Grid-like and distance codes for representing word meaning in the human brain

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ABSTRACT

Relational information about items in memory is thought to be represented in our brain thanks to an internal comprehensive model, also referred to as a "cognitive map". In the human neuroimaging literature, two signatures of bi-dimensional cognitive maps have been reported: the grid-like code and the distance-dependent code. While these kinds of representation were previously observed during spatial navigation and, more recently, during processing of perceptual stimuli, it is still an open question whether they also underlie the representation of the most basic items of language: words. Here we taught human participants the meaning of novel words as arbitrary labels for a set of audiovisual objects varying orthogonally in size and sound. The novel words were therefore conceivable as points in a navigable 2D map of meaning. While subjects performed a word comparison task, we recorded their brain activity using functional magnetic resonance imaging (fMRI). By applying a combination of representational similarity and fMRI-adaptation analyses, we found evidence of (i) a grid-like code, in the right postero-medial entorhinal cortex, representing the relative angular positions of words in the word space, and (ii) a distance-dependent code, in medial prefrontal, orbitofrontal, and mid-cingulate cortices, representing the Euclidean distance between words. Additionally, we found evidence that the brain also separately represents the single dimensions of word meaning: their implied size, encoded in visual areas, and their implied sound, in Heschl's gyrus/Insula. These results support the idea that the meaning of words, when they are organized along two dimensions, is represented in the human brain across multiple maps of different dimensionality.

Significant statement

How do we represent the meaning of words and perform comparative judgements on them in our brain? According to influential theories, concepts are conceivable as points of an internal map (where distance represents similarity) that, as the physical space, can be mentally navigated. Here we use fMRI to show that when humans compare newly learnt words, they recruit a grid-like and a distance code, the same types of neural codes that, in mammals, represent relations between locations in the environment and support physical navigation between them.

1. Introduction

One of the hallmarks of intelligent behavior is the ability to represent how items in memory are related and to perform comparative judgments over those representations. These operations are pervasive in our everyday life. If, for instance, we want to learn to play a wind instrument but we live in a poorly insulated apartment and have little money to spend, we will probably choose the flute and not the saxophone, considering the combination of their relative loudness and price. As a linguistic species, we humans use arbitrary symbols to express / recover / evaluate concepts without having to experience them directly through the senses:

we can decide that a saxophone is louder than a flute without the need to hear their sounds but relying on the long term representation of the associated words. How does the human brain represent this relational information between concepts when they are presented linguistically in the form of words?

One possibility is that we store in memory all the possible pairwise relations in a piecemeal format: flute is cheaper than clarinet (flute < clarinet); clarinet is less loud than saxophone (clarinet < saxophone); and so on. Another possibility is that we summarize this information in a single structure that spans multiple dimensions (loudness and price, in the example above) and that serves as a general and comprehensive

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model of the mutual relations existing between concepts. This latter representational model, evidently more parsimonious, is what Tolman named "cognitive map", which he thought as a general model for human cognition, but demonstrated only in the domain of spatial memory and navigation (e.g., Tolman 1948). Cognitive scientists have also later largely used spatial metaphors to conceptualize mental representations, suggesting that concepts, and words that refer to them, can be conceived as points in multidimensional internal spaces: comparing them might then be equivalent to assessing their relative position, an operation that is typical of spatial navigation (e.g., Shepard, 1962, 1964; Gardenfors 2000; Borghesani and Piazza 2017; Todd and Hills 2020).

The present study tests the hypothesis that the human brain represents word meaning using the same neuronal machinery that underlies spatial navigation.

In the human neuroimaging literature, the existence of cognitive maps of the navigable physical space has been associated with two kinds of neural codes. The first one is the grid-like code, an hexagonally symmetric modulation of brain activity as a function of movement direction, representing the angular relationship between locations in the environment (Doeller et al., 2010). This signal likely originates from grid-cells, neurons that activate when the animal, moving in the environment, traverses the vertices of putative hexagonal lattices that cover the navigable surface (Hafting et al., 2005; Jacobs et al., 2013). The second one is a distance-dependent code, a modulation of brain activity that scales with the physical distance between real-world locations (e.g. Morgan et al., 2011; Nielson 2015). At a single neuron level the origin of this signal remains to date debated, although place-cells, characterized by partially overlapping bell-shaped tuning functions centered on specific locations, might be likely candidates.

Beyond the domain of spatial navigation, both grid-like and distance-dependent codes have been recently observed for non-spatial stimuli when organized into bi-dimensional structures, such as visual shapes (Constantinescu et al., 2016), odours (Bao et al., 2019), and real-life objects (Theves et al., 2019, 2020). In a previous study (Viganò and Piazza 2020) we presented subjects with both words and objects organized in a 2D space during a categorization task, and we reported, using fMRI, that they evoked both a distance and a directional response. However, due to design limitations, we could not restrict the analyses to the trials where only words were presented, leaving open the possibility that at least part of the observed responses reflected perceptual rather than purely semantic coding. Moreover, importantly, we could not determine whether the observed direction-dependent modulation of the entorhinal activity reflected a 6-fold grid-like periodicity or rather a 2-fold periodicity, as the number of movement directions we sampled was too small to disentangle the two.

In the current study, we overcame the aforementioned limitations with a novel experimental design in which we taught adult subjects the meaning of nine novel words as arbitrary labels of a set of artificial stimuli varying orthogonally along two dimensions (size and pitch, see Methods and Fig. 1). Crucially, (i) the neural activity evoked by accessing word meaning was measured by exclusively presenting words, thus ruling out the direct influence of perceptual aspects; (ii) the experimental design provided a sufficiently dense sampling of directions to appropriately test the grid-like code and (iii) a sufficiently variable set of distances to identify the brain regions supporting the distance code both in the bidimensional space and in each single dimension.

2. Methods

2.1. Participants

For this study, we recruited a total of 31 students (21 female, mean age: 23.7 yrs, std: 3.2 yrs) from the University of Trento, Italy. All of them had normal or corrected-to-normal vision and were right-handed. Four participants did not reach a satisfactory performance of 80% of correct responses during the semantic comparison task at the end of

the training and were therefore excluded from the study. In total, 27 participants entered the analysis. The study was approved by the local Ethics Committee (Comitato Etico per la Sperimentazione con l'Essere Umano, University of Trento, Italy), in accordance with the Declaration of Helsinki. All participants gave written consent before the experiment. The privacy rights of the participants were observed in accordance with the guidelines of the Ethical Committee of the University of Trento.

2.2. Stimulus space

We developed a set of 9 novel multisensory objects by orthogonally manipulating the size of an abstract shape (Fig. 1a) and the pitch of a sound the objects produced during a small animation. This led to a stimulus space where each object represented the unique combination of one size and one pitch level. The visual angles subtended by the objects were 3.75, 5.73 , 7.64 °. The pitches of the sounds were 500, 750, and 1000 Hz. These values were partially based on previous work from our lab (Viganò and Piazza 2020) where we measured, using a psychophysical staircase approach, the Just Noticeable Difference for size levels and pitch changes, separately, of a similar object space. As the objective for the current experiment was to make the objects clearly distinguishable one from another, the perceptual distance between two subsequent levels of size or of pitch would approximately correspond to 10 average JNDs of our previous report, thus ensuring their discriminability. No finer psychophysical measure was attempted. Objects were animated by simulating a small squeezing; their presentation lasted a total of 750 ms, and sounds were presented at the apex of the squeezing period for 200 ms. We assigned a novel word to each object as illustrated in Fig. 1b. Stimuli were presented foveally using MATLAB Psychtoolbox (MathWorks) in all experimental phases, at a distance of ~130 cm. Each word subtended a visual angle of 3.58 ° horizontally and 2.15 ° vertically and was presented with black Helvetica font on a gray background. Crucially, the bidimensional arrangement of the stimulus space was never shown to participants.

