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Navigating through the ebbs and flows of language

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Is progress in understanding the neural basis for spatial navigation relevant to the human language faculty? Not so much at the shortest scale, where movement is continuous, a recent study in the space of vowels suggests. At a much larger scale, however, that of the verbalization of run-away thoughts, a rich phenomenology appears to involve critical contributions by some of the brain structures also involved in spatial cognition. Their interactions may have to be approached with models operating at an integrated cortical level, and allowing for the compositionality of multiple local attractor states. A useful window on the latching dynamics enabled by cortico-cortical interactions may be offered by altered states of consciousness. As an example, psychedelic states have been reported to alter the graph properties of functional connectivity in the cortex so as to facilitate wide-ranging trips.

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Searching for a word, steering a conversation, going off on a tangent... navigation-related metaphors abound around our use of language, but it was only recently, with the elucidation of several neural mechanisms serving spatial cognition, particularly in rodents, that it became possible to consider whether and how such metaphors could capture processes occurring in our brain, as we speak.

Short-range navigation

The discovery of grid cells in rats, and subsequently in other species, has suggested that across mammals local metric information may be expressed, in the entorhinal cortex, by the activity of these cells. Such information can be used, as several theoretical models indicate, to navigate between nearby positions. On the other hand, a BOLD signal has been observed in humans with approximate 6-fold symmetry, which could be generated by grid-like neurons. In a remarkable paper [1] it was reported that a similar 6-fold symmetric signal can be observed, in fMRI, with subjects moving around short distances in a ‘conceptual’ space, realized by a bird drawing, with legs and neck of variable length. As the two parameters can be varied continuously and independently, despite being related both to vertical extensions, they span effectively a portion of a two-dimensional space, or of a plane. What about language? In the language domain most variables are categorical and do not vary continuously, so a grid code would not appear to be relevant. In phonology, however, vowel sounds can be described, to a good approximation, as locations on a portion of a plane, a trapezoid where the two dimensions correspond to the first two formant frequencies of the acoustic signal, and also to the extent of opening the vocal tract and to

the location of the main occlusion, when articulating a vowel. Each language utilizes a limited set of standard vowels, which behave as categorical variables; but the underlying space is continuous, and since different languages and even different speakers arrange their standard sets differently, we need to navigate the continuum, at least a bit, any time we listen to another speaker. Although most standard vowels in any given language are equivalent to static positions, each in a loosely defined sizable portion of vowel space, it is also possible to engineer short trajectories, similar to diphthongs. No grid-like 6-fold symmetric signal was seen, however, in an EEG study of such short diphthong-sounding trajectories [2]. It appears, instead, that the value of the second formant is approximately coded at a much grosser scale, by the position of the hotspot of activity (likely due to massive neural populations) in the superior temporal gyrus [3]. While grid-like units may not therefore be involved, these observations still fit the theoretical notion of dynamical continuous attractor, in which neural activity ‘flows’ continuously but into a path for each standard sound. Many such attractors can be kept in memory in a recurrent network [4]. If vowels, and the other sounds of language, are encoded as dynamical attractors, the transitions between them can be regarded as discrete jumps, allowing for the wide combinatorics typical of language compositionality. Indeed, the working of the phonological output buffer, a key short-term memory store involved in language production, can be analyzed in terms of saltatory, or ‘latching’ dynamics, even in the context of sign language [5].

A description in terms of latching dynamics becomes even more cogent when dealing with longer-range navigation, as is that in the space of thoughts. Thoughts come in packets of variable size, and how we compose the packets is much more variable than how we proceed within each packet. We may be wondering which reference to look at after making ourselves a cup of coffee, but not really how to make coffee or how to look at a reference, those are preassembled schemata [6]. In terms of navigation, the trajectories between nearby ports in the Mediterranean are relatively fixed, the real compositionality is in deciding the sequence of ports to visit.

Navigating thoughts during mind-wandering

The human mind has a marked propensity to wander away from the perceptual ‘here and now’. We daydream about a future holiday while walking, we remember our last conversation with a friend while attending a class, current concerns pop into our minds while watching a movie. These are instances of ‘mind-wandering’: more than goal-directed navigation, it resembles a goal-free drift, away from an ongoing task or external event towards (chains of) mentally constructed experience [7]. The most paradigmatic form of mind-wandering is both stimulus-independent (internally generated) and task-unrelated [8], but streams of thoughts can also be triggered by incidental external stimuli (a song leads us to think of a past experience; e.g., [9, 10]), or even the task at hand (we realize it is boring and start fantasizing) [8]. Also, at times we let our mind wander deliberately [11]. Once initiated, either because cued internally or externally, mind-wandering moves rather freely from thought to thought, which makes it a ‘wandering’, a navigation from port to port, and distinguishes it from deliberate thinking [7]. How do we mentally construct complex events alternative to direct experience? What triggers them, and what ‘grammar’ underlies the

precise transitions we make, in memory space, from one mental content to the next, as we mind-wander?

