Information-theoretic tools to understand distributed source coding in neuroscience

Ariel K. Feldman, Praveen Venkatesh, Douglas J. Weber, and Pulkit Grover, *Senior Member, IEEE*

Abstract—This paper brings together topics of two of Berger's main contributions to information theory: distributed source coding, and living information theory. Our goal is to understand which information theory techniques can be helpful in understanding a distributed source coding strategy used by the natural world. Towards this goal, we study the example of the encoding of location of an animal by grid cells in its brain. We use information measures of partial information decomposition (PID) to assess the unique, redundant, and synergistic information carried by multiple grid cells, first for simulated grid cells utilizing known encodings, and subsequently for data from real grid cells. In all cases, we make simplifying assumptions so we can assess the consistency of specific PID definitions with intuition. Our results suggest that the measure of PID proposed by Bertschinger et al. *(Entropy, 2014)* provides intuitive insights on distributed source coding by grid cells, and can be used for subsequent studies for understanding grid-cell encoding as well as broadly in neuroscience.

Index Terms—Distributed source coding, grid cells, neuroscience, Partial Information Decomposition

I. INTRODUCTION

A natural question that arises when examining problems of representation in life sciences is: how does one understand a code found in nature? In this work, we explore this question by investigating the context of encoding of an animal's location by *grid cells* in the brain's entorhinal cortex. The focus of our work is on examining which information-theoretic tools are applicable to the problem. Grid cell encoding, widely studied in neuroscience and understood to be a sophisticated form of encoding [1]–[10], brings together two of Berger's main contributions to information theory spanning decades: distributed source coding, and neural encoding of information. It is widely accepted that the grid cells perform a distributed source coding, where the animal's location is the source being encoded. Berger's pioneering works in distributed source coding [11]–[19] were deep and impactful contributions to the field, creating problems that are still actively pursued today, and tools that are actively utilized. Less well known are his contributions to theoretical neuroscience. Berger

Ariel K. Feldman is with the Neuroscience Institute, Carnegie Mellon University, Pittsburgh, PA 15213 USA (e-mail: arielfeldman@cmu.edu).

Praveen Venkatesh is with the Allen Institute and the University of Washington, Seattle, WA 98109 USA (e-mail: praveen.venkatesh@alleninstitute.org).

Douglas J. Weber is with the Mechanical Engineering Department and Neuroscience Institute, Carnegie Mellon University, Pittsburgh, PA 15213 USA (e-mail: dougweber@cmu.edu).

Pulkit Grover is with the Electrical and Computer Engineering Department and Neuroscience Institute, Carnegie Mellon University, Pittsburgh, PA 15213 USA (e-mail: pgrover@andrew.cmu.edu).

wrote (through a long and fruitful collaboration with William Levy [20]–[26] as well as beyond [27]–[31]) a set of deeply theoretical works on "Living information theory", the topic (and the title) of his 2002 Shannon lecture [31]. The focus of these works is on understanding encoding by neurons in the brain, from single neurons to neural populations, from fundamental information-theoretic principles. What drove much of his work is what is called the "Efficient Coding Hypothesis" in neuroscience, which posits that the brain is efficient at its use of resources [31].

Sreenivasan and Fiete were the first to suggest that grid cells' encoding of location, which is our focus here, is efficient [2] in a Shannon-theoretic sense. They suggest that grid cell "modules" (with each module encoding a phase in the space) are spatial representations of short-period clocks (with different periods), tiling the space for efficient (and, in fact, error-resilient) representation. The work is one of many in the field that examines grid cell encodings [3].

The focus of this work is not to contribute to this still evolving literature. Instead, we focus on understanding which information-theoretic tools can be applied to grid cell data, and can provide deeper understanding of the problem. In particular, of interest to us are tools from *Partial Information Decomposition* (PID), which provide a richer set of inferences than classical measures of conditional entropy and mutual information. The need for definitions for PID was first raised in neuroscience [32], [33] (see [34] for a nice tutorial) with the objective of identifying synergistic information, when present, and various definitions were developed over the years [35]–[37]. Our focus is on understanding which PID definition *should* and *can* be used to understand neural encoding[1].

To understand which definitions *should* be used, we use simulated grid cells with random binning of space (in the style of Wyner-Ziv/Slepian-Wolf coding [38], [39]). We then create "parity" grid cells that, together with the random-binning grid cells, create Hamming coded grid cells. We use the resulting simulated data and the intuition of Hamming codes as a playground to test whether our chosen measure provide insights consistent with information-theoretic understanding of random binning and Hamming codes. We observe that while a commonly used PID definition (of Williams and Beer [35]) does not transfer well to this domain, the definition posed by Bertschinger et al. (often called "BROJA PID", where BROJA is an acronym of last names of the authors) [37] provides answers consistent with information-theoretic intuition. To

---

[1]In the spirit of Berger's note on thinking "critically about information-theoretic concepts and methods and then apply only those that genuinely transfer to the new territory" [31].

assess whether this definition *can* be used in practice, we apply it on real neural data. Again, in the spirit of identifying whether the chosen definition is appropriate, we use cells that appear to be from the same grid cell module (i.e., differing only in phase, but not in scale of representation; see Section IV-E). In Section IV-E, we estimate BROJA PID for real grid cells likely from the same module to estimate unique, redundant, and synergistic information in these cells. We run two PID analyses. While the first PID analysis, on fine-grained location, is shown to be equivalent to a conditional entropy analysis (Section IV-C), the second (on very coarse-grained location, left vs right half) provides different insights. Our observations are in line with expectations of grid cell representations from the same module, further supporting the potential of using the BROJA PID definition in neuroscience.

In summary, the main contributions of this work are as follows:

- We connect the encoding used by grid cells to represent location with information-theoretic techniques for distributed source coding, specifically, to random binning. We further use this connection to generate a set of Hamming coded grid cells for baseline understanding of random binning-based strategies.
- We use real grid cell data (from [10]) to quantify conditional entropy *scaling* of grid cell representations, as a cell's output (codeword symbol) is conditioned on an increasingly large set of other cells' outputs (other codeword symbols). Our analysis reveals that there is significant dependence in binning across encoders, which is expected as they are presumably drawn from the same module.
- To perform a deeper analysis, we first inform the choice of a suitable definition of Partial Information Decomposition (PID) in this context, and then estimate the PID quantities to understand how different cells together represent information about the location. Specifically, we study two cases: how grid cells represent the location itself, and how they represent crude information about the location, namely left versus right half of the environment.

Throughout this work, to estimate PID quantities, we use the estimator developed in [40] for BROJA PID (definition developed in Bertschinger et al. [37]). The spiking data analyzed here is freely available, and was collected in Trettel et al. [10] by implanting electrodes in the medial entorhinal cortex of rats during an open field exploration experiment.

II. PRELIMINARIES

A. *Partial information decomposition as a tool for understanding neural encoding*

Historically, measures of entropy [41] and mutual information [32], [42] have been applied in addressing questions about information content, especially in neural contexts, including in the pioneering work of Berger [11]–[19]. Entropy captures the uncertainty in a random variable, A, with distribution $p(a)$, where $\mathcal{A}$ is the set of values that A can take and may be expressed as: $H(A) = -\sum_{a \in \mathcal{A}} p(a) \log_2 p(a)$, whereas mutual information quantifies the dependence between the

two variables as the average *reduction* in the uncertainty (i.e. entropy) of one random variable from its unconditional entropy to the value given the value of another $I(A; B) = H(A) - H(A|B)$.