2.3. Training sessions (pre scanning)

The experiment comprised 4 training sessions and one fMRI scanning session (Fig. 1c). The training sessions were distributed over three consecutive days, one session per day during the first two days, and two sessions in the third day. The neuroimaging session occurred on the day after the last training session. During the first three training sessions, participants were first presented twice with the individual multisensory objects (in random order), each appearing next to their written name. Then subjects performed three tasks: a recognition, a production, and a semantic comparison task (see below for details). During the fourth training session they performed the semantic comparison task only.

2.3.1. Recognition task

During the recognition task in each trial participants were presented with one multisensory object and then with the 9 object names vertically listed in random order. They had to select the one corresponding to the object by pressing a number from 1 to 9 on the keyboard. The selected name turned blue to indicate that the selection was made. If the answer was correct, the name turned green and a trumpet sound was played; if the answer was incorrect, the selected name turned red, a buzzer sound was played, and the correct name turned green, so that the subjects profited from the incorrect trials to learn. The objects were presented in random order, four times each.

2.3.2. Production task

During the production task in each trial participants were presented with one multisensory object and were asked to type its name using the computer keyboard. The letters that the subject typed appear on the screen, one next to the other. The response was considered correct only if all the three letters were typed correctly. Participants did not have
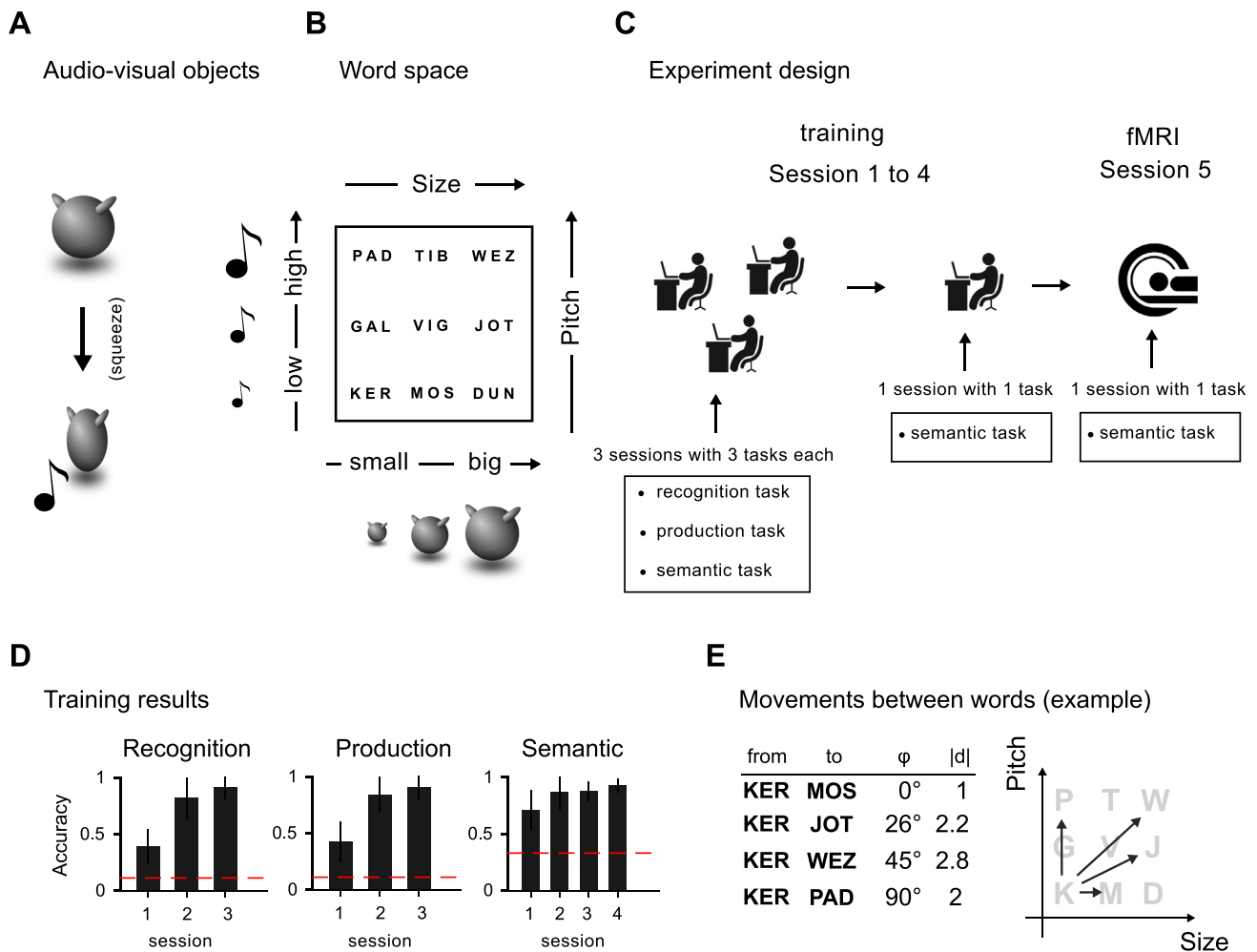
Fig. 1. (a) - Example of audiovisual object. Nine audiovisual objects were created by manipulating the size of a shape and the pitch of an associated sound, produced during a short squeezing animation. **(b)** - **Word space.** Each audiovisual object was given an abstract name, that could be conceived as a location in a 2D word space. (**c**) - **Experiment design.** Participants were taught the name of each object over 4 training sessions, using a combination of associating, naming, and semantic tasks (see Methods), and were eventually tested on the semantic task during an fMRI session. **(d)** - **Training results**. Participants performed highly above chance by the end of the training, and were admitted to the fMRI scanning session. (**e**). **Movements between words.** - Comparing two word meanings required to recover their relation in the underlying word-space, defined by specific angular positions and distances.

the possibility to delete typed letters. Once the last letter was typed, the name turned green if it was the correct one, or red if it was incorrect: in this last case, participants were also informed about the correct name of the object with a screen message. Audio feedback was provided as in the previous task. The objects were presented in random order, four times each.

2.3.3. Semantic comparison task

In the semantic comparison task participants were presented, for each trial, with two words in rapid sequence, one after the other. Words lasted 250ms on the screen, with a pause of 250ms between them. Then, after a reflection period of 4 (+/- 1.5) s, they were presented with one of these two questions: "has there been an increase, decrease, or no change in size?" or "has there been an increase, decrease, or no change in pitch?" Participants could not know in advance which question was about to be presented, and therefore had to mentally consider both features. They could respond by pressing one of three buttons: 1 to indicate an increase, 2 to indicate a decrease, and 3 to indicate no change. If the answer was correct, a trumpet sound was played; if the answer was incorrect, a buzzer sound was played; in both cases, an informative visual feedback was provided (e.g., "Correct/wrong, size increased!"). Outside

the scanner, the semantic task consisted of 144 trials (all the pairs between different words, repeated twice, once with a question about the implied size, once with a question about the implied pitch, randomly presented). On the first training session, participants had no time limit to answer, but this was set to 4 s on the second training session, and to 2 s in the third and fourth ones. This was done to foster automatisation.

