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Obstructions to convexity in neural codes

Caitlin Lienkaemper [a,*], Anne Shiu [b], Zev Woodstock [c,1]

[a] *Department of Mathematics, Harvey Mudd College, 301 Platt Boulevard, Claremont, CA 91711-5901, USA*
[b] *Department of Mathematics, Texas A&M University, Mailstop 3368, College Station, TX 77843-3368, USA*
[c] *Department of Mathematics and Statistics, James Madison University, Roop Hall 305, MSC 1911, Harrisonburg, VA 22807, USA*

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ABSTRACT

How does the brain encode spatial structure? One way is through hippocampal neurons called place cells, which become associated to convex regions of space known as their receptive fields: each place cell fires at a high rate precisely when the animal is in the receptive field. The firing patterns of multiple place cells form what is known as a convex neural code. How can we tell when a neural code is convex? To address this question, Giusti and Itskov identified a local obstruction, defined via the topology of a code's simplicial complex, and proved that convex neural codes have no local obstructions. Curto et al. proved the converse for all neural codes on at most four neurons. Via a counterexample on five neurons, we show that this converse is false in general. Additionally, we classify all codes on five neurons with no local obstructions. This classification is enabled by our enumeration of connected simplicial complexes on 5 vertices up to isomorphism. Finally, we examine how local obstructions are related to maximal codewords (maximal sets of neurons that co-fire). Curto et al. proved that a code has no local obstructions if and only if it contains certain "mandatory" intersections of maximal codewords. We give a new criterion for an intersection of maximal codewords to be non-mandatory, and prove that it

* Corresponding author.
E-mail addresses: clienkaemper@g.hmc.edu (C. Lienkaemper), annejls@math.tamu.edu (A. Shiu), zwoodst@ncsu.edu (Z. Woodstock).
[1] Present address: Department of Mathematics, Box 8205, NC State University, Raleigh, North Carolina, 27695-8205.

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classifies all such non-mandatory codewords for codes on up to five neurons.

1. Introduction

The brain's ability to navigate within and represent the physical world is fundamental to our everyday experience and ability to function. How does the brain accomplish this? For their work shedding light on this question, neuroscientists John O'Keefe, May Britt Moser, and Edvard Moser won the 2014 Nobel Prize in Physiology and Medicine. Their work led to the discovery of place cells, grid cells, and head direction cells, all of which take part in rodents' and other animals' mechanisms for representing, navigating through, and forming memories of their environments.

This paper focuses on place cells, which are hippocampal neurons which become associated to regions of the environment known as their receptive fields or place fields. When an animal is located in a place cell's receptive field, the place cell fires at a higher rate than when the animal is outside the place field. The firing patterns of a collection of place cells describe an animal's position within its environment. These receptive fields have been experimentally observed to be approximately convex regions of space. *Convex codes* are those neural codes (firing patterns) that can arise from the activity of place cells with convex receptive fields.

Which neural codes are convex? What are signatures of convexity or non-convexity? Curto et al. [3,4] and Giusti and Itskov [5] addressed these questions using combinatorial topology and commutative algebra, and gave complete answers for codes on up to four neurons. Curto et al. achieved this classification by organizing neural codes according to their simplicial complexes, and, additionally, by focusing on *local obstructions* to convexity. Earlier, Giusti and Itskov had introduced this concept and proved that codes with local obstructions are necessarily non-convex. Curto et al. proved that local obstructions have the following interpretation: for each simplicial complex Δ, there is a set of "mandatory" codewords whose presence in a code (whose simplicial complex is Δ) is required to avoid local obstructions [3]. Therefore, a code must contain all its mandatory codewords to be convex. Moreover, the mandatory codewords are necessarily intersections of maximal codewords. This motivates the following questions:

Question 1.1. Is every code which has no local obstructions convex?

Question 1.2. Is every intersection of maximal codewords a mandatory codeword?

Question 1.3. For codes on five neurons, which have local obstructions? Which are convex?