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# Searching for knowledge.

# The neurophysiology behind the exploration of hippocampal cognitive maps.

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# Abstract

Exploring and interacting with the environment is crucial for animals' survival. Neurons in the hippocampal formation support spatial exploration through locomotion, and eye movements in primates, as well as memory. However, how the hippocampus supports exploration across different cognitive domains remains unclear. In this thesis I will provide evidence that hippocampal rhythms support exploration of conceptual domains, further strengthening the parallels between spatial and mnemonic exploration. I will then show that attention underlies exploration of visual space giving rise to the grid-like response, a typical signature of spatial navigation. These findings deepen our understanding of the role of human's hippocampal formation in cognition and open new avenues for research, particularly regarding the potential role of attention in navigating conceptual spaces.

# *Summary*

The ability to perceive, interpret and respond to the environment is a crucial aspect of an animal's daily life. In order to survive and thrive in complex, ever-changing environments animals must gather information from their surroundings, integrate it with previous knowledge and their current goals and eventually plan actions accordingly, all this within seconds.

In the middle of last century, Tolman (1948) coined the term “cognitive map” to describe the set of learned relationships between events that the animals use to interpret external stimuli and guide their response. Tolman goes further and hypothesizes that a “comprehensive-enough” map is needed to perform flexible behavior when the animal is facing novel external stimuli. An example of this are rats that familiarized with the environment and later were able to use their knowledge to go directly to the reward after it was introduced (Tolman & Honzik 1930) or go to the reward after the learned path was blocked (Tolman, Ritchie & Kalish 1946).

It has then been suggested that such map-like representation has a remarkable neural correlate in a set of space-sensitive neurons in the medial temporal lobes (MTL) of the mammalian brain, specifically in the hippocampal-entorhinal system (O’Keefe & Nadel, 1978). This brain region in fact contains neurons that respond to different spatial variables, such as position or heading direction (for reviews see Grieves & Jeffrey, 2017; Moser et al., 2017).

Furthermore, there is now evidence that neurons in the same brain area play a broader role in cognition, supporting understanding of relationships between elements (relational reasoning; Eichenbaum & Cohen 2014), for instance sounds organized according to their pitch (Aaronov et al., 2017).

It has thus been proposed that space is actually only one example of relational computations that the MTL system is carrying out (Eichenbaum, 2017), but the MTL is actually implicated in supporting flexible behavior more broadly (Behrens et al., 2018). The currently held view is in fact that these computations might have been developed originally to support spatial cognition and later recycled to provide the necessary structure to organize and explore declarative knowledge (Bottini & Doeller, 2020; Eichenbaum & Cohen 2014; Buzsaki & Moser, 2013; Bellmund et al., 2018).

In the first chapter of this thesis, I will describe the current evidence of the involvement of the hippocampal-entorhinal system in spatial and non-spatial relational knowledge.

Neural activity in this brain area is in fact responsive to spatial variables at both the cellular and population level. At the cellular level, neurons can be classified according to their firing, with specific neurons firing for a given place (O’Keefe, 1976) or heading direction (Taube, Muller & Ranck, 1990), or at multiple places in the environment (Hafting et al., 2005). At the population level, oscillations arising from their coordinated activity (Buzsaki & Draguhn, 2004), and especially theta and gamma (see e.g., Colgin, 2016), correlates with spatial variables (Kunz et al., 2019; Herweg & Kahana, 2018), such as distance traveled (Bush et al., 2017).

In primates, these cells fire for positions defined according to gaze location (Killian et al., 2012; Wirth et al., 2017) or saccade direction (Killian et al., 2015), suggesting that the typical way in which a species explores the environment has an effect on the neural activity in the hippocampal formation (Piza et al., 2024). Similarly, neural oscillations in the MTL are affected by visual exploration, for instance theta rhythm undergoes phase reset after a saccade (Jutras et al., 2013; Hoffman et al., 2013).

Furthermore, these same neural signatures have been found also during the exploration of more abstract domains. For instance, there is evidence of cells firing for specific sound frequencies (Aronov et al., 2017) or at multiple locations in a two-dimensional emotion space (Qasim et al., 2023).

At the mesoscopic level, there is an extensive literature regarding the involvement of theta oscillations in spatial navigation (Kunz et al., 2019) as well as episodic memory formation and retrieval (Herweg et al., 2020a), however there is no direct evidence for its involvement in the navigation of a conceptual domain.

In the second chapter I will present a study in which we leveraged the verbal fluency paradigm to investigate the electrophysiological mechanisms underlying the exploration of conceptual spaces in humans. In a verbal fluency task people are asked to name all the concepts that they can think of from a given semantic category. It has been shown that, in this task, the adopted strategies are similar to foraging in spatial domain (Hills et al., 2012), thus allowing to draw parallels with navigation in physical space. We used intracranial eeg to record brain activity directly from the hippocampus and investigated the presence of power increases when people find concepts in their memory. Theta rhythm in this time window has in fact been associated to the distance traveled in a spatial navigation task (Bush et al., 2017), and to the semantic distance between recalls in an episodic memory task (Solomon et al., 2019a).

First, we found an increase in theta and gamma power in the hippocampus before word onset. Furthermore, this power increase was specific to the hippocampus, in that the lateral temporal lobe, a region implicated in language and semantics, has different theta and gamma dynamics. Second, we showed that theta power correlates with semantic distance and temporal interval between subsequent words whereas gamma power correlates with the temporal distance between words. This finding provides the first direct evidence for the involvement of theta oscillations in the exploration of a conceptual space. Theta oscillations in the hippocampus, thus, are present when animals explore the environment through their body or through eye movements and even when they explore their internal conceptual space.

The link between exploration through eye movements and exploration of conceptual spaces is particularly interesting. Eye movements offer interesting insights about participants behavior during spatial navigation (Lakshminarasimhan et al., 2020; Zhu et al., 2022) and decision making (Ferro et al., 2024) but, most interestingly, in our lab it has recently been demonstrated that spontaneous eye movements can reflect the organization of concepts in mental space (Viganò et al., 2024). For instance, people generating random numbers move their eyes according to a left-to-right magnitude-based ordering (Dehaene et al., 1993), with larger eye movements reflecting larger differences between consecutive numbers. Similarly, peoples eye movements reflect the organization of colors in the color wheel.

The hypothesis that eye movements reflect the internal organization of memory is further being tested in the lab under different perspectives. Within this line of research, I will present as a third chapter of this thesis a study in which we ask whether eye movements are actually necessary to observe typical signatures of navigation, such as the grid-like response. Eye movements are often interpreted as being the reflection of the focus of attention (e.g., Kustov & Robinson, 1996), and even when asked to fixate people make small eye movements that are associated with the attentional focus (Yuval-Greenberg et al., 2014; Engbert & Kiegl 2003). It is thus possible that eye movements in the aforementioned studies reflect movements of attention in mental space, thus representing a behavioral signature of attentional movements. In non-human primates this is the case, with grid-like firing being present when covertly attending to peripheral visual locations (Wilming et al., 2018). To test whether this is the case also in humans we used magnetoencephalography and a novel, non-invasive method to investigate the presence of a grid-like response based on frequency-tagging. While participants were fixating at the center of the screen, they were presented with visuo-spatial trajectories in their visual periphery and successfully performed a location memory task. In the medial temporal lobe we observed a higher response for trajectories with a 60° periodicity compared to control periodicities, a signature of grid-like response. People made small eye movements during the task that were not correlated with the grid-like response.

With this second experiment we thus demonstrated that movements of attention can elicit a signature of spatial navigation such as the grid-like response, independently of eye movements. Attentional movements can thus be a mechanism through which people move around their mental space.

In the final chapter of the thesis, I will discuss the implications of these findings in light of the existing literature and further elaborate on the proposal that attention can be a mechanism through which conceptual spaces can be explored.

# *Chapter 1*
# *Introduction*

## *Space-related activity in the hippocampal formation*

Although spatial representations in the brain have been attributed to a wide network of areas, comprising frontal, parietal and temporal regions (Epstein et al., 2017), in the last 50 years there has been a strong interest in the medial-temporal lobe (MTL) due to the findings of specialized cells whose firing can be modulated by spatial variables such as position or heading direction of an animal in the environment (Grieves & Jeffery, 2017; Moser et al., 2017).

This interest sparked thanks to the discovery of “place cells” in the rats’ hippocampus, neurons that fired specifically when the animal traversed one location in space ( O’Keefe & Dostrovsky, 1971). The firing fields of multiple hippocampal place cells cover the local environment in which the animal is placed and thus provide a spatial code from which the animals’ position can be inferred (O’Keefe, 1976; Wilson & McNaughton, 1993), with precision possibly limited to the animals size (Hazon et al., 2022). This finding was interpreted by O’Keefe and Nadel (J. O’Keefe & Nadel, 1978) as providing the neural underpinnings of what Tolman (1948) termed a “cognitive map”, i.e. a learned set of relationships between environmental stimuli (as well as stimuli and consequences of actions on them) that is used to guide behavior.

While place cells signal a single location in the environment, “grid cells”, located one in the medial entorhinal cortex (Hafting et al., 2005; Sargolini et al., 2006) have multiple, regularly-spaced firing fields that provide information about the environmental structure. Firing fields of a grid cell can be thought of as positioned at the vertices of repeating equilateral triangles, eventually forming a hexagon that covers the navigated environment. Grid cells are characterized by a phase (the vertices’ position in angular coordinates), orientation relative to an external reference point and the spacing between vertices (Hafting et al., 2005). They are organized in modules with consistent phase and orientation within the module but distinct spacing (Gu et al., 2018; Stensola et al., 2012), increasing along the dorsal to ventral axis of the EC, allowing to map the whole environment at different levels of granularity (Hafting et al., 2005; Stensola et al., 2012; Barry et al., 2007).

While place and grid cells provide a representation of the environment based on position, another set of cells, defined “head-direction cells”, is modulated by the heading direction of the animal. These were first found in rats’ presubiculum and parasubiculum (Taube, Muller & Ranck, 1990) but then also in other areas such as the retrosplenial cortex (Cho & Sharp., 2001) and anterior thalamus (Taube, 1995).

More recently, several other cells have been identified in the hippocampal-entorhinal system that encode specific aspects of navigational behavior, such as for instance the “object-vector cells” which fire in response to distance and direction from objects in the environment (Høydal et al., 2017) or “border cells” firing for in proximity of environmental borders (Solstad et al., 2008).

These findings have been pioneered by studies on rodents and have then been extended to other mammals including human and non-human primates (Herweg & Kahana, 2018), whose hippocampal-entorhinal system is highly similar in structural and functional terms (Garcia & Buffalo, 2020; Clark & Squire, 2013; Manns & Eichenbaum, 2006).

In humans however, direct recordings of neural activity can only be obtained from patients with electrodes implanted to monitor epileptic seizures. By having these patients navigate virtual reality environments, Ekstrom and colleagues (2003, and later Miller 2013) reported the existence of place-cells in the human hippocampus, Jacobs and colleagues (2013, and later Nadasdy 2017) reported grid-cells in the entorhinal cortex, while Tsitsiklis and colleagues (2020) reported the presence of heading-direction neurons.

The necessity of invasive neural recordings for the study of grid cells in humans has been overcome in a landmark study by Doeller and colleagues (2010) who identified a proxy for the periodic firing of grid cells in non-invasive functional magnetic resonance imaging (fMRI). More specifically, the authors reported that fMRI activity in the entorhinal cortex recorded during movements in virtual reality that are 60° periodic, (thus mimicking the spatial periodicity of grid cells firing fields), is higher than control periodicities. The possibility of observing cellular-like activity at the voxel level (where each voxel corresponds to millions of neurons) is consistent with the finding that grid-cells are organized into modules with similar firing fields size and orientation (Stensola et al., 2012; see Kunz 2019 for a discussion on how this may be achieved). This indirect, grid-like measure, in line with direct recordings (Jacobs et al., 2013), demonstrated the existence of a broader set of areas in humans that show a 60° periodic (or hexa-directional) modulation, comprising the medial prefrontal cortex as well as the entorhinal cortex. Moreover, this methodological advance opened the possibility to study grid-like activity non-invasively in humans, which was until then limited to highly invasive recordings in epileptic patients, leading to numerous discoveries in the context of both spatial and conceptual navigation in healthy human participants (Bellmund et al., 2018).

More recently, other non-invasive methods have been developed to study heading direction in ecological settings using mobile, non-invasive neuroimaging (Griffiths et al., 2024).

A parallel line of research has identified similar signatures of navigation being reflected in the extracellular recordings in the hippocampal formation (Kunz et al., 2019; Colgin, 2016). Such recordings, termed local field potentials (LFP), usually exhibit rhythmic patterns denoted as oscillations.

Two oscillation frequencies are prominent in the hippocampal formation: theta (Buzsaki, 2002; Buzsaki, 2005; Colgin, 2013), ranging between 3 and 8 Hz, and gamma (Colgin & Moser, 2010; Fernandez-Ruiz et al., 2023; Buzsaki & Schomburg, 2015), ranging between 30 and 150 Hz, as well as their cross-frequency coupling (Buzsaki & Wang, 2012; Jensen 2007, Colgin, 2015).

Theta oscillations are a slow rhythm, in the range of 3-8 Hz, lasting around 200 ms per cycle (Vanderwolf, 1969). Theta oscillations are most regular in frequency and have the largest amplitude in cornus ammonis 1 (CA1) of the hippocampus (Buzsaki, 2002). However, given its slow cycle, theta is thought to coordinate activity of a large number of neurons (Buzsaki, 2002) and enable communication between hippocampus and its connected structures in the limbic system such as the entorhinal cortex (Mitchell & Ranck, 1980) or septum (Nerad & McNaughton, 2006). Single neurons phase-lock to hippocampal theta oscillations both within the hippocampus (Jacobs et al., 2007, Rutishauser et al., 2010) and in other regions (Sirota et al., 2008) even in the absence of local theta oscillations (Schonaut et al., 2024).

In rodents they appear to be faster than in humans (Jacobs, 2014), in which a fast and a slow theta oscillation has been identified and associated with spatial and mnemonic functions respectively (Goyal et al., 2020). Theta oscillations have in fact been consistently associated with an "active" state of the brain (Vanderwolf, 1969). Hippocampal theta power is higher during periods of movement compared to moments of stillness in both real and virtual environments and in both humans and rodents (Bush et al., 2017; Ekstrom et al., 2005; Bohbot et al., 2017; Aghajan et al., 2017; Graves et al., 2023; Mao et al., 2021; Vanderwolf, 1969; Buzsaki et al., 1983). Theta power and frequency scale with movement speed (Aghajan et al, 2017; Mao et al., 2021; Fuhrmann et al., 2015), paralleling the finding of single neurons being modulated by speed (Spalla et al., 2022; Kropff et al., 2015; McNaughton et al., 1993). Moreover, theta power increases with the length of the path taken (Bush et al., 2017), even in the absence of sensory information (Vass et al., 2016). Theta power not only is related to movement, but also exhibits a grid-like modulation (Chen et al., 2018; Maidenbaum et al., 2018), it increases close to boundaries (Lee et al., 2018; Stangl et al., 2020) and is modulated by distance to the goal (Liu et al., 2023).

Gamma oscillations instead are faster, (>30 Hz) and are considered a mesoscopic signal reflecting local synchronous neural firing (Buzsaki & Wang, 2012). For instance, it has been shown that hippocampal neurons (including place cells, Senior et al., 2008) fire synchronously within ~10-30 ms (Harris et al., 2003; Umbach et al., 2022; a time window that matches that of spike timing dependent plasticity (Magee & Johnston, 1997; Markram et al., 1997) forming a "cell assembly" whose synchronous activity allows to efficiently activate downstream "reader" neurons (Buzsaki, 2010). Similar principles of gamma oscillations have reported in a variety of cortical and subcortical areas (Buzsaki & Wang, 2012) and it has thus been suggested that gamma oscillations reflect a general mode of neural assembly activity (Fernandez-Ruiz et al., 2023; Fries, 2009; Fries et al., 2007) such as providing a transient activation (Tal et al., 2020; Van Ede et al., 2018) for specific information "packets" to be transmitted (Fernandez-Ruiz et al., 2023; Fries, 2009; Freeman, 2003). In fact, it has been shown that different gamma frequencies separate information transmission within the hippocampal formation (Colgin et al., 2009; Schomburg et al., 2014) by engaging different cell assemblies (Senior et al., 2008). For instance, slow gamma underlies communication between CA1 and CA3 while fast gamma between CA1 and the medial entorhinal cortex such that neurons in each area where phase locked to the respective CA1 gamma rhythm and the different gamma rhythms occurred at distinct phases of the CA1 theta cycle (Colgin et al., 2009). Fast and slow gamma thus can engage place cells representing current or future location, respectively (Bieri et al., 2014; Zheng et al., 2016). Similar dissociation between fast and slow gamma have been demonstrated for communication between hippocampus and medial and lateral entorhinal cortices, respectively (Igarashi et al., 2014; Fernandez-Ruiz et al., 2021).

Gamma oscillations are usually nested within theta cycles (Colgin & Moser, 2010), giving rise to what is known as cross-frequency coupling (Aru et al., 2015; Hyafil et al., 2015), which in the case of theta-gamma is often expressed in an amplitude modulation of gamma with respect to the phase of theta (i.e., phase-amplitude coupling, PAC). Theta-gamma PAC has been implicated in spatial memory performance (Vivekananda et al., 2019; Tort et al., 2008;

Newman et al., 2013). One possible explanation for the theta-gamma PAC is its relation to neural firing. In fact, neurons tend to fire at specific phases of both theta and gamma (Lisman & Jensen, 2013), however only theta has a long-enough temporal window that allows long-range communication (Von Stein & Sarnthein, 2000) thus PAC can be an effective way to precisely synchronize neuronal assemblies across areas.

To sum up, we have seen that both single neurons and neural oscillations are related to spatial variables, such as position or heading direction. These findings have been pioneered in rodents but extended also to other mammalian species such human and non-human primates. However, some differences exist between species. First, in their peripheral sensing organs: rodents are nocturnal animals that use their whiskers and olfaction to explore the environment (Deschenes et al., 2012), while primates are diurnal animals that mainly rely on vision (Rolls & Wirth 2018; Meister & Buffalo, 2016; Kaas et al., 2021). These differences are reflected in the hippocampal neural response: in primates space seems to be mainly represented according to gaze location rather than the actual body position. In the next paragraph I will present findings linking MTL neural activity to gaze behavior.

## *Representation of visual space in the hippocampal formation*

The extension of the aforementioned findings to primates has been paralleled by the discovery that spatial-responsive cells are sensitive to a different way of exploring the environment, namely vision. When looking at pictures or their surroundings, primates naturally move their eyes (Yarbus, 1967) so that the fovea (the region of the eye with maximal visual acuity) gets centered on specific portions of the image that are of interest, aiding recognition and memory. Recognition memory is in fact reduced with increasing distance from the fixation (Nelson & Loftus, 1980) and increases with the number of fixations to the object to be memorized (Pertzov et al., 2009). Furthermore, restricting eye movements results in worse memory (Henderson et al., 2005) and worse navigation performance (Lakshminarasimhan et al., 2020). Visual exploration is thus fundamental and, even in the absence of eye movements, humans move their head to compensate, with temporal characteristics that resemble that of saccades (Gilchrist et al., 1997). Head and eye movements are in fact tightly coupled (Bizzi et al., 1971; Freedman & Sparks, 1997) and allow gathering information about the animal's surroundings (Schroeder et al., 2010). This behavior results in a sequence of eye movements followed by fixations that enable exploration of the environment (Noton & Stark, 1971), akin to the movements required to grasp objects in the environment (Rolls & Wirth 2018: Kaas, 2013). Saccades (rapid, ballistic eye movements) can thus be conceived as movements within the field of view (Bicanski & Burgess, 2019), allowing to acquire information about the surroundings before moving the body. It has thus been suggested that exploration through eye movements and locomotion are supported by the same neural mechanism (Nau et al., 2018a).

Invasive studies in monkeys have demonstrated that saccades modulate single units in the MTL (Ringo et al., 1994). This finding was then extended to show the presence of “spatial view cells” in the hippocampus, which respond selectively to where the monkey is looking at (Corrigan et al., 2023; Wirth et al., 2017; Georges-Francois et al., 1999; Sobotka et al., 1997), “spatial view grid-cells” in the entorhinal cortex whose firing is modulated by eye-movements that have an hexagonal periodicity (Killian et al., 2012) and “saccade-direction cells”, firing for the direction at which saccades are directed (Killian et al., 2015). These cells bear a strong resemblance with place-, grid- and head-direction cells that are typically reported in studies of physical navigation and have several properties that mimic rodents' spatial-cells, e.g., place coding is disrupted during passive transportation (Nishijo et al., 1997).

Interestingly, recent studies in freely-moving primates have uncovered that the majority of cells in the primate hippocampus respond to many spatial variables with the majority exhibiting mixed selectivity (Mao et al., 2021). Spatial position is encoded in hippocampal neurons (Ludvig et al., 2004; Hazama & Tamura 2019; Gulli et al., 2019; O'Mara et al., 1994) and can be accurately decoded from hippocampal neural populations (Piza et al., 2024; Gulli et al., 2019), however the majority of individual neurons respond to vision-derived spatial variables such as head- or eye-movements (Piza et al., 2024; Mao et al., 2021). This discrepancy with rodents is interpreted as a consequence of different exploration strategies between species (Piza et al., 2024).

The link between MTL and viewing behavior can also be observed at the population level.

Similarly to the findings in single units, human hippocampal theta is mostly correlated with visual rather than spatial variables (Watrous et al., 2011).

Eye movements themselves modulate activity in the hippocampus, even in darkness (Sobotka & Ringo, 1997), with naturally-occurring saccades direction modulating low-theta phase and saccade amplitude modulating theta power (Doucet et al., 2019). Interestingly, saccades during natural vision occur at the theta rhythm (Otero-Millan et al., 2008; Näher et al., 2024) suggesting a potential relation between the hippocampal dominant rhythm and information sampling behavior (Lakatos et al., 2008; Schroeder et al., 2010; Leszczyncki & Schroeder, 2019). Saccade onsets in fact reset hippocampal theta phase (Jutras et al., 2013; Hoffman et al., 2013; Doucet et al., 2019; Katz et al., 2020). This is interpreted as allowing the hippocampus to be in an optimal state to retain information from the newly fixated location (Meister & Buffalo 2016; Leszczyncki & Schroeder, 2019), given the relationship between MTL theta phase and long-term synaptic potentiation (Hyman et al., 2003; McCartney et al., 2003).

Several other pieces of evidence in support of a role for the MTL in the representation of visual space come from non-invasive neuroimaging experiments in humans. For instance, Nau et al., (2018b) report a grid-like signal in the entorhinal cortex elicited by actively tracking with the eyes a dot moving on a screen in fixed directions. The authors further demonstrate that this response was not present in a control condition in which the surrounding arena moved while the dot remained fixed, concluding that movements of gaze are driving the observed effect, rather than motion of the visual stimulus per se. A similar six-fold symmetry related to gaze direction in an unconstrained visual search task has been reported by Julian and colleagues (2018), who further demonstrated the sensitivity of the measured grid-like code to environmental geometry, such that the rotation of a rectangular environment by 30° resulted in a rotation of the grid orientation by a comparable degree, mimicking known grid-cells' properties identified in rodents' locomotion (Stensola et al., 2015).

Another relevant study comes from Staudigl and colleagues (2018), who recorded magnetic brain activity (and direct neural recordings from one epileptic patient) while participants were studying pictures of outdoor and indoor scenes. By dividing the data according to gaze direction recorded with an eye tracker, they demonstrated that gamma-band activity (90 ± 30 Hz) is hexa-directionally modulated, i.e., there is higher power in directions that are multiples of 60° than control periodicities, and this effect is localized in the MTL.

Taken together, this evidence suggests a link between the MTL and viewing behavior.

Viewing behavior and the hippocampus are also related through memory-guided eye movements (Ryan & Shen, 2020; Meister & Buffalo 2016; Kragel & Voss 2022), whereby the eyes move according to memorized content, recapitulating the exploration strategy adopted during encoding (Wynn et al., 2020; Johansonn et al., 2022). Another proposed function for the hippocampal formation is in fact that of encoding and retrieving memories, of which eye movements can be an integral part (Noton & Stark, 1971). Starting from the seminal evidence of patient HM who, after hippocampal resection, could not form new memories (Scoville & Milner, 1957), the literature abounds with reports of hippocampal involvement in memory which will be reviewed in the next paragraph.

## *Non-spatial, relational representations*

A parallel line of research has implicated the hippocampal formation in the storage and retrieval of declarative knowledge (Squire, 1992; Eichenbaum & Cohen, 2004). The hippocampus has an anatomically-privileged position to receive inputs from multiple cortical and subcortical sources (Squire et al., 2004; Lavenex & Amaral, 2000; Felleman & Van Essen 1991). These separate sources of information are bound by the hippocampus to form a unitary representation of episodes or events (Squire, 1992; Squire et al., 2004; Davachi, 2006) by providing the spatiotemporal context (O'Keefe & Nadel, 1978; Schonaut et al., 2023; Nielsen et al., 2015) that enables encoding the relation between elements of experiences (Eichenbaum & Cohen 2014; Bellmund et al., 2018).

Most of the early studies on memory come from neuropsychology. Patients with hippocampal damage show memory deficits (reviewed in Nadel & Moscovitch, 1997) for relations in spatial, temporal and associative domains alike (Konkel et al., 2008) leading to the suggestion that the hippocampus is critical for the formation of long-term memory. These findings were paralleled by neural recordings showing increased firing when learning and retrieving associations between stimuli (Wirth et al., 2003; Messinger et al., 2001; Ison et al., 2015; Biane et al., 2023: Young et al., 1994; Liu et al., 2023; Staresina et al., 2019; Kunz et al., 2024).

Similarly to findings in the spatial domain where individual neurons code for a specific location in the environment, there are several reports of cells in the MTL responding to specific items. A first interesting finding is that of "concept cells", cells that respond to specific concepts (e.g., Jennifer Aniston) irrespective of the modality of presentation and during recall of the same concept (Quiroga et al., 2005; Quiroga et al., 2009). These neurons share some characteristics of place cells, for instance their selectivity to specific items (Quiroga, 2012). Recent evidence has further implicated the reactivation of these cells when pronouns referring to memorized concepts are read (Dijksterhuis et al., 2024). Similarly, there is evidence of single neurons coding for higher-levels of abstraction such as conceptual categories (Reber et al., 2019) or events in a movie (Gelbard-Sagiv et al., 2008).

Further evidence in favor of this multi-domain relational processing comes from studies drawing parallels between the neural responses in spatial and non-spatial domains. In spatial navigation tasks, hippocampal neurons increase firing to signal memorized locations (Qasim et al., 2019), specific events during exploration such as lap number (Sun et al., 2020) or relative location across environments (Miller et al., 2015), whereas in a mental navigation task entorhinal neurons signal memorized temporal intervals (Neupane et al., 2024). Furthermore, it has been shown that cells in the MTL can respond to other arbitrary, non-spatial dimensions such as time (Kraus et al., 2013; Umbach et al., 2020; Schonaut et al., 2023), sounds (Aronov et al., 2017), abstract schemas (Baraduc et al., 2019), relations (Bausch et al., 2021) or conjunction of items (Kolibius et al., 2023). Further evidence for the involvement of spatial codes in the organization of abstract knowledge comes from a recent study in humans showing a grid-like response for pictures organized according to their emotional valence (Qasim et al., 2023). An extensive literature has then demonstrated the presence of a grid-like response in fMRI for memorized stimuli arranged in a two-dimensional space, be them shapes (Costantinescu et al., 2016), audio-visual objects (Viganò et al., 2020), odors (Bao et al. 2019; Raithel et al., 2023), social information (Park et al. 2021; Liang et al., 2024), abstract reward values (Nitsch et al. 2023) and action-outcome relations (Barnaveli et al. 2024).

There is also an extensive literature linking theta and gamma oscillations in the hippocampal formation to memory encoding and retrieval (Herweg et al., 2020a; Etter et al., 2023a), both in the spatial (e.g., Herweg et al., 2020b) and, in non-spatial domain (e.g., Kota et al., 2020), mainly in the context of episodic memory tasks. Some of the studies reported above find a correlation between hippocampal theta and memory performance, for instance Jutras and colleagues (2013) showed a higher hippocampal theta phase synchronization following saccades for later remembered items or Vivekananda and colleagues (2019) found a higher theta for remembered items during a location memory task. The timing of theta oscillations is causally involved in spatial memory tasks, such that interfering with theta oscillations frequency impacts spatial memory (Quirk et al., 2021; Etter et al., 2023b). In the episodic memory domain, hippocampal theta power increases during encoding of later remembered items (Lega et al., 2012; Joensen et al., 2023) and prior to recall events (Rudoler et al., 2023; Solomon et al., 2019a). Similarly, hippocampal theta phase is synchronized across trials during encoding and retrieval (ter Wal et al., 2021; Kota et al., 2020) and synchronizes with a widespread network of brain areas (Solomon et al., 2017; Watrous et al., 2013) of which the entorhinal cortex is a main hub (Solomon et al., 2019b) and with the cortex influencing hippocampal activity during retrieval (Gattas et al., 2023).

Gamma activity is involved in memory formation (Jutras et al., 2009; reviewed in Griffiths & Jensen, 2023), with fast gamma involved in encoding of new memories, contrasting with slow gamma that seemed to be more related to spatial processing (Zheng et al., 2016). Similarly to the spatial domain, neural assemblies are associated with specific gamma phases in support of memory formation (Umbach et al., 2022).

Theta-gamma phase amplitude coupling is also involved in memory formation (Lega et al., 2016; Fell et al., 2003), with gamma being higher at opposite phases between encoding and retrieval (Saint-Amour di Chenaz et al., 2023).

## *Questions addressed in the thesis*

The evidence presented above suggests that hippocampal neurons respond to spatial variables, such as specific locations in space, and that in primates this firing is mostly driven by eye position rather than body position. At the same time, neurons in the hippocampus respond to specific concepts, such as Jennifer Aniston. Similarly, theta (and gamma) oscillations signal spatial information such as traveled distance, synchronize following eye movements and are involved in memory formation and retrieval.

A key question is thus to understand what kind of computations the hippocampus is carrying out to support exploration of the external space through bodily- and eye- movements as well as exploration of the internal space of memory.

Although this question will not be answered with only a few experiments, in this thesis i will address two experimental questions that can provide new insights into the cognitive mechanisms of the hippocampal formation and further move our understanding of its role in cognition. Specifically, in the next two chapters i will address the following questions:

1) What are the electrophysiological mechanisms that underlie searching for concepts in memory?

As reviewed above, theta and gamma oscillations are involved in memory encoding and retrieval. However, these oscillations have been often studied in the context of episodic memory tasks, where for instance participants are asked to memorize a list of words for later recall (e.g., Solomon et al., 2019a), a dominant paradigm since it was first introduced (Ebbinghaus, 1885). The extent to which these oscillations underlie conceptual exploration in a way that is similar to exploration of the external space is not known. However, this is a crucial piece of evidence that would demonstrate whether the hippocampus is similarly involved in the exploration of both spatial and non-spatial domains. In this respect, an interesting task is verbal fluency, during which participants are asked to name concepts from a given semantic category for two minutes. During such tasks, participants' behavior resembles strategies used in spatial navigation, thus making it suitable to test the hypothesis of a continuity between spatial and conceptual exploration. We recorded LFP from the hippocampus of epileptic patients engaged in this task to investigate the electrophysiological mechanism of finding a concept in memory. Results of this investigation are presented in chapter 2.

2) Do we observe a signature of spatial exploration such as the grid-like response when space is explored through attention?

Grid-like activity has been observed during spatial exploration, both through physical movements as well as through eye movements in primates, including humans. At the same time in non-human primates, grid-like activity underlies exploration through covert attention, i.e., when eye position is dissociated from the locus of attention, thus suggesting that movements of attention, without externally observable body- or eye- movements, can give rise to the typical grid-like response. However, it is still not known whether movements of attention elicit a grid-like response also in humans. If this is the case, we can speculate on the possible attention-based exploration of conceptual spaces and thus suggest attention as a common cognitive mechanism that enables the hippocampus to support exploration in both physical and conceptual spaces. We tested the hypothesis that attention-based exploration can give to the grid-like response in humans using magnetoencephalography in combination with a newly developed method to investigate grid-like responses based on frequency tagging. The results of this experiment will be discussed in chapter 3.

# *Chapter 2*
# *Foraging for concepts: neurophysiological mechanisms underlying mental search in semantic memory*

This chapter and the results here reported are part of an ongoing investigation. I would like to acknowledge the contribution of the coauthors in this project: Simone Viganò (equal contribution), Roberto Mai, Christian F. Doeller and Roberto Bottini.