2.4. Neuroimaging task

In the neuroimaging session participants performed the same semantic comparison task as during the last session of training, except for the absence of feedback. Also, to reduce the scanning time while sampling as many trials as possible the task question was only present in a small subsample (16.6%) of trials. This selection was randomized across participants, with half of the questions related to a change in "size" and half related to a change in "pitch" for each subject. The experiment was organized in 8 runs of 48 trials each. Participants were explicitly instructed to always think about the meaning of the two words for each trial, because they couldn't know whether a question would be subsequently presented, nor what dimension it would focus on.
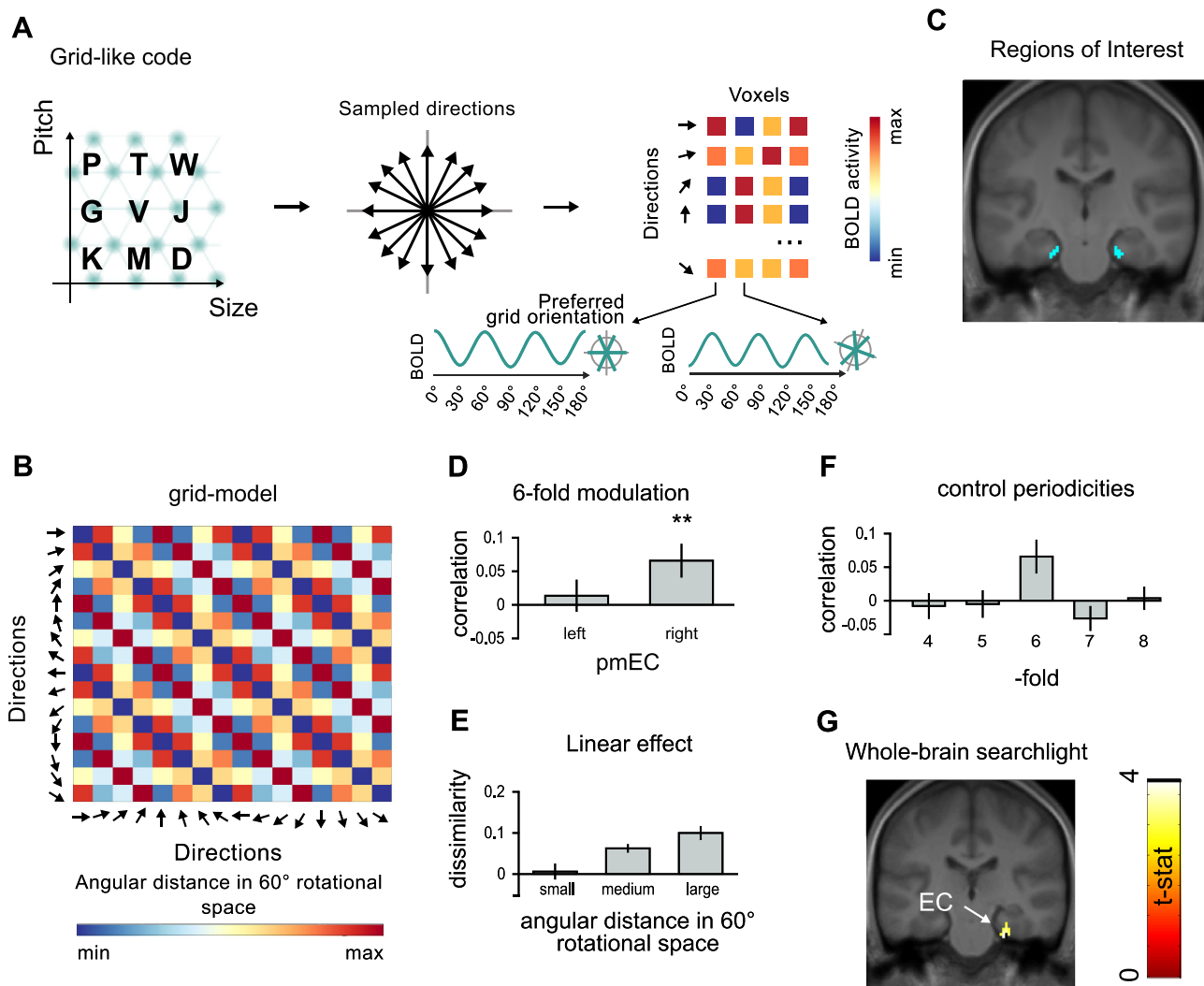
Fig. 2. **(a) - Grid-like code.** To test the hypothesis that a grid-like code underlined the representation of the novel semantic space, we looked for changes in BOLD signal as a function of movement direction (see Doeller et al., 2010 and Methods). Following physiological evidence (Stensola et al., 2012; Doeller et al., 2010), we assumed that each movement direction evoked a variable activity pattern across voxels of brain regions containing grid-cells. **(b) - Grid-model.** If an underlying grid-like code exists, then the similarity of the activity patterns evoked by different movement directions should be determined by their angular distance in the 60° rotational space (see Methods). We applied a multivariate approach (as in Bellmund et al., 2016; Bao et al., 2019; Viganò and Piazza 2020), here correlating the predicted grid-model to the neural dissimilarity matrix obtained from our Regions of Interest. **(c) - Regions of Interest.** We first focused on left and right postero-medial entorhinal cortices (pmEC), where grid cells have been recorded in rodents and humans (Hafting et al., 2005; Jacobs et al., 2013). **(d). 6-fold modulation.** The multivariate activity of the right pmEC significantly correlated (Pearson's r) with the predicted grid-model (** p <0.01). **(e). Linear effect of angular distance.** For visualization purposes, pairs of movement directions were grouped based on their angular distances in the 60° rotational space: small (<10°), medium (10 to 20°), and large (21 to 30°). The larger the angular distance between two movement directions in the 60° rotational space, the larger their dissimilarity (1 - Pearson's r). **(f) - Control periodicities.** The same analysis conducted assuming a 4-, 5-, 7-, or 8- fold symmetries resulted in no correlation (Pearson's r) with the neural dissimilarity matrix. **(g) - Whole-brain searchlight.** A whole-brain approach revealed a significant cluster in the right pmEC.

2.5. Trial selection

Given the 9 words composing our semantic space, the possible word pairs are 72 (we excluded pairs of the same word because they did not subtend any movement). Comparing their meaning was conceivable as moving in the semantic space, covering different directions and distances. With this word space we could sample 16 different movement directions (assuming the x-axis as 0°, the possible direction of movements are 0°, 26.5°, 45°, 63.5°, 90°, 116.5°, 135°, 153.5°, 180°, 206.5°, 225°, 243.5°, 270°, 296.5°, 315°, 333.5° (Fig. 2a)) and 5 different movement distances (assuming as 1 the smallest distance covered between two close objects along the horizontal or vertical axis, such as "KER" and "MOS", the distances covered in the experiment are 1, $\sqrt{2}$, 2, $\sqrt{5}$, $2\sqrt{2}$, hereafter indicated for simplicity with their increasing order: 1,

2, 3, 4, 5). Due to the spatial arrangement of the 9 discrete points of our semantic space, it was not possible to balance both directions and distances across trials. We decided to equalize the number of trials covering each direction, as our main goal was to search for a grid-like modulation of the BOLD signal as suggested by our previous experiment (Viganò and Piazza 2020), where for design constraints we could only sample 8 movement directions. Throughout the experiment, all 16 directions were sampled uniformly with 24 repetitions for each direction, equally divided between runs. Distances were only partially balanced in their presentation: distances 1 and 3, indicating movements along the horizontal and vertical axes and therefore informative for the analysis of distance coding in both the bidimensional and unidimensional spaces (see below), were balanced with 48 repetitions each; distances 2, 4, and 5 were sampled 80, 192, and 16 times each, respectively. We

corrected for this unbalanced sampling at the level of the analyses (see below).

