, the subject remained on the platform for 5 s, during which time they could rotate and view the environment but could not leave the platform. The display was then removed and a 2 s inter-trial interval followed	The VMWT was run on an IBM-compatible computer with a 17" color monitor. Arrow keys on the keyboard were used to navigate through the virtual environment. Subjects were able to navigate forward, but not backward and to turn left and right using the keyboard arrow keys (up, left and right). Also, forward movement in the pool was accompanied by the sound of moving water. The subject's position in the pool was collected in *x*, *y* coordinates recorded by the computer every 100 ms. Auditory feedback was controlled by the computer and was presented via speakers. When the platform location was discovered, a bell sounded and a verbal message saying the platform has been found appeared on the screen. When the duration of the trial exceeded 60 s without the platform location being found, an aversive tone sounded, the platform became visible and a verbal message saying the platform is visible appeared on the screen
Visual perspective taking task Langdon *et al*. (2001)	Examples and practice items preceded each set of experimental items. Four versions of the task were prepared to counterbalance for order of presentation of the two instructions (array-rotation and viewer-rotation) and, within each instruction type, order of presentation of item and appearance questions. All subjects saw questions with simple instructions first. To ensure that all subjects understood the two main instructions, subjects were encouraged to rotate the stand when shown the array-rotation examples and to get up and to move around the table when shown the viewer-rotation examples. Each subject saw a total of 24 questions with simple instructions, 48 questions with array-rotation instructions and 48 questions with viewer-rotation instructions. There were equal numbers of questions requiring yes and no decisions. The following instructions were given to the participants Item question with simple instructions: "Look at the blocks as they appear directly in front of you. Is the color in the front on your right, green?" Appearance question with simple instructions: "Look at the blocks as they appear directly in front of you. Do the blocks look like this?"3 Item questions with array-rotation instructions: "Imagine turning the stand so that the single dot is directly in front of you. Would the color in the front on your right be green? Appearance question with array-rotation instructions: "Imagine turning the stand so that the single dot is directly in front of you. Would the blocks look like this?" Item question with viewer-rotation instructions: "Imagine moving to sit in the chair with the single dot. Would the color in the front on your right be green?" Appearance question with viewer-rotation instructions: "Imagine moving to sit in the chair with the single dot. Would the blocks look like this?"	Subjects sat in front of a small table on which stood a square flat white stand. Beyond the table was a desk with a computer monitor displaying questions. Four colored blocks (red, green, yellow and blue) were arranged on the stand in a square layout. The stand was mounted on a turning platform (not visible to subjects) that allowed the stand to be rotated when explaining array rotation instructions. Prior to that, subjects were unaware that the stand could rotate. During array-rotation instructions, three small lever arms (normally concealed) were extended to label the three sides of the stand (one dot at 908, two dots at 1808 and three dots at 2708). During viewer-rotation instructions, the lever arms were hidden and three chairs (with similar labels) were placed around the table. During simple instructions, the lever arms were hidden and there were no chairs around the table. Subjects responded to all questions (see following examples) using a yes/no response pad. The computer recorded errors and latencies

fMRI – Functional magnetic resonance imaging; VMWT – Virtual Morris water task