## *Introduction*

The ability to seek resources in an environment is essential for survival. Searching behaviors vary in complexity, from plants extending roots to find water, to animals navigating their surroundings looking for food or shelter. Humans take this even further, engaging in abstract searches like browsing Wikipedia or digging through long-term memory for ideas and information. This internal form of exploration, in particular, has intrigued philosophers and cognitive scientists for centuries, leading some to suggest that organizing and searching through knowledge in our minds mirrors how we map locations - and search through them - in the physical world (e.g., St. Augustine, Confessions, Book X, 398; James 1890; Shepard et al. 1987; Lakoff & Johnson 1999; Gardenfors 2000, 2014; Bottini & Doeller 2020). In more recent years, this idea has motivated empirical investigations in cognitive science, leading to the proposal that during mental exploration of conceptual spaces (e.g., during semantic fluency tasks, where participants are asked to mention all the animals or professions they can think of), humans show similarities with the way in which animals forage for resources in the environment (Todd et al. 2012). This was supported, for instance, by the observation that people tend to retrieve together words that are similar in meaning (and thus that are close in the semantic space) and/or tend to exploit narrow categorical regions of the semantic space before focusing on other ones, mimicking "area-restricted search" behaviors that are ubiquitously observed in the animal kingdom (Laing, 1937; Tinbergen et al. 1967; Kareiva & Odell 1987; Hills et al. 2015; for reviews see Dorfman et al. 2022; Todd & Hills 2020).

Several studies in cognitive neuroscience (Constantinescu et al. 2016; Theves et al. 2019; 2020; Bao et al. 2019; Viganò & Piazza 2020, Viganò et al. 2021, 2023; Park et al. 2021; Nitsch et al. 2023; Barnaveli et al. 2024; Qasim et al. 2023) have indicated that the human brain can indeed repurpose similar areas and coding schemes to both represent spatial information about the external physical environment, as well as to internally organize more abstract or conceptual knowledge in memory in the form of relational models, usually referred to as "cognitive maps" (Tolman 1948, for reviews see Bellmund et al. 2018; Behrens et al. 2018; Bottini & Doeller 2020; Buzsaki & Moser 2013). These studies pointed to the hippocampal-entorhinal region in the medial temporal lobe of the brain, which is mostly known for its crucial involvement in spatial navigation and orientation (Moser et al., 2017) as well as in episodic memory (Squire 2004; Dickerson & Eichenbaum, 2010). Consistently, both clinical studies (e.g., Lee et al. 2021; Gleissner & Elger 2001) as well as non-invasive functional neuroimaging (e.g., e.g., Sheldon & Moscovitch 2012; Glikmann-Johnston et al. 2015; Lundin et al. 2023; Nour et al. 2023) have recently linked the hippocampus to performance in semantic fluency tasks, potentially extending its role beyond the spatial and episodic domains, to the realm of mentally search in semantic memory.

However, a clear description of the physiological mechanisms that might govern hippocampal activity in this process is currently missing. In this study, we aimed to fill this gap by examining the physiological behavior of the human hippocampus during semantic foraging using intracranial recordings, which offer an unparalleled anatomical specificity paired with high temporal resolution. By operating under the hypothesis that the hippocampus serves as a general-purpose interface for efficiently organizing and exploring information across different domains, we took inspiration from the spatial navigation literature to isolate the potential physiological signatures of searching behavior in this region.

For instance, it is now well established that when related to external exploration and navigation of the physical world, the rhythm of rodents' hippocampal activity shows a typical oscillatory pattern in the lower frequency range denoted as theta, usually up to 8 Hz (e.g., Vanderwolf et al. 1969; Herweg et al., 2020a; Jacobs, 2014). Such rhythm is known to influence the retrieval of reward locations from spatial memory (Winson, 1978), and to modulate the spatial periodicity of entorhinal grid cells (Koenig et al. 2011; Brandon et al., 2011), which are necessary for correctly orienting in the environment. The presence and importance of this rhythmic activity for spatial tasks have been confirmed in humans during experiments that involve real-life ambulation (Aghajan et al. 2017; Stangl et al. 2020) and exploration of virtual reality environments (Kahana et al. 1999; Ekstrom et al. 2005), with theta activity scaling as a function of traveled distance (e.g., Bush et al. 2017) or goal proximity during spatial search (Liu et al., 2023). Additionally, research suggests that hippocampal theta rhythm plays a role in visual search tasks in both humans and non-human primates (e.g., Jutras et al. 2013; Kragel et al. 2020; Hoffman et al. 2013) and is also involved in retrieving information from episodic memory (e.g., Solomon et al. 2019a; Rudoler et al., 2023; Lega et al., 2012). Thus, hippocampal theta rhythm could serve as a key marker for searching behaviors. Based on this evidence, we predicted that during semantic foraging tasks—where individuals mentally navigate their semantic memory to retrieve concepts—the hippocampus would display increased theta activity. This heightened theta activity is expected to reflect the characteristics of the searched semantic environment.

## *Results*

### *Exploration of conceptual spaces mimics spatial foraging behavior*

To investigate the physiological bases of searching and finding concepts in memory, we asked twenty patients with drug-resistant epilepsy, implanted with stereo-EEG (sEEG)(Figure 1a,b,c), to perform a categorical verbal fluency task (Bousfield & Sedgewick, 1944). They were instructed to name as many concepts as possible from three semantic categories - animals, cities or professions - in different runs and blocks (Figure 1d). Participants produced an average of 24.18 words (SD=7.53) with a mean inter-word time interval (ITI) of 5.37 s (SD=1.63; Figure 1f,g), without statistical differences across categories (number of words: F(2,56)=1.93, p=.155; ITI: F(2,56)=0.992, p=.377) nor across block repetitions (number of words: F(2,57)=0.095, p=.909; ITI: F(2,57)=0.418, p=.660)(see Supplementary Figure 1a,b).

How can we describe searching behavior in conceptual spaces? When referring to the spatial domain, we can do it by monitoring several factors, such as the traveled distance between visited locations (expressed for instance in meters) or the time spent to move between locations (expressed for instance in seconds). In the conceptual domain, where concepts are referred to with words, this might be less trivial. Although time could still be easily defined as the temporal interval between subsequently retrieved words (thus, ITI), a metric for their underlying semantic distance is not obvious. In cognitive science, distances between concepts are usually conceived as being the inverse of their similarity (e.g., Shepard, 1987; Gardenfors, 2000), but similarity between words can be expressed in many different ways: they can be similar to each other because their referent concepts are thematically related, or because they equally occur in a language, or are composed by the same number of letters, and so on. Following the intuition that, as it happens in physical space, more distant elements in memory might require more time to be reached (assuming constant speed), we evaluated the best model of distances between words by correlating the ITI with different distance metrics that have been used in the literature to describe their dissimilarity (the inverse of similarity, Figure 1h, see Methods). Our results indicate that participants' timing behavior was most correlated with cosine distances in a high-dimensional vector space model of word meaning (FastText, Bojanowski et al., 2016; highest Pearson's r M=0.331, CI=[0.289; 0.373], t(19)=19.191, p < .001; significantly higher than all the other models with p <0.001 Bonferroni corrected; see Supplementary Table 1 and Supplementary Table 2 for the individual comparisons), therefore we used this as a metric of semantic distance throughout the rest of our investigation (Figure 1i; see Supplementary Figure 1c for a confirmation that the effect is not affected by category).

Using this metric, we found that participants' verbalizations did not proceed randomly, but semantically related words tended to occur close to each other (t(19)=-10.846, p<0.001, M=-4.391 SD=1.810, CI=[-5.376; -3.405], see Methods)(Figure 1j). Furthermore, we noticed that on rare occasions participants deviated from this pattern, producing words with relatively higher semantic distances before returning to retrieving semantically related words (Figure 1k; see Methods). These events happened on average 29% of the time (Figure 1k, inner panel). We interpreted these transitions as corresponding to "semantic switches" (see Lundin et al. 2023 and Kumar et al. 2024 for similar measures), which occurred on average after 2-3 words (Figure 1l,m) and most likely defined changes of strategy from local exploitation of a current cluster to the next one: indeed, semantic distance was significantly lower when we computed it between words that appear within the same two subsequent switch events (“within clusters”) compared to words that appear across different switch events (“across clusters”)(t(19)=10.621, p<0.001; confirmed with a permutation approach where cluster switch were randomly positioned in each “foraging” block, 1000 permutations, p <.001)(see Methods)(Figure 1n,o). Interestingly, and in line with similar previous observations (Hills et al. 2015), ITIs were significantly correlated with semantic distances even within clusters (t(19)=18.38, p<0.001), possibly indicating the use of an associative search strategy in which the association between words is driving their selection rather the categorical membership.

Taken together, these results indicate that participants can successfully complete the semantic foraging procedure and that their search in semantic spaces is reminiscent of how animals search for resources in physical environments (e.g., Hills & Butterfill 2015; Hills et al. 2012; 2015; Todd & Hills 2002). Is this reflected in the underlying neurophysiology of the brain? Specifically, is the hippocampal theta rhythm involved in the navigation of a conceptual space?

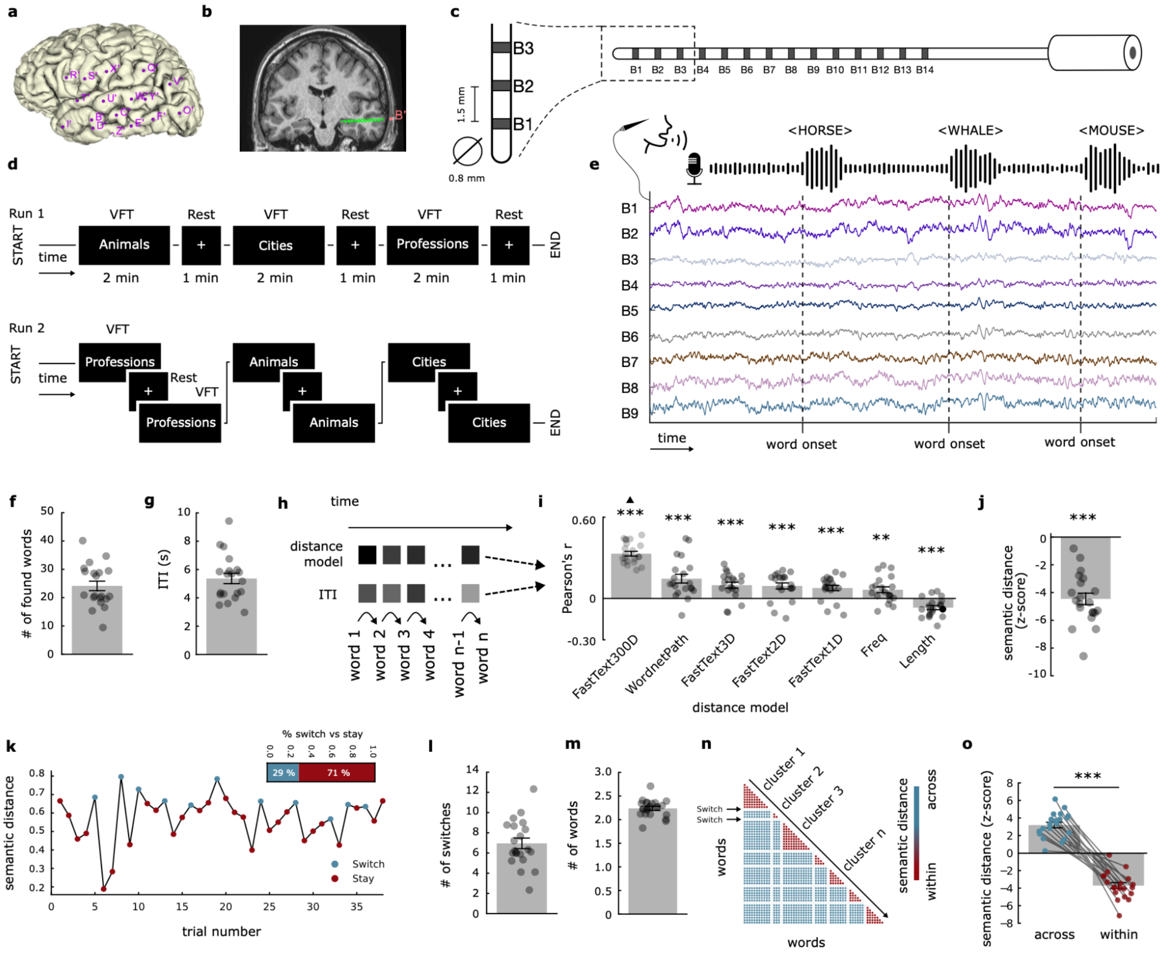


**Figure 1 - Experimental design and behavioral results. a**. lateral view with an example of the implant montage for one participant. Each purple dot is the point where an electrode, indicated with a letter, is inserted. **b**. coronal view of the brain and of an example electrode (B') traversing the temporal lobe to target the hippocampus. **c**. schematic of an electrode, with contacts indicated by numbered letters (e.g., B1, B2, B3, etc.) and the relative spacing between them, as well as diameter of the shaft. Lower number indicates more medial contacts. **d**. schematic of the foraging task procedure, where participants were asked to perform Verbal Fluency Tasks (VFT) mentally searching for names of either animals, cities, or professions in different blocks of 2 minutes, separated by short rest blocks of 1 minute (Run 1, upper). In Run 2 instead (lower), after the rest period participants perform another VFT of the same category **e**. rationale of the general approach, where the audio track recorder from a microphone is used to determine the onset of the word and then segment the sEEG trace into epochs of interest. **f**. average number of words found by participants (see also Supplementary Figure 1a for results cross categories and Supplementary Figure 1b for results across task blocks). **g.** average ITIs between subsequently retrieved words (see also Supplementary Figure 1a for results cross categories and Supplementary Figure 1b for results across task blocks). **h**. rationale of the correlational approach between ITIs and distances between words (see Methods for details). **i**. results of the correlation analysis between ITIs and different distance measures between words. Cosine distance between FastText in 300 dimensions (FastText300D) seems to be the (relative) best model of participants ITIs (see also Supplementary Figure 1c for results cross categories). **j**. average z-scored semantic distance between subsequently pronounced words. Values below zero indicate that participants did not pronounce words randomly, because the average distance between subsequent words was below that expected by random walks (see Methods). **k**. example time-series of the different word-by-word transitions for a single block of foraging, where each point represents the semantic distance between a word and the one immediately preceding. Blue dots are indicated as "switch" and defined as trials where the semantic distance is higher compared to the neighboring transitions (Hills et al., 2012; see Methods). The insert bar shows the percentage of switch events compared to stay events across all participants and task blocks. **l**. average number of switches across participants. **m**. average number of words between subsequent switches across participants. **n**. schematic of the analysis used to quantify whether the semantic distance between words that happen in the same cluster (so within two subsequent switches, indicated in red) is lower than that between words that happen across different clusters (indicated in blu). For proper statistical comparison, the analysis is then repeated by randomly shuffling the position of the switches (see Methods). **o**. semantic distances between words happening across clusters is significantly higher than that happening within clusters. Results are confirmed by a shuffling procedure (see Methods).

*** p<.001, ** p <.01, ▲ higher than all the others with p <.001 corrected.

## *Hippocampal theta power is significantly higher before finding a concept compared to after the concept has been found*

To investigate whether hippocampal theta rhythm is involved in the navigation of a conceptual space, we analyzed sEEG data (Figure 1a,b,c,e). All the participants had contacts in the medial temporal lobe, targeting the hippocampus at various coordinates (174 bipolar contacts in total, see Table 1), thus allowing us to record local-field potentials (LFP) and looking for physiological signatures of searching and finding concepts during semantic foraging. We assumed that such physiological signatures would manifest before the actual verbalization of a word (Addante et al., 2010; Fell et al., 2011; Solomon et al., 2019a), so we started our analyses by segmenting the recordings based on word onsets (Figure 2a) and we compared the time period before verbalization (-1 to 0 s, assuming people were searching for and finding concepts in this time frame) to the time period after it (from 0 to +1 s, hereafter considered as baseline, except where explicitly stated, because we considered it as a moment when the search stopped and participants were articulating and externalizing the concept they had found).

We observed that hippocampal theta (3-8 Hz) was significantly higher before compared to after word onset (t(19)=6.077, p<0.001)(Figure 2b). This effect was not dependent on the category (one-way ANOVA: F(2, 56)=0.880, p=0.420; Supplementary Figure 2a) nor block repetitions (one-way ANOVA: F(2, 57)=2.3, p=0.109; Supplementary Figure 2b), and it was replicated using different baseline periods (vs post-offset: t(19)=5.324, p<0.001; vs rest: t(19)=3.605, p=0.001; vs silence: t(19)=1.204, p=0.243; Figure 2c). Interestingly, although numerically higher, theta power was statistically indistinguishable when compared with long silence periods between words (see Methods), where participants are likely to be engaged in mentally searching for concepts. Additionally, we observed that the reported theta effect was also present in contacts recording from the lateral temporal lobe (LTL; t(19)=3.177, p=0.004)(Supplementary Figure 3), without statistically significant differences from the hippocampus (t(19)=0.563, p=0.579)(Figure 2d).

All these results are in line with the literature on spatial navigation (Bush et al. 2017; Kahana et al. 1999; Ekstrom et al. 2005), where hippocampal and cortical theta increase during movement periods compared to stationary periods, thus supporting the hypothesis that theta might be involved in both external/spatial and internal/conceptual foraging.

## *Time-frequency analysis inform on the time course of theta power increase and additionally reveals significant modulation of gamma frequencies before a concept is found*

To confirm our results at a finer temporal scale and to verify whether they are specific to theta, we looked at the whole time-frequency representation focusing on 1 s preceding the utterance of each word (see Methods). Confirming our previous analysis, we found a significant and sustained increase in hippocampal theta power (3 to 8 Hz), but also a more transient increase in the gamma frequency range, above 51 Hz (p<.05, FDR corr.)(Figure 2e). Similarly to the effect in theta, the effect in gamma was not dependent on category (one way ANOVA F(2, 56)=0.880, p=0.42; Supplementary Figure 4a) but it changed as a function of block repetitions (F(2,57)=3.644, p=0.032 Supplementary Figure 4b), and it was only partially corresponding with the effect in theta in terms of baseline selection. In fact, similarly to theta, gamma power was significantly higher than post-offset (t(19)=3.862, p=0.001) but i) was significantly higher compared to silence periods (t(19)=2.928, p=0.008) and ii) it was not statistically different from resting periods (t(19)=0.906, p=0.375)(Figure 2f). The power increase in the two frequency bands differed also in their time course: while theta power was significantly higher than the baseline across the entire time window, with a peak at -.374 s before word onset (CI=[-.384, -.35], see Methods), gamma power increase was statistically significant only earlier in time, with a peak at about -.866 s before word onset (CI=[-.866, -.786])(Figure 2g) and close to word onset becomes significantly lower than the baseline.

When applied to the LTL, these analyses revealed a different dynamic. Here, we observed a wider range of frequencies encompassing both theta and alpha bands (from 3 to 23 Hz) being significantly higher than baseline only in a confined time interval (between -1 and -0.6 s from word onset). Additionally, we observed a negative modulation of gamma frequencies, above 40 Hz in the same time window (p<.05, FDR corrected)(Figure 2h,i; see Supplementary Figure 5 for additional analyses).

Taken together these findings indicate that the period preceding word verbalization, thus when concepts are still searched for and then found, is associated with a significant increase in hippocampal theta and gamma power, while the lateral temporal lobe exhibits a more transient increase in the broader theta-alpha range and a simultaneous decrease in gamma power. In the following analyses we focused on characterizing the role of hippocampal theta and gamma in memory search. Nevertheless, LTL showed interesting temporal and frequency dynamics that are not restricted to theta and gamma and will need to be explored further in future works.

| Patient ID | Sex | Age (years) | # Trials | Hip contacts | LTL contacts | Hemisphere |
|---|---|---|---|---|---|---|
| 01 | M | 24 | 121 | 3 | 14 | L |
| 03 | F | 24 | 134 | 6 | 7 | L |
| 04 | F | 42 | 61 | 7 | 6 | L |
| 05 | F | 32 | 123 | 3 | 6 | L |
| 06 | F | 44 | 130 | 8 | 4 | L |
| 07 | F | 46 | 132 | 7 | 12 | L |
| 08 | M | 27 | 118 | 6 | 7 | R |
| 09 | M | 30 | 123 | 7 | 12 | L |
| 10 | M | 35 | 106 | 9 | 8 | L |
| 11 | M | 39 | 138 | 18 | 13 | L+R |
| 12 | M | 29 | 247 | 10 | 4 | R |
| 13 | M | 28 | 174 | 13 | 10 | L+R |
| 14 | M | 30 | 126 | 5 | 16 | R |
| 15 | F | 27 | 136 | 18 | 7 | L+R |
| 16 | M | 29 | 255 | 8 | 9 | L |
| 17 | F | 20 | 176 | 13 | 17 | L+R |
| 18 | F | 23 | 176 | 7 | 25 | L |
| 19 | F | 28 | 253 | 4 | 1 | R |
| 20 | F | 36 | 216 | 7 | 9 | R |
| 21 | M | 34 | 123 | 15 | 7 | R |
|  |  |  |  | 174 | 194 |  |

**Table 1. Participants demographics**

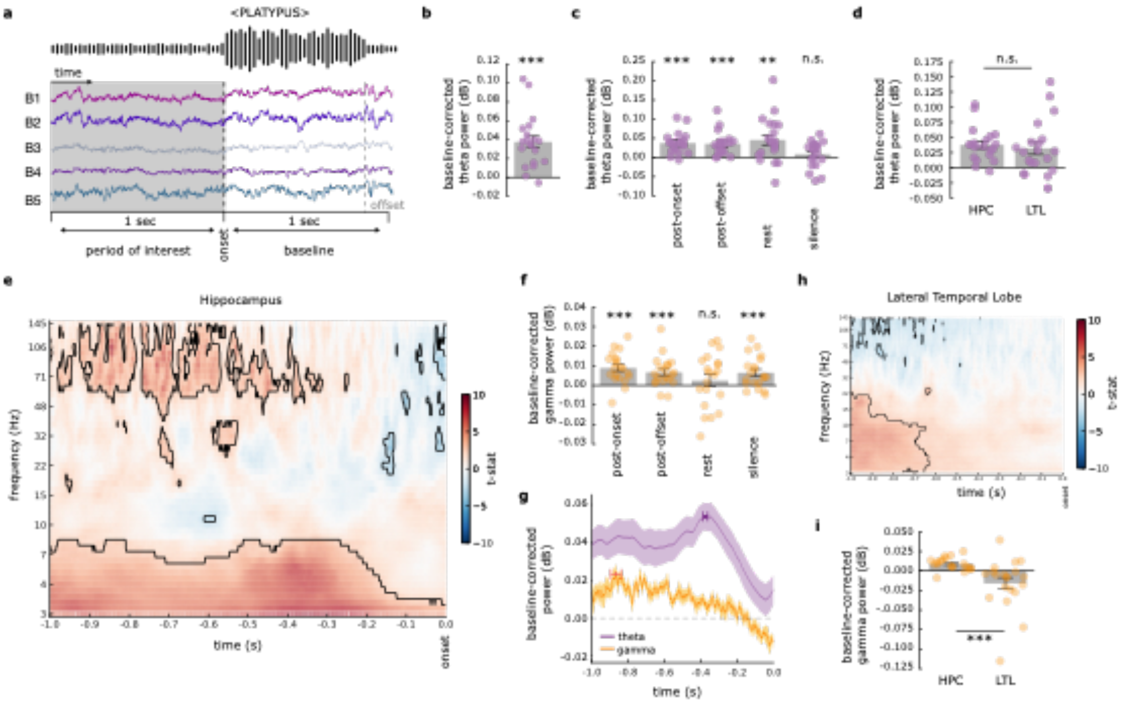


**Figure 2 Time-frequency analysis of hippocampal and lateral temporal contacts during semantic foraging** - Frequency analysis. **a**. rationale of the approach, where we compared the sEEG signal in the time window of interest (1 s before word onset) to a baseline period (1 s after word onset). **b**. theta-power (3-8 Hz) was higher before word onset (see also Supplementary Figure 2 for results cross categories and blocks). **c**. partial replication of the previous results across different baseline (see Methods). **d**. theta power increase in the period of interest is not statistically different between hippocampus (HPC) and lateral temporal lobe (LTL)(see also Supplementary Figure 3 for results in LTL cross categories and blocks). **e**. time-frequency analysis for the period of interest in the hippocampus reveals effects not only in theta band but also in gamma (see Methods). **f**. effect in gamma is partially replicated across different baselines (see also Supplementary Figure 4 for main results across categories and blocks). **g**. time course of the effect in theta and gamma. Shaded area represents standard error of the mean. The peak of the curve is indicated with a circle and a 97.5% confidence interval, estimated with a jackknife procedure (see Methods). **h.** time-frequency analysis for the period of interest in LTL reveals a different power modulation and time course for theta and gamma. **i**. direct comparison between hippocampal and LTL gamma (see also Supplementary Figure 5 for results in LTL cross categories and blocks). *** p <.001, ** p <.01, n.s. = non statistically significant (p>.05)

### ***Hippocampal rhythms are modulated by the semantic and the temporal distances between retrieved concepts during semantic foraging***

Our previous analyses have revealed a significant involvement of hippocampal theta and gamma in the process of searching for and finding concepts during semantic foraging. We thus aimed to better characterize their role in this process and which aspect of search they may reflect. In the spatial domain, one can describe searching behavior by monitoring, among other factors, the distance traversed between locations, or the time spent to do it. It has been shown that hippocampal theta is modulated as a function of traveled distance (e.g., Bush et al. 2017; Vass et al. 2016). In our behavioral analyses we found indication that semantic distances between subsequently retrieved words affected participants' behavior, influencing the time they needed to produce the next word after the previous one (Figure 1j). Therefore, we asked whether hippocampal activity (in the theta or gamma range) was reflecting this feature.

Following a similar approach from the spatial domain (Liu et al., 2023; Stangl et al., 2020) we fitted two linear-mixed models to the trial-level theta or gamma power using as predictors i) the semantic distance and ii) the temporal distance (ITI) between subsequent words and subject identity as random factor (see Methods). In other words, we tested whether pre-word onset power at trial *t* was predicted by the distance (semantic or temporal) between the word pronounced and trial *t* and the previous one. The model fitting was repeated at each time point before word onset, to investigate the temporal evolution of the effect.

In the hippocampus, we found that the power of theta was significantly predicted by the *semantic* distance between subsequent words between -1s until -0.3 s from word onset ($p < 0.05$, FDR corrected)(Figure 3a) and partially also by their *temporal* distance (ITI, between -1s and -0.77 s and between -0.22 and -0.17 s). The power of gamma, on the other hand, was predicted across several events spanning the entire time window of interest by the *temporal* distance between subsequent words (Figure 3b), but not by their semantic distance. These results seem to suggest that two key aspects of semantic foraging, namely the distance between retrieved words in the semantic space and the time spent to retrieve it, were reflected in the power of two hippocampal frequencies, theta and gamma.

Moreover, by following a previous study that reported a modulation of hippocampal theta as a function of low-dimensional semantic distance between words in an episodic verbal-recall task (Solomon et al. 2019a), we repeated our previous analysis using distances along the first Principal Component (PC) of FastText space (see Methods). Interestingly, we observed a modest but significant modulation of hippocampal theta power as a function of lower-dimensional distances at a later stage, from -0.3 to -0.18 s ($p<0.05$ FDR corrected). Consistent with the observation from previous works that the first PC of linguistic vectors is often explainable by word frequency (Hollis & Westbury 2016; Viganò et al. 2024), we found a similar, significant modulation between -0.292 and -0.23 s ($p<0.05$, FDR corrected) when we repeated our analysis modeling distance between words not with their semantic distance on PC1 but with their difference in linguistic frequency (Figure 3c). Moreover, we also found a significant modulation by linguistic frequency in an earlier time window between -1 and -0.842 s ($p<0.05$, FDR corrected). Gamma power was not significantly predicted ($p>0.05$, FDR corrected) neither by low-dimensional semantic distances (similarly to Solomon et al., 2019a), nor by linguistic frequency differences.

Our analyses indicate that hippocampal theta and gamma rhythms might be linked to the process of searching and finding concepts during mental search by representing the semantic and temporal distances, respectively, between subsequently retrieved words.

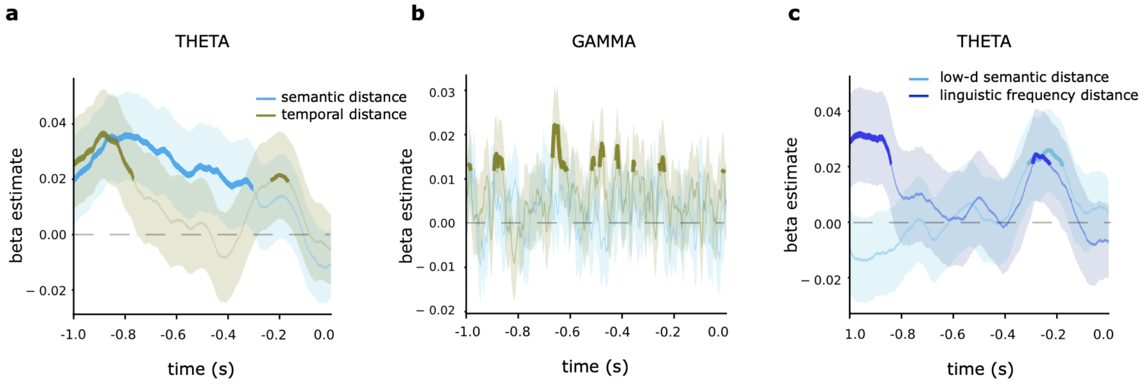


**Figure 3 - Linear mixed-models reveal a significant modulation of time and semantic distance of hippocampal theta and gamma power. a**. hippocampal theta rhythm is significantly predicted by semantic distance between subsequently produced words between -1s until -0.3 s (blue, bold line). Theta power also shows significant modulation by temporal distance between -1s and -0.77 s and between -0.22 and -0.17 s (dark green, bold line). Shaded area represents 97.5% confidence interval. **b**. hippocampal gamma is significantly predicted by temporal distance between subsequently produced words at various time points in the time window of interest (dark green, bold line). No significant modulation as a function of semantic distance is detected. **c**. hippocampal theta rhythm is significantly modulated by low-dimensional (PCA reduced, see Methods) semantic distance in a later period, between -0.3 to -0.18 s (light blue, bold line), which seems to correspond to the time period when it is also predicted by frequency distance between words (dark blue, bold line). Frequency distance also modulates theta between -0.292 and -0.23 s seconds and between -1 and -0.842 s. For all the plots, significant timepoints are p<.05 FDR corrected.

## ***Discussion***

Searching for resources in an environment is crucial for surviving. In this study we investigated whether the neuro-physiological mechanisms that are associated with searching and exploratory behaviors in the external physical world are also recruited when people direct their search internally, looking for concepts or ideas in memory. We focused on hippocampal rhythms, given their well-documented role in spatial navigation and memory (Buzsaki & Moser, 2013). We found that hippocampal theta and gamma activity is associated with searching and finding concepts during semantic verbal fluency tasks, showing increased power before a word is articulated (and thus when the concept is still searched for and then found). We also showed that theta power was mostly modulated, at least in terms of temporal extension, as a function of semantic distance between words, similarly to what happens during navigation for traveled distance (Bush et al. 2017; Vass et al. 2016), and that gamma was modulated as a function of the time passed between two subsequent words (see paragraph “The role of gamma”).

Broadly speaking, our results are in line with the proposal that the brain regions and mechanisms that evolved for spatial navigation can be repurposed to represent and manipulate more abstract conceptual information (Bellmund et al., 2018; Bottini & Doeller, 2020; Buzsaki & Moser, 2013). Previous studies focused on signatures of relational coding in the form of so-called “cognitive maps” to organize knowledge across different perceptual and conceptual domains (visual shapes, Constantinescu et al. 2016; Theves et al. 2019; 2020; odors, Bao et al. 2019; audiovisual items, Viganò & Piazza 2020, Viganò et al. 2021, 2023; social hierarchies, Park et al. 2021; value, Nitsch et al. 2023; action-outcome relationships, Barnaveli et al. 2024; emotions, Qasim et al. 2023), mostly using non-invasive functional neuroimaging. Our study, investigating the physiological bases of semantic foraging using intracranial recordings, significantly extends this body of knowledge for a number of reasons.

First, compared to previous studies, our investigation focuses on a different cognitive function, that of searching. Differently to the study of how things are represented and organized in memory, we focused on the active process of sampling this information following internal and spontaneous tendencies: in other words, rather than focusing on how the map is formed, we focus on how we read and *look* for information in it (see paragraph “A wide-eyed look at mental search and the hippocampus: a link with gaze behavior and attention?” for a more detailed discussion on this). Second, previous studies in humans, with the only exception of Qasim et al. 2023, used artificially created conceptual spaces, organized along two dimensions and where items were distributed uniformly by design. Despite having the clear merit of providing an highly controlled situation for studying the putative involvement of typical neural signatures of cognitive maps such as grid-like codes (Doeller et al. 2010), this approach falls short in his ability to generalize to real-life situations, where concepts and memories are rarely organized into uniform bidimensional spaces. In our study we decided to engage participants in the more ecological task of searching for real concepts in their semantic memory. Showing evidence of hippocampal theta and gamma involvement during the process of searching for and finding concepts and, crucially, of representing their semantic or temporal distance, is a noteworthy advancement in that it links these mechanisms to real-life conceptual knowledge. Third, verbal fluency is a task that lends itself to direct comparison with spatial behavior, given the similarity with spatial foraging in the adopted strategies (Hills et al., 2012). Our behavioral results replicate these findings further strengthening this parallel. At the same time, we showed for the first time that semantic similarity within clusters is higher than across clusters (Figure 1n, o), a crucial comparison showing that this clustering is meaningful and automated methods can be used for this purpose without relying on manual annotations as done in previous studies (Troyer et al., 1997). Furthermore, we showed that semantic distance is predictive of participants timing even within clusters, replicating previous results (Hills et al. 2015), and suggesting that associative strategies are more prominent than categorical. Nevertheless, having observed the presence of clusters in participants' exploration strategies we might wonder whether there is a signature of such tendency in the hippocampal neural activity. One way to test whether this is the case could be to run representational similarity analysis (Kriegeskorte et al., 2008) using as predictor the within/across clusters matrix (Figure 1n). Is theta still reflecting this behavioral strategy? Lundin and colleagues (2023) used functional MRI to study the neural basis of verbal fluency reporting an increase in hippocampal BOLD activity up to cluster switch. Based on this result we may predict that gamma, a probable equivalent of BOLD activity (Logothetis et al., 2001), similarly increases within clusters up to the switch trial. Another possible prediction is that bursts of activity in frequencies such as alpha or beta may be involved in inhibiting (Lundqvist et al., 2024) cluster switching, thus being higher within clusters as compared to switch trials.