2.6. Data acquisition and preprocessing

Data were collected on a 3T PRISMA MRI scanner (Siemens) with standard head coil at the Center for Mind/Brain Sciences, University of Trento, Italy. Functional images were acquired using EPI T2*-weighted scans. Acquisition parameters were as follows: TR = 1 s, TE = 28 ms, FOV = 100 mm; number of slices per volume = 65, acquired in interleaved ascending order; voxel size = 2 mm isotropic. T1-weighted anatomical images were acquired with an MP-RAGE sequence, with $1 \times 1 \times 1$ mm resolution. Functional images were preprocessed using the Statistical Parametric Toolbox (SPM12) in MATLAB following canonical steps: slice timing, realignment of each scan to the first of each run, coregistration of functional and session-specific anatomical images, segmentation, and normalization to the Minnesota National Institute (MNI) space. 7 mm smoothing was applied before subsequent analyses (GLM and MVPA), which were performed using both SPM12 and CoSMoMVPa (Oosterhof et al. 2016)(see below).

2.7. ROI selection and whole brain searchlights

For the grid-like code analysis we targeted the entorhinal cortex: although other brain regions have been previously implicated in representing non-spatial environments with a grid-like code (e.g., see Constantinescu et al., 2016; Bao et al., 2019), other studies (among which our own previous investigation, Viganò and Piazza 2020) reported it only in the entorhinal territory (Bellmund et al., 2016; Nau et al., 2018; Julian et al. 2018). Therefore, we first focused on the postero-medial entorhinal cortex (the homologous of rats' medial EC, where grid-cells have been first described (Hafting et al., 2005)). To this end, bilateral entorhinal masks were obtained from Maass et al., 2015, and were co-registered to the anatomical images of our subjects. Then, to investigate the possibility that other brain regions recruited a grid-like code during our task, we also implemented a whole-brain searchlight, using spheres of radius = 3 voxels, consistent with previous studies from our and other groups (e.g., Connolly et al., 2012; Viganò and Piazza 2020). For the adaptation analysis of the distance code, we first focused on the hippocampus, motivated by previous studies that had associated a distance-related response in the hippocampal activity in humans (e.g., Morgan et al., 2011; Theves et al., 2019, 2020). Hippocampal masks were obtained from PickAtlas (Maldjian et al. 2003). Then, in order to verify that with our ROI approach we did not miss other important areas we approached the question at the whole-brain level.

2.8. Grid RSA

In mammals, the representation of the relations between locations in the physical environment is captured by grid-cells (Bush et al., 2015), which tuning functions peak at multiple locations at the vertices of equilateral triangles tiling the entire navigable space (Hafting et al., 2005; Jacobs et al., 2013). Their presence can be inferred in humans using BOLD fMRI (Doeller et al., 2010). To test for grid-like modulation of the fMRI activity reflecting the relations between words in our experiment, we used a "grid Representational Similarity Analysis" (hereafter grid-RSA), inspired by Bellmund et al., 2016 and extensively described in Viganò and Piazza 2020, which logic is illustrated in Fig. 2a. The first step of the grid-RSA is to run a GLM modeling the directions of movement between words. For each run, 23 regressors were included: 16 regressors corresponding to the 16 possible directions of movement, implied by the comparison between two words, arbitrarily referenced to the horizontal axis; one regressor for the participants' response; six regressor for head movements (estimated during motion correction in

the preprocessing). Baseline periods were modeled implicitly, and regressors were convolved with the standard HRF. A high-pass filter with a cutoff of 100 s was applied to remove low-frequency drifts. We obtained one beta for each movement direction for each run. Following the multivariate approach of Bellmund et al., 2016, we assumed that preferred grid orientation varies, although minimally, across voxels, as empirically indicated by fMRI in humans (Doeller et al., 2010; Nau et al., 2018) and suggested by electrophysiological recording in rodents, showing that the grid orientation varies in a step-like fashion across different portions of the entorhinal cortex (Stensola et al., 2012). Previous studies showed this assumption to be plausible in both imagined physical (Bellmund et al., 2016) and conceptual (Bao et al., 2019; Viganò and Piazza 2020) spaces. Starting from this assumption, we hypothesized that within the 6-fold periodic space generated by a grid-like code two movement directions evoke a similar fMRI activity pattern if their angular distance is close to 60° or a multiple of it. Conversely, when two directions are not perfectly aligned in the 6-fold symmetry, the dissimilarity in the activity that they evoke is proportional to the difference between their angular distance and the closest multiple of 60° (hereafter referred to as "angular distance in the 60° rotational space"). Crucially, thanks to our trial selection uniformly sampling all 16 different directions, the angular distances in the 60° rotational space resulting from the combination of the selected word pairs densely sampled the angular range between 0 and 60°, while this was not the case in our previous study (Vigano and Piazza, 2020). We computed the 16×16 pairwise correlations between the brain activity evoked by word pairs corresponding to all the different 16 movement directions (averaged across runs) and correlated (Pearson's r) this neural dissimilarity matrix (Fisher transformed) with the model of their angular distance in the 60° rotational space (represented in Fig. 2B), as in traditional model-based Representational Similarity Analyses (Kriegeskorte et al. 2008). This procedure was first applied in the entorhinal ROIs, and next extended to the whole brain using a searchlight approach (sphere radius = 3 voxels). As a control for the ROI analysis, this approach was repeated by assuming a 4-, 5-, 7-, and 8- fold periodicity. Given the specific hypothesis put to test, namely that the neural dissimilarity between regions could be explained by a given periodicity in the underlying neuronal population, 1-tailed t-tests were reported at group level to quantify statistical significance. Please notice that the results remain unaltered if a 2-tailed t-test is considered. The same logic applies for all the subsequent analyses.

2.9. Control models

As explained above, our trial selection optimized balanced presentations of movement directions. Given our stimulus space composed by 9 locations, it could be possible that the brain activity patterns evoked by two similar angular distances in the 60° rotational space were similar due to the similar average distance covered by the associated movements, to their similar average starting/ending locations, or to a similar number of associated unique word pairs. To control for these potential confounds, we constructed control models. The first one predicted that two movement directions were more or less similar as a function of the average distance covered across trials. To give an example, moving from KER to DUN implies a direction of 0°, and moving from KER to TIB implies a direction of ~ 63.5°. In the 60° rotational space tested with the grid-RSA, these two movement directions should be represented similarly. One possible confounding factor however might be that they are represented similarly because, on average, the trials that implied movement along these two directions covered the same distance. In order to exclude this we computed the average distance covered for each movement direction across the experiment, and created a matrix where each entry was the difference between the average distance covered by two directions. If two orientations subtended the same average distance across the experiment, their difference, that is their dissimilarity, should be zero. This matrix did not correlate with the one assuming a 6-fold

modulation ($r = -0.12$, $p = 0.18$), thus indicating that our grid-model was not confounded with distance.