Functional neuroimaging (fMRI) and lesion evidence have linked convincingly mind-wandering with activity in the ‘default mode network’ (DMN), a set of interconnected brain regions, including the medial temporal lobes (MTLs), ventromedial prefrontal cortex (vmPFC), and the posterior cingulate cortex, whose activity is enhanced during relatively passive states and internally focused thought [7, 12]. The DMN is engaged by stimulus-independent and by task-unrelated thought, but is maximally engaged by full-fledged mind-wandering with both aspects of separation from perceptual reality [8]. What is currently unclear are the precise functional contributions of specific DMN regions to the processes governing mind-wandering, from its initial triggering to the dynamic unfolding of its content.

The vmPFC and the hippocampus and surrounding MTL structures, as part of the MTL subsystem of the DMN [8], are candidate regions for the generation of spontaneous thought. Indeed, lesions to both vmPFC [13] and the hippocampus [14, 15] hinder the (voluntary) construction of (past, future, and even atemporal) events, which are common contents of mind-wandering, though the nature of the event/scene construction impairment is different in each case [15, 16]. Constructed experience in hippocampal patients is mainly devoid of spatial references, whereas that of vmPFC patients also lacks contents and sensory details, suggesting that vmPFC plays a more general (upstream) role in event construction [17]. McCormick and colleagues have proposed that vmPFC initiates event construction by activating schematic knowledge (e.g., about the self, lifetime periods) that drives the collection of relevant individual details to be assembled into a spatially coherent scene by the hippocampus [16, see also 6, 18]. Indeed, vmPFC patients (but not hippocampal patients) are particularly impaired in event construction when the task benefits from the activation of (self) schemata [15], and are not impaired when it instead minimizes the need for self-initiation [19]. vmPFC may also govern schema-congruent transitions between the successive scenes of complex events based on event models [20, 21]. This may explain why vmPFC patients are particularly poor at simulating extended mental events [13], and may even confabulate, concocting irrelevant memory traces [6,18]. Similarly, while hippocampal patients fail to construct detailed mental scenes for navigation [22], vmPFC patients may go off path towards routes that were relevant in the past, which is reminiscent of confabulation [16]. Two recent magnetoencephalography studies show synchronized engagement of vmPFC and the hippocampus during both autobiographical memory retrieval and scene construction, with vmPFC activity driving activity in the hippocampus during both the initiation and elaboration of mental events [23,24].

Navigating with no rudder, or no sail

Would this also be the case during the spontaneous construction of mental events? A few studies have so far investigated mind-wandering in patients with damage in vmPFC vs. the hippocampus. Bertossi and Ciaramelli (2016) assessed mind-wandering in vmPFC patients and brain-damaged and healthy controls probing them to report whether their thoughts were on-task or

off-task, and about their contents, while they performed various tasks (e.g., even/odd judgements). vmPFC patients showed a reduced frequency of mind-wandering. Moreover, unlike the controls', their thoughts were never about the future, but mostly present-oriented [25]. A study confirmed that inhibiting medial prefrontal cortex activity with transcranial direct current stimulation attenuates mind-wandering [26]. By contrast, McCormick et al. (2018) found a normal frequency of mind-wandering in hippocampal patients. Hippocampal damage, however, altered the quality of mind-wandering, which was context-rich (episodic) in controls, but semanticized in hippocampal patients [27]. Present-oriented mind-wandering prevailed in hippocampal patients, too, but it was past-oriented mind-wandering that was hindered the most. A recent study also found a normal incidence of mind-wandering but reduced past-oriented thoughts in left MTL epilepsy [28]. The dissociation in the effects of focal lesions to vmPFC vs. the hippocampus on mind-wandering aligns with the finding of a recent study [29] investigating mind-wandering in two types of dementia, namely, Alzheimer's Disease (AD) and the behavioral variant of fronto-temporal dementia (bvFTD), which are associated with prominent early pathological changes in the MTLs and ventromedial (and dorsomedial) prefrontal cortex, respectively. bvFTD but not AD patients showed reduced mind-wandering and increased stimulus-bound thought. Together, this initial lesion evidence shows that vmPFC damage impairs the occurrence of mind-wandering, whereas hippocampal damage does not, suggesting that vmPFC (but not the hippocampus) the initiation of mind-wandering episodes, at least during tasks involving meaningless stimuli, as those we reviewed. Both regions, however, appear implicated in shaping the content of off-task thought, steering it towards the future (vmPFC) and populating it of (past) episodes (hippocampus). Sticking to the navigation metaphor, the contributions of the vmPFC and the hippocampus to mind-wandering would be those of the steering oars and the sail of the ship, respectively: to direct thought away from the here and now and towards constructed (future) experience, and to boost it with context-rich content (see Figure 1).