Hippocampal rhythms in verbal production tasks have been investigated in the context of episodic memory (Herweg et a., 2020a). One notable study, conducted by Solomon et al. 2019a demonstrated that hippocampal theta rhythm, monitored with sEEG, significantly correlates with the semantic distance between words recalled from previously memorized lists as part of a verbal free-recall task. These results are partially consistent with our observations, in that they too indicate a role of hippocampal theta in representing relational information between words held in memory. However, several differences between the two studies exist. First, Solomon and colleagues investigated the role of hippocampal theta in the context of episodic memory, a cognitive domain that is classically associated with hippocampus (Squire 2004; Dickerson & Eichenbaum, 2010). The nature of their task moreover, where subjects had to memorize and recall lists (that is, sequences) of words, talks to the established role of the hippocampus in constructing, memorizing, and recalling the sequential order of information (e.g., Buzsaki & Tingley, 2018). Our task, where participants are simply given a conceptual category to spontaneously sample concepts from, targets a form of memory (semantic) that is classically not attributed to the hippocampus (Squire et al., 2004, but see Duff 2020). The crucial difference in the cognitive aspects of the tasks is likely reflected by two empirical observations. First, we showed that hippocampal theta power was more extensively modulated by high-dimensional distances between words rather than by PCA-reduced low-dimensional distances, as it was in Solomon et al. This observation is potentially interesting as semantic memory is typically considered to be high dimensional (Piantadosi et al., 2024), and the hippocampus is usually considered to be able to construct low-dimensional cognitive maps (e.g., see Bottini & Doeller 2020). Our results might open the intriguing hypothesis that the hippocampus is constructing low-dimensional representations of the unfolding search experience on the fly, but this will require more extensive investigation to be tested. Such low-dimensional representation was found to correlate with low-level linguistic features such as linguistic frequency, in line with previous reports (Hollis & Westbury., 2016; Viganò et al., 2024), suggesting a possible interpretation. Second, we detected a significant activation in high-frequency gamma bands that was absent in Solomon’s work, further stressing the significant and potentially complementary role of the two investigations. The role of gamma band increase in our study seems to be related to representing the timing between produced words, but more analyses will be helpful in correctly deciphering the role of this frequency band in semantic foraging (see paragraph “The role of gamma”).

The study by Solomon and colleagues thus contributes to the extensive body of literature on hippocampal theta and spatial and episodic memory (see Herweg et al. 2020a for review). As discussed in the Introduction of this thesis, increased theta power during the encoding of items in spatial and episodic memory tasks is predictive of successful later recollection (Lega et al., 2012; Joensen et al., 2023). Although theta rhythms are sometimes also implicated in episodic non-spatial cognitive domains like in the study of Solomon and colleagues, there is less research on their role in exploring conceptual spaces. Our study offered a significant advancement in this direction, more directly linking the role of theta between spatial/external and non-spatial/internal exploration.

### *Linking the hippocampus to language processing and psycholinguistics*

As briefly mentioned above, the role of the hippocampus in semantic memory is still debated. Nevertheless, several recent findings highlight the potential role of hippocampal rhythms in retrieving semantic memories (reviewed in Duff et al., 2020). For instance, it has been shown that, in a picture-naming task, both hippocampal theta (Piai et al., 2016) and gamma (Jafarpour et al., 2017) power increase before picture presentation for sentences that have a higher congruence with respect to the presented picture as compared to less congruent sentences. As an example, theta and gamma power were higher before participants were shown the picture of a key following the sentence “she locked the door with the…” as compared to a picture of a key following the sentence “she walked in here with the …”. These results suggest that hippocampal theta may be involved in the online reactivation of the spatiotemporal context (O’Keefe & Nadel, 1978) provided by the sentence that will later help in finding the correct concept to verbalize. Our study extends this finding by showing a different contribution of the two frequency bands to finding a concept during navigation of a semantic space, namely that theta correlates with semantic distance while gamma with the temporal interval between words.

Interestingly, a close inspection of the temporal course of our results reveals a potentially intriguing parallel between the course of hippocampal theta with proposed models of language processing. A prominent model in psycholinguistics, indeed, differentiates the timing of different stages of speech production and linguistic expression, estimating them on picture naming tasks (Indefrey & Levelt 2004). In particular, the model indicates that after seeing a picture, it takes about 0.175 s to select the target concept (conceptual preparation), then 0.075 s to retrieve the correct lemma (lexical access), and finally about 0.350 s to encode the verbal form of the word, going through phonological retrieval, syllabification, and phonetic encoding. We reasoned that similar stages might apply to our semantic foraging task and that might help us in defining a more precise contribution of hippocampal rhythms before verbalization. In particular, reasoning in reverse order, we assumed that the time preceding -0.425 s from word onset, labeled as “conceptual preparation” in Indefrey and Levelt’s model, might be substituted in our task by the period of looking for different concepts, where people search their semantic memory. The following two periods, from -0.425 s to -0.350 s, and from -0.350 s to 0 s from word onset, respectively labeled as “lexical access” and “form encoding” in the model, would likely be preserved in our task, as they signal the moment of accessing the found concept with its symbol (lexical access), and then connecting it to the correct phonological and phonetic form for verbalization (form encoding). It is intriguing to note that theta power correlates with semantic distance between concepts in an early time window (from -1 to -0.3 s; Figure 3a), it shows a peak at 0.374 s (Figure 2g), and then it correlates with the difference in linguistic frequency (arguably a lower-level linguistic characteristic) from -0.292 to -0.23 s. We may speculate that this tripartite time course might resemble the tripartite model of Levelt, with a first stage dedicated to conceptual search, a second stage indicating that the concept has been found (and thus its lexical form accessed), and a third and final stage reflecting a transformation of the concept in a lower-dimensional, putatively linguistic, format. Further investigation will be needed for testing the soundness of this interpretation. In fact, we also observed a significant correlation with linguistic frequency in an earlier time window that is not predicted by the model. However, there are indications in the literature that during a verbal fluency task participants use lexical information to choose the next word after changing clusters (Hills et al., 2012). We may speculate that the earlier correlation with linguistic frequency is due to the prominence of this linguistic information in that time window, especially in the trials when there is a cluster switch. However, this needs to be further tested.

Given the linguistic nature of the task, it would also be interesting to investigate the potential relation between hippocampal activity and other, language-related cortical areas. One such area can be the lateral temporal lobe, known for being a key part of the semantic/language network (Binder et al., 2009) and conveniently targeted by our electrodes pointing to the medial surface of the temporal lobe, where the hippocampus is located (see example montage in Figure 1a,b). The finding that hippocampal activity is correlated with semantic memory does not imply that the hippocampus is the permanent storage of the memory. In fact, several studies indicate that during recall, cortical, sensory-related areas are reactivated (Simons et al., 2022). This is in line with the proposal that the hippocampus provides pointers to specific memories stored elsewhere in the cortex (Teyler & DiScenna, 1986; Teyler & Rudy 2007). One hypothesis might be that the hippocampus is coordinating the “movements” in the internal mental space by communicating with other cortical areas. For instance, there is evidence that hippocampal activity synchronizes with a large number of cortical areas (Sirota et al., 2008; Gattas et al., 2023) and that hippocampal gamma synchronizes with LTL in spatial memory tasks (Pacheco Estefan et al., 2019). Interestingly, there is also evidence that hippocampal ripples (short, high-frequency bouts) increase synchronously with cortical areas before recollection of episodic memory (Vaz et al., 2019; Norman et al., 2019). Such high-frequency activity has been suggested as a potential mechanism of information transmission (Fernandez Ruiz et al., 2023), but at the same time it may be impaired by the long-distance between the hippocampus and cortex (Buzsaki & Schomburg, 2015). It has been suggested that one way to overcome this limitation is by cross-frequency coupling (Griffiths & Jensen, 2023; Hyafil et al., 2015), whereby the phase of a lower frequency (e.g., theta) synchronizes between distant areas while high-frequency activity (e.g., gamma) synchronizes locally. In the results presented as part of the current investigation we have seen that both hippocampal and LTL theta power increase around 1 s before word onset. Further investigations are needed to understand whether this increase in theta power is accompanied by a coherent phase relationship between the two areas and whether gamma power increases at specific phases within the theta cycle (i.e., phase-amplitude coupling). Another possibility is that hippocampal and lateral temporal areas have a coherent power increase because their theta power share a common originator (Bush et al., 2017), which in rodents is identified as the medial septum (Robinson et al., 2023).

### *The role of gamma*

Our results indicate an increase in gamma power before verbalization. This finding is in line with the memory literature showing that hippocampal gamma power increases during retrieval (Staresina et al., 2016; Treder et al., 2021). Furthermore, we report for the first time that the increase in gamma power is modulated as a function of time elapsed to verbalize the next concept and not by the semantic distance between words. Although novel, we know from the literature that gamma power at the cortical level correlates with several behavioral measures including reaction times (Rieder et al., 2011) and that source-projected MEG activity in the gamma band is higher during the encoding of duration rather than encoding of color information (Kulashekar et al., 2016). Nevertheless, more investigations are needed to understand the contribution of gamma to our semantic foraging task.

In the hippocampus, gamma often co-occurs with the theta rhythm and its amplitude is higher when it's nested in theta oscillations (Colgin & Moser, 2010). Furthermore, theta and gamma interact such that gamma amplitude is higher at specific phases of theta (Lisman & Jensen 2013) and their interaction (termed phase-amplitude coupling, PAC, Aru et al., 2015) is thought to provide the neural basis for episodic memory formation and retrieval, whereby the episode is encoded in the slower theta rhythm and the single elements in distinct gamma cycles (Griffiths & Jensen, 2023) or, more generally, to enable storing and retrieving sequential information (Jensen & Lisman 2013). How would theta-gamma PAC translate to the exploration of a conceptual space? An interesting finding is that the phase at which PAC occurred has been shown to distinguish the category of viewed images (Watrous et al., 2015). We thus may expect that PAC distinguishes the clusters (i.e., categories) that participants are mentally exploring during the verbal fluency task. Another possible function of PAC is that of enabling communication between brain areas (Griffiths & Jensen, 2023; Fries, 2023; Buzsaki et al., 2012). Gamma in fact are fast oscillations that may synchronize only locally or within a short distance (Ray & Maunsell, 2015; Von Stein & Sarnthein, 2000). Theta instead, with its longer time window, synchronizes widely across the hippocampus and cortex (Sirota et al., 2008; Roux et al., 2022). The potential finding of PAC during our task can thus be in line with the hypothesis of communication with other brain areas, with fast gamma possibly routing information transmission to the neocortex via the entorhinal cortex, whereas slow gamma being a more local phenomenon within the subfields of the hippocampus (Colgin et al., 2009; Fernandez-Ruiz et al., 2021).

Another possible role of PAC in our task can be to relate distance and time traveled. We have seen that theta power scales with the distance in the space that is being explored while gamma power scales with the temporal interval between subsequent words. Following the intuition that in the external space time and distance are linked by speed, it would be interesting to see whether a similar correlation is found in hippocampal rhythms during exploration of a conceptual space and specifically whether speed is encoded in the interaction of these rhythms. In fact, we know that both hippocampal theta (McFarland et al., 1975; Slawinska & Kasicki, 1998; Sheremet et al., 2016) and gamma (Ahmed & Mehta, 2012; Zheng et al., 2016) are modulated by speed, such that power increase is mostly seen at higher frequencies within the frequency band for increasing running speeds. A first attempt in this direction can be made by borrowing the definition of speed from physics, thus as being the ratio between distance traveled and time elapsed. This quantity can be correlated with trial-by-trial variations in peak frequency and/or power in the respective frequency band as well as with the strength of the phase-amplitude coupling. Whether the aforementioned definition of speed applies to semantic spaces is however an empirical question that will need to be addressed before proceeding with such analyses.

It is also possible that the observed theta and gamma effects reflect (at least partially) separate processes. We treated gamma as a frequency band, but gamma is very heterogeneous and activity in this range may reflect distinct biological processes which can be fully dissociated only by considering the precise spatial location and cellular origin of the signal (Fernandez-Ruiz et al., 2023; Buzsaki & Wang, 2012). One particularly interesting phenomenon that has been reported in this frequency range in humans (e.g., Norman et al., 2019) is the sharp-wave ripple (SWR; Buzsaki, 2015), fast and short-lived oscillations that are thought to consolidate memories recapitulating previous experience during off-task periods (Yang et al., 2024). The presence of SWRs in the current experiment could be related to the spontaneous storage of the experience of having found a specific word, similarly to what happens for images (Norman et al., 2019). If this is the case then, we might expect that an increase in SWR rate is observed before words that are later repeated in the task as compared to words that are not repeated. Interestingly, we observe a significant difference in gamma power between blocks, which can be an indication in favor of this hypothesis, but further analyses are needed to investigate whether this increase in gamma can be ascribed to putative SWRs. Nevertheless, SWRs should be dissociated from gamma oscillations in order to correctly interpret the findings: according to a recent consensus paper (Liu et al., 2022) this dissociation can be achieved in sEEG recordings by investigating the phase-locking to theta rhythm as well as the temporal and frequency extent of the observed power increase.

### *A wide-eyed look at mental search and the hippocampus: a link with gaze behavior and attention?*

Searching behaviors in primates are not limited to movements of their bodies. In fact, primates, including humans, naturally move their eyes to explore visual scenes (Yarbus, 1967) at a rhythm within the theta range (Otero-Millan et al., 2008; Näher et al., 2023). Interestingly, evidence from monkey electrophysiology indicates that neurons in the hippocampal formation not only respond to spatial locations but mostly map the visual field during visual tasks and free exploration (Mao et al., 2021; Wirth et al., 2017; Killian et al., 2012; Piza et al., 2024). This connection between the hippocampal formation and eye movements is further supported by human invasive and non-invasive neuroimaging studies, which have shown hippocampal activity linked to eye movements across a range of tasks, including visual tracking, visual search, and relational memory (Nau 2018b; Julian et al., 2018; Staudigl et al., 2018; Kragel et al., 2020; Hoffman et al., 2013; Hannula & Ranganath, 2009; Slama et al., 2021). Additionally, neuropsychological findings revealed that amnesic patients with hippocampal damage exhibit less efficient eye-based search behaviors in the visual environment (Lucas et al., 2019; Hannula et al., 2007).

Eye movements provide a behavioral readout of planning strategies during navigation, reflecting for instance the goal location (Lakshminarasimhan et al., 2020) in simple environments while recapitulating its structure in more complex environments (Zhu et al., 2022). Furthermore, they allow to track the dynamics of spatial exploration (Zhu et al., 2022), which interestingly is impaired when eye movements are restricted (Lakshminarasimhan et al., 2020). In the memory domain, there is evidence that during recall of previously memorize pictures participants recapitulate the sequence of eye movements that were made during encoding (Wynn et al., 2020; Johansonn et al., 2022), indicating that eye movements may be an integral part of the memory trace that participants are retrieving (Noton & Stark, 1971). Similarly, while participants are keeping in memory the items that were previously presented, their eyes move to the location of the item even if the location is irrelevant for task performance (Van Ede et al., 2019) and, even when eye movements are constrained, small, fixational eye movements reflect the orientation of the to-be-remembered item (Linde-Domingo & Spitzer, 2023).

Complementing this evidence, recent work from our lab has demonstrated that spontaneous eye movements reflect the representational geometry of conceptual spaces during verbal fluency tasks (Viganò et al., 2024): when participants were saying numbers, their eyes moved according to a left-to-right magnitude-based order (Dahene et al., 1993); when participants were saying colors, their eye movements reflected distances between colors in subjects' own color wheels (Shepard & Cooper, 1992); when saying animals their eyes were moving according to the position of the animal in PC1/frequency space. In this experiment participants received no visual stimulation while sat in dim lit rooms, thus eye movements could not have been influenced by external stimulation. When there is nothing to see, participants may spontaneously move their eyes to explore their internal mental space in search of the concept to verbalize. Interestingly, these effects were observed in the 0.5 s before verbalization. The timing of these eye-movements allows us to draw an interesting parallel with the current investigation, which makes us wonder to what extent the observed effect depends on eye movements. Further experiments with concurrent eye tracking recordings are needed to answer this question. Nevertheless, a more interesting hypothesis pertains to the mechanism behind memory search. Spatial codes, such as the grid-like response, can be observed in non-human primates even without bodily or eye movements (Wilming et al., 2018), thus being driven by covert attention. Eye movements, in both human and non-human primates, have in fact been interpreted as reflecting the location of attention (Kustov & Robinson, 1996) but at the same time it should be possible to dissociate the location of attention from the current eye position (Posner, 1980). Can attention be the mechanism enabling search in conceptual space? If this is the case, also humans should exhibit typical spatial codes when their eye movements are restricted. In the next chapter I will present results of an experiment in which we focused on one specific spatial code, the grid-like response, to investigate its presence in a visual task when participants eye movements are restricted.

## Conclusions

We have observed that hippocampal theta and gamma power increase when participants are looking for and finding concepts in their mental space during a verbal fluency task. This power increase is modulated by the semantic and temporal distance between subsequent words, suggesting its functional role in the exploration of a conceptual space. These results reveal important insights about the hippocampal role in cognition, strengthening the hypothesis of a repurposing of its function across spatial and non-spatial domains (Bottini & Doeller, 2020; Bellmund et al., 2018; Buzsaki & Moser, 2013). Further analyses on this dataset are needed to fully characterize the hippocampal role in memory search, as well as further research controlling for the contribution of eye movements to the memory search process.

## *Methods*

### *Participants*

Twenty-one patients with drug-resistant epilepsy were recruited for the study. Patients underwent surgery and were implanted with intracranial stereotactic-electroencephalography depth electrodes (sEEG, Nihon-Koden) for seizure monitoring and localization of epileptic regions. All patients had at least one contact in the hippocampus. Additional information about the patients can be found in Table 1. The study was approved by the ethical committee of the University of Trento and of the Niguarda Hospital.

### *Experimental design*

Participants performed a categorical verbal fluency task for three different semantic categories (animals, professions, cities). The name of a category was presented on a computer screen for three seconds, followed by a 0.1 s long sound cue indicating the start of the task block. Participants had then two minutes to name as many concepts as possible for the given category. They were instructed to speak calmly, without rushing to avoid creating overlap between words. During these two minutes a green fixation cross was presented on a black screen, after which the fixation cross turned white and another sound cue (0.1 s) instructed participants to rest for one minute. In a first run, this alternation of verbal fluency task and rest was repeated three times, one for each category with the order of the categories randomized across participants (Figure 1d). In a second run instead, after the resting period, participants were presented again with the same category and were instructed to retrieve even more concepts than in previous blocks, with the possibility to repeat concepts that were already being said. This manipulation was introduced to address other scientific questions that are not part of the current investigation.

Before the main experimental procedure with the three aforementioned categories, participants familiarized themselves with the verbal fluency task with the category “objects”, being asked to mention for two minutes all the objects they could think of. This block was not recorded and was thus not used in the analyses.

Visual and auditory presentation, recording of participants' voices and control of experimental timings were performed using MATLAB and Psychtoolbox (Brainard, 1997). Lights were switched off during the experiment so that the room was dimly lit to minimize the influence of external visual information.

One participant (Participant ID 1) did not do the task for the “cities” category, thus for this participant only the data of the other two categories were used.

### *Experimental events definition*

Audio recordings of the participants were segmented using Audacity (https://www.audacityteam.org/). The generated time stamps were visually inspected and labelled with the pronounced word (S.V.; G.G.). Time stamps of each word were realigned to the trigger sent during the sEEG recording at the beginning of the corresponding foraging block. Epochs were defined as the time window starting 1.5 s before word onset and ending 1.5 s after word onset. Within these 1.5 s windows only 1 s was of interest, 0.5 s were included to account for edge artefacts caused by time-frequency analysis (Cohen, 2014; see later).

Additional epochs of interest were defined based on silence periods between words. We considered only silence periods at least 5 s long. These time periods were further segmented in 2 s long time windows, to match the duration of the word events and including 0.5 s to account for edge artefacts. Similarly, the resting periods were segmented in 2 s long time windows.

### *Behavioral descriptive statistics*

We evaluated participants' behavior by calculating the amount of words produced in each foraging task block as well as their inter-word time interval. We used a series of one-way analysis of variance (ANOVA) to compare the amount of words recalled between semantic categories and between repetitions of the task. Similarly, we compared the inter-word time interval across categories and across repetitions. These first analyses provided a descriptive measure of participants' exploration behavior.

### *Evaluating semantic distances as predictors of behavior*

To investigate which distance metric better accounted for participants' timing behavior, we obtained, for each word, several language-related variables and used them to compute a distance metric between subsequent words as spoken by the participants.

Specifically, we used: i) word embeddings from the Italian FastText (Bojanowski et al., 2016), both in their original dimensionality (300) and, following previous studies (Solomon et al., 2019a), reduced to a lower dimensionality (1, 2, 3 dimensions) using principal component analysis as implemented in scikit-learn (Pedregosa et al. 2011). As distance metric we used cosine for the high-dimensional vector and Euclidean for the low dimensional vectors; ii) word frequency, measured as Zipf value obtained from the publicly available Italian Subtlex corpus (Crepaldi et al., 2015). Distance was defined as the difference in frequency scores; word length, i.e., number of letters, and the distance is their difference; path distance obtained from the wordnet corpus (Miller, 1995);

Each distance measure was then correlated with the time interval between subsequent words. The rationale was that, assuming constant speed, the time interval is the best indicator of traveled distance. The semantic variable that correlates better with inter word interval can thus be interpreted as better reflecting the underlying conceptual space. This correlation was repeated for each participant, category and task block and finally averaged to obtain one correlation value per participant. Correlation values were fisher transformed and tested against zero using a two-tailed, one-sample t-test. We further tested whether the highest correlation was higher than the others using a two-tailed, paired sample t-test.

Using the distance metric that is best correlated with timing intervals between words (i.e., high-dimensional word embeddings), we evaluated whether it is capturing meaningful aspects of participants' sequence of named concepts. To this end, the word sequence of each task block was randomly shuffled 1000 times and the distance between subsequent words was recomputed. We then normalized the observed average distance between sequent words by the null distribution of 1000 average distance scores. The obtained z-scores were tested against zero using a two-tailed, one-sample t-test.

The correlation between the high-dimensional semantic vectors and ITI was repeated after removing the “switch” trials (see later) and the resulting fisher transformed correlation values tested against zero using a two-sided, one-sample t-test.

### *Behavioral signatures of foraging in conceptual spaces*

We evaluated whether naming concepts in the verbal fluency task mimicked strategies that animals use when foraging in physical space. Specifically, we tested the presence of local clusters of concepts that are visited in sequence (exploitation) followed by “switches” between clusters (exploration). We used the “similarity drop” model (Hills et al., 2012) as implemented in the “forager” package (Kumar et al., 2024) to define “switch” trials as the points where semantic distance between subsequent words is higher than its neighbors. Words in between switch trials were considered to belong to the same “cluster”. For these clusters to be meaningful, we next tested whether distances “within” clusters were smaller as compared to distances “between” clusters. This comparison was by design unbalanced due to the lower amount of switch trials, and potentially circular in that the distance we evaluated was used to define the clusters. To overcome these limitations we created a null distribution of clusters and their “within” and “between” distances by randomly shuffling 1000 times the order of words within each task block. The observed difference between “within” and “between” distances was then normalized based on the null distribution. The obtained z-score was then tested against zero using a two-tailed, one-sample t-test.

### *Intracranial stereotactic EEG recording and preprocessing*

sEEG recordings were performed at the Niguarda Hospital (Milan, Italy) using a Nihon-Koden system with a sampling rate of 1000 Hz. Data were recorded with an online reference chosen for clinical reasons. Raw data were visually inspected by expert epileptologist (R.M.), who indicated contacts and time windows contaminated by potential epileptic discharges that were subsequently marked for exclusion. One participant was excluded at this stage due to its strong epileptic activity.

Raw sEEG files were imported in Fieldtrip (Oostenveld et al., 2011) and converted to BIDS format (Gorgolewski et al., 2016). BIDS-formatted data were then loaded in python and data analysis was further carried out using MNE-python (Gramfort et al., 2013) as well as common scientific python packages (Harris et al., 2020; Virtanen et al., 2020; McKinney, 2010).

Time series data were low-pass filtered at 150 Hz to avoid aliasing artefacts (Cohen, 2014) and notch filtered at 50+-1 and 100+-1 Hz (line-noise). Data were re-referenced offline using the “bipolar” reference scheme, which subtracts the activity of neighboring contacts from medial to lateral along the sEEG electrode, effectively increasing the spatial specificity of the recordings (Mercier et al., 2022). Neighboring contacts that were localized in different brain areas based on the Desikan-Killiany atlas (Desikan et al., 2006) were not included in the analysis to avoid misinterpreting the spatial origin of the effects. After epoching based on events onset (see paragraph "*Experimental events definition*"), data were downsampled to 500 Hz to ease computational cost of the following analyses. We excluded from the analyses of sEEG data epochs that had an overlap of less than 1.5 s to avoid contamination between the period of interest and speech related activity of the previous word. This led to the exclusion of ~18% words. See Table 1 for the total number of words per participant included in the analyses. Note that distance metrics used for correlation with sEEG power (see later) were calculated based on the word sequence before words exclusion, thus reflecting the actual navigation process of the participant.

## *Electrode localization*

Electrode localization was performed based on coregistered post-implant CT and pre-implant MRI.

Anatomical electrode localization was based on the Desikan-Killiany atlas (Desikan et al., 2006) and confirmed through visual inspection of the electrical signal by an expert epileptologist (R.M.).

The following analyses were performed on contacts localized in the hippocampus (N=20). Furthermore, we defined a control region in the lateral temporal lobe, given its known role in language processing and semantic memory (Binder et al., 2009) and the availability of contacts in all participants. Lateral temporal contacts were defined as the grey-matter contacts on the same shaft of the medial temporal contacts (including hippocampal, entorhinal and parahippocampus).

## *Time-frequency analysis*

Single-trial time series were convolved with Morlet wavelets to obtain time-resolved, frequency-specific power estimates. Fifty Morlet wavelets were constructed with logarithmic spacing between 3 and 145 Hz. Line noise and its harmonics were at least 1 Hz away from the closest wavelets. Wavelet cycles were frequency dependent and ranged between 3 (lowest frequency) and 5 (highest frequency). To avoid edge artifacts due to time-frequency decomposition (Cohen, 2014), the 0.5 s at the beginning and at the end of the trial were excluded from further analyses. Following (Tallon-Baudry & Bertrand, 1999; Iemi et al., 2017; Ronconi et al., 2017) we evaluated the temporal resolution of the selected time-frequency parameter: temporal resolution for the slowest frequency we considered (3 Hz) was of ~0.160 s and 0.05 s for the fastest (145 Hz). Interpretation of effects within these latencies should thus be taken with caution as it can result from temporal smearing due to time-frequency decomposition. Power values were then log transformed given their chi-squared distribution (Percival, 1993; Manning et al., 2009).

### *Statistical analysis of theta power*

We selected frequencies in the theta range (3-8 Hz) and averaged their power across frequencies and time points. Theta power in the period before word onset was then contrasted with theta power in the period after word onset and their difference tested against zero using a two-tailed, one-sample t-test. We then repeated this contrast using different baseline periods (post-word offset, silence, rest) to account for the potential confound of motor activity in the chosen baseline. For the silence and rest periods contrast, we randomly selected an amount of segments that matched the amount of words being said by the individual participant (after trial exclusion based on temporal overlap, see previous paragraph). As control analyses we also tested whether theta power differed between the semantic categories (one-way ANOVA with factor category: cities, animals, professions) and between repetitions of the task block (one-way ANOVA with factor repetition: 1,2,3).

Next, we tested whether theta power differed between the hippocampus and lateral temporal lobe using a two-sided, paired sample t-test.

### *Statistical analysis of time-frequency*

Power in the time window before word onset was normalized with the average power in the time window after word onset. We then used a two-sided, one-sample t-test against zero at each time-frequency point. Multiple comparison correction was performed using false discovery rate (FDR, Genovese et al., 2002; Benjamini & Hochberg, 1995). This analysis was repeated for both the hippocampus and lateral temporal lobe.

### *Identifying peaks in frequency-band power*

To visualize their time course, we averaged the power in the significant frequency bands identified in the time-frequency analysis. We defined theta as being from 3 to 8 Hz and gamma as being from 51 to 145 Hz. We identified the peak in the respective frequency band by considering the highest point in the time series. We then evaluated the stability of the peak across participants using a jackknife procedure often employed to evaluate the peak-latency of event-related potentials (Ulrich & Miller, 2003). The jackknife procedure involves removing one participant from the group-level analysis and repeating the peak identification procedure. The procedure was repeated until all participants were left out once. This allowed us to obtain a distribution of peak estimates from which we computed the 97.5% confidence interval.

### *Linear-mixed models*

We used linear-mixed models to investigate whether frequency-band power was related to the relevant aspects of navigation behavior such as semantic and temporal distances. Linear-mixed models are powerful tools to assess the contribution of an independent variable on the dependent variable when multiple correlated measurements are performed (e.g., from the same participant, Laird & Ware, 1982).

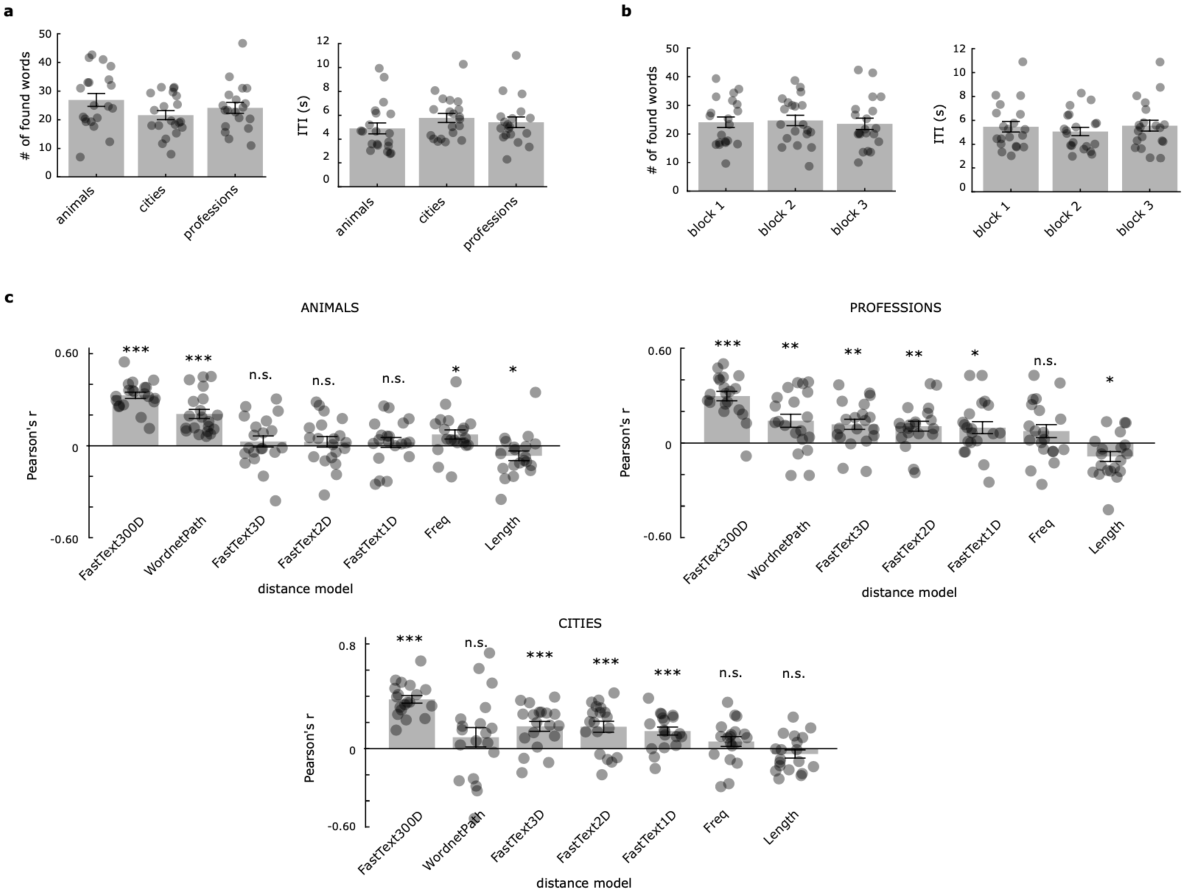
As done for the behavioral data, we modeled semantic distance using the high-dimensional FastText embeddings (Bojanowski et al., 2016). For each task block, we computed the cosine distance between subsequent word vectors, following the order in which words were spoken by the participants. Similarly, we calculated the temporal interval between subsequent words. Predictors were z-scored given their different scales allowing a more direct comparison of the resulting parameter estimates (Stangl et al., 2020). Before fitting the mixed model, we evaluated whether the correlation in the predictors (see Figure 1i) can be problematic for the interpretation of the results. To this end we computed the variance inflation factor (VIF, Montgomery et al., 2012) of the fixed effects. The VIF measures the degree to which the variance explained by one predictor is inflated due to multicollinearity with other predictors in the model. A value higher than 5-10 warrants caution in the interpretation of the models estimate. VIF for both predictors was slightly above 1 indicating that multicollinearity was not affecting the parameter estimates of the model.