Partial information decomposition (PID) is an emerging body of work [35], [37], [43] in information theory that decomposes the mutual information $\mathrm{I}(M; (A, B))$ about a random variable M contained in the tuple (A, B) into four *non-negative* terms as follows:

$$\begin{aligned} \mathrm{I}(M; (A, B)) = & \mathrm{Uni}(M : A \setminus B) + \mathrm{Uni}(M : B \setminus A) + \\ & \mathrm{Red}(M : (A, B)) + \mathrm{Syn}(M : (A, B)). \end{aligned} \tag{1}$$

$\mathrm{Uni}(M : A \setminus B)$ denotes the *unique information* about M that is present only in A and not in B. Similarly, $\mathrm{Uni}(M : B \setminus A)$ is the unique information about M present in B and not in A. The term $\mathrm{Red}(M : (A, B))$ is the redundant information about M present in both A and B, and $\mathrm{Syn}(M : (A, B))$ is the synergistic information not present in either A or B individually, but present jointly in (A, B). *All four of these terms are non-negative. Also notice that,* $\mathrm{Red}(M : (A, B))$ *and* $\mathrm{Syn}(M : (A, B))$ *are symmetric in A and B.* Conceptually, PID aims to decompose mutual information into a sum of terms representing unique, redundant and synergistic information. For completeness, a brief introduction to PID is provided in Appendix A. The following equality also holds:

$$\mathrm{I}(M; A) = \mathrm{Uni}(M : A \setminus B) + \mathrm{Red}(M : (A, B)). \tag{2}$$

B. *Grid cells as an appropriate neural population*

To gain insights about encoding in the brain from PID, we want to identify neural populations whose encoding schemes are likely to depend on a mixture of the quantities in (1). Spatially-tuned neurons have complex, and in the case of certain cell types, distributed firing fields, and thus their combinations provide a mixture of the PID quantities described in Section II-A. Grid cells, found predominantly in layer 2 of the medial entorhinal cortex, are a functional classification of mostly stellate, but also pyramidal, spatially-tuned neurons [8], [44], [45]. The characteristic firing rates of these cells are a function of the animal's physical location in space. Grid cells, along with place cells and several other spatially-tuned functional cell types, compose the neural circuitry underlying spatial reasoning; however, they differ from other spatially-tuned neurons in how they encode an animal's location. In a typical rodent experimental paradigm (spatially on the order of 1 meter^2 in lab conditions), a given grid cell will have multiple locations at which its firing rate is high, while place cells, for example, will typically only exhibit one larger favored firing location [46]. We refer to the collection of locations at which a grid cell's firing rate is heightened as that grid cell's *firing field*. The firing fields of different grid cells may overlap, indicating a potential richness in the aforementioned information quantities and thus making them an interesting encoding to understand using PID.

III. GRID CELL ENCODING AS DISTRIBUTED SOURCE CODING

We now describe grid cell encoding of location from an information-theoretic perspective. In doing so, we utilize mod-
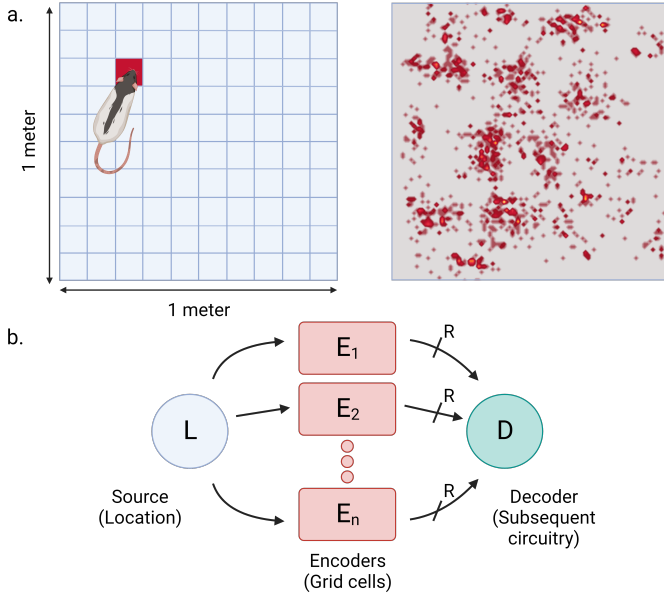
Fig. 1. a) Left, an illustration of a rat exploring the 1 m × 1 m environment, which, for the purpose of illustration, is discretized into 100 segments of size 100 cm^2 each (i.e., 10 cm x 10 cm segments). Right, the firing map of one grid cell (plotted based on data from [10]) as the rat moves through the environment. b) Grid cell encoding described through lens of distributed source coding. Multiple encoders encode the same source for reconstruction by a decoder. A rate limited (and potentially noisy) channel may connect the encoders to the decoder. Created with BioRender.com

els and results from the grid cell literature [2], [3], [47], and summarize them (with some simplification) for readers familiar with information theory. Grid cells are thought to perform a distributed source coding (see Fig. 1) of a single source, namely, the location of the animal in a limited region. For simplicity, the outputs of the encoders (individual grid cells) can be thought of as rate constrained (in nature, this abstracts the limitations on firing rate of neurons). The decoder, e.g. a subsequent region of the brain, is aware of all encoders' encoding strategies, and uses them to decode the location to some degree of precision. The environment is divided into *segments*, a simplification of what is often seen in grid cells fields[2] illustrated in Fig. 1(a). The actual degree of precision is determined by which modules of grid cells are used by the decoder (roughly, a module describes encoding strategy where all encoders represent location using 'segments' of similar size, see Fig. 1).

In this work, we assume for simplicity that the subsequent circuitry only has access to cells from a single module, which is specified by coarseness of quantization (bin size). We further assume that each cell has a deterministic binary output, depending on which segment the animal is in: it either fires (1), or does not fire (0), corresponding to a rate constraint of 1 bit in Fig. 1. We now describe how the strategy used by grid cells resembles binning strategies in distributed source coding literature. First, as discussed above, the space is quantized into segments. The quantization error

is thus bounded by the resolution of the spatial quantization. Posed as a distributed coding strategy, the quantized source is the index denoting the segment of space, and is available to each encoder. Assuming random coding, the codebooks at the k encoders are independently generated as follows: using random binning, each encoder's codebook encodes the source (i.e., the segment of space) by randomly assigning it one of 2^R bins (here, one of two bins, the '0' bin, or the '1' bin, as $R = 1$). The encoders encode using their respective codebooks. The decoder utilizes encoding of each distributed encoder, and finds the segment (if unique) that corresponds to the k bits (grid cell outputs). If not unique, the decoder declares an error. The probability of error of this strategy is bounded by the following lemma.

Lemma 1. *If k grid cells are available for N_{seg} number of segments, the following upper bound on the error probability holds for random coded grid cells:*

$$P_e \leq \frac{N_{\text{seg}} - 1}{2^k}. \tag{3}$$

In particular, if $k = (1 + \eta) \log_2 N_{\text{seg}}$, $P_e < \frac{1}{N_{\text{seg}}^{\eta}}$.

The proof is straightforward from random coding, and is included in Appendix B for completeness. Note that N_{seg} captures the distortion (quantization error) in reconstruction: the larger its value, the smaller its distortion. It is important to observe that binning in natural grid cells in a module is far from independent: the firing fields are typically phase shifts of each other [47]. However, random binning and independent coding are well understood within information theory, so they enable us to test our tools on simulated data prior to application on real data. We also note that ours is the first work where grid cell encoding has formally been connected with binning.

Why would such a distributed source coding strategy be useful? After all, if only one source is being communicated, then all encoders can coordinate, and it may appear that there is no need for distributed strategies. However, binning could still be an effective strategy here: a) binning effectively creates an error-correcting (fountain) code that is resilient to erasures (which, in biological context, can mean access to a required number of neurons, but any k neurons suffice); b) in biological plausibility of neural representations and computations, one widespread criterion is whether it can be implemented[3] in a decentralized fashion [48]–[50]; c) different questions may be answered by the same firing patterns of multiple grid cells. We explore (c) further in Section IV-E and Section V.

IV. UNDERSTANDING ENCODING OF MULTIPLE GRID CELLS

A. Simple grid cell examples

Consider the 3 examples of simple, spatially-tuned neurons in Fig. 2. Each neuron has a different firing field, and we ask different questions about the animal's location in the environment to illustrate how PID quantities change when altering the question we ask of the firing fields. We will represent

---

[2]Grid cell firing fields are often better approximated using hexagonal lattices, instead of the square lattice we use here, but that has little bearing on our analysis and conclusions, and is done purely for simplicity of exposition.