If vmPFC is necessary for the endogenous triggering of spontaneous thoughts, vmPFC patients should be able to mind-wander if externally cued. Our preliminary findings [30] show that inserting meaningful verbal cues in a vigilance task indeed increases mind-wandering frequency in vmPFC patients, suggesting vmPFC patients can engage in (and become aware of) cue-driven forms of mind-wandering. Interestingly, it is this type of cue-driven spontaneous thought to be impaired in prodromal stages of AD [31, 32]. This raises the interesting possibility that the hippocampus mediates forms of cued mind-wandering, consistent with its role in pattern-completion.

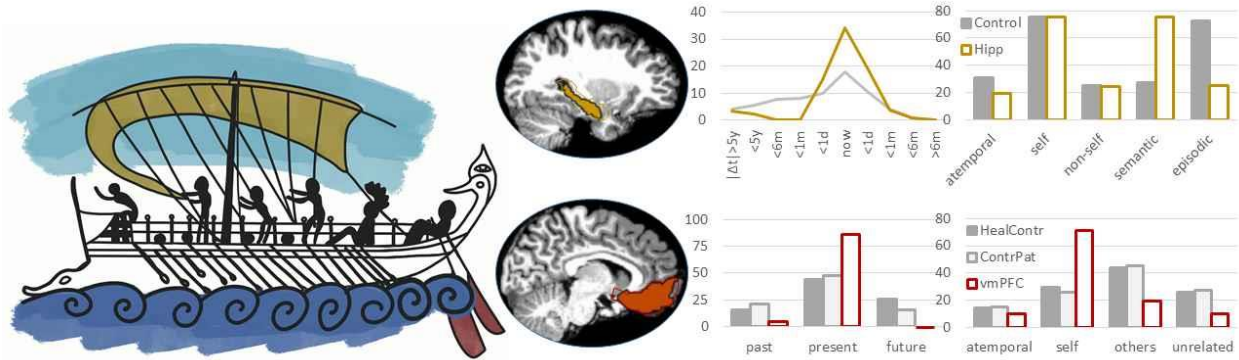


Figure 1. The effect of brain lesion on mind-wandering. The contribution of the hippocampus and vmPFC to mind wandering may be loosely compared to the boost offered by the sail (in dark yellow) and to the directionality provided by the steering oars (in dark red) in an ancient ship (left). Neuropsychological data indicates that hippocampal lesions (top right, in dark yellow, from [27]) impair the ability to imbue mind wandering with episodic content, particularly from the recent past; while vmPFC lesions (bottom right, in dark red, from [25]) reduce the initiation of mind-wandering and its steering towards the future. Art by Silvia Girardi.

Schemata and attractors in latching dynamics

Computational models conceive episodic memories as attractor states in the hippocampus, with CA3 connectivity enabling the cued retrieval of temporally-defined scenes of arbitrary content. The retrieval of attractor patterns can engage 'latching' dynamics [33], when the whole neocortex does not just settle into a single attractor, but instead hops from one attractor to the next. Such spontaneous hopping may be supplemented by 'schemata' that favor instructed transitions between locally continuous (smoothly connected) attractor states, modeling vmPFC. We have proposed [34, see also 16] that during mind-wandering vmPFC would govern neocortical latching, activating local schemata (for example about the self, one's goals, [35]) that initiate self-relevant simulations, and favoring appropriate latching across continuous memory attractors. Future-related mental simulations are especially reliant on schema-based processing, because we have no direct experience of the future, which would explain why future-based mind-wandering is particularly hindered by vmPFC damage. In contrast, the hippocampus would reinvigorate streams of thoughts in the cortex with novel (schema-incongruent) content [36, see also 7], for example past memories triggered by external stimuli or partially overlapping previous thoughts.