Following previous studies (Liu et al., 2023; Stangl et al., 2020), these metrics were entered in the following linear mixed model:

$$power_t \sim semantic\ distance\ + temporal\ distance\ +\ (1\ |\ subject)$$

where *t* indicates a given time point, *power* indicates the average frequency-band specific power. Power was either one of two frequency bands: theta (3-8 Hz) and gamma (51-145 Hz). As a measure of power we used the z-scored difference between the time window of interest and the baseline period (post-onset). This procedure was repeated for the other two predictors, semantic distance in one dimension, obtained by reducing the dimensionality of the original FastText vectors using PCA and computing the Euclidean distance between subsequent words, and the difference in linguistic frequency between consecutive words measured as Zipf value (see above paragraph). In all analyses, the distance assigned as predictor to a given trial corresponds to the distance between the word pronounced in the same trial *t* and the previous one *t-1*. For example, if in trial *t* the participant pronounced the word “dog”, the predictor for trial *t* would be the distance between the word vector for “dog” and the word pronounced in trial *t-1*. The first word of each foraging block thus has no meaningful distance and was excluded from the analyses. The analysis was carried out using pymer4 (Jolly, 2018). Significance was evaluated using an ANOVA and multiple comparison correction was carried out using FDR.

## *Supplementary results*



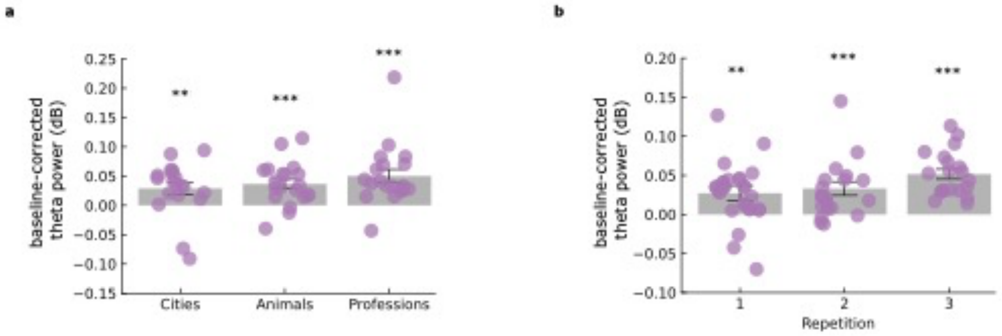
**Supplementary Figure 1** - Extended behavioral results. **a**. average number of words and ITIs as a function of category. **b**. average number of words and ITIs as a function of repetition block. **c**. average correlation between ITIs and distance measures across categories. *** p<.001, ** p <.01, * p<.05

| Comparison | df | t | p |
|---|---|---|---|
| SemDist300D | 19 | 19.191 | <0.001 |
| WordNet | 19 | 4.657 | <0.001 |
| SemDist3D | 19 | 4.708 | <0.001 |
| SemDist2D | 19 | 4.274 | <0.001 |
| SemDist1D | 19 | 4.144 | <0.001 |
| Frequency | 19 | 3.205 | 0.004 |
| Length | 19 | -4.380 | <0.001 |

**Supplementary Table 1 - Group level t-test results of the correlation of inter-word-interval with several language-related distance measures.**

| Comparison | | df | t | p |
|---|---|---|---|---|
| SemDist300D | WordNet | 19 | 7.422 | <0.001 |
| SemDist300D | SemDist3D | 19 | 10.389 | <0.001 |
| SemDist300D | SemDist2D | 19 | 10.204 | <0.001 |
| SemDist300D | SemDist1D | 19 | 10.014 | <0.001 |
| SemDist300D | Frequency | 19 | 10.530 | <0.001 |
| SemDist300D | Length | 19 | 14.203 | <0.001 |

**Supplementary Table 2 - Pairwise t-test of the correlation between high-dimensional semantic distance and other language-related distance measures**



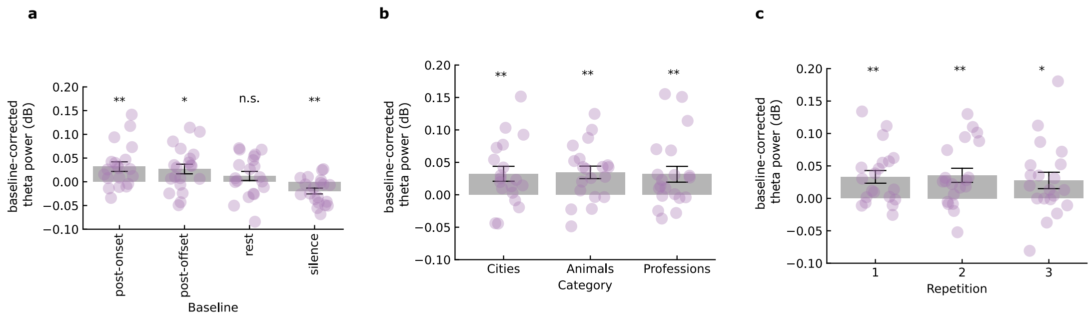
**Supplementary Figure 2** - Control analyses on hippocampal theta. **a**. average theta power in hippocampus as a function of categories. **b**. average theta power in hippocampus as a function of block repetition. *** p<.001, ** p <.01, * p<.05

| **Category** | **df** | **t** | **p** |
|---|---|---|---|
| Cities | 19 | 2.750 | 0.013 |
| Animals | 19 | 4.498 | <0.001 |
| Profession | 19 | 4.457 | <0.001 |

**Supplementary Table 3 -** Control analyses on hippocampal theta: t-test results on the individual categories.

| **Repetition** | **df** | **t** | **p** |
|---|---|---|---|
| 1 | 19 | 2.808 | 0.011 |
| 2 | 19 | 3.821 | 0.001 |
| 3 | 19 | 8.043 | <0.001 |

**Supplementary Table 4 -** Control analyses on hippocampal theta: t-test results on the individual task repetitions



**Supplementary Figure 3** - Control analyses on LTL theta. **a**. average theta power in LTL as a function of different baseline. **b**. average theta power in LTL as a function of categories. **c**. average theta power in LTL as a function of block repetition. *** p<.001, ** p <.01, * p<.05

| **Baseline** | **df** | **t** | **p** |
|---|---|---|---|
| post-onset | 19 | 3.177 | 0.004 |
| post-offset | 19 | 2.646 | 0.015 |
| rest | 19 | 1.179 | 0.252 |
| silence | 19 | -2.994 | 0.007 |

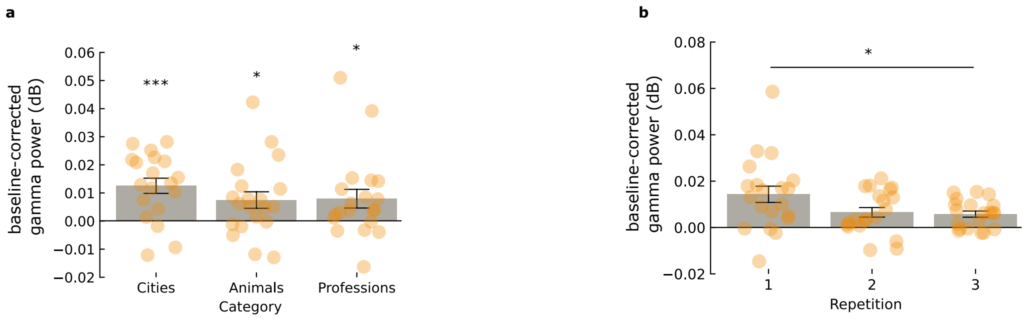
**Supplementary Table 5 -** Control analyses on LTL theta: t-test results on the individual categories.

| **Category** | **df** | **t** | **p** |
|---|---|---|---|
| Cities | 19 | 2.811 | 0.011 |
| Animals | 19 | 3.576 | 0.002 |
| Profession | 19 | 2.594 | 0.017 |

**Supplementary Table 6 -** Control analyses on LTL theta: t-test results on the individual categories.

| **Repetition** | **df** | **t** | **p** |
|---|---|---|---|
| 1 | 19 | 3.392 | 0.003 |
| 2 | 19 | 3.271 | 0.004 |
| 3 | 19 | 2.182 | 0.041 |

**Supplementary Table 7 -** Control analyses on LTL theta: t-test results on the individual task repetitions



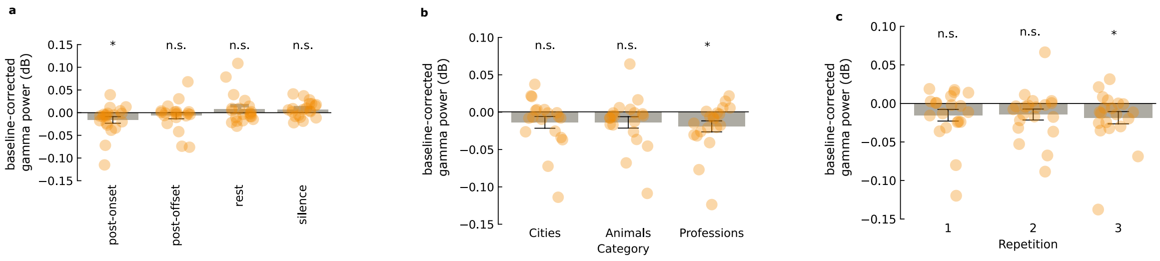
**Supplementary Figure 4** - Control analyses on hippocampal gamma. **a**. average gamma power in the hippocampus as a function of categories. **b**. average theta power in the hippocampus as a function of block repetition. *** p<.001, ** p <.01, * p<.05

| **Category** | **df** | **t** | **p** |
|---|---|---|---|
| Cities | 19 | 4.716 | <0.001 |
| Animals | 19 | 2.527 | 0.020 |
| Profession | 19 | 2.437 | 0.024 |

**Supplementary Table 8 -** Control analyses on hippocampal gamma: t-test results on the individual categories.

| **Repetition** | **df** | **t** | **p** |
|---|---|---|---|
| 1 | 19 | 4.074 | <0.001 |
| 2 | 19 | 3.169 | 0.005 |
| 3 | 19 | 4.346 | <0.001 |

**Supplementary Table 9 -** Control analyses on hippocampal gamma: t-test results on the individual task repetitions



**Supplementary Figure 5** - Control analyses on LTL gamma. **a**. average gamma power in LTL as a function of different baseline. **b**. average gamma power in LTL as a function of categories. **c**. average theta power in LTL as a function of block repetition. *** p<.001, ** p <.01, * p<.05

| **Baseline** | **df** | **t** | **p** |
|---|---|---|---|
| post-onset | 19 | -2.208 | 0.039 |
| post-offset | 19 | -0.917 | 0.370 |
| rest | 19 | 1.121 | 0.275 |
| silence | 19 | 1.756 | 0.095 |

**Supplementary Table 10 -** Control analyses on LTL gamma: t-test results on the individual categories.

| **Category** | **df** | **t** | **p** |
|---|---|---|---|
| Cities | 19 | -1.740 | 0.098 |
| Animals | 19 | -1.796 | 0.088 |
| Profession | 19 | -2.580 | 0.018 |

**Supplementary Table 11 -** Control analyses on LTL gamma: t-test results on the individual categories.

| **Repetition** | **df** | **t** | **p** |
|---|---|---|---|
| 1 | 19 | -2.029 | 0.056 |
| 2 | 19 | -2.031 | 0.056 |
| 3 | 19 | -2.348 | 0.029 |

**Supplementary Table 12 -** Control analyses on LTL gamma: t-test results on the individual task repetitions

# Chapter 3

# MEG frequency tagging reveals a grid-like code during attentional movements

This chapter contains a modified version of the following scientific article: *Giari G., Vignali L., Xu Y., Bottini R. (2023), MEG frequency tagging reveals a grid-like code during attentional movements, Cell Reports, Volume 42, Issue 10, 113209 October 31, 2023.*

The journal author rights are reported in Appendix. The following materials were used: Introduction, Results, Discussion, Methods, Figures and Supplementary Materials

## Introduction

Understanding the surrounding environment is fundamental for animals' survival. To this end, sensory information is organized into so-called "cognitive maps," an internal model of the environment that supports flexible behavior (Tolman, 1948)

Cognitive maps are thought to be instantiated at the neural level through several neurons responding to spatial variables (Moser et al., 2017). Among these, grid cells in the entorhinal cortex exhibit multiple firing fields that cover the navigable surface with a 60° rotational symmetry (6-fold, Hafting et al., 2005). The finding of spatially modulated cells has been pioneered in rodents, and comparable evidence has been reported in humans in virtual navigation tasks, with invasive direct neural recordings (Jacobs et al., 2013; Nadasdy et al., 2017) but also using non-invasive functional magnetic resonance imaging (fMRI; Doeller et al., 2010).

Interestingly, in primates the neural mechanisms that evolved to support spatial exploration through locomotion seem to be recruited when space is explored through eye movements (Rolls & Wirth, 2018; Nau et al., 2018a). In non-human primates, grid cells exhibit their hexagonal firing also when space is explored through saccadic eye movements (Killian et al., 2012; Meister et al., 2018). Similarly, Staudigl and colleagues (2018) reported in humans a higher gamma-band power (60–120 Hz) in the medial-temporal lobe (MTL) for saccades aligned to the participants' grid. Moreover, grid-like responses in the human MTL have been reported using fMRI during visual search (Julian et al., 2018) and smooth pursuit (Nau et al., 2018b).

Findings of a grid-like response during visual exploration suggest the possibility of an attentional mechanism taking place (Bicanski & Burgess, 2019). Gaze position can be conceived as being the overt index of the currently attended location. Attention, however, can also be covertly deployed to peripheral spatial locations without moving the eyes (Posner, 1980). Interestingly, a grid-like response in entorhinal cells has been reported in non-human primates trained to maintain central fixation while covertly paying attention to a dot moving in the periphery (Wilming et al., 2018). However, in humans there is no evidence of grid-like responses being dissociated from overt visual exploration of the environment.

We set out to investigate whether grid-like coding can be elicited, in humans, by movements of covert attention using frequency tagging (FT; Norcia et al., 2015; Tononi et al., 1998). Following previous studies (Posner, 1980; Wilming et al., 2018), we defined covert attention as being the orientation of attention toward spatial locations achieved independently of directly observable eye movements. Instead of relying on currently established non-invasive methods to detect grid-like responses (Stangl et al., 2019), we developed a method that enables one to obtain an objective index of neural response that does not require participants' overt behavior (Norcia et al., 2015). In fact, FT relies on the brain's ability to track regularities embedded within a periodic presentation of stimuli, offering the advantage of measuring periodic neural responses with high signal-to-noise ratio.

Our FT method relied on rhythmic visual presentation of trajectories, appearing in fixed sequences of angles linearly spaced by either 15° or 30° in different trials (Figure 1A). This sequential "clock-like" presentation allowed to embed multiple spatial periodicities at different temporal intervals within the sequence. For instance, in the 30° resolution, trajectories separated by 60° (6-fold, i.e., grid-cell periodicity) appeared at 3 Hz, while trajectories separated by 90° (4-fold, control periodicity) appeared at 2 Hz. The aforementioned frequencies were thus "tagged" with different spatial periodicities (Figure 1B). If any of these regularities were being tracked, a response at the corresponding frequency would emerge in the magnetoencephalography (MEG) signal (Figure 1C). Compared to current non-invasive methods, the recurrent presentation of 6-fold regularities avoids the need to estimate the grid orientation with the maximal periodic response. A peak at the frequency corresponding to the presentation of 6-fold trajectories is itself an index that during the stimulation there was a successful recognition of a 6-fold periodicity in the trajectories' presentation. Crucially, this FT measure does not depend on the participant-specific preferred orientation: the same frequency response should be observed if the grid is aligned to any of the trajectories in the sequence. In fact, the continuous clock-like presentation allows a consistent temporal interval between the preferred trajectory (i.e., orientation) and its 60° multiples, irrespective of the participant-specific orientation. We recorded MEG and eye tracking while participants attended to the FT presentation. We quantified the neural tracking of the spatial periodicities using inter-trial coherence (ITC; Ding & Simon, 2013) and observed a grid-like response: the frequency tagged with the 6-fold periodicity shows higher ITC than control periodicities. At sensor level this effect was found in clusters encompassing occipital and temporal sensors, whereas at source level this effect was found specifically in the MTL. Concurrently recorded gaze location and participants' accurate performance allowed us to ascribe the observed effect to covert attention. In a control experiment we used the same FT design with non-spatially structured stimuli. We observed a different response profile, indicating the dependency of the effect observed in the spatial experiment on covert movements of attention.

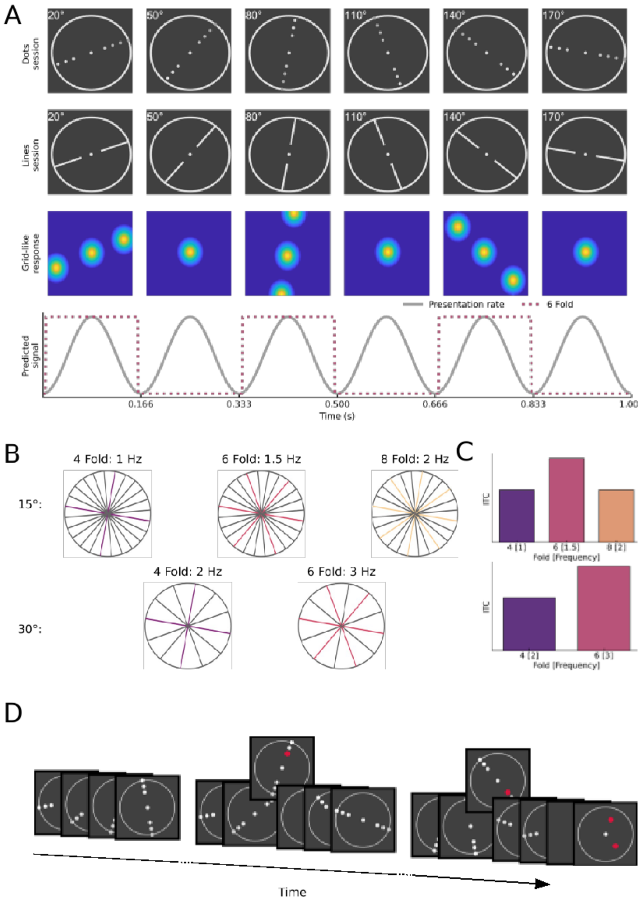


**Figure 1 Frequency tagging design**

(A) Example of a sequence at 30° resolution. Individual trajectories were presented continuously every 0.166 s (6 Hz). The same trajectories were presented in one session as dots moving from one side to the other of the circular arena (6 dots are shown here for visualization purposes; in the experiment 16 dots were presented) and in another session as static lines. Crucially, within this sequential presentation were embedded additional spatial regularities. For instance, trajectories separated by 60° (6-fold) appear every 0.333 s (3 Hz). See Videos S1–S4 for examples of trials of the different sessions and of the different angular resolutions.

(B) Multiple spatial regularities can be embedded within the sequential presentation of linearly spaced trajectories. Specifically, spatial regularities embedded in the 15° resolution include 90° (4-fold, purple) appearing every 1 s (1 Hz), 60° (6-fold, pink) appearing every 0.666 s (1.5 Hz), and 45° (8-fold, yellow) appearing every 0.5 s (2 Hz). The 30° resolution instead includes 4-fold appearing every 0.5 s (2 Hz) and 6-fold appearing every 0.333 s (3 Hz). The 6-fold periodicity corresponds to the grid-like periodicity, whereas the others act as control periodicities. Having two angular resolutions allows to "tag" different frequencies with the same spatial periodicity: 6-fold trajectories occur at 3 Hz in the 30° resolution and at 1.5 Hz in the 15° resolution, enabling an estimation of the neural tracking that is not tied to a specific chosen frequency.

(C) Predictions. If the spatial regularities were being tracked, a response at the corresponding frequency would be visible in the frequency spectrum. Isolating the frequencies of interest should then reveal a higher neural tracking for the frequency tagged with 6-fold (pink) as compared to 4-fold (purple) and 8-fold (yellow) in the 15° resolution (top) as well as a higher response for the frequency tagged with 6-fold as compared to 4-fold in the 30° resolution (bottom).

(D) Task. During the trajectories' sequence (both sessions) two red dots appeared for 0.025 s in random locations along the trajectory. To ensure spatial attention, timing of their appearance was randomized but constrained between 19 s and 33 s for the first dot and between 37 s and 39 s for the second dot. At the end of the trial, two red dots were presented again and participants had to indicate whether their position was consistent with the one they were keeping in memory.

# Results

## Participants were covertly tracking the spatial trajectories

Twenty-three healthy volunteers completed two MEG recording sessions. In one session, trajectories were formed by dots moving from one side to the other in a circular arena, similar to the method used by Nau et al. (2018b) In another session, the same trajectories were presented as static lines. Participants were instructed to fixate at the center of a screen while attending to the trajectories. To ensure they were paying attention to the stimuli, they were asked to perform a location memory task (Figure 1D). This consisted of two red dots appearing at random positions along the trajectories and at random times within the trial sequence. Participants had to remember the dot's exact position, and their memory was tested at the end of each trial. Performance overall was accurate (Figure 2A), except for one participant that was excluded from further analyses.

Gaze-location data confirmed that participants were keeping central fixation (4.5° visual angle; Wilming et al., 2018) throughout the trial (Figure 2B). To further make sure that any MEG response can be ascribed to covert attention, trials in which fixation was maintained for less than 80% of the time were excluded from further analyses. This threshold was used during the recording session to warn participants of excessive eye movements and was thus kept during the analysis stage, but the main findings are replicated using a more stringent threshold of 95% of time (Figure S4).

Taken together, participants' behavior as reflected in task performance and gaze position indicates successful covert tracking of the spatial trajectories.

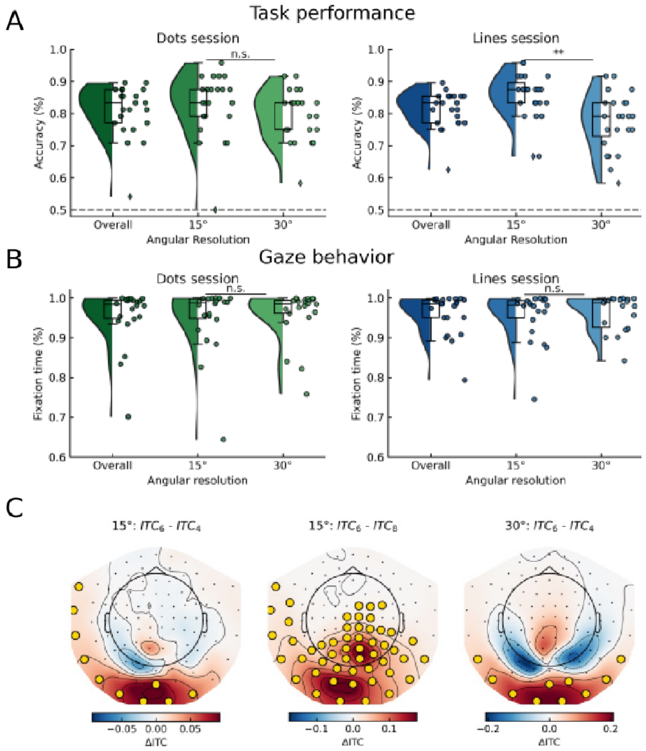


**Figure 2 Covert tracking of spatial trajectories elicited a grid-like response detectable with frequency tagging**

(A) Accuracy in the location memory task, averaged over angular resolutions as well as separately for each angular resolution. Performance was overall good (dots session: mean = 80%, SD = 7%; lines session: mean = 81%, SD = 5%) except for one participant (diamond point in the plot) whose accuracy (dots: 54%; lines: 62%) was two SDs below group mean in both sessions. This participant was excluded from further analyses. After separating the responses in the two angular resolutions, we observed higher accuracy in the 15° resolution (t(22) = 3.18, p = 0.004) in the lines session, while no difference was observed in the dots session (t(22) = 1.71, p = 0.099).

(B) Fixation time during the trials, expressed as percentage, averaged over angular resolutions as well as separately for each angular resolution. Participants kept central fixation (4.5° visual angle from the center of the screen[16]) for the majority of the time during the trial. No differences in fixation behavior were found between angular resolutions (dots session: t(21) = −1.06, p = 0.300; lines session: t(21) = −1.16, p = 0.257). Green shades indicate dots session, blue shades indicate lines session. Lines above data points indicate significance (n.s., not significant; *p < 0.05; **p < 0.01; ***p < 0.001).

(C) Significant clusters at sensor level in which $ITC_6$ is greater than control ITCs, indicating a grid-like response in occipito-temporal sensors. In the 15° resolution, $ITC_6$ is greater than $ITC_4$ (p = 0.038 cluster corrected, left) and $ITC_6$ is greater than $ITC_8$ (p < 0.001 cluster corrected, center). In the 30° resolution, $ITC_6$ is greater than $ITC_4$ (p = 0.047 cluster corrected, right). No clusters were found in which control periodicities were higher than 6-fold periodicity.

See Figures S1 and S2 for results of the individual sessions.

## *MEG FT detects a grid-like response in humans during covert attentional movements*

As a first step, we sought to understand whether the FT method was able to detect a grid-like response by quantifying the neural tracking of the spatial periodicities with ITC at sensor level. This analysis is based on the signal as recorded by MEG but will provide limited spatial information. After standard MEG preprocessing, the time series of each trial was divided into shorter segments, which then underwent a semi-automatic artifact rejection procedure (see STAR Methods). Individual segments were decomposed in the frequency domain with a fast Fourier transform (FFT), and this complex representation was used to calculate ITC following previous studies (Ding et al., 2016; Henin et al., 2021). Having observed no statistical differences in the ITC response between the dots and lines sessions in the predicted source-level region of interest (ROI) analysis, we averaged the results and carried out our main analyses on this averaged ITC value (see "grid-like response was localized in medial-temporal sources" for the formal comparison and Figures S1 and S2 for the individual session results).

The ITC of the frequencies corresponding to the 6-fold periodicity ($ITC_6$) was compared to the ITC at the frequency of the control periodicities ($ITC_4$ and $ITC_8$) with a two-sided cluster-permutation test (Maris & Oostenveld, 2007), separately for each angular resolution. For the sensor-level analysis we focused on magnetometers, given their higher sensitivity to deep sources as compared to gradiometers (Hari & Salmelin, 2012). This analysis revealed significant clusters encompassing occipital and temporal sensors in which $ITC_6$ was higher than the control periodicities (Figure 2C). Specifically, in the 15° resolution we observed a cluster in which $ITC_6$ was greater than $ITC_4$ ($p = 0.038$ cluster corrected) and a cluster in which $ITC_6$ was greater than $ITC_8$ ($p < 0.001$ cluster corrected). In the 30° resolution, we observed a cluster in which $ITC_6$ was greater than $ITC_4$ ($p = 0.047$ cluster corrected). No cluster was found in which control periodicities' ITCs were greater than $ITC_6$.

This analysis indicates that covert attentional movements in humans also elicit a grid-like response, similarly to non-human primates (Wilming et al., 2018). The limited spatial resolution of sensor-level analyses localized this response in occipito-temporal sensors, with similar topographies giving rise to the grid-like effect in both angular resolutions (Figure S10B).

## *Grid-like response was localized in medial-temporal sources*

We performed source localization to investigate which brain areas were responsible for the grid-like effect observed at sensor level. We used a linearly constrained minimum variance beamformer (Van Veen et al., 1997) to reconstruct the time series of brain activity in each voxel and computed the ITC at the frequencies corresponding to the tagged spatial periodicities (see STAR Methods).

We focused our analysis on the MTL (Figure 3A, left), given the a priori hypothesis of its involvement in the generation of the 6-fold periodic response. The average ITC value in this ROI was compared across sessions with a two-way repeated-measures analysis of variance (ANOVA) with factors session (dots, lines) and periodicity (15° resolution: 4-, 6-, 8-fold; 30° resolution: 4-, 6-fold) to evaluate whether the neural tracking of the spatial periodicities is elicited differently by moving dots or static lines. This analysis was repeated for each hemisphere and each angular resolution. We found no significant periodicity × session interaction (15°: left, $F(2,42) = 2.42$, $p = 0.101$; right, $F(2,42) = 1.44$, $p = 0.248$; 30°: left, $F(1,21) = 1.40$, $p = 0.25$; right, $F(1,21) = 0.19$, $p = 0.66$). The ITC values of the two sessions (dots and lines) were thus averaged together and used for further analyses (see Figures S1 and S2 for the individual session results).

Most interestingly, the ANOVA identified a main effect of periodicity in both hemispheres, and in both the 15° resolution (left: $F(2,42) = 9.27$, $p < 0.001$; right: $F(2,42) = 16.46$, $p < 0.001$; Figure 3B, left) and 30° (left: $F(1,21) = 8.63$, $p = 0.008$; right $F(1,21) = 11.89$, $p = 0.002$; Figure 3C, left). Planned paired t test indicated that in the 15° resolution, $ITC_6$ was significantly greater than both $ITC_4$ and $ITC_8$ in both hemispheres (Table 1). In the 30° resolution, $ITC_6$ was significantly greater than $ITC_4$ in both the left and right MTL (Table 1). Taken together, these results suggest the presence of a grid-like response in the MTL during covert attentional movements.

To investigate whether the grid-like effect was specific to the MTL, we compared the MTL with two control ROIs, the lateral occipital and precentral cortices (Figure 3A, center and right). We conducted a two-way repeated-measures ANOVA with factors ROI (MTL, lateral occipital, precentral) and periodicity (15° resolution: 4-, 6-, 8-fold; 30° resolution: 4-, 6-fold) separately for each hemisphere and each angular resolution. We found a significant two-way interaction in the 15° resolution (Figure 3B) in both the left hemisphere ($F(2.51, 52.75) = 29.62$, $p < 0.001$) and right hemisphere ($F(2.17, 45.66) = 20.82$, $p < 0.001$). Post hoc t test indicated that the effect was indeed specific to the MTL, as in neither the lateral occipital nor the precentral ROI was $ITC_6$ greater than both control periodicities (Table 1). In the 30° resolution (Figure 3C) we observed a significant two-way interaction in the left hemisphere ($F(1.35, 28.27) = 4.94$, $p = 0.025$) and the right hemisphere ($F(1.39, 29.13) = 4.79$, $p = 0.026$). Post hoc t tests confirmed that in the control regions $ITC_6$ was not greater than both control periodicities (Table 1).

To localize this effect at the cortical level, we performed a conjunction analysis (Nichols et al., 2005). This analysis revealed clusters of voxels in the bilateral MTL that survived an uncorrected threshold ($p < 0.005$) (Figure 3D). In addition, a cluster-permutation test at the cortical level identified significant clusters encompassing the MTL in both 15° and 30° resolution (Figure S3).

Given their higher sensitivity to deep sources (Hari & Salmelin, 2012), we also repeated source analysis using only magnetometers. We did not find differences from the main results reported above (Figure S5).

These results confirm that the grid-like response elicited by covert attentional movements originated in the MTL and was not present in control regions.