[3]In fact, a stronger constraint is often imposed, where learning also must happen in a decentralized fashion (see, e.g. [48]).
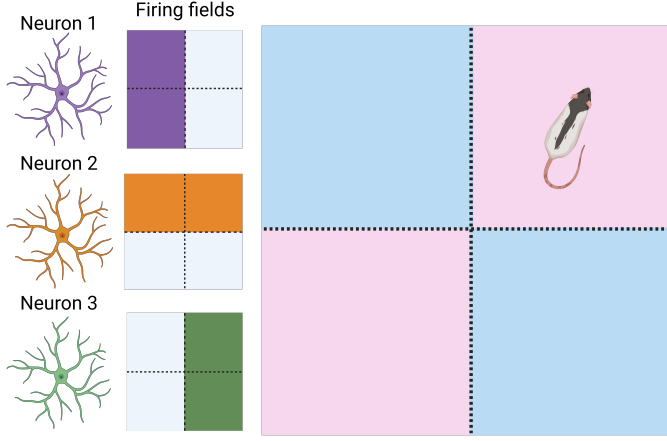
Fig. 2. Partial information decomposition: Using very simplified examples of spatially-tuned neurons, we discuss how combinations of 3 different firing fields can be decomposed into unique, redundant and synergistic information, based on different questions about the animal's location. In this illustration, each neuron's firing field covers exactly half of the space. Neuron 1 fires when the rat is in the left half of the environment, neuron 2 fires when the rat is in the top half, and neuron 3 fires when the rat is in the right half of the environment. The color of the quarters of space in the figure correspond to the operation $\mathbb{1}_{N_1} \oplus \mathbb{1}_{N_2}$. Created with BioRender.com.

whether or not neuron i fired with the indicator function $\mathbb{1}_{N_i}$. For simplicity, this is assumed to be a deterministic function of the location, i.e., $\mathbb{1}_{N_i} = 1$ if the animal is within the firing field, and 0 if not. Suppose we were to ask whether the animal is in the left half of the environment (i.e., M is whether the animal is in the left half), and we were given access to the firing of neurons 1 and 2, where Neuron 1 ($\mathbb{1}_{N_1}$) only fires when the animal is in the left half of the environment, and Neuron 2 ($\mathbb{1}_{N_2}$) only fires when the animal is in the top half of the environment. Intuitively, using PID, we should discover that the information from these neurons about the animal's position, *specifically regarding the left vs. right half of the environment*, is entirely unique. In other words, $\mathrm{I}(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = \mathrm{Uni}(M : \mathbb{1}_{N_1} \setminus \mathbb{1}_{N_2}) = 1$ bit. In contrast, if we were to ask the same question (keep M the same), but use the firing of neurons 1 and 3, where neuron 3 ($\mathbb{1}_{N_3}$) fires only when the animal is in the right half of the environment, we would find that the information provided by the neurons is entirely redundant. Given the output of neuron 1, we will always know the output of neuron 3, and vice versa — the information they possess about the question M is the same. This is expressed as $\mathrm{I}(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_3})) = \mathrm{Red}(M : \mathbb{1}_{N_1}, \mathbb{1}_{N_3}) = 1$ bit.

Expanding our question, consider the case regarding information about the quadrant the animal is in (upper left, upper right, lower right, or lower left) contained in neurons 1 and 2, which have independent firing fields (in that one is only a function of the x-axis value, and the other of the y-axis value). The question now has 4 possible answers, which we can represent with 2 bits. Due to the rate constraint of 1 bit per neuron (it either fires or does not), we still know $\mathrm{I}(M; \mathbb{1}_{N_i})$ is maximally 1 bit for neuron i. The knowledge that neuron 1, for example, fired would reduce our uncertainty of which quadrant the animal is in by half

— only the upper left and lower left quadrants would be the remaining candidates. Likewise, knowing neuron 2 fired leaves us only two possible quadrants — the upper left or the upper right. Given their firing fields are independent, redundant information must be 0 bits. It follows, then, that $\mathrm{I}(M; \mathbb{1}_{N_1}) = 1$ bit and $\mathrm{I}(M; \mathbb{1}_{N_2}) = 1$ bit. By applying constraint (1), $\mathrm{I}(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = \mathrm{Uni}(M : \mathbb{1}_{N_1} \setminus \mathbb{1}_{N_2}) + \mathrm{Uni}(M : \mathbb{1}_{N_2} \setminus \mathbb{1}_{N_1})$.

Suppose we were to ask a more complex question, such as that represented by the "XOR operation" in Fig. 2, which divides the environment into two pink quarters and two blue quarters. Given neurons 1 and 2, to determine if the animal is in a pink or blue quarter of the space (M), neither cell on its own reduces uncertainty in the question. Knowing just neuron 1 fired means there is equal probability the animal is in either a pink or blue quarter; the same goes for knowing just neuron 2 fired. However, when able to access the firing of *both* neurons, performing $\mathbb{1}_{N_1} \oplus \mathbb{1}_{N_2}$ not only reduces uncertainty in the answer to the question, but answers it completely. Thus, the information provided by neurons 1 and 2 about this question is entirely synergistic: $\mathrm{I}(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = \mathrm{Syn}(M : (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = 1$ bit.

The problem of understanding grid cell distributed source coding of location is a complex one, and requires careful consideration of the PID definition used to assess grid cell information content, as well as the message that the PI decomposition is obtained for.

B. Selecting an appropriate PID measure

Within the scope of this work, we focus on two of the most relevant PID measures. The first is the measure proposed in the work of Williams and Beer [35], which was the first work that imposed the constraint (1). Williams and Beer focused on quantifying redundant information, imposing 3 axioms: the symmetry axiom, the self-redundancy axiom, and the monotonicity axiom [35], [37]. We refer the reader to the original works for the definitions of these axioms. While there is broad awareness of shortcomings of this measure [36], [37], [51] in theory, it has nevertheless been used in some recent neuroscience works [52], [53]. The second measure, BROJA PID [37], focuses on defining the unique information and redundant information in terms of the marginal distributions $P(m, a)$ and $P(m, b)$, using the same notation as Section II-A. This measure also follows the 3 axioms from [35], as well as an additional identity axiom, as was first defined in [51]. From the formulation of this measure, which is detailed in [37], we expect BROJA PID to outperform the measure of Williams and Beer in neuroscientific applications. Grid cells provide a concrete example which reveals some of the limitations of the measure of [35] in an existing neuroscience context, and how [37] yields a more intuitive PID quantification.

Consider the case in which two spatially-tuned neurons have independent encoding schemes (such as neuron 1 and neuron 2 in Fig. 2, each containing 1 bit of information about the location of the animal). By definition, then, the firing of one neuron should not decrease our uncertainty about the firing of the other neuron. Using the constraint (1), we can assess

whether the estimators defined in [35] and [37] match the conditions of our example. The estimator posed by Williams and Beer would simplify (1) to the following:

$$I(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = \text{Red}(M : (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) +$$
$$\text{Syn}(M : (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})).$$

In the above simplification, the value of $I(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2}))$ is 2 bits. The Williams and Beer measure would attribute the mutual information of location and each neuron's firing to the redundant information contained in both, and none to unique information contained within each neuron's firing, which would maximally be 1 bit of information. Thus, the remaining 1 bit would be attributed to synergistic information.

However, because the two neuron encodings are independently generated, intuitively, we know that this should not be the case, as is discussed in Section IV-A. The knowledge of the firing of one neuron should not decrease the uncertainty about the firing of the other, and the redundant information between them should be 0 bits. When we apply the BROJA PID [37], we see the constraint (1) simplify instead to:

$$I(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2})) = \text{Uni}(M : \mathbb{1}_{N_1} \setminus \mathbb{1}_{N_2}) +$$
$$\text{Uni}(M : \mathbb{1}_{N_2} \setminus \mathbb{1}_{N_1}).$$

In this simplification, the value of $I(M; (\mathbb{1}_{N_1}, \mathbb{1}_{N_2}))$ remains 2 bits. The BROJA PID measure correctly decomposes the mutual information about location to the unique information contained in each neuron's firing, and redundant information between the neurons is assigned 0 bits.