The second model we verified took into account the starting/ending location of each movement direction. The two movements in the above example, for instance (KER —> DUN and KER —> TIB) might be similar because they share the same starting point. To test for this possibility, we took all the trials that implied a movement in a given direction and for each direction, we created a vector of 9 elements corresponding to the 9 words (or locations) in the word-space, and we filled it with the number of times a given word appeared as starting (or ending) point. For instance, the direction 0 ˚ had a starting-point vector equal to [6 2 0 6 2 0 6 2 0], meaning that participants started 6 times from KER, 2 times from MOS, 0 times from DUN, 6 times from GAL, and so on. It is already clear at this point that the geometry of our word space imposed some constraints, such as it was impossible to move at 0 ˚ starting from words such as DUN or WEZ, because they are at the extreme of the space. We computed all the pairwise correlations between the 9-elements vectors and constructed a competing 16×16 model of how much similar movement directions were. Notice that the starting and the ending location models were exactly identical because generated by specular vectors. Again, this was a consequence of spatial constraints imposed by the geometry of the word space (e.g., movements to the right can't be done if you start from the right boundary, and movements to the left can't be done if you start from the left boundary). This model did not significantly correlate with the 6-fold grid-model ($r = 0.13$, $p = 0.13$). The third control model took into account the fact that by design some directions were estimated by more unique word pairs than others (e.g., direction at 45 ˚ was subtended by 5 unique word pairs, while direction at 26 ˚ only by 2). We thus computed a model based on the matrix containing all the pairwise absolute differences between the number of unique word pairs that subtended two given directions. This model did not significantly correlate with the 6-fold grid-model ($r = -012$, $p = 0.18$).

A fourth control model took into account the fact that the similarity of the activity patterns evoked by two directions could depend on the similarity of the kind of motor response they elicit. For instance, directions at 26 ˚ (e.g., KER → JOT), 45 ˚ (e.g., KER → WEZ), and 62 ˚ (e.g., KER → TIB) all share the same motor preparation (both features *increased*). In order to verify whether similarity between directions was confounded by the motor preparation that they implied, we performed a correlation between the 6-fold model and the model of motor preparation similarities between directions. The two models did not correlate ($r = -0.13$, $p = 0.12$).

Finally, our last control model took into account that the similarity of the patterns evoked by the directions could be confounded by the *difficulty* of the motor response they required to prepare. Some directions implied more complex decisions (and motor preparations) compared to others. For instance, directions at 26, 45, 62, 206, 225, and 243˚ all share the same difficulty in motor preparation (both features increased OR decreased, thus the decision to be made and the motor response to be prepared were easy). In order to verify whether similarity between directions was confounded by the *difficulty* of the motor response they implied, we correlated the 6-fold model and a model of difficulty similarity between directions. The two models did not correlate ($r = 0$, $p = 1$).

Although we proved that our trials were sampled in such a way that a grid-like code could be tested without being confounded by the above mentioned confounding factors, we further tested that the neural dissimilarity between directions in our ROIs could not be significantly explained by neither of them (see Results), and therefore applied the same model-based grid-RSA describe above, but now testing the control models introduced in this paragraph.

2.10. Distance-dependent adaptation

A word pair presented during a trial implied also a distance covered in the word-space, that should reflect the proximity in their meaning, another signature of the cognitive map. We looked for this signal in brain activity using BOLD adaptation, by reasoning that the closer two words were in the word space, the stronger the suppression in their evoked activity should be. We ran three separate GLMs in SPM12 for each participant. All of them comprised regressors for participants' responses and head movements as in the previous analyses but changed in their main regressor of interest. In the first GLM we added a regressor with the onsets of each trial, and two parametric modulators. The first modulator indicated, for each trial, the number of trials that had passed from the last time that a trial covering the same distance in the semantic space was presented. This step was necessary for correcting for the biased sampling of distances, and excluded from the main regressor (the following parametric modulator) any suppression in the BOLD signal caused by uneven sampling. The second modulator indicated, for each trial, the distance covered in the bi-dimensional space. This model served to search for distance-dependent adaptation in the 2D space. In the second GLM the parametric modulator indicated the distance covered along size (ignoring differences in pitch), while in the third GLM it indicated the distance covered along pitch (ignoring differences in size). Group effects were computed by running a second level analysis in SPM12 on the results of the three first-level GLMs. For the only scope of visualization of the linear suppression effects, we run 3 additional GLMs adding separate regressors for the different distance levels covered in the bidimensional space, or along size, or pitch. In this way we could extract, after the second-level analysis, the group-level parameter estimate for each individual distance level and visualize them in Fig. 3.

3. Results

3.1. Behavioral training results

Before the fMRI session, for 3 days we taught participants the meaning of 9 novel words (Fig. 1b) as the names of 9 audiovisual objects (see Methods). We engaged them in (i) a recognition task, where they had to recognize the correct name of each object among the 9 possible alternatives; (ii) a production task, where, after an object presentation, they had to type its correct name; and iii) a semantic comparison task, where they had to compare the meaning of two names with respect to one of their implied sensory features at a time (e.g. deciding whether KER, compared to GAL is larger, smaller, or identical in *size*)(see Methods). By the end of the training, participants reached a high performance in all the three behavioral tasks: 92% correct (std = 9%) in the recognition task, 91% (std = 10%) in the production task, and 93% (std = 6%) in the semantic comparison task (Fig. 1d), indicating that they fully mastered the novel semantic space.

3.2. fMRI results

During fMRI participants were presented with sequences of words, organized in pairs, and they were instructed to process their meaning as, rarely, they would be presented with comparative questions involving either the size or pitch of the objects they referred to (this was identical to the semantic task presented during training). Performance in the scanner was high (89% correct (std = 8%); average RTs = 898 ms (std = 164 ms)). We reasoned that a sequential presentation of two words implied a movement in the underlying conceptual space with a given direction and covering a given distance (Fig. 1e). This allowed us to implement a series of multivariate and univariate analyses to look for the two codes that are to date known in the human neuroimaging literature as signatures of bidimensional cognitive maps: the grid-like code and the distance code.