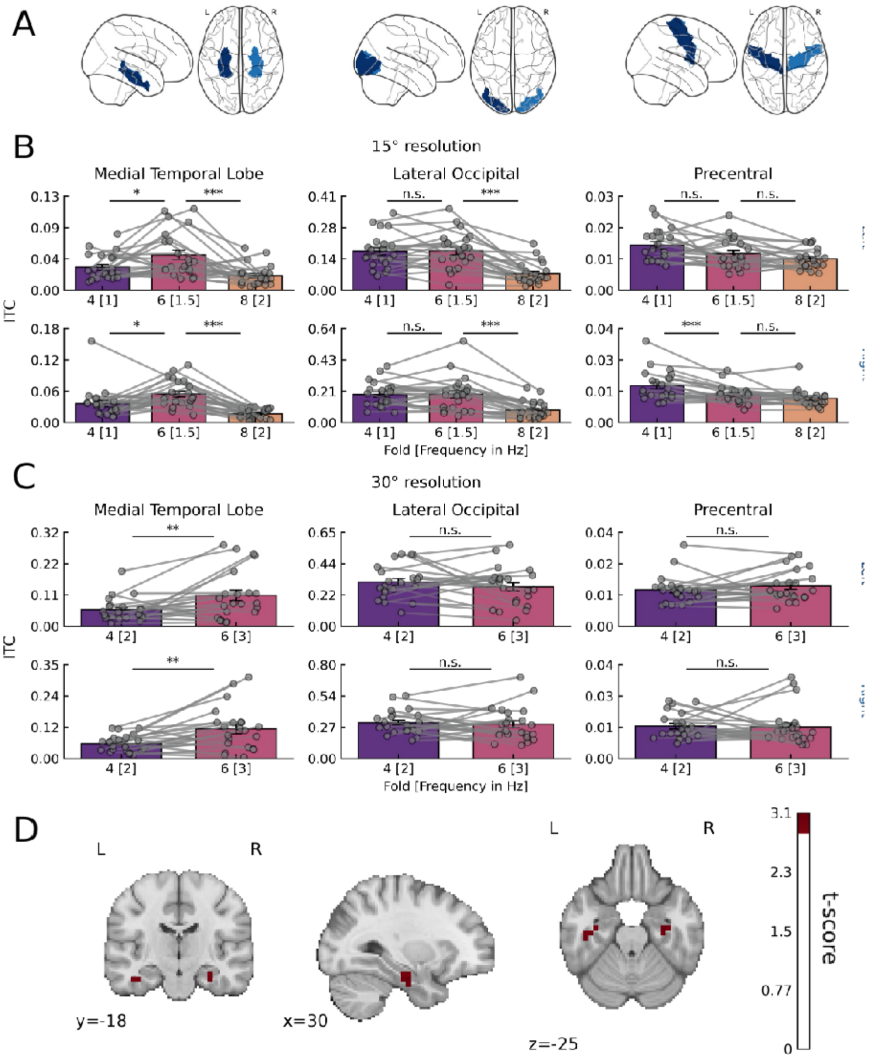


**Figure 3 Grid-like response during covert attention originated in the MTL**

(A) Regions of interest (ROIs) selected for the source-level analyses. From left to right: medial-temporal lobe (MTL; hippocampus, entorhinal, and parahippocampal cortices), lateral occipital, and precentral. Dark blue indicates left hemisphere and light blue indicates right hemisphere.

(B) Inter-trial coherence (ITC) in the ROIs for each frequency tagged with spatial periodicities at 15° resolution demonstrate the presence of a grid-like response, i.e., the frequency tagged with the 6-fold spatial periodicity (pink) was higher than both control periodicities (4-fold: purple; 8-fold: yellow) in the MTL (left) in both the left hemisphere (top) and right hemisphere (bottom). The grid-like effect was specific to the MTL in that in neither the lateral occipital (center) nor precentral (right) control ROI was the 6-fold periodicity higher than both control periodicities.

(C) ITC in the ROIs for each for each frequency tagged with spatial periodicities at 30° resolution demonstrate the presence of a grid-like response in the MTL ROI (left) in both the left (top) and right (bottom) hemisphere, with the 6-fold periodicity (pink) being higher than the 4-fold periodicity (purple). This effect was specific to the MTL in that neither the lateral occipital nor precentral ROI show a comparable periodicity preference. Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s., not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

(D) Conjunction analysis (15°: $ITC_6 > ITC_4$ and $ITC_6 > ITC_8$; 30°: $ITC_6 > ITC_4$) at the cortical level ($p < 0.005$ uncorrected) demonstrated the specificity to the MTL of the grid-like effect.

See Figures S1 and S2 for results of the individual sessions.

| Angular resolution | Hemisphere | ROI | Comparison | df | t | P | Sig. |
|---|---|---|---|---|---|---|---|
| 15° | Left | MTL | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | 2.35 | 0.028 | * |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 3.92 | <0.001 | *** |
|  |  | Lat. Occipital | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | 0.07 | 0.937 |  |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 6.43 | <0.001 | *** |
|  |  | Precentral | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | -1.93 | 0.066 |  |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 1.83 | 0.08 |  |
|  | Right | MTL | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | 2.45 | 0.022 | * |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 6.80 | <0.001 | *** |
|  |  | Lat. Occipital | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | 0.06 | 0.949 |  |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 6.09 | <0.001 | *** |
|  |  | Precentral | 6-Fold [1.5 Hz] vs 4-Fold [1 Hz] | 21 | -4.15 | <0.001 | *** |
|  |  |  | 6-Fold [1.5 Hz] vs 8-Fold [2 Hz] | 21 | 1.82 | 0.081 |  |
| 30° | Left | MTL | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | 2.92 | 0.008 | ** |
|  |  | Lat. Occipital | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | -1.01 | 0.322 |  |
|  |  | Precentral | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | 1.07 | 0.294 |  |
|  | Right | MTL | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | 3.43 | 0.002 | ** |
|  |  | Lat. Occipital | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | -0.39 | 0.698 |  |
|  |  | Precentral | 6-Fold [3 Hz] vs 4-Fold [2 Hz] | 21 | -0.14 | 0.884 |  |

*Table 1. Pairwise comparison between tagged frequencies in the different ROIs in the spatial experiment.* Post-hoc t-tests at source level in each ROI identified a significantly higher $ITC_6$ as compared to control folds in the 15° resolution in both the left and right MTL. The same pattern was not present in the control regions. Similarly, in the 30° resolution $ITC_6$ was higher than $ITC_4$, specifically in the MTL.

## *Gaze location does not influence the grid-like response*

We then conducted further analyses on the eye-tracker data to investigate the presence of eye movements within the fixation window that could be induced by the presentation of the stimuli and their potential relation with the observed grid-like response.

First, we replicated the analysis conducted by Wilming and colleagues (2018) to directly assess the time-resolved consistency between gaze location and stimuli position (Figure 4A).

We separately computed the Euclidean distance of the eyes to the center and of the stimuli (dots) to the center at each time point. These distance measures would be correlated if the eyes were following the dots. However, at the group level we did not observe any correlation, neither in 15° ($t(21) = -1.169$, $p = 0.255$) nor in the 30° resolution ($t(21) = -0.814$, $p = 0.424$). Moreover, no difference was present between the 15° and 30° resolutions ($t(21) = -0.409$, $p = 0.686$). Thus, at least according to the standards adopted by Wilming and colleagues, attentional tracking during the task was not accompanied by consistent eye movements (at least in the case of the moving dot session, to which this kind of analysis could be applied). Moreover, by comparing the eye position in the moments directly before and after the appearance of the target dots, we found that the presentation of the target did not induce a consistent shift of gaze location (Figure S6), indicating that task-relevant stimuli were not influencing gaze behavior.

We then directly assessed the similarity between gaze locations during the presentation of different trajectories in both the dots and lines sessions. We used Gaussian kernel density estimate to calculate the heatmaps of fixations (Wynn et al., 2020) for each trajectory, focusing on the predefined 4.5° × 4.5° fixation window (Figure 4B). The average pairwise correlations between the heatmaps were very high overall (dots session: 15°, $r = 0.97 \pm 0.01$; 30°, $r = 0.98 \pm 0.005$; lines session: 15°, $r = 0.97 \pm 0.01$; 30°, $r = 0.98 \pm 0.005$; Figure 4C), indicating that individual participants' gaze location was similar across trajectories.

However, despite the high similarity, we found that fixation maps of trajectories that were similar to each other were negatively correlated with the angular difference between trajectories (Figure 4D). Fisher-transformed r scores were significantly different from zero (dots session: 15°: $r = 0.71 \pm 0.09$, $t(21) = -20.232$, $p < 0.001$; 30°: $r = 0.82 \pm 0.064$, $t(21) = -26.486$, $p < 0.001$; lines session: 15°: $r = 0.69 \pm 0.08$, $t(21) = -25.224$, $p < 0.001$; 30°: $r = 0.81 \pm 0.05$, $t(21) = -32.202$, $p < 0.001$), indicating that individual participants' fixation similarity was (slightly) higher for trajectories that had smaller angular difference.

Given that the spatial trajectories induced a small but consistent bias in participants' gaze location, we next investigated whether this effect could influence the observed grid-like response. To this end we computed the slope of the correlation from the previous analysis and averaged it across sessions. This measure was taken as an index of the extent to which an individual participant's gaze was modulated by the angular difference between the trajectories. We then computed the slope of the grid-like effect in the left and right MTL, separately for each angular resolution: for the 15° resolution we fit a quadratic model centered on 6-fold to individual participants' ITC data in the MTL (see Figure 6 for similar analysis at the group level), while for the 30° resolution we fit a linear model. The slope of each model was taken as an index of the strength of the grid-like response. We then correlated the slopes of the MEG and eye-tracker effects to investigate whether the participants that exhibited the strongest grid-like effect were also exhibiting a high modulation of the fixation pattern by the trajectories' presentation. We did not find any correlation (Figure 4E) in neither 15° (left hemisphere: $r(20) = -0.11$, $p = 0.618$; right hemisphere: $r(20) = -0.06$, $p = 0.789$) or 30° resolution (left hemisphere: $r(20) = -0.22$, $p = 0.335$; right hemisphere: $r(20) = -0.30$, $p = 0.172$).

As an additional control, we replicated the previous results using the time-resolved gaze angle instead of the gaze location represented in the heatmaps (Figure S7), strengthening the observation of a lack of correlation between gaze behavior and the grid-like effect.

Taken together, these results indicate that the presented spatial trajectories induced a small but consistent bias in participants' gaze location. Although it is unclear to what extent this fixation bias reflects shifts of attention along the presented trajectories (see the control analysis inspired by Wilming et al. (2018) and the lack of correlation with the magnitude of the 6-fold effect), we cannot completely rule out this possibility. Indeed, there is an ongoing debate regarding whether miniature eye movements are inherently linked to shifts in spatial attention and can be taken as an index of covert attention (Lowet et al., 2018; Liu et al., 2022; Yu et al., 2022). Nevertheless, grid-like coding seems to emerge in the absence of directly observable, overt oculomotor exploration of the visual environment, as previously reported in non-human primates (Wilming et al., 2018).

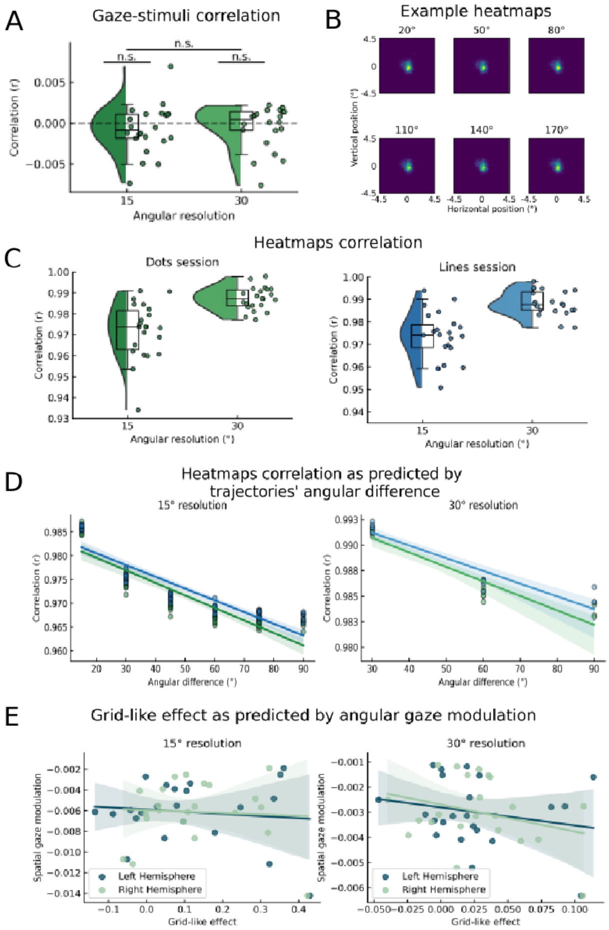


**Figure 4 Gaze location does not influence the grid-like response**

(A) Correlation across time between Euclidean distance of the eye to the center and the dot to the center, replicating the analysis conducted by Wilming and colleagues.[16] We did not observe any correlation at the group level, neither in 15° (t(21) = −1.169, p = 0.255) nor in 30° resolution (t(21) = −0.814, p = 0.424), and no difference was observed between the two angular resolutions (t(21) = −0.409, p = 0.686).

(B) Heatmaps (restricted to the fixation window) from one example participant for each trajectory in the 30° resolution.

(C) Average pairwise correlation (within-subject) between trajectory-specific heatmaps. Correlations were overall high in both the dots (green) and lines (blue) session.

(D) Group-average correlation as a function of angular difference for both the dots (green) and lines (blue) sessions, in both 15° (left) and 30° (right) resolution. We observed a significant negative correlation in all cases (dots session: 15°: r = 0.71 ± 0.09, t(21) = −20.232, p < 0.001; 30°: r = 0.82 ± 0.064, t(21) = −26.486, p < 0.001; lines session: 15°: r = 0.69 ± 0.08, t(21) = −25.224, p < 0.001; 30°: r = 0.81 ± 0.05, t(21) = −32.202, p < 0.001), indicating that trajectories with higher correlation were close in angular space.

(E) Grid-like effect as a function of the angular gaze modulation. The slope of the grid-like effect in each hemisphere was correlated with the slope of the correlation between the pairs of heatmaps and their angular difference. We found no correlation in either hemisphere and in neither the 15° (left) nor 30° resolution (right) (all p > 0.172).

See Figure S7 for the same analyses using gaze angle.

### ***Temporal structure of the FT design cannot explain the grid-like response***

Temporal regularities in stimuli presentation constitute the most important feature of FT designs (De Rosa et al., 2022). When multiple regularities are present (as in our case), their interaction can result in additional neural responses at frequencies corresponding to any sum of the originally tagged frequencies and their multiples (i.e., intermodulation; Norcia et al., 2015; Gordon et al., 2019). Intermodulation of salient rhythms inherent to the previously presented FT design (e.g., presentation rate and “turn” of the clock-like presentation; Cracco et al., 2022) could potentially provide an alternative interpretation of the effects that were observed (Figure S8).

We thus conducted a control experiment to rule out the possibility that the grid-like response reported in the previous experiment was the by-product of other temporal regularities. Specifically, we designed another FT task having the same temporal regularities (i.e., the repeating sequences) but using non-spatially structured stimuli (i.e., letters). In the spatial experiment sequences were of different duration in the two angular resolutions, due to a difference in the number of trajectories. We replicated this feature using a different number of letters in the sequences (15°: 12 letters, from A to N; 30°: 6 letters, from A to F; see STAR Methods and Figure S9).

Data from 22 healthy participants who took part in this non-spatial experiment were analyzed following the same approach used in the spatial experiment (see STAR Methods). If the temporal structure of stimulus presentation and the interaction between multiple frequencies were the cause of the results in the spatial experiment, we should see a preference for the frequency that was previously tagged with 6-fold periodicity (i.e., 1.5 Hz in 15° resolution and 3 Hz in 30° resolution) in this non-spatial experiment as well. To test this hypothesis, we extracted the ITC of the frequencies that in the spatial experiment were tagged with spatial regularities (Figure 1B) and compared them at both sensor level and source level, both within and between experiments.

At sensor level, a two-sided cluster-permutation test (Figure 5A) in the condition that corresponded to the 15° angular resolution identified an occipito-temporal cluster in which ITC at the frequency corresponding to 6-fold spatial periodicity ($ITC_{Cont6}$) was greater than ITC at the frequency corresponding to 4-fold ($ITC_{Cont4}$) ($p < 0.001$ cluster corrected) and two clusters in which ITC at the frequency corresponding to 8-fold ($ITC_{Cont8}$) was higher than $ITC_{Cont6}$, one located in left temporal sensors ($p = 0.010$) and one in right frontal sensors ($p = 0.005$). In the condition corresponding to 30°, we identified an occipito-temporal cluster in which $ITC_{Cont6}$ was greater than $ITC_{Cont4}$ ($p = 0.013$ cluster corrected). The condition corresponding to the 15° resolution showed clearly different results compared to the spatial experiment, with sensors in which $ITC_{Cont8}$ was greater than $ITC_{Cont6}$. In the condition corresponding to the 30° resolution, with only one control periodicity, it was more difficult to characterize a grid-like response as compared to a more general response elicited by the temporal structure. Nevertheless, the topographies of the two experiments were different (Figure S10A), indicating a different neural origin of the effect. Moreover, we found a high correlation of the grid-like response (i.e., the difference between $ITC_6$ and $ITC_4$) between angular resolutions in the spatial experiment and not when correlating the corresponding frequencies of the non-spatial experiment (Figure S10B).

We then reconstructed the sources of the signal to further explore the effects elicited by the temporal structure and ensure that a 6-fold preference was not present in the MTL. Finally, we compared the ITC values in the ROIs between experiments using ANOVAs and Bayesian model comparison.

In the 15° condition (Figure 5B), a mixed ANOVA with experiment as between-subjects factor and ROI and periodicity as within-subjects factor identified a significant three-way interaction in both the left hemisphere ($F(2.73,114.58) = 39.43$, $p < 0.001$) and right hemisphere ($F(2.77, 116.27) = 22.93$, $p < 0.001$), indicating different patterns of ROI × periodicity interaction across the two experiments (spatial vs. non-spatial). Indeed, in the MTL the $ITC_{Cont6}$ was never greater than both the control periodicities. Moreover, contrary to the spatial version of the experiment, the frequency preference showed similar trends in both the MTL and the control regions (see Figure 5B and Table S1 for post hoc pairwise comparison within each ROI). To directly compare $ITC_6$ with both control ITCs at the same time, we fitted (within each experiment) linear (L) and quadratic (Q) models to the group-level data and compared their goodness of fit with Bayes factor (BF; Wagenmakers, 2007). In the MTL ROI (Figure 6A), we found very strong evidence (Raftery, 1995) for the quadratic model centered on the 6-fold periodicity over the linear model in both the left hemisphere ($BF_{QL} = 150.05$) and right hemisphere ($BF_{QL} = 2{,}203.92$) in the spatial experiment. Conversely, in the non-spatial experiment, we found positive evidence for the linear model over the quadratic model in the left hemisphere ($BF_{LQ} = 8.07$) and weak evidence in the right hemisphere ($BF_{LQ} = 2.04$). This is confirmed at the cortical level, where the right MTL shows very strong evidence in favor of the quadratic model over the linear model in the spatial experiment (Figure 6B).

In the 30° resolution (Figure 5C), we found a significant three-way interaction (experiment × ROI × periodicity) in the left hemisphere ($F(1.3, 54.7) = 11.14$, $p < 0.001$) but not in the right hemisphere ($F(1.23, 51.84) = 2.56$, $p = 0.109$). Post hoc comparisons (Figure 5C and Table S1) revealed that a preference for the frequency that was previously tagged with 6-fold spatial periodicity was found in the bilateral MTL but, contrary to the spatial experiment, also in a control region, the left lateral occipital.

Taken together, these results demonstrated that the FT temporal structure generated different neural responses based on the task. The presentation of spatial sequences and their covert attentional tracking resulted in a grid-like response specific to the MTL. The same temporal structure but no spatial allocation of attention instead produced different response profiles across the whole brain. In the 15° condition, we observed a linear increase of ITC with the frequency. In the 30° condition, it was more difficult to characterize the grid-like response as independent from other temporal regularities given the presence of a single control periodicity. Nevertheless, differences in both topographies and control regions make the MTL grid-like effect specific to the spatial experiment, suggesting differences in the mechanisms that gave rise to the observed response in the non-spatial experiment. In this respect, the left lateralization may be suggestive that lexical regularities (which have been shown to be detectable with FT; Lochy et al., 2015; Lochy et al., 2018) were playing a role.

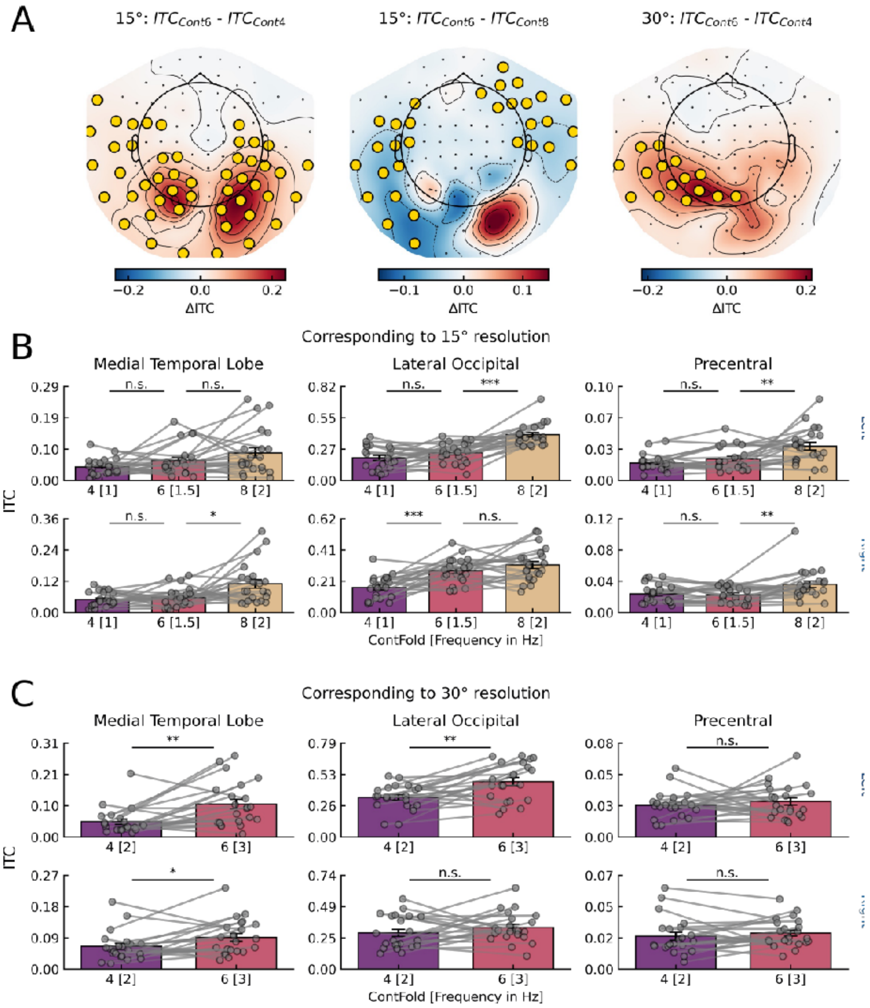


**Figure 5 Temporal structure of the frequency-tagging design does not elicit a grid-like response**

(A) Sensor-level clusters observed in the non-spatial experiment comparing the frequencies tagged with spatial periodicities in the spatial experiment. In the condition corresponding to 15°, ITC$_{Cont6}$ was greater than ITC$_{Cont4}$ ($p < 0.001$ cluster corrected, left) whereas ITC$_{Cont6}$ was lower than ITC$_{Cont8}$ (left-temporal cluster, $p = 0.010$; right-frontal cluster $p = 0.005$, center). In the condition corresponding to 30°, instead ITC$_{Cont6}$ was greater than ITC$_{Cont4}$ ($p = 0.013$, right)

(B) In the condition corresponding to 15° resolution, a significant three-way interaction (experiment × ROI × periodicity) indicates different response profiles between the spatial (Figure 3B) and non-spatial experiment. In the non-spatial experiment, no significant differences between frequencies were identified in the left MTL ROI (top left), while in the right (bottom) MTL ITC$_{Cont6}$ was significantly lower than ITC$_{Cont8}$.

(C) In the condition corresponding to 30° resolution, a significant three-way interaction (experiment × ROI × periodicity) indicates different response profiles between the spatial (Figure 3C) and non-spatial experiment only in the left (top) and not in the right (bottom) hemisphere. This significant interaction was caused by ITC$_{Cont6}$ being greater than ITC$_{Cont4}$ in the left lateral occipital, in that no differences between experiments were found in the MTL. Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s., not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$).

See Table S1 for statistics of the pairwise comparisons.

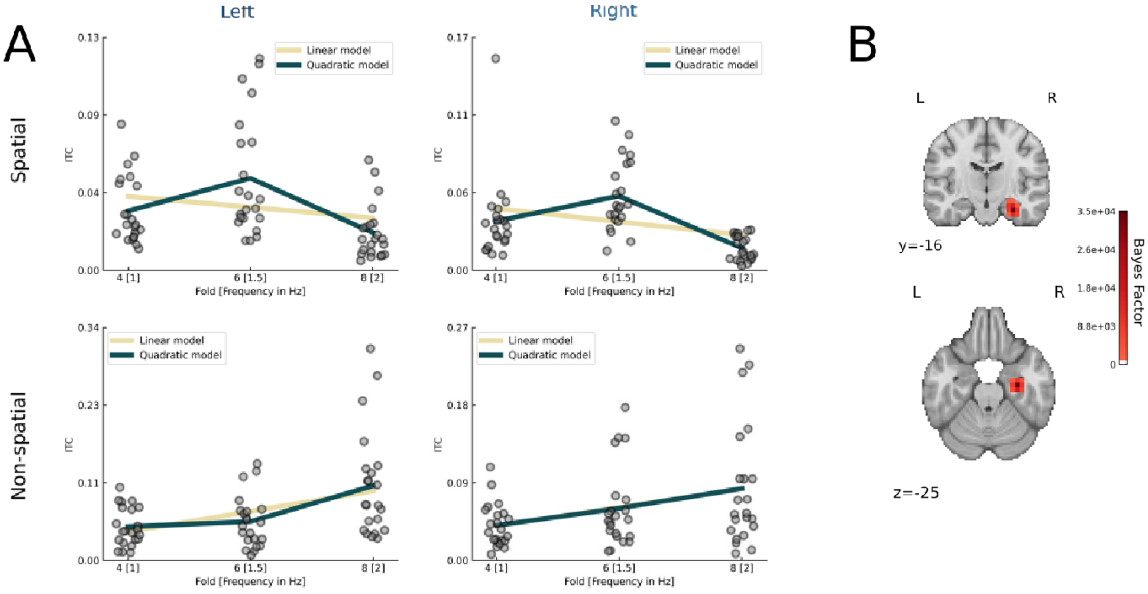


**Figure 6 Bayesian model comparison identifies a quadratic trend in the spatial experiment and a linear trend in the non-spatial experiment**

(A) In the spatial experiment (top), there was very strong evidence in favor of a quadratic model centered on $ITC_6$ as compared to a linear model in both the left ($BF_{QL}$ = 150.05) and right ($BF_{QL}$ = 2203.92) hemispheres. Conversely, in the non-spatial experiment, there was positive evidence for a linear model as compared to a quadratic model in the left hemisphere ($BF_{LQ}$ = 8.07), while there was weak evidence for the linear model in the right hemisphere ($BF_{LQ}$ = 2.04).

(B) Voxel-wise model comparison in the spatial experiment identified very strong evidence for the quadratic model as compared to the linear model in the MTL.

## *Discussion*

We demonstrated that a grid-like response, i.e., a preference for spatial trajectories aligned with a 6-fold periodicity as compared to control periodicities, was elicited in the human MTL by movements of attention. This effect arises in the absence of directly observable eye movements during the exploration of the environment, providing evidence that also in humans covert attention induces grid-like responses.

To this end, we used an eye tracker in combination with MEG FT. The proposed method relies on the periodic visual presentation of spatial trajectories. Crucially, unbeknownst to participants, these trajectories exhibited spatial regularities corresponding to the periodic firing of grid cells. This resulted in a grid-like response that was specific to the MTL, thus demonstrating the biological plausibility of the cellular-level signal that was picked up non-invasively with MEG. Moreover, in a control experiment, we provided evidence that the grid-like signal depended on covert movements of attention and not on the temporal structure of our task.

## *Covert attention elicited a grid-like signal in the human MTL*

Previous literature had already demonstrated that overt visual exploration can result in a grid-like response in the MTL (Killian et al., 2012; Meister & Buffalo, 2018; Staudigl et al., 2018; Julian et al., 2018; Nau et al., 2018b), strengthening the relationship, in primates, between the neural mechanisms supporting spatial exploration through bodily and ocular movements (Rolls & Wirth, 2018; Nau et al., 2018a). Gaze location is often considered a proxy for spatial attention. However, attention can also be covertly moved in space independently of eye movements (Posner, 1980), resulting in a similar grid-like response in non-human primates (Wilming et al., 2018). Here we demonstrated that a grid-like response was present also in humans while attention was covertly deployed to spatial locations.

By confirming findings from non-human primates, we provided comparable evidence across species for an attentional mechanism being able to give rise to grid-like responses. The current results allow for an interesting hypothesis regarding the general role of hippocampal cognitive maps in representing knowledge. Indeed, grid-like coding in the entorhinal cortex emerges also when people mentally explore relational links between non-spatial stimuli, such as visual objects (Constantinescu et al., 2016), odors (Bao et al., 2019), social attributes (Park et al., 2021), or word meanings (Viganò & Piazza, 2020). The attention-modulated activation of grid-like coding provides a suitable mechanism supporting the activation of the same hippocampal machinery during the navigation of conceptual spaces: where there is nothing to see and nowhere to move, but internal attention can be moved across the mental space.

In primates, attention and eye movements are tightly linked (Rizzolatti et al., 1987; Corbetta et al., 1998; Smith et al., 2012; Awh et al., 2006), and it is possible that even spontaneous endogenous shifts of attention cannot be completely dissociated from gaze behavior, such as microsaccades (Yuval-Greenberg et al., 2014). Indeed, we found that similar trajectories induced similar biases in eye position, albeit very small. Across participants, however, the strength of this bias did not predict the grid-like effect, suggesting that it may not reflect attentional movements along the relevant spatial trajectories. However, if attentional movements cannot be completely dissociated from gaze behavior and if the navigation of conceptual spaces is mediated by attention, it could be possible that spontaneous eye movements would reflect the structure and navigation of abstract relational spaces. Future studies should investigate whether this is the case.

## *FT as a non-invasive tool to assess the grid-like response*

A second purpose of the present study was to develop an alternative non-invasive method that allows detection of the grid-like response. The seminal paper by Doeller and colleagues (2010) opened the possibility to study the proxy of a cellular response non-invasively, giving rise to numerous discoveries on the functioning of grid-like response in humans. While this method has been used successfully in both healthy participants and special populations (Kunz et al., 2015; Bierbrauer et al., 2020), it relied on participants' compliance to perform a task and undergo long training procedures. This greatly limited the possibility to investigate grid-like signals with populations that instead may have problems in performing cognitive tasks, such as patients, or may not be able to undergo long experiments, such as children.

We developed a method to detect a grid-like response based on FT that overcomes these limitations and can be used to further advance our understanding of grid-like responses in the human brain. FT in fact has been employed successfully in special populations (de Heering & Rossion, 2015; Buiatti et al., 2019; Vettori et al., 2020). Moreover, FT can be used to study high-level cognitive processes, such as attention (Müller et al., 2003; Kim et al., 2007) or understanding spatial relations (Adibpour et al., 2021).

Taken together, our results indicate that the proposed method is a valid alternative to the now standard non-invasive analytical approaches to detect a grid-like signal, with the advantage of requiring less effort from the participants and thus being potentially useful in special populations.

## ***Limitations of the study***

In the present study we investigated the so-called grid-like response, a macro-scale proxy for the grid-cell response (Doeller et al., 2010). The relationship between grid-cell properties at the micro-scale and grid-like signal at the meso-scale and macro-scale, however, still have to be clarified (Kunz et al., 2019). Our FT paradigm, as well as other paradigms used in non-invasive neuroimaging (fMRI, MEG), may be able to capture such signal capitalizing on the coordinated activity of populations of conjunctive grid cells exhibiting similar orientations (Doeller et al., 2010; Stensola et al., 2012). Nevertheless, it is also possible that 6-fold symmetry occurs independently at different levels of brain organization, with different and specific biological and behavioral relevance (Kunz et al., 2019). Future studies combining investigations at the micro-scale and meso-scale may shed light on the precise mechanism relating different levels of spatial representations.

Furthermore, studies recording field potentials will allow us to pinpoint the exact spatial origin of the signal we measured non-invasively with MEG. Mounting evidence demonstrates the ability of MEG to detect signals from deep brain structures such as the hippocampus (Ruzich et al., 2019; Pu et al., 2018). Indeed, we observed a grid-like response specifically in the MTL and not in control regions, in line with other MEG studies focused on grid-like coding (Staudigl et al., 2018; Convertino et al., 2023). Nevertheless, distinguishing between subfields of the MTL may still be difficult, although simulation studies suggest it is possible (Stephen et al., 2005).

## STAR Methods

### Resource availability

### Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact Roberto Bottini, roberto.bottini@unitn.it.

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

- Data reported in this paper will be shared by the lead contact upon request.

- All original code has been deposited at DOI 10.17605/OSF.IO/TV2CU

- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

### Experimental model and study participant details

Twenty-four participants (12 male, age M = 25,88 years; SD = 4,84) were recruited to participate in the spatial experiment that consisted in two magnetoencephalography (MEG) sessions, conducted in different days (maximum eight days apart). One participant did not show up for the second session and was excluded from the analysis. Another sample of twenty-four participants (9 male, age M = 23,91 years; SD = 3,51) were recruited to participate in the non-spatial experiment.