The redundant information is nonzero using Williams and Beer. PID is also observed for our more realistic simulated grid cell examples in Section IV-D. The proof for that is included in Appendix D.

Hence, we choose to use the BROJA PID measure [37]. We include a brief summary of the definitions of both measures in Appendix A, and refer the reader to the original works for a full discussion of the technical details.

C. PI Decomposition of Location Representation by Deterministic Grid Cells

Lemma 2. *For any 3 random variables L, Y_1, Y_2 such that $Y_i = f_i(L)$ for $i = 1, 2$, where $f_i(\cdot)$ are deterministic functions, the following holds:*

$$\text{Uni}(L : Y_1 \setminus Y_2) = H(Y_1 | Y_2).$$

The proof is in Appendix C.

In a deterministic setting where a grid cell is certain to either fire or not fire at any location l, Lemma 2 says that the unique information that a grid cell's output carries with respect to another grid cell's output about location becomes a conditional entropy term. I.e., the message M is the location L, and the Y_i's are the outputs of single or multiple grid cells, as those are deterministic functions of L. When applied to neural data, Lemma 2 enables us to verify that the unique information term of our PID estimator matches the conditional entropy quantity $H(Y_1|Y_2)$. As Lemma 2 only applies in the deterministic case, we choose to move forward with the

assumption of a deterministic setting for validation purposes. Despite this limitation, we expect that the application of the BROJA PID estimator would be appropriate for a probabilistic model of grid cell encoding.

This Lemma guides our choice of messages and analyses on simulated and real grid cells, in Sections IV-D and IV-E.

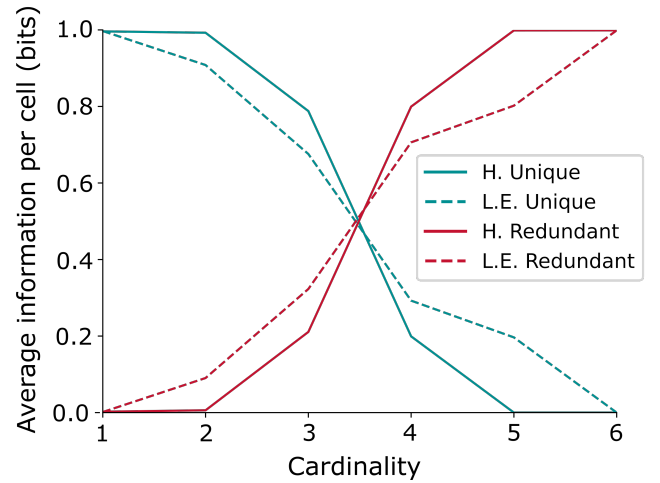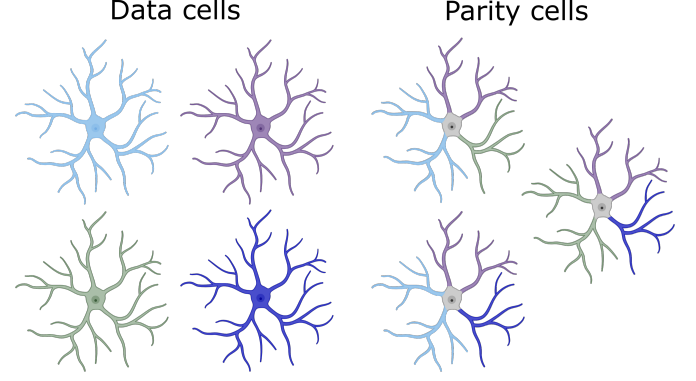### D. Simulated Hamming-coded grid cells

Fig. 3. Simulated data: Average redundant and unique information about location contained in one grid cell, with respect to a set $\mathcal{S}$ of other grid cells, as the cardinality of $\mathcal{S}$ grows, for both Hamming(7,4) coded grid cells (H.) and grid cells coded using a less efficient error correcting code (L.E.). Created with BioRender.com

In this study, for two distributed location coding strategies, we obtain the PI decomposition for one grid cell's representation of location in relation with a set $\mathcal{S}$ of other grid cells (where the size of $\mathcal{S}$ is varied). Specifically, the Hamming coded grid cells (H. in Fig. 3) use random binning for the first 4 grid cells' outputs. Here, we divide the space into 100 square segments (10cm $\times$ 10cm). Then, each segment is binned in to the '0' bin or the '1' bin randomly, with probability half (as is done in Section III). The parity relationships described by the (7,4)-Hamming code are used to encode the remaining 3 symbols (the code length is kept short for computational efficiency of estimation) in an element/segment-wise fashion. The "less efficient" (L.E. in Fig. 3) code uses the following coding strategy: it encodes the first four symbols using random binning, and the remaining three symbols using pairwise XORs, with the code being: $[X_1, X_2, X_3, X_4, X_1 \oplus X_2, X_1 \oplus X_3, X_3 \oplus X_4]$.

Because of Lemma 2, a PID analysis turns out to be equivalent to a conditional entropy analysis. This is because, with deterministic encoding, the PI decomposition of location has zero synergistic information. From the proof in Appendix C, we know that the set Δ_p (in the BROJA definition of PID quantities in [37]) collapses to a single point set in the deterministic case, and thus $\text{Syn}(M : (Y_1, Y_2)) = \text{I}(M; (Y_1, Y_2)) - \inf_{q \in \Delta_p} I_q(M; Y_1|Y_2) = 0$, i.e., the synergistic information is zero. This is also observed in Fig. 3, which also shows average unique and redundant information for Hamming-coded and less-efficiently-coded grid cells. Precisely, the plot shows $\bar{U}_s = \frac{1}{n} \sum_{i=1}^{n} \frac{1}{\binom{n-1}{k}} \sum_{\mathcal{S} \subseteq \mathbf{X}: X_i \notin \mathcal{S}, |\mathcal{S}| = s} \text{Uni}(L : X_i \setminus \mathcal{S})$, and $\bar{R}_s = \frac{1}{n} \sum_{i=1}^{n} \frac{1}{\binom{n-1}{k}} \sum_{\mathcal{S} \subseteq \mathbf{X}: X_i \notin \mathcal{S}, |\mathcal{S}| = s} \text{Red}(L : (X_i, \mathcal{S}))$. The sum of these two quantities is constant, and is the average mutual information between L and X_i (averaged over i).

The average unique information measure, $\bar{U}_s$, is related[4] to the efficiency of a code: for efficient codes, parallel channels should communicate independent information, and hence one expects that $\bar{H}_s$ stays high as $|\mathcal{S}|$ increases, and then collapses all at once. I.e., more efficient representations should exhibit a sharp fall as the cardinality of the set $\mathcal{S}$ grows. At some point while increasing the size $|\mathcal{S}|$, the average unique information any given grid cell has, with respect to the grid cells in $\mathcal{S}$, about the exact location in space, should suddenly drop. The inclusion of one additional symbol should provide *exclusively* redundant information about exact location. We illustrate this concept next through comparing two coding strategies for encoding using multiple grid cells.

In Fig. 3, as compared to a less efficient error correcting code, the Hamming(7,4) neurons demonstrate a steeper fall as the cardinality of $\mathcal{S}$ increases (esp. from 3 to 4), and the less efficient code shows a fall in conditional entropy that is more gradual and starts earlier.

Overall, for this thought experiment of simulated grid cells with distributed coding strategies of different efficiencies, the BROJA PID measure continues to provide quantification consistent with intuition.