3.2.1. A grid-like code in entorhinal cortex

To test for a grid-like code we used Representational Similarity Analysis (RSA, Kriegeskorte et al. 2008), a multivariate analytical approach that, capitalizing on the small but reliable variability in grid orientation across voxels (Doeller et al., 2010; Nau et al., 2018), has been previously
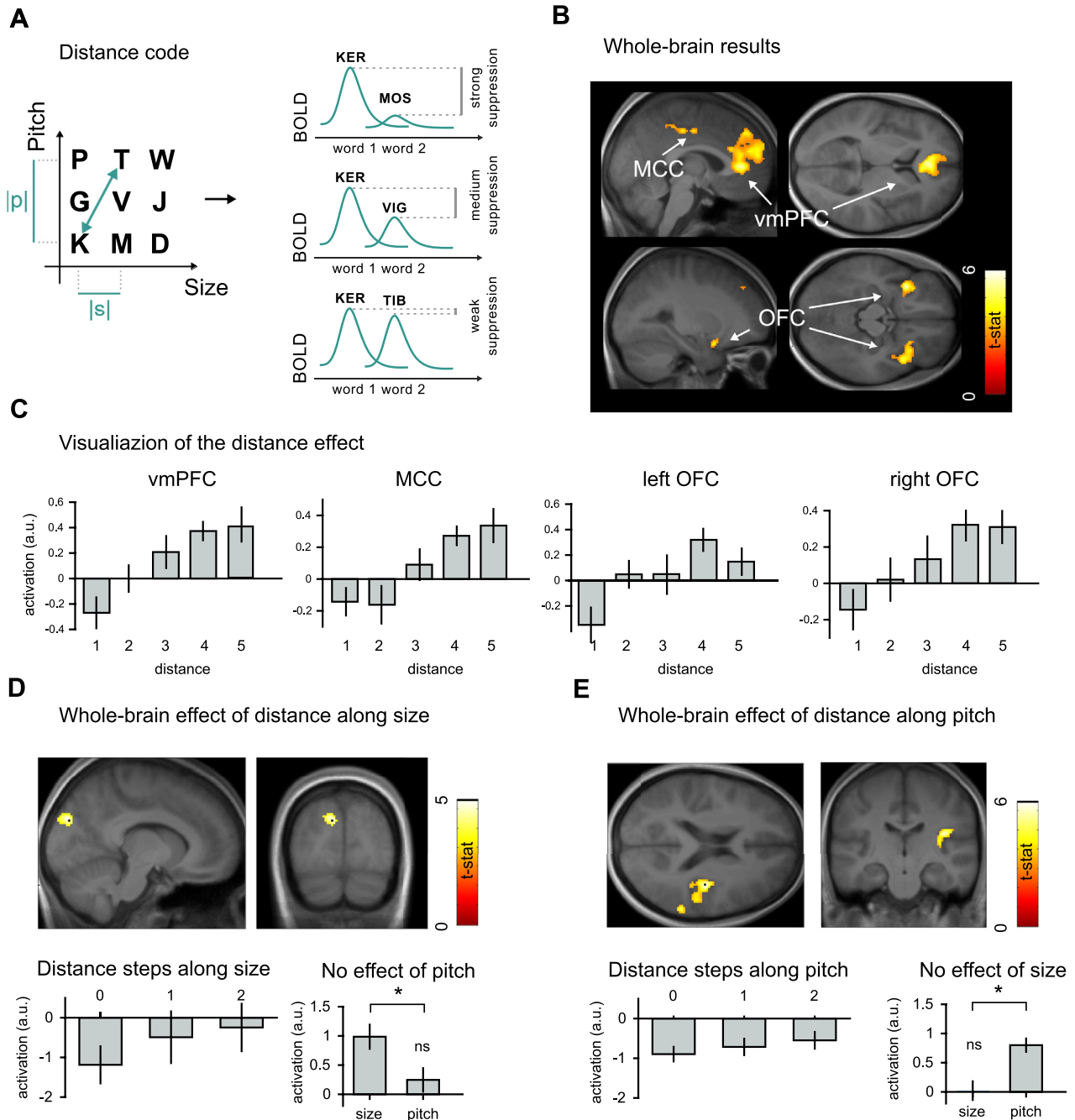
Fig. 3. (a). Distance code. We expected that words that are close in a conceptual space would elicit strong BOLD suppression, that can be measured using fMRI adaptation, as it happens for locations that are close in the environment during spatial navigation tasks (e.g., Morgan et al., 2011). **(b) - Whole-brain analysis.** A whole- brain analysis revealed significant clusters in the medial prefrontal cortex (mPFC), orbitofrontal cortex (OFC), and middle cingulate cortex (MCC). **(c) - Visualization of the distance effect.** BOLD signal in these brain regions increased linearly with the distance covered in the semantic space. **D–E - Whole-brain analyses for distances along size and pitch separately.** Motivated by recent models of how the different components of the meaning of words can be represented in different brain regions (Borghesani and Piazza 2016), we applied the same distance analysis but now considering only the distances between words along either the visual (size of the object) or the sound (pitch of the object) dimensions, separately. On the left side we show the results of the analysis that focused on distances along size, revealing a significant cluster in the occipital cortex, at the level of secondary visual areas (BA18). On the right side we show the results for distances along pitch, revealing a significant cluster in the auditory cortex, at the level of Heschl' gyrus/Insula. For both results, we reported in the lower panels the linear increment of BOLD signal as a function of distance for that specific dimension. Moreover, we show that the visual cluster does not respond to distances along the acoustic dimension, and that the auditory cluster does not respond to distances along the visual dimension.

successfully applied to detect a grid-like signature in the BOLD signal in entorhinal cortex (EC) and other related regions (Bellmund et al., 2016; Bao et al., 2019; Viganò and Piazza 2020). We started by focusing on the postero-medial EC (pmEC, Fig. 2c, see Methods), the human homologous of the rodent medial EC, where grid-cells have been originally described

(Hafting et al., 2005). If an hexadirectional modulation existed in the pmEC, then the similarity between the activity evoked by two movement directions should be directly modulated by their angular distance in the 60° rotational space. This was quantified by correlating the dissimilarity matrix between pairwise BOLD activity patterns with a model of their

dissimilarity in the 6-fold space, computed as the difference between their angular distance and the closest multiple of 60 ° (Fig. 2a)(see Methods). We observed a significant correlation in right pmEC (t (26) = 2.77, p = 0.0051), but not in left pmEC (t (26) = 0.6, p = 0.28)(Fig. 2d; see Fig. 2e for a visualization of how pattern dissimilarity between directions in right pmEC scales as a function of their angular distance in a 60 ° rotational space). To further characterize this result, we applied additional controls. First, we verified that the distributed activity in the right pmEC did not significantly correlate with other competing periodicities, such as four (t (26) = −0.44, p = 0.66), five (t (26) = −0.26, p = 0.60), seven (t (26) = −1.54, p = 0.93), and eight (t (26) = 0.24, p = 0.41) -fold symmetries (Fig. 2f). Second, we verified that the similarity existing between movement directions in this region could not be explained by three competing models (see Methods) addressing the potential effects of the average distance covered by all the trials across directions (t (26) = −0.10, p = 0.54), of the starting/ending points in the word-space (t (26) = 0.56, p = 0.29), or of the number of unique word pairs used to sample the different directions (t (26) = −0.82, p = 0.41). Also, it did not correlate with the similarity between the specific motor response that elicited by these directions (which for instance is identical for directions at 26 and 62°)(t (26) = - 1.22, p = 0.23), nor with the similarity of the complexity of the motor response to be prepared (e.g., directions at 26 and at 206.5° are similarly complex because they require to prepare just one finger)(t (26) = −0.56, p = 0.58). Additionally, we showed that the 6-fold model did not correlate significantly with the activity of the antero-lateral EC (ROIs selected from Maass et al., 2015; left alEC: t (26) = 1.38, p = 0.18; right alEC: t (26) = 1.49, p = 0.15), which is the homologous of the lateral EC in rodents (where grid-cells have not been found, see Hargreaves et al. 2005). Finally, to explore the possibility that the same 6-fold modulation was similarly evoked in other brain regions (as indicated for instance in Constantinescu et al., 2016), we applied a whole brain searchlight. This revealed a single cluster located precisely in the right pmEC (MNI(x,y,z) = 26, −24, −30; p <0.005 at voxel level, q <0.05 at cluster level, uncorrected)(Fig. 2g).

3.2.2. Bi-dimensional distance code in prefrontal cortices and uni-dimensional distance code in sensory regions

Next, we looked for the second signature of a cognitive map typically reported in human neuroimaging studies of spatial navigation: a distance code. Even if in our previous work (Viganò and Piazza 2020) we didn't observe a distance-dependent adaptation effect in hippocampal activity, other researchers (Morgan et al., 2011; Theves et al., 2019, 2020) did, therefore we started our analyses by looking at the hippocampal region of interest. Neither the left (t (26) = −0.09, p = 0.53) nor the right (t (26) = −0.89, p = 0.81) hippocampus showed a distance-dependent adaptation effect. Also, we did not see this effect in the pmEC (left mpEC: t (26) = 0.65, p = 0.51; right pmEC: t (26) = 0.02, p = 0.97), nor in the alEC (left alEC: t (26) = −1.48, p = 0.15; right alEC: t (26) = 0.80, p = 0.42). We then applied a whole-brain analysis to test for such an effect in other brain regions. We found highly significant clusters (threshold p<0.001, FWE corrected at cluster level with q = 0.05) in medial prefrontal cortex (mPFC)(MNI(x,y,z) = −2 36 6), left (MNI(x,y,z) = −36 14 −16) and right (MNI(x,y,z) = 44 12 −12) orbitofrontal cortex, and middle cingulate cortex (MCC) (MNI(x,y,z) = −6 −14 42)(Fig. 3b–c).