Current work is relating behavioral observations of mind-wandering in vmPFC vs. hippocampal patients with the behavior of a Potts network endowed with latching dynamics, schema instantiation, and a hippocampal content booster [37]. On this view, the network can be in a 'no latching' phase, corresponding to reduced mind-wandering, a 'finite latching' phase, when the mind moves frequently and freely from one thought to the next, or an 'infinite latching' phase, when latching dynamics go on spontaneously and indefinitely (akin to confabulation) [33,37]. One insight from these modelling studies [38] is that brain dynamics may be affected significantly by quantitative changes in some relevant model parameters, much subtler than the gross changes that would correspond to brain lesions: a critical parameter 10% higher, for example, may set the

network in a different phase, i.e., a different ‘state of mind’. Complementary to lesion studies, then, another window into human cognition and its underlying mechanisms is offered by contrasting distinct mind states. We touch here on this wide-ranging theme by briefly considering psychedelic states of consciousness.

Insights from psychedelic states

The term psychedelic is rooted in Greek (from *psyche*, soul and *deluon*, reveal), and can be translated as soul, or mind-revealing. This term was defined due to many psychedelics users reporting having access to suppressed contents of long term-memory and making conceptual connections unusual in their ordinary states. Despite the plentiful literature describing ‘trip’ experiences with psychedelic substances such as psilocybin, lysergic acid diethylamide (LSD), and N,N-dimethyltryptamine (DMT) [39, 40, 41], few behavioral studies have evaluated the effect of psychedelics on thought and language.

Early studies provided insight into the role of psychedelics in language modulation. Spitzer et al. have reported that psilocybin increases indirect semantic associations, those not evident at a first analysis, but that associate two concepts through an intermediate concept (e.g. lemon-sweet, lemon-sour-sweet) [42], apparently enhancing spreading activation in semantic networks. Family et al. have reported that subjects under the influence of LSD make more errors in a naming-pictures task consisting in the substitution of the target with a semantically related word [43]. Kuypers et. al. have observed that subjects under Ayahuasca effects, a brew containing DMT, have intensified creative divergent thinking and diminished convergent thinking in picture association tasks [44].

Those results suggest that psychedelics affect the space of thoughts by effectively extending the range of possible associations, as if latching dynamics guided by local schemata were weakened in favor of a larger diversity of transitions, hence more flexible, remote associations. A study by Kraehenmann et al. evaluating audio-recorded mental imagery indicates an increase in ‘primary process’ thinking under LSD effects, again characterized by unlikely combinations of events, and allowing contradictory or illogical connection of ideas, with unaffected ‘secondary processes’ (reflective, logical) thinking [45] – which instead prevail in ordinary mental states and inhibit the accessibility of irrelevant contents [45].

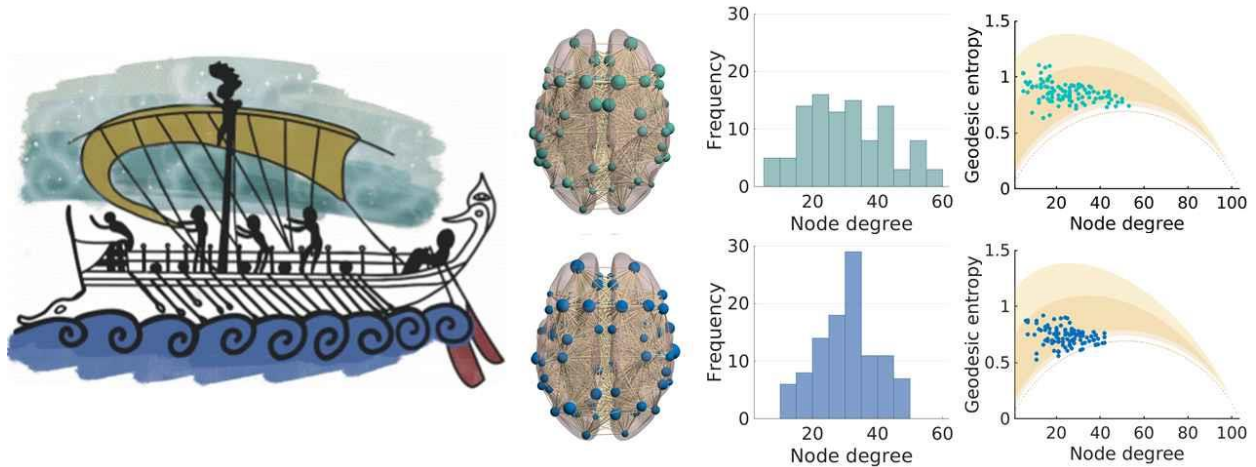


Figure 2. The effect of psychedelic substances on thought dynamics. Changes in mind dynamics are observable even in the absence of brain lesion. Initial studies suggest that psychedelic substances may increase the scope of spontaneous thoughts, at the expense of predefined schemata, with the enhanced perception perhaps afforded by climbing on the mast, in the navigation metaphor (left). In the statistics extracted from measures of functional connectivity in the cortex (middle), this may be reflected in relatively subtle changes (right). Here the top row shows a wider distribution of node degrees (right-center) and a slightly increased geodesic entropy (right) after Ayahuasca consumption relative to before (bottom row, see [46,47] for details). Art by Silvia Girardi.