All had normal or corrected to normal vision and no history of neurological disorders. Prior to each session they gave written informed consent to participate in the experiment. All procedures were approved by the ethical committee of the University of Trento.

### Method details

### Spatial experiment design

The experiment consisted in the visual presentation of spatial stimuli (trajectories). These were defined dividing a circle in 24 and 12 equidistant points, resulting in two angular resolutions (15° and 30°) that were presented in different trials. These points were rotated 10° clockwise to avoid trajectories to appear along the cardinal axes. Each trajectory connected two opposite points (i.e., 180° apart) in the circle.

In separate recording sessions these trajectories were presented to the same participants either as a sequence of dots, moving from one end to the other of the circle, or as static lines, covering the whole trajectory at once. The order of the sessions was counterbalanced across participants. Note that static lines lack directionality, effectively reducing the number of trajectories to half. That is, a trajectory starting at 20° and ending at 200° occupied the same portion of space as a trajectory starting at 200° and ending at 20°. In the dots session half of the trajectories were presented as starting from the opposite side of the circle, effectively making opposite trajectories indistinguishable between each other. The total number of trajectories is thus 12 in the 15° resolution and 6 in the 30° resolution.

Stimuli were generated using MATLAB (version 2012b, The Mathworks, Natick, MA, USA) and presentation was controlled using PsychToolbox (Brainard, 1997).

A new trajectory was presented every 0.166 s (6 Hz) using a typical frequency-tagging (FT) approach (Figure 1). In the "lines" session, a new line appeared at the presentation rate of 6 Hz crossing the circle from one end to the other with a break around the fixation window. In the "dots" session individual trajectories were presented at 6 Hz but they were formed by 20 dots, appearing in successive positions along the trajectory at the rate of 0.0083 s (corresponding to the 120 Hz refresh rate of the screen) and covering the whole trajectory before the appearance of the next one. Of these 20 dots, the 4 central dots were excluded to avoid presenting them within the fixation window. In each trial were presented 264 trajectories, for a total duration of 44 s. These appeared sequentially, in a clock-like fashion (e.g., 20°, 50°, 80°, 110° etc … in the 30° resolution, Figure 1A), with clockwise/counter-clockwise direction balanced across participants. Crucially, the periodic presentation of regularly spaced trajectories allowed to embed multiple spatial periodicities in the trajectories' sequence, each appearing at fixed and distinct temporal intervals such that each spatial periodicity "tags" a unique frequency (Figure 1B). Specifically, at 15° resolution, trajectories separated by 60° (6-fold) appear every 0.666 s (1.5 Hz), trajectories separated by 90° (4-fold) every 1 s (1 Hz) and trajectories separated by 45° (8-fold) every 0.5 s (2 Hz). At 30° instead, trajectories separated by 60° appear every 0.333 s (3 Hz) while trajectories separated by 90° appear every 0.5 s (2 Hz). Note that 6- and 4-fold occur in both spatial resolutions, but tagging different frequencies in each. This enables an estimation of their neural tracking that is not tied to a specific chosen frequency as well as direct comparison between responses in the two spatial resolutions.

Multiple sequences with the same trajectories' order were presented in a trial to allow the emergence of a frequency-tagged response to the different spatial periodicities. Specifically, individual sequences lasted 2 s (15°) and 1 s (30°), with each sequence containing one instance of each trajectory. With the clock-like presentation one sequence corresponds to half-turn of the clock. The starting trajectory of the sequence was randomized across trials such that each trajectory was used as a start twice (15°) or four times (30°) over the experiment.

Participants were instructed to fixate in the center of the screen while paying attention to the trajectories that were shown in the periphery. To avoid following saccades, we defined a fixation window of 4.5° of visual angle[16] in which no visual stimulus was presented, except for a fixation dot that remained on the screen center for the whole trial duration. This fixation window size was used also to restrict participants gaze behavior: at the end of each trial, a warning message appeared on the screen if the participant's gaze was outside the fixation window for more than 20% of the trial time (8.4 s).

To ensure participants were covertly tracking the trajectories, we asked them to perform a location memory task (Fig., 1D). Two red target dots appeared at random position along a trajectory for 0.025 s. The timing of their appearance was randomized but constrained between 19 and 33 s for the first dot and between 37 and 39 s for the second dot. This timing was chosen to ensure participants were focused until the end of the FT presentation. Participants were instructed to remember the exact position of these two red target dots for future recall. At the end of each trial two red test dots appeared in three possible configurations, each with equal probability: i) test dots occupy the same spatial positions as target dots; ii) only one test dot does not occupy the same position of the target dots; iii) there was no overlap between test and target dots. Participants had to respond via button-press with the right index finger to indicate same position and with the right middle finger to indicate different position, irrespective of the number of dots being in a different position. The probability of these occurrences was 50%.

The experiment was divided in six blocks of eight trials each, for a total of 48 trials, 24 in each angular resolution. In each block there were four consecutive trials of the same angular resolution, and the resolution presented as first was randomized and balanced across blocks.

The timing of the presentations was controlled by the computer. A 15 s break was included after every trial, while 30 s were allowed after 4 consecutive trials. After each break, a 3 s countdown informed participants that a new trial was about to start. The trial then only started after participants had fixated for at least 500 ms within a 2° visual angle fixation window centered on the fixation dot. After each block participants were allowed a longer, self-timed, break of about 2 min.

### ***Non-spatial experiment design***

With this control experiment we wanted to test the hypothesis that temporal regularities inherent to the FT design can generate a periodic neural response that is comparable to the grid-like signal measured in the spatial experiment. Temporal regularities are defined here by the number of stimuli presented in the sequence and the individual sequences' duration, which varied between the angular resolutions of the spatial experiment. We thus reproduced these features using stimuli without spatial structure. Specifically, we reproduced the temporal structure of the 15° resolution by creating a sequence of 12 letters (A to N). Similarly, the 30° resolution was reproduced by creating a sequence of 6 letters (A to F).

Individual letters were visually presented every 0.166 s (6 Hz) with contrast modulation (Lochy et al., 2015; Lochy et al., 2018). Other potentially salient temporal regularities that may be tagged by this FT design include the sequence duration. Sequences corresponding to the 15° resolution lasted 2 s (0.5 Hz) while sequences corresponding to 30° resolution lasted 1 s (1 Hz). Frequencies of interest in the spatial experiment are not tagged with spatial regularities anymore. Any effect observed at these frequencies cannot be ascribed to spatial regularities but should be interpreted as arising from the intermodulation of the presentation rate and other potentially salient rhythms such as the sequence rate.

Participants were instructed to fixate in the center of the screen while paying attention to the letters' sequences. Moreover, to keep them engaged, twice during a trial and with the same time constraints as in the spatial experiment the fixation dot turned red for 0.025 s, a change that the participants were instructed to promptly detect (max 3 s) via right index finger button press.

## *MEG and eye-tracker acquisition*

MEG data were acquired at the Center for Mind/Brain Sciences of the University of Trento with an Elekta Neuromag 306 MEG system (Elekta, Helsinki, Finland), composed of 102 magnetometers and 204 planar gradiometers, placed in a magnetically shielded room (AK3B, Vakuumschmelze, Hanau, Germany). The head-shape of the participants was digitized (Fastrak Polhemus, Inc., Colchester, VA, USA) prior to acquisition in each session, along with fiducial points (nasion, left and right periauricular) and five head position indicator (HPI) coils, three placed on the forehead and one behind each ear. Both fiducials and HPIs were digitized twice to ensure precision (<2 mm difference).

Before entering the MEG, participants performed a short practice block (4 trials, 2 of each angular resolution) to familiarize with the FT design and the task. They received written instructions before the practice and feedback on their performance after each trial.

Participants sat upright in the MEG chair with their head as close as possible to the dewar. The eye-tracker (Eyelink 1000 Plus, SR Research Ltd., Ottawa, Canada) was positioned to ensure optimal recording of both eyes. A nine-point calibration procedure was carried out before each block.

Continuous MEG data were recorded at 1000 Hz with hardware bandpass filters in the range 0.1–330 Hz. Along with MEG, we also recorded the time series of a photodiode that tracked the colour-change of a small square on the top-left corner of the screen (not visible to the participants). This color-change was coded as indicating the start of a trial and was used in the analysis to correct for potential delays in the stimuli presentation. Eye-tracker was recorded separately for each trial at a sampling rate of 1000 Hz. Stimuli were projected on a translucent whiteboard, positioned 1 m in front of the participant, using a ProPixx projector (Vpixx Technologies, Canada) at a 120 Hz refresh rate. Responses were collected using a MEG compatible button response box (Vpixx Technologies, Canada).

After each session a 5 min empty-room measurement was recorded to be used for noise modeling in the source reconstruction procedure.

Four blocks from different participants had technical issues and were not included in the final analysis.

## *MEG and eye-tracker preprocessing*

Raw task data and empty-room MEG time series were visually inspected to identify sensors with jumps and noise throughout the recording session. Artifactual sensors (M = 7.59, SD = 6.75) were excluded and interpolated through MaxFilter (temporal signal suppression; Taulu & Simola, 2006). Raw task data was subsequently realigned to the recording block that minimized the Euclidean distance across blocks, separately for each session.

Further processing and visualization were conducted in python using MNE-python (Gramfort et al., 2013) as well as common scientific python packages (Harris et al., 2020; Hunter et al., 2007; Virtanen et al., 2020; McKinney, 2010; Seabold & Perktold, 2010; Waskom, 2021).

After application of MaxFilter, continuous raw data were filtered (High pass: 0.1 Hz, Low-pass: 40 Hz) and segmented into 44 s–long trials, starting from the onset of the first trajectory. Trial onset was corrected for potential delays using a photodiode: we replaced the MEG-recorded trigger with the actual time indicated by the change in the photodiode time series, thus setting the trial onset to the actual presentation of the first trajectory on the screen as viewed by the participant.

Hence, for each trial we quantified fixation behavior by computing the percentage of time the right eye position was within the 4.5° fixation window. Trials in which this metric was below 80% of the trial time (35.6 s) were excluded from further analysis (percentage of rejected trials: spatial experiment: dots session: 5.7%; lines session: 5.1%; non-spatial experiment: 7.69%). In the non-spatial experiment one participant was excluded at this stage due to the low number of trials left after exclusion (33%).

In a control analysis (dots and lines session only, Fig.S4), we removed trials with fixation time below 95% (41.8 s). This led to the exclusion of one participant for which the total number of trials left was below 33%, leaving 21 participants for this control analysis.

To ensure consistent timing across trials in the appearance of the spatial periodicities, trials were realigned to the first presentation of the 350° trajectory, reducing their length to 40 s and 42 s in the 15° and 30° resolution, respectively.

To increase the signal-to-noise ratio (Benjamin et al., 2021), trials' time series were further divided in shorter, non-overlapping segments of 8 s and 6 s, resulting in 5 and 7 segments per trial in the 15° and 30° resolution, respectively. Segment duration was chosen for multiple reasons: i) It allows an integer number of repetitions of each individual sequence (4 and 6); ii) each segment contains an integer number, as well as a high number, of cycles of the frequencies of interest and enables as a high frequency resolution (0.125 Hz and 0.167 Hz), resulting in output frequencies that match the tagged frequencies. Segmented data underwent a semi-automatic artifact rejection procedure in which both variance and kurtosis were computed over time for each channel, akin to the visual artifact rejection procedure implemented in the Fieldtrip package (Oostenveld et al., 2011), and subsequently averaged across channels to obtain a metric per segment. Segments above two standard deviations in each individual metric were visually inspected for the presence of artifacts (e.g., remaining channel jumps, muscle artifacts, blinks). If visual inspection confirmed the presence of an artifact, the segment was marked as bad and excluded from further analyses. This procedure led to the exclusion of an additional 0.68% of segments in the dots session of the spatial experiment and 1.04% of segments in the lines session, while 0.83% of segments were excluded in the non-spatial experiment.

## *Frequency analysis*

Artifact-free segments were subjected to a fast-Fourier transform (FFT) separately for each channel (at sensor-level) or voxel (at source level). From the complex representation of each segments' time series in the frequency domain we computed the inter-trial coherence (ITC) as follows:

$$ITC = (\frac{1}{N}\sum_{n=1}^{N} cos\theta_n)^2 + (\frac{1}{N}\sum_{n=1}^{N} sin\ \theta_n)^2$$

where θ is the phase of the individual segment (n) as obtained from the FFT (Ding & Simon, 2013; Ding et al., 2016; Henin et al., 2021).

This metric quantifies the synchronization of the neural response across segments and ranges from 0 to 1, where 1 indicates perfect synchronization. We then isolated the ITC at the single individual frequencies "tagged" with the spatial periodicities (see "Spatial experiment design" and Figure 1B), given the narrowband response afforded by the FT method. For comparison, the same frequencies were selected in the non-spatial experiment. However, these frequencies bore no spatial meaning, as in this control experiment they were not tagged with spatial regularities.

## *Source reconstruction*

Structural T1-weighted images were acquired at the Center for Mind/Brain Sciences of the University of Trento in a 3T Siemens Prisma scanner (Siemens, Erlangen, Germany) with a Multi-Echo MPRAGE (MEMPRAGE) sequence with the following parameters: FoV = 256mm; Voxel Size = 1 × 1 × 1 mm3; TR = 2530 ms; TE1 = 1.69ms; TE2 = 3.55ms; TE3 = 5.41ms; TE4 = 7.27ms and a flip angle of 7°. Two participants of the spatial experiment did not perform the MRI session.

Anatomical images were segmented using Freesurfer 7 (Fischl, 2012) to obtain subject-specific anatomical parcellations.

Coregistration of the digitized head position and the reconstructed structural surfaces was performed separately for each session. First the three fiducial points were matched, followed by an iterative closest-point match algorithm that minimizes the distance between the digitized head shape and the skin surface. For the two participants without MRI this procedure consisted in warping the Freesurfer template to match their digitized head shape and derive a subject-specific template. As recently demonstrated, using a template produces highly similar results than using the subject-specific T1 image (Vinding & Oostenveld, 2022).

A single shell boundary-element method model was created to define a volume source space by filling the inner skull surface with equidistant (5 mm) voxels.

Inverse solution was based on linearly-constrained minimum variant (LCMV) beamformer (Van Veen et al., 1997). A beamformer approach was chosen given its better resolution in estimating subcortical activity (Ruzich et al., 2019; Pu et al., 2018). A time domain solution was preferred to be able to reconstruct multiple frequencies at source level using a single spatial filter, such that the observed differences cannot be ascribed to differences in the inversion algorithm. Artifact-free segments, including data of both magnetometers and gradiometers, were used for source reconstruction. From these we estimated the empirical data covariance (separately for the 15° and 30° resolutions) while subject specific empty-room recordings were used to model noise and account for the different contributions of the two sensor types. Both data and noise covariance matrices were regularized with 5% of the sensors' power and their rank was reduced to the residual degrees of freedom after application of MaxFilter (Westner et al., 2022). Inversion kernel dimensionality was reduced by one dimension, as suggested for MEG data with single-shell headmodel. Dimensionality of the inversion kernel was further reduced by retaining (through SVD) the dipole orientation that maximized power, resulting in a scalar beamformer. No depth weighting was applied. Beamformer weights were normalized using the 'unit-noise-gain-invariant' option. The FFT and then ITC were computed at each voxel from the reconstructed time series as detailed in the frequency analysis section.

In a control analysis we replicated the source reconstruction procedure detailed above but using only magnetometers data (Figure S5).

## *Quantification and statistical analysis*

### *Behavioral analysis*

Accuracy (percentage of correct responses) was computed separately for each session and each angular resolution. We used a dependent samples t test to compare these metrics across angular resolutions, separately for each session. One participant of the spatial experiment was excluded from further analysis due to performance being two standard deviation below the group mean in both session. Similarly, one participant in the non-spatial experiment was excluded based on the same criterion.

### *Sensor-level cluster-permutation test*

A two-sided cluster-based permutation test (Maris & Oostenveld, 2007) was used to compare the ITC at the frequency corresponding to the 6-fold spatial periodicity ($ITC_{6:}$ 1.5 Hz in the 15° resolution, 3 Hz in the 30° resolution) to the ITC of the control spatial periodicities (15° resolution: $ITC_8$ 2 Hz, $ITC_4$ 1 Hz; 30° resolution: $ITC_4$ 2 Hz), separately for each angular resolution and each control periodicity. For this analysis we considered only magnetometers, given their higher sensitivity to deep brain structures as compared to planar gradiometers (Hari & Salmelin, 2012).

In brief, a one-sample t test is performed at each channel on the difference between conditions (i.e., spatial periodicities). The channels that survived an uncorrected threshold of $p < 0.05$ are retained to form spatial clusters based on a predefined adjacency matrix with ~6 neighbors per channel. This procedure was repeated 10000 times, each time shuffling the condition labels and retaining the highest cluster statistic (t-score). A p value corrected for multiple comparisons is obtained by comparing the cluster statistic observed from the actual contrast with the distribution of permuted cluster statistics.

The same analysis was applied to the non-spatial experiment data, comparing the frequencies that in the spatial experiment were tagged with spatial regularities.

### *Source-level ROI analysis*

Source level analysis focused on subject-specific anatomical regions of interest (ROIs) obtained from the Freesurfer parcellation. Specifically, we created an MTL ROI encompassing the entorhinal and parahippocampal cortex, from the Desikan-Killiany atlas (Desikan et al., 2006), and the hippocampus, obtained from Freesurfer's own subcortical parcellation (Fischl et al., 2002). We included control ROIs from the Desikan-Killany atlas to confirm the specificity of the effect in the medial temporal lobe. As control ROIs we used the lateral occipital, to test for an effect in visual cortex given the visual nature of the task. The precentral ROI was chosen as a region that was supposed to be distant from the effects of interest.

Subject-specific, average ITC values within each ROI were entered into series of analysis of variance (ANOVA) in R (R Core Team, 2022). First, a two-way repeated measures ANOVA with factors session (dots, lines) x periodicity (15° resolution: 4-, 6-, 8-fold; 30° resolution: 4-, 6-fold) was aimed at investigating differences in the neural tracking in the MTL ROI between the dots and lines sessions. This analysis was repeated for each hemisphere and each angular resolution. Results showed no statistically significant session × periodicity interaction, suggesting that a similar response profile could be observed across sessions. All subsequent analyses will therefore consider the average across session as input.

A two-way repeated measures ANOVA with factors ROI (MTL, lateral occipital, precentral) x periodicity (15° resolution: 4-, 6-, 8-fold; 30° resolution: 4-, 6-fold) investigated differences across ROIs in the neural tracking of the spatial periodicities. Planned paired t-tests were conducted to evaluate whether $ITC_6$ was greater than ITC of the control periodicities in each ROI.

Last, we compared the spatial experiment to the non-spatial experiment. We conducted a three-way mixed ANOVA with experiment (spatial, non-spatial) as between-subjects factor and ROI (MTL, lateral occipital, precentral) and periodicity (15° resolution: 4-, 6-, 8-fold; 30° resolution: 4-, 6-fold) as within-subject factors.

Greenhouse-Geisser correction was applied to the degrees of freedom in case sphericity assumption was violated.

### *Conjunction analysis*

ROI analysis is biased by *a-priori* selection of a limited number of regions, effectively neglecting contributions from other parts of the brain. To assess whether this constraint hinders the interpretation of our findings we additionally computed a whole-brain conjunction analysis (Nichols et al., 2005). This consists in computing the individual contrasts between $ITC_6$ and ITC of the control periodicities, separately for each cortical voxel and for each angular resolution. The resulting t-maps are then combined by retaining, for each voxel, the minimum t-value across all contrasts and angular resolutions. Resulting t-maps are plotted at an uncorrected threshold of $p < 0.005$.

This analysis highlights the commonalities between contrasts, thus providing the best visualization of the spatial specificity of the grid-like effect, that is independent of the specific tagged frequencies and angular resolutions.

### *Source-level cluster-permutation test*

We also performed a cluster-permutation test (Maris & Oostenveld, 2007) at the cortical level. In the 15° resolution we contrasted $ITC_6$ to the averaged $ITC_4$ and $ITC_8$. In the 30° resolution we contrasted $ITC_6$ to $ITC_4$. The procedure was the same as the one described in the paragraph “Sensor-level cluster-permutation test”, except that in these analyses clusters were formed by voxels in volume source space instead of sensors.

### *Gaze- and dot-position correlation*

We investigated whether the eyes were following the dots by replicating the control analyses conducted by Wilming and colleagues (2018). First, the eye tracker data were downsampled to 120 Hz to match the screen refresh rate, at which dots were presented. Then, for each trial, we computed the Euclidean distance between the eye position and the center of the screen at each time point. Similarly, the Euclidean distance was computed between the dot position and the center of the screen at each time point. The time points when a blink was detected were excluded from both vectors before computing the Euclidean distance. We then correlated the resulting distance vectors. A positive correlation would indicate that the eyes were following the dot. The resulting r values were fisher transformed and entered in a one-sample t test against zero, separately for 15° and 30° resolution, and in a dependent samples t test to compare between the angular resolutions. This analysis was conducted only for the dots session, for which we could precisely estimate one spatial location of the stimuli per time point.

### *Gaze distance to target dot*

We investigated whether the presentation of target dots induced a shift in gaze location toward the target dot location. Separately for each target dot presentation, we computed the Euclidean distance between the eye position and the target dot position. We then selected two time windows of interest: −0.05 to 0 s and 0.05 to 0.1 s relative to target dot onset (see

Liu et al., 2022 for a similar time window definition), i.e., “before” and “after” the target dot onset. If the eye had followed the dot, its distance in the “after” time window would have been smaller as compared to the “before” time window. We thus compared the average gaze distance between time windows using a paired samples t test, separately for each session and angular resolution.

### *Spatial gaze modulation*

We implemented further control analyses on the eye-tracker data to investigate gaze behavior in both the dots and the lines session.

We segmented the trial time series according to the presentation of the trajectories and concatenated the time windows corresponding to the same trajectory (separately for each session and angular resolution), excluding all time points in which gaze was outside the fixation window.

The aggregated time series were transformed into heatmaps using Gaussian kernel density estimate (Wynn et al., 2020), as implemented in scipy with default parameters.

This process was repeated for each individual trajectory resulting in 12 and 6 heatmaps for 15° and 30° angular resolution, respectively (Figure 4B for an example of 30° resolution heatmaps). Each pair of heatmap (separately for each angular resolution) was then correlated using Pearson correlation, resulting in 66 correlation values in 15° resolution and 15 values in 30° resolution. The average (within-subject) pairwise correlation is reported in Figure 4C and in the main text. We then computed the angular difference between the pairs of trajectories. This difference was normalized between 0° and 90° to account for the circularity of the angular measure. The vector of pairwise correlations between the heatmaps was then correlated with the vector of corresponding angular differences. The resulting correlation values were fisher transformed and entered in a one sample t test against zero.

Similarly, the aggregated time series of gaze location were used to compute the gaze angle with respect to the screen center for each trajectory. Gaze-angles distributions (12 in 15°, 6 in 30°; Figure S7A) of each trajectories pair (66 in 15°, 15 in 30°) were compared using Kuiper’s test (Kuiper, 1960), whose test statistic “V” indexes the difference between pairs of circular distributions, with larger values indicating larger differences. The average (within-subject) test statistic is reported in Figure S7B. The normalized angular difference was correlated with the corresponding V score. The resulting r scores were fisher transformed and tested at the group-level against the null hypothesis of no correlation.

### *Correlation between gaze and grid-like effects*

We further investigated whether gaze behavior was playing a role in the generation of the grid-like response. To do this we computed correlation between the grid-like measure and the measure of trajectory-based gaze similarity as obtained in the previous analyses. As grid-like measure we used the slope of a quadratic model fitted on the ITC response in MTL of each subject in the 15° resolution (see “*Bayesian model comparison”* for a similar analysis on the group-level data). Similarly, in the 30° resolution we used the slope of a linear model. As trajectory-based gaze similarity measure we used the slope of the correlation between trajectories' angular difference and the corresponding similarity measure (r for heatmaps, v for gaze-angles distributions). We computed Pearson's correlation between these measures to investigate whether participants that showed a higher grid-like effect were also the ones whose gaze was more influenced by the presentation of the trajectories.

### Bayesian model comparison

To directly compare the $ITC_6$ with both control ITCs at the same time, we fitted linear and quadratic models to the group-level ROI data at 15° resolution. For both linear and quadratic models we computed the Bayesian information criterion (BIC), a metric that quantifies goodness of fit while accounting for the number of parameters included in the model. Results were compared using a Bayes Factor (BF; Wagenmakers, 2007). In brief, BF is computed as follows:

$$BF_{QL} = exp(\Delta BIC_{LQ} \ / \ 2)$$

where $\Delta BIC_{LQ}$ is the difference in the BIC obtained for each model. QL indicates the evidence in favor of the quadratic (Q) over the linear (L) model and vice versa. This formulation is consistent with the “unit information prior”. The BF quantifies the strength of the evidence for one model as compared to the other and can be interpreted according to standard guidelines (Raftery, 1995).

### Topographies' correlation

Having observed a similar, significant frequency preference in both experiments in the 30° resolution, we sought to quantify the extent to which this similar response is expressed in the pattern of sensor level activity. To this end, we correlated the group-average topography of the ITC difference between frequencies tagged with 6- and 4-fold periodicity between the spatial (i.e., Figure 2C, right) and non-spatial experiment (i.e., Figure 5A, right) in the 30° resolution.

Moreover, we reasoned that a grid-like response should be relatively independent of the granularity of the space that is used in its investigation, thus providing a similar response pattern in both spatial resolutions that were tested in the current experiment.

To investigate this, we computed the (within-participant) similarity of the topographies of the grid-like effect (i.e., $ITC_6$ - $ITC_4$) between the 15° and 30° angular resolutions. We focused on 6- and 4-fold periodicities given that they were common between angular resolutions.

Similarly, in the non-spatial experiment we computed the correlation of the topographies ($ITC_{Cont6}$ - $ITC_{Cont4}$) between the conditions corresponding to the 15° and 30° resolutions. Correlation values were fisher transformed before further analysis. A one-sample t test was used to investigate whether the correlations at the group level were significantly different from zero. An independent samples t test was instead used to compare the correlation scores across experiments.

## *Supplementary results*

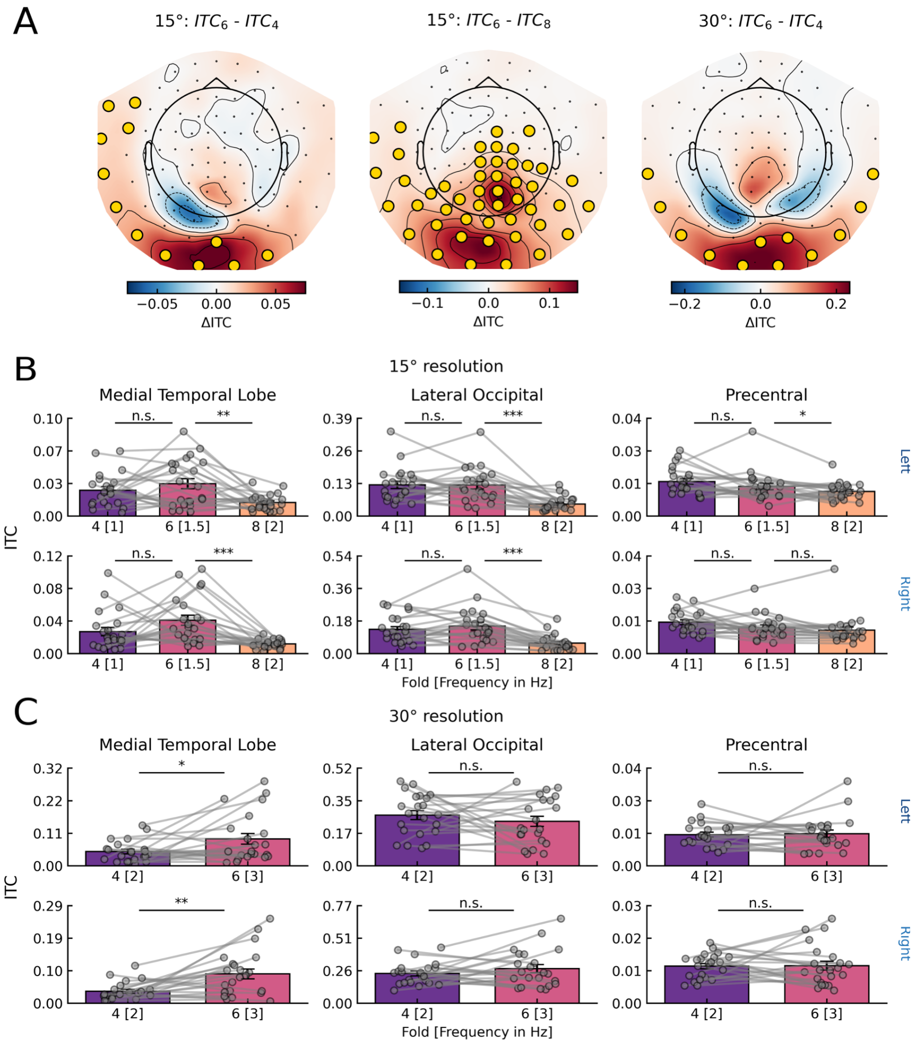


*Figure S1. Sensor- and source-level results for the dots session. Related to Fig. 2 and Fig. 3*

A) Significant clusters at sensor-level in which $ITC_6$ is greater than control ITCs. In the 15° resolution $ITC_6$ is greater than $ITC_4$ (left, $p=0.009$ cluster corrected) and $ITC_6$ is greater than $ITC_8$ (center, $p<0.001$). In the 30° resolution $ITC_6$ is greater than $ITC_4$ (right, $p=0.011$). No clusters were found in which control periodicities are higher than 6-fold periodicity.

B) A two-way repeated measures ANOVA with factors periodicity (4-, 6-, 8-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in both the left (top, $F(4, 84)=13.49$, $p<0.001$) and right hemisphere (bottom, $F(4, 84)=13.667$, $p<0.001$). Planned paired t-test did not identify significant differences between $ITC_6$ and $ITC_4$ in neither the left ($t(21)=1.14$, $p=0.266$) nor the right hemisphere ($t(21)=1.70$, $p=0.102$) but a significantly greater $ITC_6$ than $ITC_8$ in both the left ($t(21)=3.31$, $p=0.003$) and the right hemisphere ($t(21)=4.49$, $p<0.001$). In the lateral occipital no significant differences were identified between $ITC_6$ and $ITC_4$ in neither the left ($t(21)=-0.07$, $p=0.944$) nor the right hemisphere ($t(21)=1.01$, $p=0.323$) but a significantly greater $ITC_6$ than $ITC_8$ in both the left ($t(21)=4.02$, $p<0.001$) and the right hemisphere ($t(21)=6.35$, $p<0.001$). In the precentral ROI we did not find significant differences between $ITC_6$ and $ITC_4$ in neither the left ($t(21)=-1.25$, $p=0.223$) nor the right hemisphere ($t(21)=-1.48$, $p=0.151$) but a significantly greater $ITC_6$ than $ITC_8$ in the left ($t(21)=2.09$, $p=0.048$) but not the right hemisphere ($t(21)=1.23$, $p=0.230$).

C) A two-way repeated measures ANOVA with factors periodicity (4-, 6-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in the left (top, $F(2, 42)=3.40$, $p=0.042$) but not in the right hemisphere (top, $F(2, 42)=2.20$, $p=0.123$). However, planned paired t-tests identify a significantly greater $ITC_6$ as compared to $ITC_4$ in both the left ($t(21)=2.25$, $p=0.034$) and right hemisphere ($t(21)=3.62$, $p=0.001$). No significant differences between the ITCs were found in any control region (left: lateral occipital: $t(21)=-0.93$, $p=0.361$; precentral: $t(21)=0.21$, $p=0.831$; right: lateral occipital: $t(21)=1.14$, $p=0.263$; precentral: $t(21)=0.09$, $p=0.922$).

Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

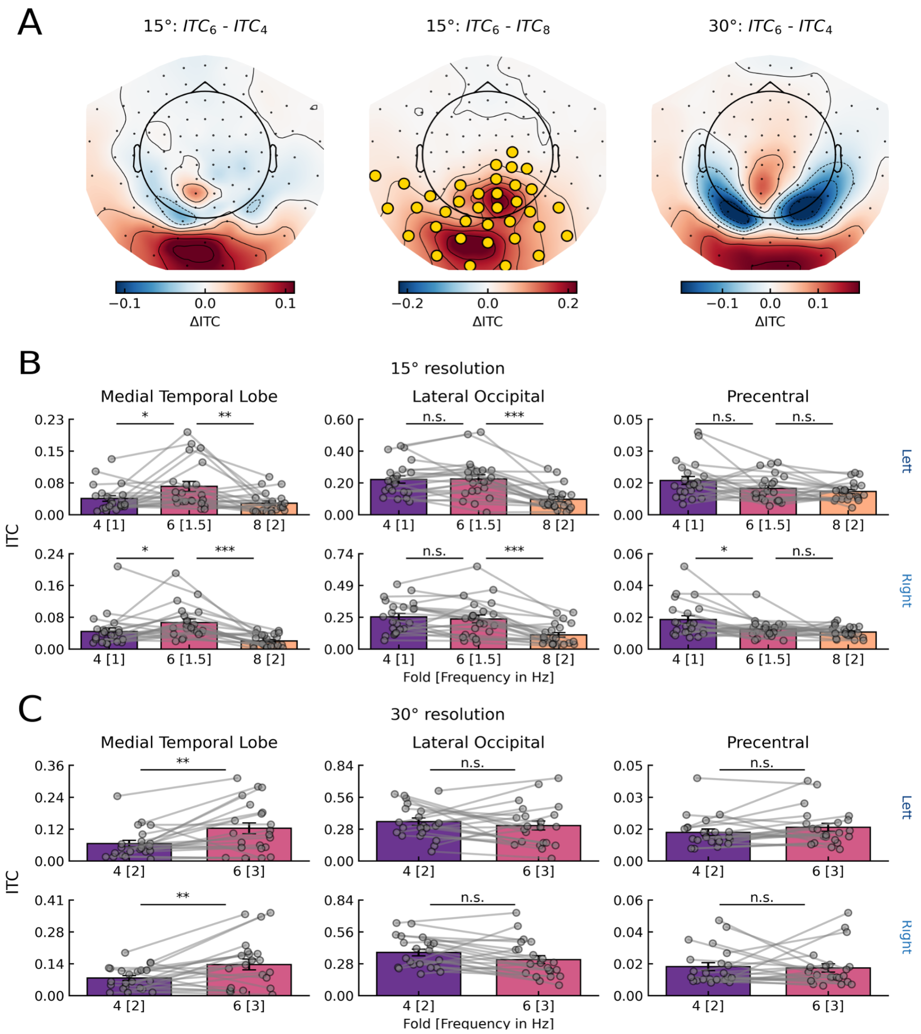


*Figure S2. Sensor- and source-level results for the lines session. Related to Fig. 2 and Fig. 3*

A) Cluster-permutation test at sensor-level identifies a significant cluster in which $ITC_6$ is greater than $ITC_8$ ($p=0.007$ cluster corrected). No significant clusters were found in the other contrasts (all $p>0.1$), although topographies were very similar to the dots session.

B) A two-way repeated measures ANOVA with factors periodicity (4-, 6-, 8-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in both the left (top, $F(4, 84)=26.15$, $p<0.001$) and right hemisphere (bottom, $F(4, 84)=17.27$, $p<0.001$). Planned paired t-test identified significant differences between $ITC_6$ and $ITC_4$ in the left ($t(21)=2.39$, $p=0.026$) and the right hemisphere ($t(21)=2.17$, $p=0.040$) as well as a significantly greater $ITC_6$ than $ITC_8$ in both the left ($t(21)=3.13$, $p=0.005$) and the right hemisphere ($t(21)=5.39$, $p<0.001$). In the lateral occipital no significant differences were identified between $ITC_6$ and $ITC_4$ in neither the left ($t(21)=0.19$, $p=0.848$) nor the right hemisphere ($t(21)=-0.78$, $p=0.439$) but a significantly greater $ITC_6$ than $ITC_8$ in both the left ($t(21)=5.79$, $p<0.001$) and the right hemisphere ($t(21)=5.26$, $p<0.001$). In the precentral ROI we did not find significant differences between $ITC_6$ and $ITC_4$ in the left ($t(21)=-1.77$, $p=0.089$) but a significant difference in the right hemisphere ($t(21)=-2.62$, $p=0.015$) while no significant differences were found between $ITC_6$ than $ITC_8$ neither in the left ($t(21)=1.00$, $p=0.325$) nor in the right hemisphere ($t(21)=1.14$, $p=0.267$).

C) A two-way repeated measures ANOVA with factors periodicity (4-, 6-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in the left (top, $F(2, 42)=4.15$, $p=0.023$) and in the right hemisphere (top, $F(2, 42)=10.78$, $p<0.001$). Planned paired t-tests identify a significantly greater $ITC_6$ as compared to $ITC_4$ in both the left ($t(21)=3.21$, $p=0.004$) and right hemisphere ($t(21)=2.84$, $p=0.009$). No significant differences between the ITCs were found in any control region (left: lateral occipital: $t(21)=-0.83$, $p=0.413$; precentral: $t(21)=1.44$, $p=0.162$; right: lateral occipital: $t(21)=-1.92$, $p=0.067$; precentral: $t(21)=0.23$, $p=0.817$).

Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

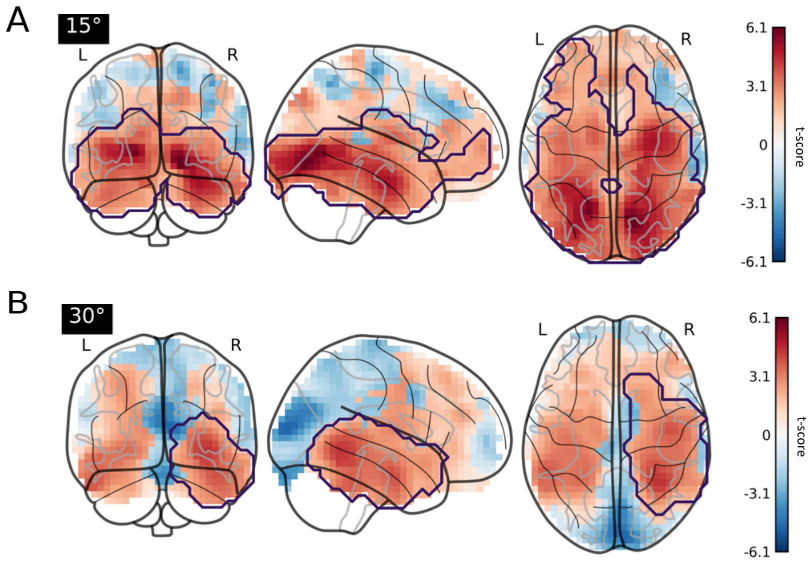


*Figure S3. Source-level cluster permutation test. Related to Fig. 3.*

A) Cluster-permutation test (10000 permutations, cluster-forming threshold p=0.05) comparing $ITC_6$ with the average of $ITC_4$ and $ITC_8$ in the 15° resolution identified a significant cluster (p=0.001, highlighted) encompassing MTL regions.

B) Cluster-permutation test (10000 permutations, cluster-forming threshold p=0.05) comparing $ITC_6$ with $ITC_4$ in the 30° resolution identified a significant cluster (p=0.053, highlighted) encompassing the right MTL.

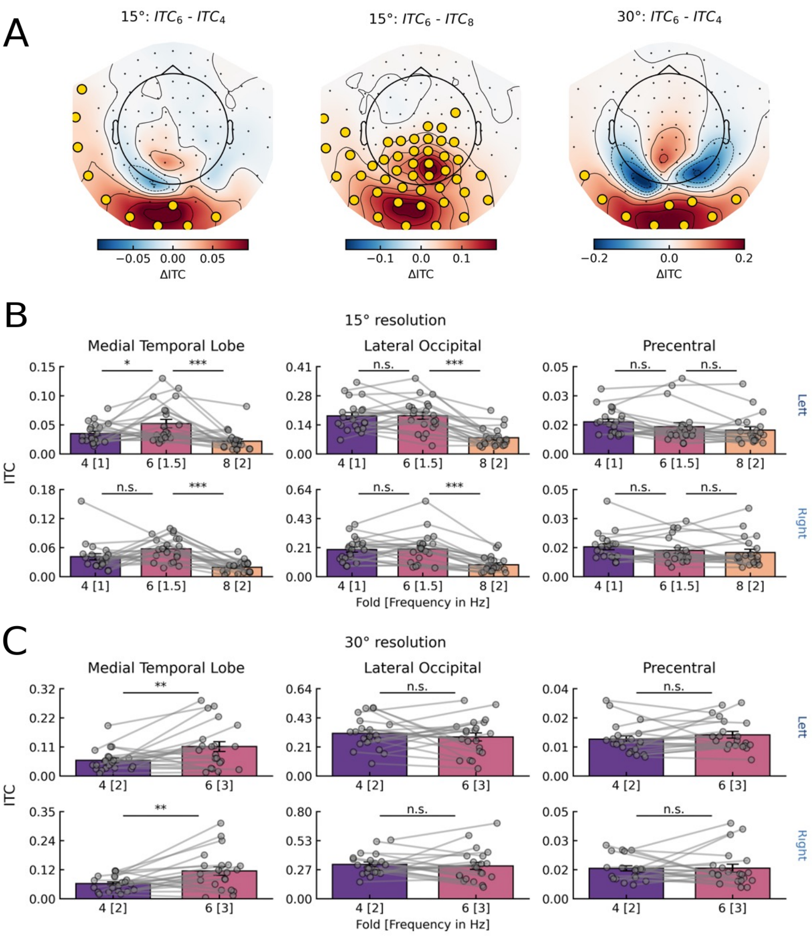


*Figure S4. Increasing fixation threshold does not influence the grid-like effect. Related to Fig. 2 & 3.*

A) A cluster permutation test at sensor-level (10000 permutations, cluster forming threshold p=0.05) identified significant clusters in which $ITC_6$ is greater than control ITCs, indicating a grid-like response in occipito-temporal sensors. In the 15° resolution $ITC_6$ is greater than $ITC_4$ (left, p=0.025) and $ITC_6$ is greater than $ITC_8$ (center, p=0.001). In the 30° resolution $ITC_6$ is greater than $ITC_4$ (right, p=0.054). No clusters were found in which control periodicities were higher than 6-fold periodicity.

B) A two-way repeated measures ANOVA with factors periodicity (4-, 6-, 8-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in both the left (top, F(2.54, 50.75)=26.76, p<0.001) and right hemisphere (bottom, F(2.22, 44.35)=21.17, p<0.001). Planned paired t-test identified significant differences between $ITC_6$ and $ITC_4$ in the left (t(20)=2.09, p=0.049) and the right hemisphere (t(20)=1.99, p=0.059) as well as a significantly greater $ITC_6$ than $ITC_8$ in both the left (t(20)=3.90, p<0.001) and the right hemisphere (t(20)=6.12, p<0.001). In the lateral occipital no significant differences were identified between $ITC_6$ and $ITC_4$ in neither the left (t(20)=0.09, p=0.929) nor the right hemisphere (t(20)=0.23, p=0.814) but a significantly greater $ITC_6$ than $ITC_8$ in both the left (t(20)=6.45, p<0.001) and the right hemisphere (t(20)=6.30, p<0.001). In the precentral ROI we did not find significant differences between $ITC_6$ and $ITC_4$ in the left (t(20)=-1.57, p=0.131) nor in the right hemisphere (t(20)=-1.64, p=0.116). No significant differences were found between $ITC_6$ and $ITC_8$ neither in the left (t(20)=1.44, p=0.163) nor in the right hemisphere (t(20)=0.84, p=0.406).

C) A two-way repeated measures ANOVA with factors periodicity (4-, 6-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in the left (top, F(1.32, 26.48)=3.75, p=0.053) and in the right hemisphere (top, F(1.3, 25.99)=3.88, p=0.05). Planned paired t-tests identify a significantly greater $ITC_6$ as compared to $ITC_4$ in both the left (t(20)=2.87, p=0.009) and right hemisphere (t(20)=3.21, p=0.004). No significant differences between the ITCs were found in any control region (left: lateral occipital: t(20)=-0.72, p=0.476; precentral: t(20)=1.26, p=0.220; right: lateral occipital: t(20)=-0.42, p=0.674; precentral: t(20)=0.05, p=0.959).

Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s.: not significant; *: p < 0.05; **: p < 0.01; ***: p < 0.001

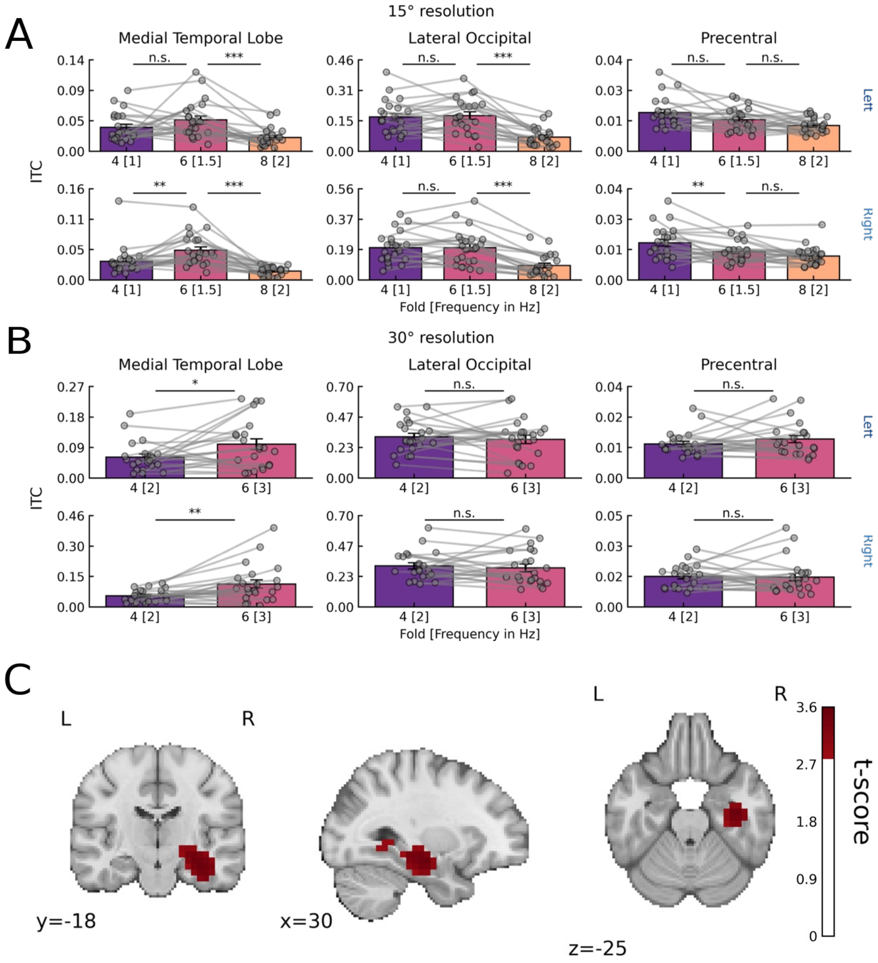


*Figure S5. Source reconstruction using only magnetometers. Related to Fig. 3.*

A) A two-way repeated measures ANOVA with factors periodicity (4-, 6-, 8-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in both the left (top, F(2.31, 48.58)=24.80, p<0.001) and right hemisphere (bottom, F(2.11, 44.94)=23.06, p<0.001). Planned paired t-test identified significant differences between ITC$_6$ and ITC$_4$ in the right (t(21)=3.47, p=0.002) but not in left hemisphere (t(21)=1.51, p=0.143). A significantly greater ITC$_6$ than ITC$_8$ was instead observed in both the left (t(21)=4.73, p<0.001) and the right hemisphere (t(21)=5.67, p<0.001). In the lateral occipital no significant differences were identified between ITC$_6$ and ITC$_4$ in neither the left (t(21)=0.45, p=0.650) nor the right hemisphere (t(21)=-0.01, p=0.987) but a significantly greater ITC$_6$ than ITC$_8$ in both the left (t(21)=6.50, p<0.001) and the right hemisphere (t(21)=7.31, p<0.001). In the precentral ROI we did not find significant differences between ITC$_6$ and ITC$_4$ in the left (t(21)=-1.92, p=0.068) but a significant difference in the right hemisphere (t(21)=-2.86, p=0.009) while no significant differences were found between ITC$_6$ than ITC$_8$ neither in the left (t(21)=2.05, p=0.052) nor in the right hemisphere (t(21)=1.94, p=0.065).

B) A two-way repeated measures ANOVA with factors periodicity (4-, 6-fold) and ROI (MTL, lateral occipital, precentral) identified significant interactions in the right hemisphere (F(1.52, 32.02)=5.40, p=0.015) but not in the left (F(1.28, 26.87)=2.61, p=0.11). Planned paired t-tests identify a significantly greater ITC$_6$ as compared to ITC$_4$ in both the left (t(21)=2.47, p=0.021) and right hemisphere (t(21)=3.41, p=0.002). No significant differences between the ITCs were found in any control region (left: lateral occipital: t(21)=-0.61, p=0.542; precentral: t(21)=1.06, p=0.300; right: lateral occipital: t(21)=-0.51, p=0.609; precentral: t(21)=-0.16, p=0.870).

Gray dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s.: not significant; *: p < 0.05; **: p < 0.01; ***: p < 0.001

C) Conjunction analysis (15°: ITC$_6$ > ITC$_4$ & ITC$_6$ > ITC$_8$ & 30° ITC$_6$ > ITC$_4$) at the cortical level (p<0.005 uncorrected) demonstrated the specificity to the MTL of the grid-like effect.

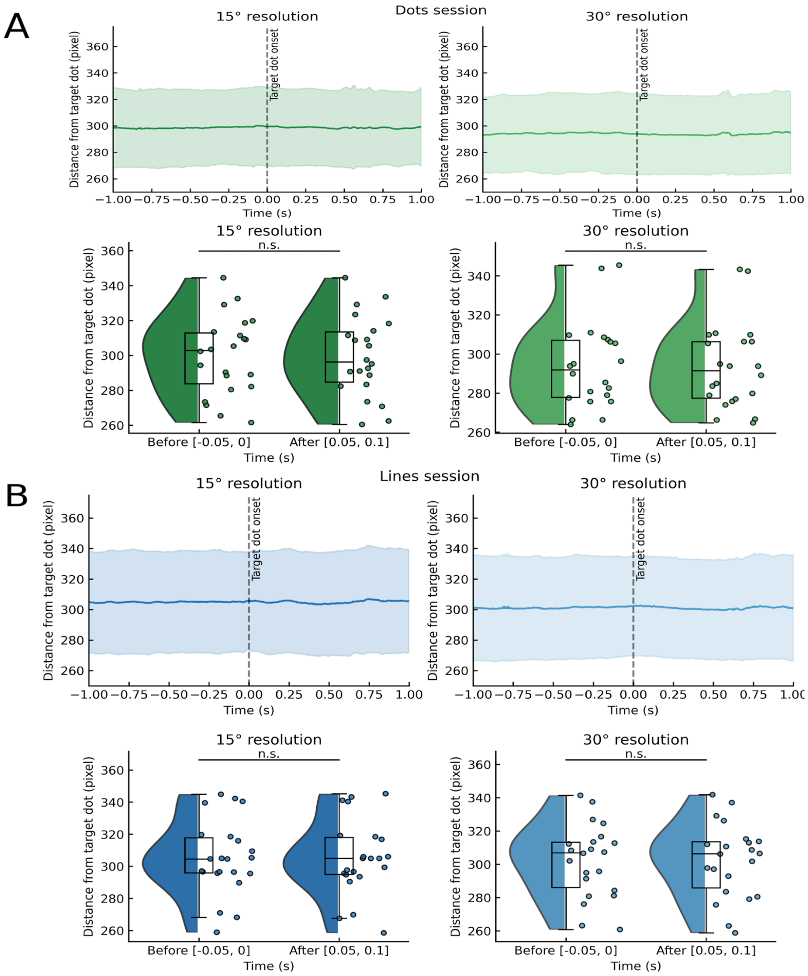


*Figure S6. No gaze shift following the presentation of target dots. Related to Fig. 4*

We investigated whether the presentation of the to-be-memorized target dots induced a shift in gaze location towards the position of the dots. To this end, we realigned the eye tracker time series to the appearance of the dot. We then computed the Euclidean distance of the eye to the target dot location, for both the dots (A, top) and lines (B, top) sessions. To directly compare the shift in gaze location depending on the presentation of the dots we selected 50 ms time windows before (-0.05 to 0 s) and after (0.05 to 0.1 s) dots onset. If the eye moved following the dot the distance in the “after” time window would be smaller than “before". This was not the case, neither in the dots (15°:, 30°: ; A, bottom) nor in the lines session (15°: t(21)=0.088, p=0.930; 30°: t(21)=-0.269, p=0.790, B, bottom).

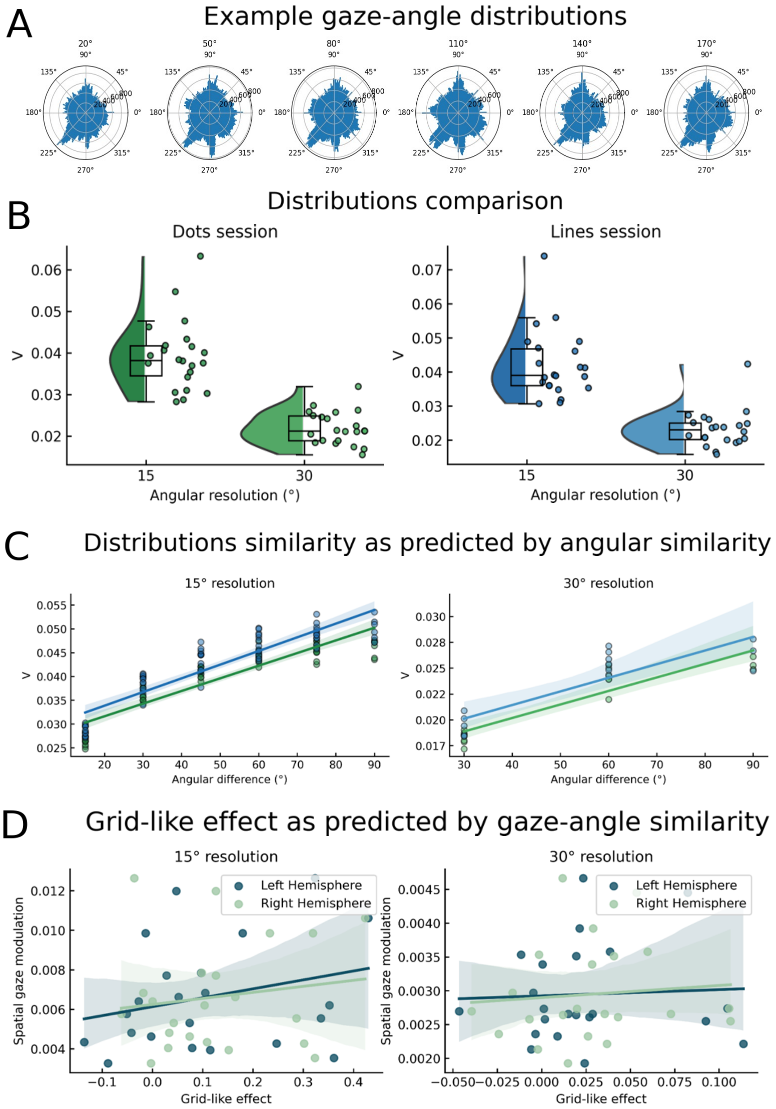


*Figure S7. Gaze angle does not influence the grid-like response. Related to Fig. 4.*

A) Gaze-angles distributions (restricted to the fixation window) from one example participant for each trajectory in the 30° resolution.

B) Average pairwise v-score (within-subject) between gaze-angles distributions. V-scores were overall low, both in the dots (green) and lines (blue) session, indicating a small difference between distributions.

C) Group-average v-score as a function of angular difference, for both the dots (green) and lines (blue) sessions, in both 15° (left) and 30° (right) resolution. We observed a significant positive correlation in all cases (dots session (green): 15° (left): r=0.577±0.150, t(21)=12.696, p<0.001; 30° (right): r=0.592±0.119, t(21)=17.260, p<0.001; lines session: 15°: r=0.69±0.112, t(21)=15.630, p<0.001; 30°: r=0.514±0.130, t(21)=13.493, p<0.001), indicating that trajectories with higher distribution similarity were closer in angular space.

D) Grid-like effect as a function of the angular gaze modulation. The slope of the grid-like effect in each hemisphere was correlated with the slope of the correlation between the pairs of gaze-angles distributions and their angular difference. We found no correlation in neither hemispheres and neither in the 15° (Left Hemisphere: r=0.27, p=0.232; Right Hemisphere: r=0.15, p=0.511; left panel) nor in the 30° resolution (Left Hemisphere: r=0.05, p=0.824; Right Hemisphere: r=0.09, p=0.684; right panel).

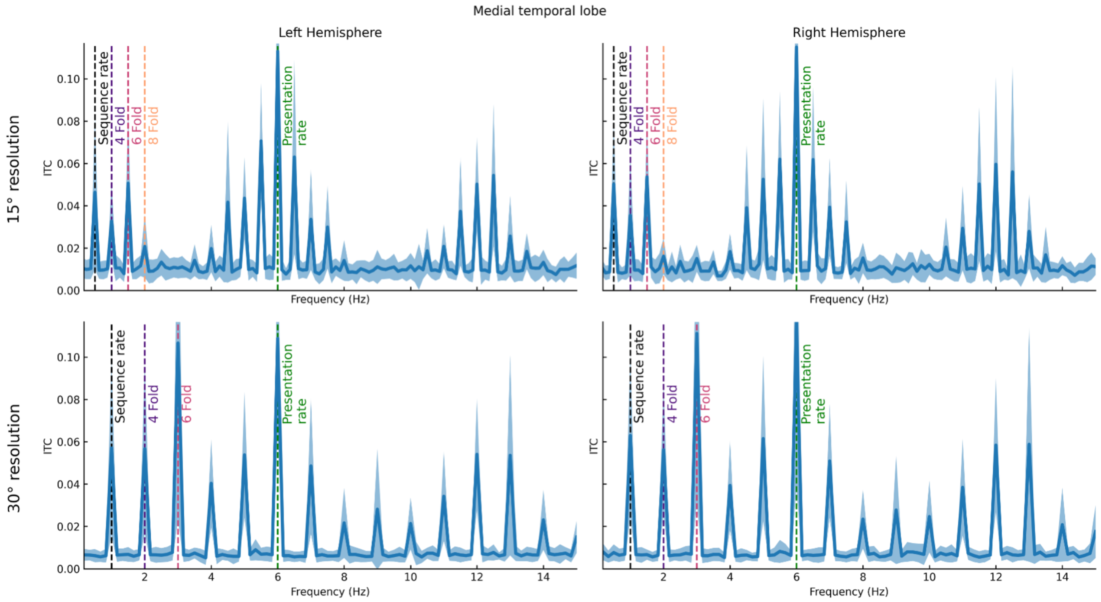


*Figure S8. Intermodulation effect in the spatial experiment. Related to Fig. 3*

Multiple peaks were present in the frequency spectrum (0.1-15 Hz) in the MTL ROI (left column: left hemisphere; right column: right hemisphere), not only the presentation rate and the ones tagged with spatial regularities. The lowest (in Hz) prominent peak was the one at the “sequence rate”, i.e., the time interval at which an individual sequence of unique trajectories was repeatedly presented (0.5 Hz in 15° resolution (top), and 1 Hz in 30° resolution). In other words, the time interval to complete one “turn” of the clock-like presentation. Note that one sequence (or turn) corresponded to half of the clock, given the lack of directionality that made opposite trajectories indistinguishable: e.g. a trajectory starting at 20° and ending at 200° occupied the same portion of space than a trajectory starting at 200° and ending at 20°. The peaks corresponding to the spatial regularities (highlighted) could then be reinterpreted as being the harmonics of this “sequence rate” peak or the intermodulation between the “sequence rate” and the presentation rate. Intermodulations are in fact any sum of the multiples of the original frequencies, e.g. considering 30° resolution 1 Hz (f1, sequence rate) and 6 Hz (f2, presentation rate), intermodulation components can arise at f1+f2=7Hz, f2-f1=5Hz, f2-f1*2=4Hz, f2*2-f1=11Hz etc.. Although the frequency tagged with 6-fold periodicity was the one with the highest ITC (excluding presentation rate), we could not rule out the possibility that its ITC was a byproduct of these intermodulation components. In fact, intermodulation components can give rise to a frequency spectrum similar to the one we found in the MTL (see Gordon et al., 2019 Fig. 2). This finding motivated us to run a control experiment to investigate the effect that temporal regularities corresponding to a sequence rate have on the neural response.

Blu lines indicate average ITC across subjects. Shaded area indicates standard deviation.

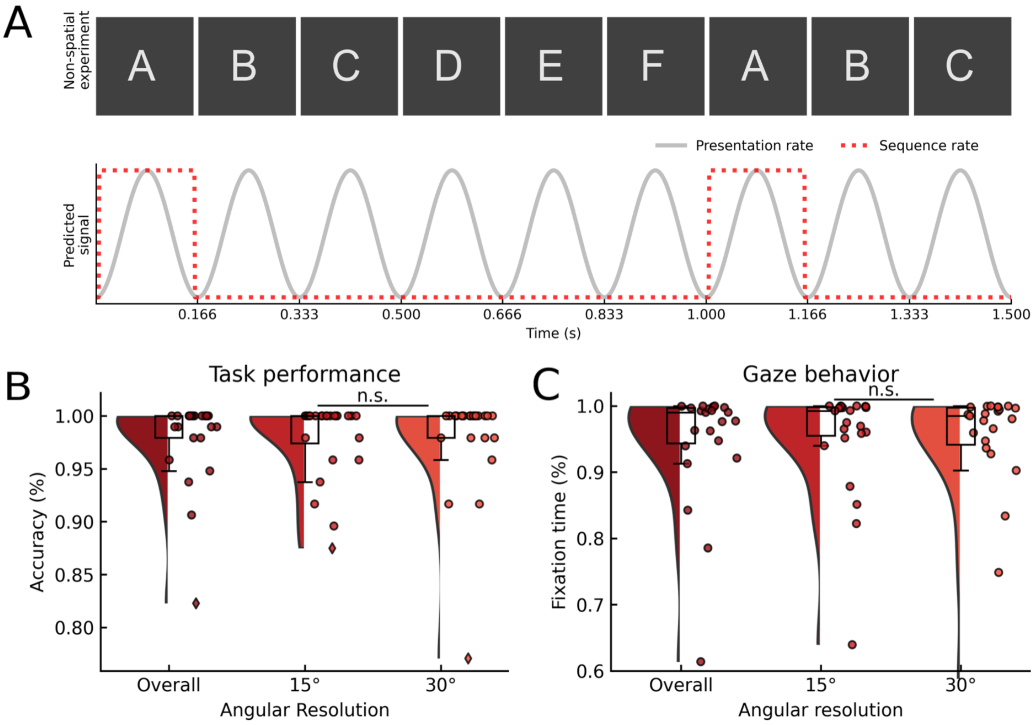


*Figure S9. Design of the non-spatial experiment and behavioral results. Related to Fig. 5*

A) Example of a sequence of letters corresponding to the 30° resolution. Individual letters were presented continuously every 167 ms (6 Hz). This same sequence of letters (A to F) was presented repeatedly every 1 s (1 Hz), generating a rhythm corresponding to the temporal structure of the sequence that corresponds to the presentation of a 30° sequence in the spatial experiment. Similarly, the 15° condition is mimicked by creating a sequence of 12 letters (A to N) that was repeated every 2 s (0.5 Hz) corresponding to the time required to present a sequence of trajectories linearly-spaced by 15° in the spatial experiment. With this presentation no frequency is tagged with spatial periodicity. The frequencies of interest of the spatial experiment (e.g., 2 and 3 Hz in 30°) in fact correspond to the presentation of letters A and D and A and E, respectively.

B) Accuracy in the color-change detection task, averaged over angular resolutions as well as separately for each angular resolution. Participants were overall accurate (M=97.87%, SD=4.02%) except for one participant (diamond point in the plot) whose accuracy (82%) was two standard deviations below the group mean and was thus excluded from further analyses. No difference was found between conditions (t(23)=0.13, p=0.896).

C) Fixation time during the trials, expressed as percentage, averaged over angular resolutions as well as separately for each angular resolution. Participants were keeping fixation within a 4.5° fixation window for the majority of the time during the trial. Trials in which fixation was maintained for less than 80% of the time were excluded from further analyses and this led to the exclusion of one participant due to the low amount of trials left.

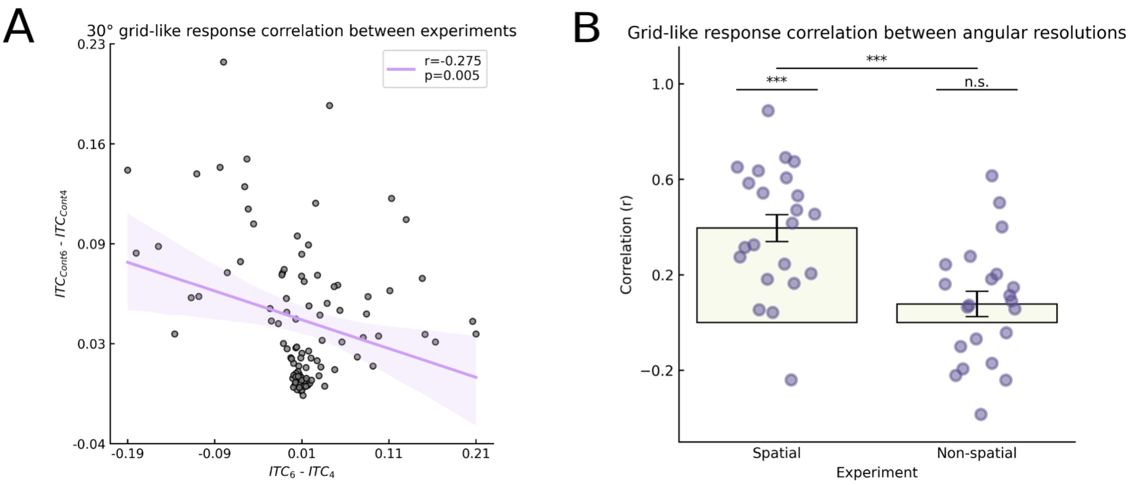


*Figure S10. Topographies correlation between experiments. Related to Fig. 6.*

A) Although the cluster-permutation test identified similar frequency preferences in the spatial and non-spatial experiment, in the 30° condition (see Fig 2C and 4A in main text), topographies seemed quite different, suggesting that these frequency preferences may rely on different neural mechanisms. To directly assess the similarity of the neural response between the experiments, we correlated the group-level topography of the grid-like response in the 30° condition between the spatial and non-spatial experiment and found a significant negative correlation (r(100)=-0.227, p=0.005) suggesting differences in the neural mechanism generating the measured response, even if a significant difference in the frequencies of interest is found in both experiments.