Additionally, we looked for brain regions representing distances along the visual and the acoustic dimensions separately. A distance-dependent adaptation relative to size was observed mostly in the visual cortex, at the level of Brodmann area 18 (MNI(x,y,z) = −10, −84, 28)(Fig. 3d) and, to a lesser extent, in the right inferior frontal gyrus (MNI(x,y,z) = 52, 16, 10); a distant-dependent adaptation to pitch was observed in the auditory cortex, both in right Heschl's gyrus/Insula (MNI(x,y,z) = 38, −18, 20))(Fig. 4f), in the superior temporal gyrus (MNI(x,y,z) = 62, −52, 8) and in MCC (MNI(x,y,z) = −2, −12, 44) (all p<0.001 and FWE corrected at q<0.05). Importantly, the distance effect of implied size in occipital cortex was statistically different from the one

of the implied pitch in the same area (size ≠ pitch, t (26) = 2.58, p = 0.02) (Fig. 3e), and the opposite pattern was observed in Heschl's gyrus/Insula (size ≠ pitch, t(26) = 3.71, p = 0.0009), indicating a segregation of the two implied sensory components at this stage of the representation of word meanings.

4. Discussion

In this study we asked whether during a semantic comparison task, the human brain represents word meanings using a cognitive map. We tested this hypothesis by looking for two typical signatures of the cognitive map for bi-dimensional spaces: the grid-like and the distance-dependent modulation of the BOLD signal.

We taught adult subjects the meaning of nine novel words as arbitrary labels of a set of artificial stimuli varying orthogonally along two dimensions. Using RSA and fMRI adaptation we uncovered signatures of a grid-like code in the right entorhinal cortex, and of a distance code in prefrontal, orbitofrontal, and mid cingulate cortices. We also proved that the projections of the position of each word onto the two axes of the semantic space (representing size and pitch, respectively) were also independently encoded in the brain: size (irrespective from pitch) in the occipital cortex and pitch (irrespective from size) in the superior temporal cortex.

These results significantly go beyond the ones previously reported in the literature, first because they relate to the processing of purely symbolic stimuli, thus extending previous data that had associated a grid-like code to sensory processing (e.g., Constantinescu et al., 2016; Bao et al., 2019), or to a mixture of symbols and sensory stimulation (Viganò and Piazza 2020). Second, in the realm of symbol processing it is the first one reporting a clear demonstration of a 6-fold directional (grid-like) modulation of the BOLD signal in the hippocampal formation, complementing previous reports of a distance-modulated response in those regions (Theves et al., 2019, 2020, Solomon 2019). Finally, our study is the first one concurrently investigating spatial codes of different dimensionalities for symbolic representations, highlighting an important interplay between sensory and associative regions in representing concepts.

4.1. An entorhinal grid-like map of word meanings

Our primary finding was that the same grid-like modulation of the BOLD signal that is recorded in humans during virtual navigation of the physical surface is also present, in the right postero-medial entorhinal cortex, when they compare the meaning of words, at least in the case where meaning can be projected onto a well-structured bidimensional space. The hallmark of the grid-like code - the 6-fold periodicity - was here demonstrated by sampling a sufficiently high number of directions (N = 16) in the discrete word space to rule out lower periodicities (in Viganò and Piazza 2020 due to too small number of sampled directions we could not determine whether the EC directional modulation was generated by a 6- or by a 2-fold rotational symmetry signal). Importantly, as we here presented exclusively symbolic stimuli, we could rule out the possibility (existing in Constantinescu et al., 2016, in Bao et al., 2019, and in Viganò and Piazza, 2020) that the grid-like code is solely recruited during direct processing of sensory features. Rather, we demonstrate that it can also be triggered during processing of purely symbolic stimuli. Because in our species we use symbols to refer to the most diverse types of experiences and representations, our result suggests that the entorhinal cognitive map has the flexibility to represent conceptual spaces at large (Tolman 1948; O'Keefe & Nadel 1987; Bellmund et al., 2018). This is particularly useful to represent relational knowledge between concepts: not only we know what "saxophone" means (what it looks like, how it sounds, etc.) but we also know that it is much smaller than a piano and much louder than a flute. This form of relational knowledge is an essential part of our semantic memory.

Our results are also in line and extend those of Theves et al. (2019, 2020): there, the authors trained participants to associate pictures of real-life objects to points of a novel perceptual space, and demonstrated using fMRI that the activity evoked by objects' pictures in the hippocampus reflected their newly acquired distances. Using real-life objects as indices of a perceptual space is however rather artificial compared to how humans typically refer to concepts (using words), and could potentially trigger unwanted and competing similarity effects due to pre-existing knowledge about the objects. Our words, on the contrary, being novel to the subjects, did not suffer from this limitation. Moreover, words, being linguistic stimuli, have been shown to have a stronger abstraction power in referring to and recalling conceptual knowledge (e.g., Lupyan 2008; Edmiston and Lupyan 2015; Lupyan and Thompson-Schill 2011), that makes them a better choice to organize and recall details of a conceptual space. On a related note, our findings also extend the result of Solomon et al. (2019), who used intracranial recordings to demonstrate that neurons in the human hippocampus are sensitive to the semantic distance (as computed using word2vec-derived subspaces) between real words recalled from a list. This study, as well as those by Theves and colleagues (2019, 2020), however, did not report a grid-like code during symbol processing. Our study is to our knowledge the first showing that this code is evoked in the entorhinal cortex during the processing of word meanings during a semantic comparison task.

It's crucial to notice that the general and comprehensive relational arrangements of word meanings in our experiment (a 3 by 3 grid) was never explicitly shown to participants. Rather, subjects constructed it on the basis of their experience of the individual relationals existing between objects (and therefore between the related words, exactly as predicted by the cognitive map hypothesis (Tolman 1948; Behrens et al. 2018). Interestingly, relational inference has been shown to be dependent on the hippocampal-entorhinal circuit in rats for perceptual stimuli (Buckmaster et al. 2004; Bunsey & Eichenbaum 1996; Eichenbaum & Cohen 2007), and seems to also support conceptual representations in humans (Viganò & Piazza, under rev; Park et al. 2020). Another additional interesting aspect of our findings is the right lateralization of the entorhinal grid-like effect that, although fully consistent with our previous study using words and multisensory objects (Viganò and Piazza 2020), one might not expect here as we are dealing with linguistic, symbolic material. The lateralization could be potentially explained by the lack of grammatical/syntactic structure in our word-space. A clear prediction in this sense would be that by manipulating the transitions between words in such a way to create grammar-like dependencies or structures, the left entorhinal cortex could be more strongly recruited.

Finally, our results can be related to the increasing neuroimaging evidence linking subportions of the anterior temporal lobe to the processing of words and their relationships, such as in the case of the perirhinal cortex (e.g., Liuzzi et al., 2015, Martin et al., 2018). At the current stage of research, it is unknown whether and how the entorhinal and the perirhinal cortex communicate during semantic processing, nor whether the perirhinal cortex implements other kinds of spatial codes to represent word meanings. In this respect, the fact that the antero-lateral entorhinal cortex, closer to the perirhinal territory, did not show a grid-like code in our study, might indicate that this effect is strictly localized to more posterior regions (a finding that is further corroborated by our searchlight approach). Future studies should focus on the interplay between these areas of the medial ATL to offer a more precise view of the different representational geometries characterizing these different regions.