E. Real grid cells

1) Data: Using data from Trettel et al. [10], we analyze grid cells across 5 rats exploring an open field of size 1m × 1m. For our analyses, we use 5 grid cells from one session for each rat. To determine the firing fields for these grid cells, we first segment the space into bins of size 6.25 cm^2 (2.5cm × 2.5cm). A bin was considered to be in the grid cell's firing field if, when comparing the total spike count in that bin with the total time spent in the bin, the grid cell's firing rate was at least 1 spike/second. Upon visual inspection, as is illustrated in Fig. 4, these firing fields matched our expectations of what a grid cell firing field would look like, and appear to be from the same module within each rat, based on the size of their firing fields.

---

[4]Because unique information is the same as conditional entropy for deterministic grid cells (Lemma 2), the unique information that is plotted in Fig. 3 is the same as the average conditional entropy term: $\bar{H}_s = \frac{1}{n} \sum_{i=1}^{n} \frac{1}{\binom{n-1}{k}} \sum_{\mathcal{S} \subseteq \mathbf{X}: X_i \notin \mathcal{S}, |\mathcal{S}| = s} H(X_i|\mathcal{S})$.
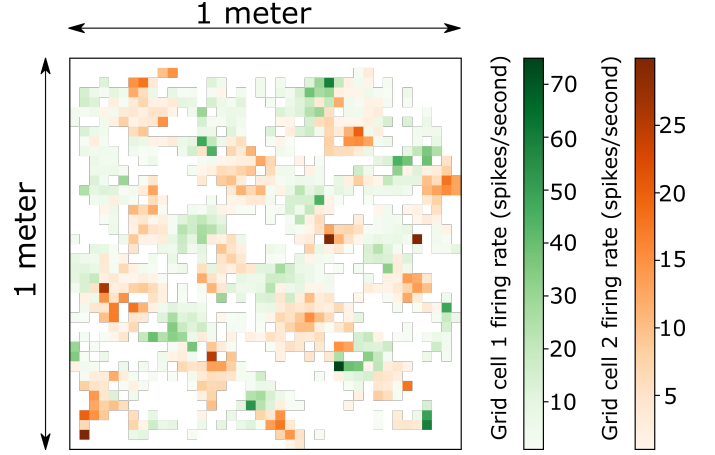

Fig. 4. An example of two grid cells' firing fields from the same rat, during the same open field exploration session, overlaid. Bins depicted are of size 2.5cm × 2.5cm.

2) Expected results: Because the entire 1m × 1m space is divided into segments of 2.5cm × 2.5cm, the total information about location is at most $\log_2(1600) \approx 10.64$ bits. When the message M is the fine-grained location, we expect each cell to have a mutual information of at most 1 bit with the message (because each cell's output is treated as binary). Because the cells are drawn from the same module, we expect them to have small but not negligible redundancy about location. Knowing one cell's output provides us some information about another cell's output. E.g., if their firing fields have very little overlap, then the firing of one cell would imply that the other cell likely did not fire. From Section IV-C and Appendix C, because our mappings are deterministic, we expect synergistic information about fine grained location to be zero. As we increase the cardinality of the set $\mathcal{S}$ of other cells, given that each cell provides at most 1 bit of information, and the total information about the location is > 10 bits, we expect unique information to fall, but not to very small values.

For coarse grained information (message is whether the animal is present in left vs right half), we expect each cell by itself to carry little information (in a mutual information sense) about the message. Thus, we expect unique and redundant information in each cell to be small. We also expect, for $\mathcal{S}$ of small cardinality, that synergistic information will be small, as a few cells are unlikely to reveal with high probability which half the animal is in. However, with enough cells from the same module (which we did not observe in this dataset), we expect synergistic information to jump sharply to a large value.

3) Results: We computed our average conditional entropy measure (average unique information), $\bar{H}_s$, on data collected from 5 grid cells from the same animals in [10]. The result from one rat is shown in Fig. 5 (top plot, top curve), and we include results from the other 4 in Appendix E. We see that average conditional entropy (unique information) falls gradually but consistently, and by the time the cardinality of the set $\mathcal{S}$ reaches 4, it has fallen substantially. This suggests that there is significant pairwise dependence, and even more substantial 3-way, 4-way, and 5-way dependence between grid cell representations (that grows gradually). This suggests that
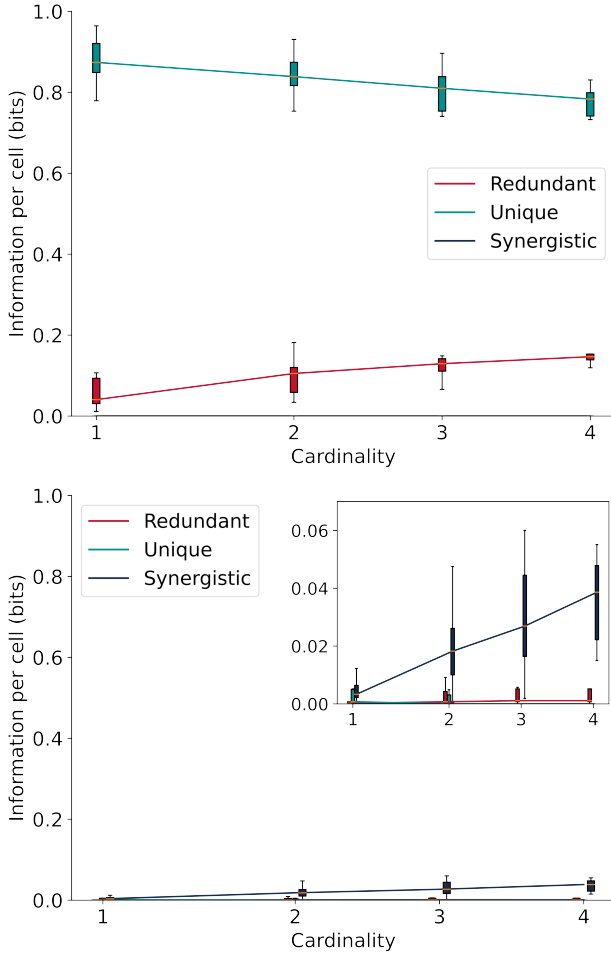
Fig. 5. PI decomposition using the BROJA definition when the message is fine-grained (top plot) and coarse-grained (bottom plot) location. When the message is fine-grained location, each cell largely has unique information about location with respect to other cells, with only a little redundant information that increases to a significant value as the number of other cells is increased. However, when the message is a coarser grained location (here, the message is whether the animal is in the left or the right half), very little information is contained even in 5 cells. Jitter is introduced in the bottom plot for visual clarity.

grid cells' encoding has significant but not large dependence (a 5th grid cell still offers unique information over 4 grid cells).

We next perform PID analyses on this real grid cell data to understand how they represent *crude* information about location: specifically, the message M now is whether the animal is in the left or right half of the environment. Here, information about the message from the same grid cell firing data is now probabilistic — a single grid cell's firing no longer tells us deterministically if the animal is in one half or the other, but rather has different probabilities of firing. Without the deterministic setting needed in Lemma 2, conditional entropy is not equivalent to unique information for a given grid cell, and thus is no longer a good measure of information represented by that neuron. Hence, a PID analysis is needed, where we use estimators from [40].

The resulting PID analysis, setting M as a random variable indicating left vs right half, is shown in Fig. 5. Our analysis reveals that the PID quantities are quite small, and that, within

them, synergistic information dominates. This is expected, as the firing field for any one grid cell should not, in general, be informative about which half of the environment an animal is in, setting the value $\mathrm{Uni}(M : X_i \setminus \mathcal{S})$ to zero. Since the mutual information $\mathrm{I}(M; X_i)$ of a single grid cell output with the message (whether the animal is in the left or right half) should be almost zero (because grid cell firing fields are typically not concentrated in one half of the environment), by (2), both $\mathrm{Uni}(M : X_i \setminus \mathcal{S})$ and $\mathrm{Red}(M : (X_i, \mathcal{S}))$ are also almost 0. Thus, synergistic information dominates.

Broadly, all of these inferences are consistent with our expectations in Section IV-E2.