B) We reasoned that the spatial resolution that defines the space should not influence the grid-like response, thus if grid cells are contributing to the signal we are measuring we should observe a high correlation between the grid-like response in the 15° and 30° resolution, but only in the spatial experiment. To test this hypothesis, we measured the (within-subject) similarity between the multivariate grid-like response (i.e. the difference between the tagged frequencies that are in common between the two resolutions) in the 15° and 30° resolution in both the spatial and non-spatial experiment. Purple dots indicate individual subjects. Error bars indicate standard error of the mean. Lines above data points indicate significance (n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$)

Confirming the prediction, we found a significant correlation at the group level between the 15° and 30° topographies in the spatial experiment (t(21)=6.09, p<0.001) and not in the non-spatial experiment (t(21)=1.48, p=0.151), with the correlation in the spatial experiment being higher than in the non-spatial experiment (independent samples t(42)=3.99, p<0.001).

These results indicate that although univariate analyses identify comparable differences in the ITC response in both the spatial and non-spatial experiment, the multivariate topographical pattern can provide additional information and distinguish the neural tracking of the spatial periodicities as compared to a response to the temporal regularities.

| Angular resolution | Hemisphere | ROI | Comparison | df | t | p | Sig. |
|---|---|---|---|---|---|---|---|
| 15° | Left | MTL | Cont$_6$ [1.5 Hz] vs Cont$_4$ [1 Hz] | 21 | 1.74 | 0.094 | |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | 1.41 | 0.171 | |
| | | Lat. Occipital | Cont$_6$ [1.5 Hz] vs Cont$_4$ [1 Hz] | 21 | 1.65 | 0.112 | |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | -6.09 | <0.001 | *** |
| | | Precentral | Cont$_6$ [1.5 Hz] vs Cont$_4$ [1 Hz] | 21 | 2.04 | 0.053 | |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | -2.85 | 0.009 | ** |
| | Right | MTL | Cont$_6$ [1.5 Hz] vs Cont$_4$ [1 Hz] | 21 | 0.73 | 0.468 | |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | -2.70 | 0.013 | * |
| | | Lat. Occipital | Cont$_6$ [1.5 Hz] vs Cont$_4$ [1 Hz] | 21 | 4.83 | <0.001 | *** |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | -1.61 | 0.121 | |
| | | Precentral | Cont6 [1.5 Hz] vs Cont4 [1 Hz] | 21 | -0.45 | 0.652 | |
| | | | Cont$_6$ [1.5 Hz] vs Cont$_8$ [2 Hz] | 21 | -3.19 | 0.004 | ** |
| 30° | Left | MTL | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 3.40 | 0.002 | ** |
| | | Lat. Occipital | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 3.49 | 0.002 | ** |
| | | Precentral | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 0.76 | 0.450 | |
| | Right | MTL | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 2.28 | 0.032 | * |
| | | Lat. Occipital | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 1.13 | 0.267 | |
| | | Precentral | Cont$_6$ [3 Hz] vs Cont$_4$ [2 Hz] | 21 | 0.88 | 0.388 | |

*Table S1. Pairwise comparison between frequencies at source level in the non-spatial experiment. Related to Fig. 4*

We ran post-hoc t-tests at source level in each ROI to investigate whether a frequency preference was present in the non-spatial experiment (see Fig. 3 and Table 1 for the same tests in the spatial experiment).

In the condition corresponding to 15° resolution (top), in the left hemisphere we found no significant difference between the ITCs (ITC$_{\text{Cont6}}$ vs ITC$_{\text{Cont4}}$: t(21)=1.74, p=0.094; ITC$_{\text{Cont6}}$ vs ITC$_{\text{Cont8}}$: t(21)=-1.41, p=0.171) while in the right we found a significant difference between ITC$_{\text{Cont6}}$ and ITC$_{\text{Cont8}}$ (t(21)=-2.70, p=0.013) and no significant difference between ITC$_{\text{Cont6}}$ and ITC$_{\text{Cont4}}$ (t(21)=0.73, p=0.468). In control regions Post-hoc t-tests in the left lateral occipital show that ITC$_{\text{Cont8}}$ was greater than ITC$_{\text{Cont6}}$ (t(21)=-6.09, p<0.001) while no significant difference was found between ITC$_{\text{Cont60°}}$ and ITC$_{\text{Cont90°}}$ (t(21)=1.65, p=0.112). The opposite effect was found in the right lateral occipital, with ITC$_{\text{Cont60°}}$ being greater than ITC$_{\text{Cont4}}$ (t(21)=4.83, p<0.001) but no significant difference between ITC$_{\text{Cont6}}$ and ITC$_{\text{Cont8}}$ (t(21)=-1.61, p=0.121). In the left precentral ROI instead we found that ITC$_{\text{Cont8}}$ was significantly higher than ITC$_{\text{Cont6}}$ (t(21)=-2.85, p=0.009) while no significant difference was found between ITC$_{\text{Cont6}}$ and ITC$_{\text{Cont4}}$ (t(21)=2.04, p=0.053). Similarly in the right hemisphere only ITC$_{\text{Cont8}}$ was greater than ITC$_{\text{Cont60°}}$ (t(21)=-3.19, p=0.004) but no significant difference was found between ITC$_{\text{Cont6}}$ and ITC$_{\text{Cont4}}$ (t(21)=-0.45, p=0.652).

In the condition corresponding to the 30° resolution (bottom), post-hoc t-tests in the MTL revealed a significantly greater ITC$_{\text{Cont6}}$ than ITC$_{\text{Cont4}}$ (left: t(21)=3.40, p=0.002; right: t(21)=2.28, p=0.032). In the right hemisphere we found no significant difference between the ITCs in neither control ROI (lateral occipital: t(21)=1.13, p=0.267, precentral: t(21)=0.88, p=0.388). Post-hoc t-tests in the left hemisphere demonstrate that, in the lateral occipital, $ITC_{Cont6}$ was greater than $ITC_{Cont4}$ (t(21)=3.49, p=0.002) while no difference was found in the precentral ROI (t(21)=0.76, p=0.450).

# Chapter 4
# Discussion

From the simplest forms of life to mammals, movements and actions are an essential part of their daily experience. To be able to efficiently move within the surrounding environment, animals need to understand the relations between elements in it and how they can interact with them. The existing literature suggests a prominent role of the hippocampal formation in supporting the exploration of external space, both through locomotion and through vision, as well as supporting the encoding and retrieval of spatial and non-spatial memories, which are essential for more efficient interactions.

For instance, during locomotion, neurons in the hippocampus respond to specific locations in the environment (O'Keefe & Dostrovsky, 1971) while neurons in the entorhinal cortex map several positions providing a reference frame for exploration (Hafting et al., 2005). In freely-moving primates, neurons in the hippocampal formation respond to spatial locations, but the majority of their responses is related to a different form of spatial exploration, vision (Mao et al., 2021; Piza et al., 2024). At the same time, neurons in the hippocampal formation of both rodents and primates respond to abstract, non-spatial information such as specific concepts (e.g., Jennifer Aniston, Quiroga et al., 2006) and map abstract relational domains such as emotions (Qasim et al., 2023). Single neuron activity is orchestrated by neural oscillations (Singer, 1999; Buzsaki & Draghun, 2004). Oscillations create windows of enhanced (at the peak) or reduced (at the trough) excitability allowing neurons to reach their firing threshold more easily or more difficultly, respectively (Buzsaki, 2006). In the hippocampal formation two prominent oscillations have been identified, theta and gamma (Kunz et al., 2019; Colgin, 2016). These have been implicated in both spatial exploration through locomotion (Vanderwolf, 1969; Herweg et al., 2018) and eye movements (Jutras et al., 2013) as well as memory (Herweg et al., 2020a; Griffits & Jensen, 2023).

The experiments presented as part of this thesis further support the involvement of the hippocampal formation across different cognitive domains. First extending the function of hippocampal theta oscillations to reflect distances in naturalistic conceptual spaces during a "semantic foraging" task. Second, by reporting the presence of a typical neural signature of spatial representations, the grid-like response, as dissociated from observable actions and thus during movements of attention.

I can now answer the questions outlined in the introduction:

1) What are the electrophysiological mechanisms that underlie searching for concepts in memory?

We have observed that hippocampal theta and gamma power increase when participants are looking for and finding concepts in their mental space during a verbal fluency task. This power increase is modulated, respectively, by the semantic and temporal distance between subsequent words, suggesting its functional role in the exploration of a conceptual space. These results reveal important insights about the hippocampal role in cognition, strengthening the hypothesis of a repurposing of its function across spatial and non-spatial domains (Bottini & Doeller, 2020; Bellmund et al., 2018; Buzsaki & Moser, 2013).

2) Do we observe a signature of spatial exploration such as the grid-like response when space is explored through attention?

Grid-like response in humans MTL can be elicited by visual presentation of spatial trajectories that participants were attending to but not following with their eyes. That is, participants were moving their attention along the visually presented trajectories, as indexed by successful performance on a spatial memory task, and this was sufficient to elicit a grid-like response. This finding highlights the possibility that movements of attention underlie exploration of conceptual spaces.

## *Are other spatial variables represented in the hippocampal formation during the exploration of conceptual spaces?*

Theta oscillations have been associated with the active state of the brain since their initial discovery (Vanderwolf, 1969), with hippocampal theta power being higher during periods of locomotion (Bush et al., 2017; Aghajan et al., 2017) as well as during episodic memory encoding and retrieval (Lega et al., 2012). Movements in the external environment are trivially observed and can be easily operationalized into numerical variables to look for their modulation of brain activity. In the spatial navigation literature, theta oscillations have thus been further shown to be modulated by the distance traveled (Bush et al., 2017; Vass et al., 2016), distance to the goal location (Liu et al., 2023), by the environmental boundaries (Stangl et al., 2020; Seeber et al., 2024; Lee et al., 2018), speed (McFarland et al., 1975; Slawinska & Kasicki, 1998; Sheremet et al., 2016), and can reflect the structure of the environment through an hexa-directional modulation that mimics the firing of grids cells (Maidenbaum et al., 2018; Chen et al., 2018). These effects imply that theta in the hippocampal formation is not only higher during periods of movement but that its activity is functionally related to spatial exploration, potentially allowing animals to search in their environments and reach their goals.

If the neural machinery in the hippocampal formation has been repurposed to serve exploration of abstract conceptual domains (Bellmund et al., 2018; Behrens et al., 2018; Bottini & Doeller, 2020; Buzsaki & Moser, 2013) we should observe similar effects in conceptual domains. This line of research has produced a large amount of studies implicating a proxy of the grid-cell response measured through non-invasive neuroimaging in representing different conceptual domains (Constantinescu et al. 2016; Theves et al. 2019; 2020; Bao et al. 2019; Viganò & Piazza 2020, Viganò et al. 2021, 2023; Park et al. 2021; Nitsch et al. 2023; Barnaveli et al. 2024; Qasim et al. 2023). The most interesting study in this line of research was conducted by Qasim and colleagues (2023), who showed the first single-cell evidence in humans of a grid-like response during recall of images that, unbeknownst to the participants, were organized according to a two-dimensional emotion space. Similarly to spatial grid cells, these grid-like cells were theta modulated, suggesting the involvement of theta oscillations in the mapping of a conceptual domain. Apart from this example there was no clear evidence in the literature for the involvement of theta oscillations in the exploration of an abstract domain. A first attempt has been made by Solomon and colleagues (2019a), who showed that during a free recall task theta power is modulated by the low-dimensional semantic distance between subsequent words. While this finding provides some interesting preliminary evidence for how theta is contributing to the recall of verbal lists, it falls short of demonstrating the involvement of theta in the exploration of long-term memory. Free recall is one of the most used paradigms in memory research. It provides a well controlled experimental setting, however it is sequential in nature, both in the presentation of the list items as well as in the recall strategies with the well known primacy and recency effects (Ebbinghaus, 1885). Sequence coding is one of the main functions of the hippocampus (e.g., Buzsaki & Tingley, 2018) that allows to situate memories in a spatiotemporal context. A comprehensive investigation of the involvement of the hippocampus, and specifically of theta, in long-term memory is thus missing, although both neuropsychology and neuroscience suggest this possibility (see Duff et al., 2020 for a review). In the first study presented as part of this thesis we aimed to fill this gap in the literature and suggested that theta is modulated as a function of distance in naturalistic conceptual space, mimicking the findings in the spatial navigation literature. Although still under investigation, the preliminary results presented as part of this thesis extend the involvement of hippocampal theta (and gamma) to the exploration of non-spatial domains. This is evidenced by several parallels between our findings and the spatial navigation literature (Bush et al., 2017; Ekstrom et al., 2005). For instance, we found an increase in theta power before verbalization as compared to periods of “immobility” (such as after having found a word or during rest) but no differences with respect to periods of silence between words in which participants are likely looking for concepts in their mental space. Theta power was mostly modulated by the distance in high-dimensional semantic space, which likely reflects the organization of long-term memory, whereas Solomon et al., (2019a) found a stronger correlation with lower dimensional spaces. The finding of a correlation with a low-dimensional embedding speaks in favor of a low-level linguistic strategy for recall of words lists, in that low-dimensional embeddings have been shown to correlate with lexical aspects such as word frequency (Hollis & Westbury, 2016; Viganò et al., 2024).

Our study demonstrated that theta in a conceptual domain is modulated by the distance between words. This provides the first evidence that allows us to draw further parallels between spatial and conceptual navigation. However, in the spatial navigation literature, theta has been shown to signal several other spatial variables, such as distance to the goal, boundaries, or speed. An interesting question is thus whether theta is similarly modulated by other variables during conceptual navigation. One prominent model of how the hippocampal formation supports navigation is based on only two variables, speed and direction (continuous attractor network, Burak & Fiete 2009), suggesting their prominence for accurate navigation. Speed is in fact a change in distance per unit of time, thus reflecting the combination of distance and time from which both can be inferred. Interestingly, models trained to predict next items in a sequence using only velocity signals (i.e., differences between subsequent images) can accurately perform such tasks and reproduce grid-like firing fields (Iyer et al., 2024). In our experiment we found that theta power was modulated by both distance and time while gamma by time. It would be interesting thus to test whether these correlations could be explained by speed (whose definition can be borrowed from physics as the ratio between semantic distance and time elapsed between verbalizations) or by their phase amplitude coupling. Nevertheless, more carefully controlled experiments would be needed to test whether this is the case. For instance, one could pace participants' speech using a metronome at varying speed and predict that i) within each speed condition, semantic distance modulation of theta persists but ii) theta power shifts to higher theta band for increasing speed. Another important aspect of navigation is the heading direction. A first attempt to show directional coding in conceptual domain has been shown by Viganò and colleagues (2021), who demonstrated that a set of regions outside of the medial temporal lobe, including thalamus and medial parietal cortex, were modulated by the implied direction between consecutive concepts shown to the participants, who previously learned their two-dimensional configuration. Interestingly, these regions are the same in which has been shown the presence of head direction cells in rodents (Taube, 1998), which are themselves theta-modulated. It would be thus reasonable to expect the finding of a theta modulation by direction in conceptual space in brain regions where head directions cells are found.

## *Attention and eye movements in the hippocampal formation as a signature of conceptual navigation*

In the third chapter we speculated that movements of attention can be a mechanism through which the hippocampal formation supports the exploration of conceptual spaces. I will now elaborate on this hypothesis.

The definition of attention dates back to James (1890) and is now a fundamental concept across cognitive science and computer science (Lindsay, 2020), where it is used to describe the process of selectively focusing on one or a few elements from a larger set for further, more effective processing. This selective attention mechanism allows systems with limited resources, whether biological or artificial, to maximize their capacity by dedicating full cognitive or computational resources to the most relevant elements at any given time (Carrasco, 2011). Attention is crucial in perception (Tsotsos, 1990), where the sensory systems are constantly bombarded by a multitude of stimuli from the environment. Only some of these stimuli however are relevant at any given time, thus attention helps to filter the irrelevant ones to prioritize the relevant for further processing. This prioritization eventually will lead to encoding in memory only some elements of the environment (Uncapher & Rugg, 2009, Chun & Turk-Browne, 2007). Additionally, attention is not only involved in the initial encoding of information but also plays a crucial role in retrieving relevant elements from memory that align with the current goals or tasks (Van Ede & Nobre, 2022; Chun et al., 2011)

In primates, attention and eye movements are tightly linked such that eye position is often interpreted as reflecting the overt location of the focus of attention (Henderson, 2003; Kowler et al., 1995; Rizzolatti et al., 1987). Primates' eyes have a specialized central region (fovea) that provides maximal visual acuity at the spatial location where it is directed (Wassle & Boycott, 1991), allowing better visual processing of the foveated object, as evidenced by the higher representation of this region in the brain's visual system (Perry & Cowey 1985). To explore and better understand the contents of their visual field, primates actively and rapidly move their eyes (saccades) allowing them to gather higher-resolution information (Van der Stigchel 2006; Findlay & Gilchrist 2003, Schroeder et al., 2010). The selection of the visual region to explore is therefore indicative of the current attentional focus of the viewer. Nevertheless, both exogenous and endogenous factors influence the deployment of visual attention (Wolfe & Horowitz 2004; Rust & Cohen 2022). Usually, the location at which gaze is directed is the one that is most salient due to its visual characteristics, such as color or contrast (Itti & Koch, 2001), or has the highest behavioral relevance, such as being a goal in a task (Henderson 2017).

It is currently debated whether eye movements are a useful readout of attentional mechanisms or an integral part of attention (Lowet et al., 2018; Liu et al., 2022; Yu et al., 2022). However, it has been shown that it is possible to dissociate the focus of attention from the currently-gazed location (Posner, 1980; Juan et al., 2004) although this often results in the presence of smaller fixational eye movements (Martinez-Conde et al., 2004) that track attentional focus (Engbert & Kiegl, 2003; Yuval-Greenberg et al., 2014).

Both eye movements and attention exert an effect at the neural level (Awh et al., 2006; Corbetta & Shulman, 2002). A set of subcortical (thalamus, superior colliculus) and cortical structures (superior parietal lobule, intraparietal sulcus, frontal eye fields) has been identified using invasive recordings and electrical stimulation in non-human primates (Moore & Fallah 2001; Kustov & Robinson, 1996; Bisley & Goldberg 2003; Thompson et al., 1997; Müller et al., 2004) as well as non-invasive recordings in humans (Corbetta et al., 1998; Nobre et al., 2000). Collectively these studies suggest that attention and eye movements modulate these brain structures by increasing neural activity at the attended location, thus increasing perceptual sensitivity in the attended spatial region. The finding of a shared substrate between attention and eye movements was initially used to support their interdependence; however more recent evidence has demonstrated that at the neuronal level control of attention and eye movements can be separated. There are both neurons that show mixed selectivity and neurons that fire for eye movements and not for attention, and vice versa (Juan et al., 2004; Thompson et al., 2005). Similar increases in neural firing for attended locations were found in sensory regions outside of this “attention network”, for instance in visual (Reynolds & Chelazzi, 2003) and auditory (Fritz et al., 2007) areas indicating the influence of attention on sensory processing. Recent evidence has further shown that both eye movements and attention are rhythmic within the theta range (Fiebelkorn & Kastner, 2019). Eye movements in primates usually occur at 3-4 Hz (Otero-Millan et al., 2008; Näher et al., 2022), similarly signatures of attention at both the behavioral level, such as enhanced sensitivity at time intervals corresponding to theta (Landau & Fries 2012; Fiebelkorn et al., 2013; but see Brookshire, 2022) and neural level, such as increased neural excitability (as indexed by gamma oscillations) are rhythmic at the same theta range (Fiebelkorn et al., 2018; Helfrich et al., 2018). Further hypotheses have suggested that attended visual objects can propagate from early visual areas for downstream computations through gamma band synchronization (Fries 2005; Fries 2015; Fries 2023, but see Vinck et al., 2023 and Spyropoulus et al., 2024 for evidence against this hypothesis).

Attention and eye movements thus modulate various cortical and subcortical areas. Despite the hippocampus being considered a critical component of the visual hierarchy according to a prominent model of the visual system (Felleman & Van Essen, 1991), it has garnered comparatively less focus in research on the neural correlates of attention. Nevertheless, there is some evidence that the hippocampus is modulated by attentional processes (reviewed in Aly & Turk-Browne, 2017).

In the context of spatial navigation, a potential index of attention is whether the animal is actively engaged in the task (Rowland & Kentros 2008). When animals are not engaged in a spatial task, less place cells emerge as compared to when the animal is engaged, (Pettit et al., 2022) and their firing fields are less temporally stable, i.e., localized firing is lost over time, whereas better task performance correlates with increased place field stability (Kentros et al., 2004). Furthermore, when the environment was task relevant, place cells were more stable, whereas when a task-relevant odor was present, they reduced their stability (Muzzio et al., 2009). Similarly, groups of place cells can be distinguished based on their anchoring to local or distal cues depending on which are more salient in the environment, with alternating increase in firing for each cue every 1 s (Fenton et al., 2010). This alternation has been reported in several other studies, mainly in relation to the theta rhythm. For instance, there is evidence that alternating cycles of theta represent distinct information, such as different spatial contexts (Jezek et al., 2011), possible future directions (Vollan et al., 2024; Kay et al., 2020), or different heading directions (Brandon et al., 2013), suggesting their potential role in allocating attention to different aspects of the task the animal is currently facing.

One of the most relevant aspects of a spatial navigation task is the goal location. According to Rowland & Kentros (2008) we can thus expect that paying attention to goal location modifies the firing of place cells. This is indeed the case: Hollup and colleagues (2001) demonstrated an accumulation of place-cells firing fields towards the goal location while Lee et al., (2006) showed that this shift occurs over learning. Furthermore, place cells increase their firing rate when moving towards a goal while conversely decreasing their firing when moving away (Aoki et al., 2019). More recently, a similar effect has been demonstrated for grid cells, in which a shift of the firing fields towards goal location is observed (Butler et al., 2019), with this restructuring evolving over learning (Boccara et al., 2019). Similar effects have been reported in a spatial navigation task in humans using fMRI (Muhle-Karbe et al., 2023) and most interestingly, in a conceptual navigation task, with increasing hexadirectional symmetry in proximity of the goal compared to locations further apart (Viganò et al., 2023). These findings, along with other evidence, suggest that the spatial code in the hippocampal formation is less stable than initially thought and is potentially under cognitive influences. It has further been suggested that distortions of the spatial metric might represent the true informative signal encoded in these spatial maps (Ginosar et al., 2023).

Another interesting finding is that actively exploring the environment with head movements induces the formation of place fields or their potentiation, accompanied by an increase in theta power compared to periods without head movements (Monaco et al., 2014). This finding is notable because it relates the active process of sampling information from the environment to the formation of a memory trace, specifically a place field. Actively sampling the environments through motor routines is a core aspect of active sensing (Schroeder et al., 2010). In line with this hypothesis, not only head movements influence hippocampal formation but also the amount of eye movements (i.e., visual sampling) increases hippocampal activity (Liu et al., 2017). When exploring the environment through eye movements, the hippocampal formation theta rhythm resets to be in an optimal stage (trough of the oscillation, Hasselmo et al., 2002) for information encoding (Jutras et al., 2013; Hoffman et al., 2013) where the input from the entorhinal cortex (the last relay of cortical information into the hippocampus) is maximal. Being in the optimal stage after an eye movement means that information can be more efficiently stored in memory through synaptic plasticity: long-term potentiation is in fact more prominent at the trough of the oscillatory cycle (Hyman et al., 2003). On the contrary, when information needs to be retrieved from memory, theta is at its peak, when recurrent dynamics with CA3 are present and lead to long-term depotentiation. In line with this proposal, a recent study by

Kragel & colleagues (2020) found that, during a spatial memory test, theta phase was at its peak when participants were looking at the spatial location that matched the one they held in memory while theta was at its trough when looking at the target object presented in a new spatial location. This dissociation fits nicely with the model by Hasselmo and colleagues (2002) and has been interpreted as reflecting different modes of sampling, either from memory or from the environment, respectively (Kragel & Voss, 2022). This distinction is also reminiscent of the effects found by Fiebelkorn & Kastner (2018) in the attentional network, in which they identified a “good” theta phase associated with more effective sampling of environmental information and a “bad” theta phase associated with shifting of attention to a different spatial location. It would be interesting to test whether these similarities reflect meaningful and coordinated operations between brain areas. Theta is in fact known for its role in long range coordination and is thus a plausible mechanism for information transmission across brain areas (Sirota et al., 2008; Roux et al., 2022). Of particular interest would be to test the directionality of the communication: we may expect that when shifting attention there is a higher influence of the hippocampus towards the cortex, signaling where to look next in the environment (Summerfield et al., 2006), while a higher influence of the cortex towards the hippocampus would be presented in the sampling phase to allow for efficient information transmission and eventually encoding in memory.

The proposed role of attention in the navigation of conceptual spaces was to operate “when there is nothing to see and nowhere to move, but internal attention can be moved across the mental space” (Giari et al., 2023). For example, borrowing from Bellmund et al, 2018, imagine you need to buy a car. You might value engine power and weight, and therefore select these as relevant feature dimensions to organize your conceptual space of cars (Bellmund 2018, Fig. 1). Organizing the elements in space is only the beginning, the crucial part is using this knowledge to decide which car to buy. How then do we “move” within this conceptual space to evaluate the options and eventually buy our new car? We can achieve this, for instance, by iteratively focusing on one relevant portion of the space, evaluating it, and then moving to the next until finding the best option. This process William James’s classical definition of attention (1890): attention “*is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, and consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others”*. Interestingly, this process can be thought of as akin to a visual search task, one of the most used paradigms to study attention (Duncan, 1989), in which a target object is hidden among distractors. in the example, the target car is hidden among irrelevant options and our goal is to select the appropriate one.

Moving and searching are verbs that imply actions. During locomotion, actions allow us to navigate and are readily observable. In navigating the internal space of our memories, actions can be movements of attention, of which eye movements can provide a useful readout.

In line with this proposal, there is evidence that even when there is no visual stimulation, participants make eye movements. For instance, during delay periods of a visual working memory task, when there is nothing relevant on the screen, participants’ eyes move towards the location where the item they were keeping in mind was originally presented, even if the location is irrelevant for task performance (Van Ede et al., 2019). Furthermore, even when eye movements are constrained to the central part of the screen, small, fixational eye movements reflect the orientation of the presented items, peaking after the disappearance of the item and ramping during the delay period (Linde-Domingo & Spitzer, 2023).

These latter studies are particularly interesting because they suggest that even when there is no relevant visual information presented to participants, their eyes move in a meaningful way, possibly reflecting the influence of a cognitive mechanism. Nevertheless, eye movements were reflecting aspects of visual materials presented as part of the experiment, leaving open the question about the involvement of the eyes "when there is nothing to see" thus truly recapitulating internal memory organization and search. When "looking at nothing", such as in a darkened room or in front of a blank screen, participants still make meaningful eye movements, for instance reflecting the magnitude comparison between auditorily presented numbers (Salvaggio et al., 2019) or the serial order of auditorily presented numbers (Sahan et al., 2022).

Numbers are a particularly interesting conceptual space that allows experimental testing in naturalistic settings while at the same time knowing the underlying structure of the space. In fact, it has been demonstrated that numbers are organized on a line according to their magnitude, going from left (lower numbers) to right (higher numbers) in western cultures (Deahene et al., 1993; Fias et al., 1996). This was originally demonstrated through a faster response time when the mapping between magnitude and manual response is congruent, but, interestingly, similar evidence is present in eye movements. Loetscher and colleagues (2010) showed that spontaneous eye movements made in darkness reflected the numbers that participants are verbalizing: high numbers were pronounced when the eyes moved to the right while lower numbers when the eyes moved to the left, and similarly for the vertical dimension with high numbers when the eyes moved higher and low numbers when the eyes moved lower. This finding was further extended by Viganò and colleagues (2024) who showed that eye movements not only reflect the position of numbers along the horizontal and vertical dimensions but that they can be also a useful readout of two-dimensional conceptual spaces such as colors and even reflect linguistic properties of higher dimensional spaces such as animals.

These preliminary findings suggest that attention and eye movements reflect the organization of conceptual information in memory. However, further research is needed to investigate this claim. For instance, several open questions that we can address are:

- How do we move through conceptual spaces?

The findings presented above suggest that eye position reflect the relative distances between items in conceptual space (i.e., the structure). However, a key question is how do we move and search within the space. This question can be addressed by evaluating the fine-grained, temporal evolution of gaze position. A sudden change in gaze position, as indexed by a saccade, can reflect the rapid shift of attention to a different portion of the conceptual space. Changes in position however can be more gradual, akin to a smooth pursuit. We may thus look for the prevalence of specific eye movement types during conceptual search. We may expect that both saccades and more gradual changes occur during conceptual search, but these may be reflected in different conceptual distances between verbalizations. For instance, assuming constant timing between verbalizations (Viganò et al., 2024), a saccade may reflect a larger distance as compared to a more gradual movement.

- Are eye movements a readout of the exploration or do they play a causal role?

Some studies have shown that restricting eye movements has behavioral consequences, for instance negatively impacting navigation performance (Lakshminarasimhan et al., 2020). Other studies instead have shown that even when restricted, eye movements were reflecting task-relevant information (Linde-Domingo & Spitzer, 2023). This contradictory evidence leaves open the question of their relevance for attention. This question can be addressed in multiple ways: i) similarly to other studies we can restrict participants eye movements during a conceptual search task. However, given that there is nothing to see on the screen we may expect that participants would still be able to do the task, so differences with unrestricted movements may be expected more in the "quality" of the navigation. For instance, restricting eye movements may result in lower exploration or shorter transitions between subsequent concepts. ii) we can interfere with eye movements during a conceptual search task. participants can be presented with a sequence of dots and asked to both follow the dots with their eyes and at the same time verbalize concepts. If eye movements are functional to the exploration, we can expect that a larger distance between the visually presented dots results in a larger distance in conceptual space (if the participants are following the dots with their eyes).

The ultimate test for the role of eye movements in conceptual search is whether early blind people (i.e., people that have lost functional vision at early age) show eye movements that are related to the conceptual search, the presence of which would speak in favor of an attentional mechanism in conceptual search of which they eye movements are a readout. On the contrary, the lack of eye movements during conceptual search in blind can be due to the eye movement being an integral part of the memory for the concept (Noton & Stark, 1971), that recapitulate the spatiotemporal context in which the memory was acquired (Wynn et al., 2019).

- What is the relationship between hippocampal activity and attention in the context of conceptual search?

We have shown in Chapter 2 that the power of hippocampal theta reflects semantic and temporal distances in the navigated conceptual space. However, in a similar task also eye movements reflect linguistic distances in conceptual spaces (Viganò et al., 2024). To what extent then are these mechanisms related? What is the direction of the relationship (if any)? Are eye movements driving the increase in theta power and, as a consequence, the exploration of the space, or is the increase in theta power that reactivates the memory trace and, eventually, the eye moves? This question can be addressed by concurrent recording of temporally resolved brain activity and eye position. We can then test, for instance, the temporal relationship between the observed effects. If the time series of theta power is predictive of the eye movement we can, to some extent, infer the direction of the relationship (Granger, 1969). Nevertheless, causal manipulations would be needed to claim the directionality.

Irrespective of the directionality, if eye movements and theta are related, we may expect that some of the effects found for theta may be reflected in eye movement patterns. For instance, in rodents navigating a t-maze, theta has been shown to signal future turns (Kay et al., 2020), alternating between left and right turns at different oscillatory cycles until the decision is made. First question to be asked is whether a similar alternation between left and right is observed in a conceptual space. Numbers provide a useful testbed for this hypothesis during a conceptual search task, given their linear arrangement. Eye movements may then similarly reflect this alternation between possible options.

## ***Conclusions***

The evidence presented as part of this thesis further advances our understanding of the hippocampal formation role in cognition. First, I have provided evidence that directly links the theta and gamma rhythm of the hippocampal formation to navigation in conceptual space. Second, I have shown that a typical signature of spatial and conceptual navigation is present in humans that are covertly exploring the visual environment. Taken together these results suggest that the hippocampal formation supports exploration across cognitive domains. How the hippocampus contributes to exploration of both spatial and conceptual domains is however still not known. In the discussion I proposed that attention can be a domain-free mechanism that the hippocampus is using to support navigation and suggested ways in which this proposal can be tested.

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# Appendix

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**MEG frequency tagging reveals a grid-like code during attentional movements**

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