4.2. Medial prefrontal, orbitofrontal, and mid cingulate cortices represent the travelled distance between words

Cognitive maps for spatial knowledge have been inferred also by distance codes, that reflect the proximities between physical locations in the environment (Morgan et al., 2011). The proximity between word meanings in our 2D word-space were represented in medial prefrontal, orbitofrontal, and mid cingulate cortices. Both medial prefrontal and orbitofrontal cortices have been previously linked to the representation of physical (Doeller et al., 2010; Jacobs et al., 2013) and abstract spaces (Schuck et al., 2016; Constantinescu et al., 2016; Viganò and Piazza 2020; Stalnaker et al., 2015; Wikenheiser and Schoenbaum 2016). Our results confirm these previous findings. Less clear is the role of the mid cingulate cortex in representing semantic distance in our study. Both medial prefrontal and mid cingulate regions are situated in the medial aspect of the cerebral cortex and are highly connected, in macaques, to the entorhinal cortex (Insausti et al., 1987). However, in order to discern their specific roles additional studies will be needed.

Similarly to our previous report (Viganò and Piazza 2020) but contrasting with others (Constantinescu et al., 2016 and Bao et al., 2019), we did not find an hexadirectional grid-like response in mPFC. Rather, mPFC was strongly modulated by distance. One possibility is that the mPFC amplifies the representation that is relevant for the ongoing task (Lee, Yu, Lerman, Kable 2020). In both our current and previous study participants performed comparative judgements, which may evoke a distance-dependent representation in mPFC. On the contrary, in both Constantinescu et al., 2016 and Bao et al., 2019, participants, prompted with a continuously changing stimulus, were asked to imagine the effects of those changes akin to a mental simulation of a movement, which may more heavily rely on the grid-like representation of direction.

Lastly, but crucially, similarly to our first report on words and objects (Viganò and Piazza 2020) we did not find a distance-modulated response in the hippocampus, previously reported by other studies (Morgan et al., 2011; Theves et al., 2019, 2020). One possibility is that in our two studies we had a much longer training regime (4 days in the current experiment, 9 days in Viganò and Piazza 2020) compared to Theves et al., 2019 (2 days) and Theves et al. 2020 (1 day). This might have shifted the representation of distances in more neocortical regions (such as mPFC), known to encode long term memories. An alternative, more speculative explanation is that distance relations in abstract and discrete material are represented in more frontal regions, while those between locations or simple perceptual stimuli are supported by the hippocampus. Interestingly, a distance-modulated code between abstract task-related decisional states was previously observed in frontal areas (Shuck et al. 2016). A carefully designed experiment addressing this specific question with an ROI approach, ideally in combination with high-field magnets, might be the more accurate way to experimentally approach the issue.

4.3. Sensory regions represent proximities of word meanings along separate dimensions

Finally, we also showed that the one-dimensional distance between word meanings was also represented in the brain, and it was so in the sensory cortices (specifically in occipital cortex and superior temporal gyrus for the implied visual and the implied acoustic dimension, respectively) that are likely involved in encoding the sensory aspects of the stimuli when they are physically presented to the subjects. Indeed, these two regions have been previously implicated in representing the real-life size of objects (Coutanche and Koch 2018; Julian et al. 2017) and the pitch of acoustic stimuli (Zhang et al. 2019), respectively. This finding has important implications for our understanding of how the human brain represents and compares the meaning of words. Previous studies showed that when subjects process words that refer to common concrete objects, the implied average size or sound are separately represented in visual and auditory areas, respectively (e.g., Borghesani et al., 2016 2019a; Coutanche 2019; Kiefer et al., 2008). Borghesani and Piazza (2017) suggested that semantic representations of concrete words can be conceived as points in multidimensional spaces where different dimensions represent the different characteristics that define the meaning of a word. According to this proposal, these different dimensions can be represented, at the brain level, both conjunctively and separately. While we have shown above that prefrontal and entorhinal cortices represent them conjunctively using 2D spatial codes, we further showed

that these dimensions are also represented separately in those brain regions typically recruited to encode the sensory features of the objects referred to by the words. Interestingly, Borghesani et al. 2019a showed, using a time-sensitive approach (magnetoencephalography) that conjunctive and separate representations of dimensions are evoked very quickly and in parallel when processing the meanings of concrete words, around 200 ms from stimulus onset. This potentially indicates that the human brain simultaneously constructs multiple and complementary maps of different dimensionalities of the same conceptual space. On a broader perspective, these maps could represent information along multiple dimensions in convergence zones (e.g., entorhinal cortex, vmPFC), integrating the representation of individual dimensions that are encoded in more sensory regions (e.g., visual cortex, auditory cortex), as also hypothesized in hub-and-spoke models of semantic knowledge (Patterson et al., 2007).

4.4. Conclusions and further directions

The knowledge we have about the world comprises not only information about individual concepts, but also how they relate to each other. One way to represent this knowledge is the use of a "cognitive map", an internal and comprehensive model of the mutual relations between elements of our experiences, being them perceptual or conceptual (Tolman et al., 1948; Behrens et al. 2018; Bellmund et al., 2018; Bottini and Doeller 2020). With the current experiment we showed that two brain signatures typical of cognitive maps for bi-dimensional spaces, the grid-like code and the distance code, are recruited when humans process words - the building blocks of our language - when their relations can be captured by a 2D structure. We also showed that together with such 2D representations, the brain concurrently represents individual dimensions of the word space. This suggests that the brain generates multiple maps of different dimensionalities of the same conceptual space. Several crucial issues remain open, and will direct future research. First, grid-cells in rats have been shown to alter the typical periodicity of their firing rate when the geometrical structure of the physical environment deviates from regular shapes (e.g., rectangular or circular arenas compared to trapezoidal ones, see Krupic et al., 2015), and this is also related with poorer spatial memory (Bellmund et al., 2020). Conceptual spaces are usually more chaotic and less well structured than what we have tested so far in artificial situations and we might expect the grid-like or the distance signatures of a cognitive map to be at least partially degraded when the structure of a conceptual space deviates from perfect regularity and homogeneity. Second, the knowledge we have about things in the world is tremendously rich and usually hardly reducible to two dimensions. Whether these representational codes, or the bi-dimensional representational format usually assumed for the cognitive map, also hold for multidimensional spaces will be an important matter of future investigation. At the moment, we still lack a precise and conclusive description of how the grid-like code might behave when more than two dimensions (that is, three dimensions) are considered during spatial navigation (but see Kim et al. 2017; Kim andMaguire 2018), and this problem is even more pronounced in the case of conceptual spaces. Do brain regions such as the entorhinal cortex, the hippocampus and the medial prefrontal cortex represent multiple dimensions at all, or they reduce the dimensionality of representations for instance via selection or compression, as few recent studies seem to suggest (e.g., Theves et al., 2020; Mack et al., 2019; Bottini and Doeller 2020)? Future studies will be crucial to respond to these questions.

Ethics statement

The study was approved by the local Ethics Committee (Comitato Etico per la Sperimentazione con l'Essere Umano, University of Trento, Italy), in accordance with the Declaration of Helsinki. All participants gave written consent before the experiment, and were assured that their individual data would remain confidential and shared only for purposes related to the original research question, in accordance with the guidelines of the Ethics Committee of the University of Trento regardings privacy rights.

Data and code availability statement

In compliance with the guidelines on data sharing and privacy from the Ethics Committee of the University of Trento, the imaging data of individual subjects are available from the corresponding author only for purposes related to the original research question. Group-level brain activation maps are available at https://neurovault.org/collections/9394/. The code used for the multivariate analyses is available at https://github.com/s-vigano/gridwords. Univariate analyses were conducted within the Statistical Parametric Mapping (SPM) toolbox environment, following the procedures described in the Methods section. Data/code sharing procedures are in line with the requirements of the University of Trento.

Declaration of Competing Interest

The authors declare no conflict of interest.

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