V. DISCUSSION

The goal of this paper, through theoretical results, toy examples, realistic examples, and real-world data analysis, is on understanding which tools from information theory provide intuitive insights on a distributed source coding strategy chosen by nature. The focus is on discerning which definition from partial information decomposition provides intuitive descriptions of these coding strategies. Several examples suggest that BROJA PID provides more intuitive quantification of PID quantities than the Williams and Beer PID definition. It is important to note that there are other PID definitions as well (see, e.g., [54]–[56]), and a similar rigorous examination of their use in neuroscience should be done before they are used. This work adds to increasing evidence that the BROJA PID definition provides useful insights. However, we are also interested in examining the "O"-Information definition [56] in this context, as that specific definition does not require choice of a message.

The focus here is not on obtaining new neuroscientific insights as several simplifications were made in order to have intuition on what the PID estimates could be, so that we could understand which PID definition is more applicable. Thus, while this work focused on single grid cell modules with binary deterministic mapping, future work will examine use of BROJA PID to understand distributed source coding in cases where the firing field is not deterministic or binary. It will also examine coding by several modules, a problem of deep interest in neuroscience. There, because of different spatial resolution of different modules, we expect successive refinement strategies, another area where Berger made substantial contributions [14], [57], [58], to play a critical role.

REFERENCES

[1] E. I. Moser, Y. Roudi, M. P. Witter, C. Kentros, T. Bonhoeffer, and M.-B. Moser, "Grid cells and cortical representation," *Nature Reviews Neuroscience*, vol. 15, no. 7, pp. 466–481, 2014.
[2] S. Sreenivasan and I. Fiete, "Grid cells generate an analog error-correcting code for singularly precise neural computation," *Nature neuroscience*, vol. 14, no. 10, pp. 1330–1337, 2011.
[3] R. W. DiTullio and V. Balasubramanian, "Dynamical self-organization and efficient representation of space by grid cells," *Current opinion in neurobiology*, vol. 70, pp. 206–213, 2021.
[4] D. Bush, C. Barry, D. Manson, and N. Burgess, "Using grid cells for navigation," *Neuron*, vol. 87, no. 3, pp. 507–520, 2015.
[5] M. Klukas, M. Lewis, and I. Fiete, "Efficient and flexible representation of higher-dimensional cognitive variables with grid cells," *PLoS computational biology*, vol. 16, no. 4, p. e1007796, 2020.

[6] A. Mathis, A. V. Herz, and M. Stemmler, "Optimal population codes for space: grid cells outperform place cells," *Neural computation*, vol. 24, no. 9, pp. 2280–2317, 2012.

[7] X.-X. Wei, J. Prentice, and V. Balasubramanian, "A principle of economy predicts the functional architecture of grid cells," *Elife*, vol. 4, p. e08362, 2015.

[8] Y. Gu, S. Lewallen, A. A. Kinkhabwala, C. Domnisoru, K. Yoon, J. L. Gauthier, I. R. Fiete, and D. W. Tank, "A map-like micro-organization of grid cells in the medial entorhinal cortex," *Cell*, vol. 175, no. 3, pp. 736–750, 2018.

[9] P. Venkatesh and P. Grover, "Understanding encoding and redundancy in grid cells using partial information decomposition," in *Computational and Systems Neuroscience (Cosyne)*, 2020.

[10] S. G. Trettel, J. B. Trimper, E. Hwaun, I. R. Fiete, and L. L. Colgin, "Grid cell co-activity patterns during sleep reflect spatial overlap of grid fields during active behaviors," *Nature neuroscience*, vol. 22, no. 4, pp. 609–617, 2019.

[11] T. Berger, Z. Zhang, and H. Viswanathan, "The CEO problem [multiterminal source coding]," *IEEE Transactions on Information Theory*, vol. 42, no. 3, pp. 887–902, 1996.

[12] T. Berger, "Multiterminal source coding," *The information theory approach to communications*, 1978.

[13] R. Zamir and T. Berger, "Multiterminal source coding with high resolution," *IEEE Transactions on Information Theory*, vol. 45, no. 1, pp. 106–117, 1999.

[14] J. Chen and T. Berger, "Successive Wyner–Ziv coding scheme and its application to the quadratic Gaussian CEO problem," *IEEE Transactions on Information Theory*, vol. 54, no. 4, pp. 1586–1603, 2008.

[15] J. Chen, X. Zhang, T. Berger, and S. B. Wicker, "An upper bound on the sum-rate distortion function and its corresponding rate allocation schemes for the CEO problem," *IEEE Journal on Selected Areas in Communications*, vol. 22, no. 6, pp. 977–987, 2004.

[16] A. Kaspi and T. Berger, "Rate-distortion for correlated sources with partially separated encoders," *IEEE Transactions on Information Theory*, vol. 28, no. 6, pp. 828–840, 1982.

[17] T. Berger and R. W. Yeung, "Multiterminal source encoding with one distortion criterion," *IEEE Transactions on Information Theory*, vol. 35, no. 2, pp. 228–236, 1989.

[18] Z. Zhang and T. Berger, "New results in binary multiple descriptions," *IEEE Transactions on Information Theory*, vol. 33, no. 4, pp. 502–521, 1987.

[19] H. Viswanathan and T. Berger, "The quadratic Gaussian CEO problem," *IEEE Transactions on Information Theory*, vol. 43, no. 5, pp. 1549–1559, 1997.

[20] T. Berger and W. B. Levy, "A mathematical theory of energy efficient neural computation and communication," *IEEE Transactions on Information Theory*, vol. 56, no. 2, pp. 852–874, 2010.

[21] W. B. Levy, T. Berger, and I. A. Fleidervish, "Neural computation at the thermal limit," *arXiv preprint arXiv:1408.6777*, 2014.

[22] T. Berger, W. B. Levy, and J. Xing, "Energy efficient neurons with generalized inverse Gaussian interspike interval durations," in *2011 49th Annual Allerton Conference on Communication, Control, and Computing (Allerton)*. IEEE, 2011, pp. 1737–1742.

[23] W. B. Levy and T. Berger, "Design principles and specifications for neural-like computation under constraints on information preservation and energy costs as analyzed with statistical theory," in *2012 IEEE International Symposium on Information Theory Proceedings*. IEEE, 2012, pp. 2969–2972.

[24] M. Sungkar, T. Berger, and W. B. Levy, "Mutual information and parameter estimation in the generalized inverse Gaussian diffusion model of cortical neurons," *IEEE Transactions on Molecular, Biological and Multi-Scale Communications*, vol. 2, no. 2, pp. 166–182, 2016.

[25] T. Berger, J. Xing, and W. B. Levy, "Generalized inverse Gaussian (GIG) models for energy-efficient neurons," in *Proceedings of the 2013 Information Theory and Applications Workshop (ITA), San Diego, CA, USA*. Citeseer, 2013, pp. 10–15.

[26] W. B. Levy, T. Berger, and M. Sungkar, "Neural computation from first principles: Using the maximum entropy method to obtain an optimal bits-per-joule neuron," *IEEE Transactions on Molecular, Biological and Multi-Scale Communications*, vol. 2, no. 2, pp. 154–165, 2016.

[27] T. Berger, "Rate-distortion theory," *Wiley Encyclopedia of Telecommunications*, 2003.

[28] J. Xing, T. Berger, M. Sungkar, and W. B. Levy, "Energy efficient neurons with generalized inverse Gaussian conditional and marginal hitting times," *IEEE Transactions on Information Theory*, vol. 61, no. 8, pp. 4390–4398, 2015.

[29] J. Xing, T. Berger, and T. J. Sejnowski, "A Berger-Levy energy efficient neuron model with unequal synaptic weights," in *2012 IEEE International Symposium on Information Theory Proceedings*. IEEE, 2012, pp. 2964–2968.

[30] P. Suksompong and T. Berger, "Capacity analysis for integrate-and-fire neurons with descending action potential thresholds," *IEEE transactions on information theory*, vol. 56, no. 2, pp. 838–851, 2010.