There is initial evidence on the neural mechanisms behind psychedelics-induced reductions of mind constraints, although the accompanying changes in functional connectivity appear relatively subtle. fMRI studies indicate functional brain networks with a higher segregation, which may be counterintuitive, in individuals under the effect of Ayahuasca than in ordinary mind states, as reflected in increased average ‘geodesic distance’ and clustering coefficient [46]. The information entropy (variability) of the degree distribution of functional connectivity between brain regions is, however, higher under Ayahuasca influence, reflecting a less constrained network [46]. Geodesic entropy, which reflects the diversity of distances of nodes within functional networks, also increases under Ayahuasca effects [47], suggesting that, on average, each brain region is subject to a greater diversity of influences, at least in terms of topology, in individuals under psychedelic effects. The increase of entropy in brain networks was also reported by studies of other psychedelics such as psilocybin [48] and LSD [49]. These results suggest that the functional brain networks of individuals in psychedelic (compared to ordinary) states are less constrained. Indeed, psychedelic substances have been shown to be effective in the treatment of depression, a condition characterized by unduly constrained mind states [50].

Psychedelics modulate DMN activity. fMRI studies have reported decreased activity in several regions of DMN, including the medial prefrontal cortex (mPFC) and posterior cingulate cortex, in individuals under the influence of psilocybin [51] and Ayahuasca [52]. A similar reduction of DNM activity also characterizes experienced meditators, who are more capable to control mind-wandering compared to non-meditators [53]. Psychedelic and meditative states have

in common an increase of (present) self-consciousness and a reduction of future self-projection. Although in psychedelic states the mind is reportedly free to wander, the relation between psychedelics and mind-wandering is not entirely understood. Experienced Ayahuasca users have in fact reduced mind-wandering, perhaps as an acquired compensatory mechanism to preserve executive functioning [54]. A study evaluating psychedelic microdosing also shows that most users experience a significant decrease in mind-wandering, though subtypes of mind-wandering were not investigated [55].

Thus, the studies on psychedelics corroborate a link between the DMN and mind-wandering. We conjecture that a decrease in mPFC activity would disarticulate schemata-coupling and schema-congruent transitions, which can also lead to an increase in unexpected mental contents observed under psychedelic effect [46]. It is still not clear whether higher doses of psychedelic substance would increase the experience (or awareness) of mind-wandering, altering latching dynamics. More in general, although neuroimaging data gives us initial insight on neuronal mechanisms underlying the effects of psychedelic-induced brain states, and analytical tools to characterize them are being developed [56, 57, 58] a comprehensive theory supported by quantitative mathematical modeling is sorely needed to elucidate their correlation with thought dynamics.

We expect to see, in the near future, more pioneering studies on language-related navigation at this larger scale, which sails effectively in a sea of thoughts more than in a pool of individual words. Reviewing recent studies, we can already infer that navigation in the sea of thoughts involves distinct brain regions in non-straightforward interaction with each other. Studies of neuropsychological patients and of subjects in psychedelic states suggest a major role of the DMN, especially the mPFC, in mind-wandering. Suitable models have just begun to be developed, but they already point at the complexity associated with the latching dynamics arising from the interactions of multiple local attractor networks.

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* This study links mind-wandering with brain injury located within the default mode network (DMN). The authors tested mind-wandering in patients with brain damage and healthy controls and studied the link between mind-wandering and brain damage with traditional lesion mapping techniques and a novel lesion network pattern analysis revealing brain networks mainly affected by focal lesions. The results show that reduced mind-wandering is related to damage in several DMN nodes, including the vmPFC and the parietal cortex, and generally reduced connectivity within the DMN.

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* This study investigates the construction of future events pertaining to the self or to another person in patients with lesions to the vmPFC or the MTL and healthy controls. vmPFC patients were impaired in the construction of self-relevant but not other-relevant future events, while MTL patients were impaired in either, though they showed a self-benefit in event construction. These results suggest that vmPFC and the MTL play distinct roles in event construction, with vmPFC implicated in activating high-level self-related knowledge, and the MTL assembling individual details of any event.

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