[31] T. Berger, "Living information theory," *IEEE information theory society newsletter*, vol. 53, no. 1, p. 1, 2003.

[32] E. Schneidman *et al.*, "Synergy, redundancy, and independence in population codes," *J. Neurosci.*, vol. 23, no. 37, pp. 11 539–11 553, 2003.

[33] I. Gat and N. Tishby, "Synergy and redundancy among brain cells of behaving monkeys," in *NIPS*, 1999, pp. 111–117.

[34] N. M. Timme and C. Lapish, "A tutorial for Information Theory in Neuroscience," *eNeuro*, vol. 5, no. 3, 2018.

[35] P. L. Williams and R. D. Beer, "Nonnegative decomposition of multivariate information," *arXiv:1004.2515 [cs.IT]*, 2010.

[36] V. Griffith and T. Ho, "Quantifying redundant information in predicting a target random variable," *Entropy*, vol. 17, no. 7, pp. 4644–4653, 2015.

[37] N. Bertschinger, J. Rauh, E. Olbrich, J. Jost, and N. Ay, "Quantifying unique information," *Entropy*, vol. 16, no. 4, pp. 2161–2183, 2014.

[38] A. Wyner and J. Ziv, "The rate-distortion function for source coding with side information at the decoder," *IEEE Transactions on information Theory*, vol. 22, no. 1, pp. 1–10, 1976.

[39] D. Slepian and J. Wolf, "Noiseless coding of correlated information sources," *IEEE Transactions on information Theory*, vol. 19, no. 4, pp. 471–480, 1973.

[40] P. K. Banerjee, J. Rauh, and G. Montúfar, "Computing the unique information," in *2018 IEEE International Symposium on Information Theory (ISIT)*. IEEE, 2018, pp. 141–145.

[41] H. B. Barlow *et al.*, "Possible principles underlying the transformation of sensory messages," *Sensory communication*, vol. 1, no. 01, 1961.

[42] G. Lewen, W. Bialek, and R. D. R. Van Steveninck, "Neural coding of naturalistic motion stimuli," *Network: Computation in Neural Systems*, vol. 12, no. 3, p. 317, 2001.

[43] V. Griffith and C. Koch, "Quantifying synergistic mutual information," in *Guided Self-Organization: Inception*. Springer, 2014, pp. 159–190.

[44] C. Domnisoru, A. A. Kinkhabwala, and D. W. Tank, "Membrane potential dynamics of grid cells," *Nature*, vol. 495, no. 7440, pp. 199–204, 2013.

[45] H. Pastoll, H. L. Ramsden, and M. F. Nolan, "Intrinsic electrophysiological properties of entorhinal cortex stellate cells and their contribution to grid cell firing fields," *Frontiers in neural circuits*, vol. 6, p. 17, 2012.

[46] J. O'keefe and L. Nadel, *The hippocampus as a cognitive map*. Oxford university press, 1978.

[47] E. Moser and M. Moser, "Grid cells," *Scholarpedia*, vol. 2, no. 7, p. 3394, 2007, revision #144456.

[48] Y. Bahroun, D. Chklovskii, and A. Sengupta, "A normative and biologically plausible algorithm for Independent Component Analysis," *Advances in Neural Information Processing Systems*, vol. 34, 2021.

[49] D. Lipshutz, Y. Bahroun, S. Golkar, A. M. Sengupta, and D. B. Chklovskii, "A biologically plausible neural network for multichannel canonical correlation analysis," *Neural computation*, vol. 33, no. 9, pp. 2309–2352, 2021.

[50] B. A. Olshausen and D. J. Field, "Sparse coding with an overcomplete basis set: A strategy employed by V1?" *Vision research*, vol. 37, no. 23, pp. 3311–3325, 1997.

[51] M. Harder, C. Salge, and D. Polani, "Bivariate measure of redundant information," *Physical Review E*, vol. 87, no. 1, p. 012130, 2013.

[52] A. I. Luppi, J. Cain, L. R. Spindler, U. J. Górska, D. Toker, A. E. Hudson, E. N. Brown, M. N. Diringer, R. D. Stevens, M. Massimini *et al.*, "Mechanisms underlying disorders of consciousness: Bridging gaps to move toward an integrated translational science," *Neurocritical Care*, vol. 35, no. 1, pp. 37–54, 2021.

[53] A. I. Luppi, P. A. Mediano, F. E. Rosas, J. Allanson, J. D. Pickard, R. L. Carhart-Harris, G. B. Williams, M. M. Craig, P. Finoia, A. M. Owen *et al.*, "A synergistic workspace for human consciousness revealed by integrated information decomposition," *BioRxiv*, 2020.

[54] A. J. Gutknecht, M. Wibral, and A. Makkeh, "Bits and pieces: Understanding information decomposition from part-whole relationships and formal logic," *Proceedings of the Royal Society A*, vol. 477, no. 2251, p. 20210110, 2021.

[55] K. Gurushankar, P. Venkatesh, and P. Grover, "Extracting unique information through Markov relations," in *2022 58th Annual Allerton Conference on Communication, Control, and Computing (Allerton)*. IEEE, 2022, pp. 1–6.

[56] F. E. Rosas, P. A. Mediano, M. Gastpar, and H. J. Jensen, "Quantifying high-order interdependencies via multivariate extensions of the mutual information," *Physical Review E*, vol. 100, no. 3, p. 032305, 2019.

[57] L. Lastras and T. Berger, "All sources are nearly successively refinable," *IEEE Transactions on Information Theory*, vol. 47, no. 3, pp. 918–926, 2001.

[58] J. Chen and T. Berger, "Distributed source coding via successive refinement," in *42nd Annual Allerton Conference on Communication, Control, and Computing*, 2006, pp. 1–5.

APPENDIX A
A BRIEF INTRODUCTION TO PARTIAL INFORMATION DECOMPOSITION

The Partial Information Decomposition (PID) framework decomposes the mutual information $I(M; (A, B))$ about a random variable M contained in (A, B) into four *non-negative* terms as follows:

$$I(M; (A, B)) = \text{Uni}(M : A\backslash B) + \text{Uni}(M : B\backslash A) + \text{Red}(M : (A, B)) + \text{Syn}(M : (A, B)).$$

$\text{Uni}(M : A\backslash B)$ is the unique information about M that is present only in A and not in B; $\text{Uni}(M : B\backslash A)$ is the unique information about M that is in B and not in A. $\text{Red}(M : (A, B))$ is the redundant information about M present in both A and B, and $\text{Syn}(M : (A, B))$ is the synergistic information not present in either of A or B individually, but present jointly in (A, B).

Irrespective of the exact definition of individual PID terms, the following identities hold [35], [37]:

$$I(M; A) = \text{Uni}(M : A\backslash B) + \text{Red}(M : (A, B)). \quad (4)$$

$$I(M; A \mid B) = \text{Uni}(M : A\backslash B) + \text{Syn}(M : (A, B)). \quad (5)$$

Given the three equations (1), (4) and (5), and four unknowns (the four PID terms), the PID terms are not uniquely specified. However, defining any one of the terms (e.g., $\text{Uni}(M : A\backslash B)$) is sufficient to obtain the other three.

Williams and Beer define the redundant information as $I_{\min}$:

Definition 1 (Redundant information $I_{\min}$ in [35]).

$$I_{\min}(M; A, B) = \sum_m p(m) \min\{I(M = m; A), I(M = m; B)\} \quad (6)$$

BROJA PID defines the unique information:

Definition 2 (BROJA Unique Information [37]). *Let Δ be the set of all joint distributions on (M, A, B), and Δ_p be the set of joint distributions with the same marginals on (M, A) and (M, B) as their true distribution, i.e., $\Delta_p = \{Q \in \Delta : q(m, a) = \Pr(M=m, A=a) \text{ and } q(m, b) = \Pr(M=m, B=b)\}$. Then, $\text{Uni}(M : A\backslash B) = \min_{Q \in \Delta_p} I_Q(M; A|B)$.*

APPENDIX B
PROOF OF LEMMA 1

Random coding: each segment of each grid cell's encoding is randomly assigned a value 1 or 0. The k-bit output of k grid cells is received at the decoder. The decoder finds the segment (if unique) that corresponds to the k bits. The probability that an incorrect segment, say the (i, j)-th segment, also has the same k-bit encoding is $\frac{1}{2^k}$ due to random coding. Now, the probability that *any* of the incorrect $N_{\text{seg}} - 1$ segments have the same k-bit encoding is, by union bound, $\frac{N_{\text{seg}} - 1}{2^k}$.

APPENDIX C
PROOF OF LEMMA 2

Proof. From the definition of Unique Information in BROJA PID [37],

$$\text{Uni}(L : X_1 \setminus X_2) = \inf_{q \in \Delta_p} I_q(L; X_1 | X_2), \quad (7)$$

where Δ_p is a set of 3-way joint distributions on L, X_1, X_2 such that:

$$\Delta_p = \{q(l, x_1, x_2) : q(l, x_1) = p(l, x_1), q(l, x_2) = p(l, x_2)\}. \quad (8)$$

Now,

$$p(l, x_1) = p(l)p(x_1|l) = \begin{cases} p(l).1 & \text{if } x_1 = f_1(l) \\ 0 & \text{otherwise} \end{cases}.$$

Note that $q(l, x_1) = p(l, x_1)$ from the definition of Δ_p (and hence, also, $q(l) = p(l)$).

Similarly,

$$p(l, x_2) = \begin{cases} p(l).1 & \text{if } x_2 = f_2(l) \\ 0 & \text{otherwise} \end{cases}.$$

Now, we claim that Δ_p is a single point set, i.e., $\Delta_p = \{p\}$ and hence $q = p$. To see this, let us examine $q(l, x_1, x_2) \in \Delta_p$:

$$\begin{aligned} q(l, x_1, x_2) &= q(l)q(x_1|l)q(x_2|l, x_1) \\ &= \begin{cases} q(l).1 & \text{if } x_1 = f_1(l), x_2 = f_2(l) \\ 0 & \text{otherwise} \end{cases} \\ &= \begin{cases} p(l).1 & \text{if } x_1 = f_1(l), x_2 = f_2(l) \\ 0 & \text{otherwise} \end{cases} \\ &= p(l, x_1, x_2). \quad (9) \end{aligned}$$

I.e., the optimization in (7) is over a singleton, $q = p$. Thus,

$$\begin{aligned} \text{Uni}(L : X_1 \setminus X_2) &= I(L; X_1|X_2) \\ &= H(X_1|X_2) - H(X_1|X_2, L) \\ &= H(X_1|X_2), \end{aligned}$$

where the last equality follows from the observation that X_1 is a deterministic function of L. $\square$

APPENDIX D
$I_{\min} = 1$ FOR RANDOMLY-BINNED GRID CELLS FOR REPRESENTING LOCATION

Here, we compute $I_{\min}$ for N_{seg} (quantized) source locations, each randomly ($\text{Ber}(1/2)$) assigned a value by each encoder (independently).

$$\begin{aligned} I_{\min}(L; X_1, X_2) &= \sum_l p(l) \min_i I(L = l; X_i) \\ &\overset{(a)}{=} \sum_l p(l) \min_i \sum_{x_{ij}} p(x_{ij}|l) \log \frac{p(l, x_{ij})}{p(l)p(x_{ij})} \\ &= \sum_l \min_i \sum_{x_{ij}} p(l, x_{ij}) \log \frac{p(l, x_{ij})}{p(l)p(x_{ij})}. (10) \end{aligned}$$

In (a), note that the notation (borrowed from [35]) is slightly unusual, with the following definition: $I(L = l; X_i) :=$

$\sum_{x_{ij}} p(x_{ij}|l) \log \frac{p(l,x_{ij})}{p(l)p(x_{ij})}$, where x_{ij} are the (binary) realizations of X_i. Then, say $f(l)$ is the output of the grid cell. Let us examine the term inside the $\min_i$ for a fixed l, say l_0

$$\min_i \sum_{x_{ij}} p(l_0, x_{ij}) \log \frac{p(l_0, x_{ij})}{p(l_0)p(x_{ij})}$$

$$\overset{(b)}{=} \min_i \sum_{\{x_{ij}\ s.t.\ x_{ij}=f(l_0)\}} \frac{1}{N_{\text{seg}}} \log \left(\frac{\frac{1}{N_{\text{seg}}}}{\frac{1}{N_{\text{seg}}} \times \frac{1}{2}} \right)$$

$$\overset{(c)}{=} \min_i \frac{1}{N_{\text{seg}}} \overset{(d)}{=} \frac{1}{N_{\text{seg}}}, \qquad (11)$$

where (b) follows from noting that $p(l_0, x_{ij}) = \frac{1}{N_{\text{seg}}}$ if $f(l_0) = x_{ij}$ and 0 otherwise, and because $p(l_0) = \frac{1}{N_{\text{seg}}}$ and $p(x_{ij}) = \frac{1}{2}$. Also, (c) holds because the set $\{x_{ij}\ s.t.\ x_{ij} = f(l_0)\}$ is a single point set, since only one value of x_{ij} satisfies $x_{ij} = f(l_0)$. Further, (d) holds because the term inside the $\min$ in the LHS of (d) does not depend on i. From (10), (11), we get:

$$I_{\min}(L; X_1, X_2) = \sum_l \frac{1}{N_{\text{seg}}} = 1. \qquad (12)$$

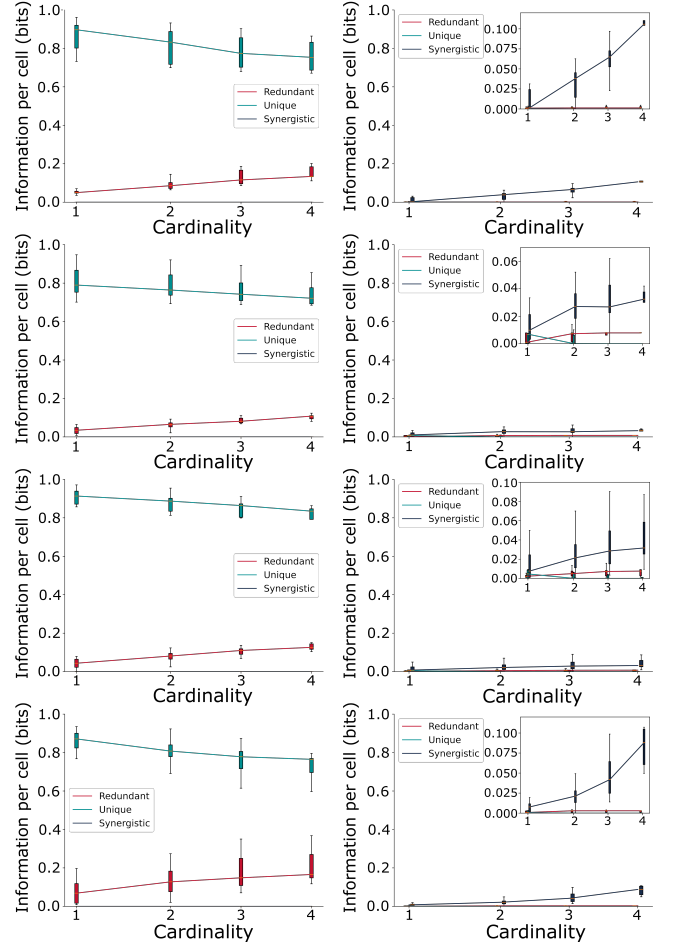## APPENDIX E
ADDITIONAL GRID CELL PID ANALYSES

Fig. 6. The figure provides PI decomposition for a fine-grained message (left) and a coarse-grained message (right), as described in Section IV-E, on 4 other rats (5 cells from each, likely belonging to the same module). The figures confirm that, qualitatively, the PID behavior is the same across animals for either choice of the message. Jitter is introduced in the right plots for visual clarity.