Neural codes are lists of subsets of neurons that fire together. Of particular interest are neurons called place cells, which fire when an animal is in specific, usually convex regions in space. A fundamental question, therefore, is to determine which neural codes arise from the regions of some collection of open convex sets or closed convex sets in Euclidean space. This work focuses on how these two classes of codes — open convex and closed convex codes — are related. As a starting point, open convex codes have a desirable monotonicity property, but here we show that closed convex codes do not possess the same property. We additionally show that, even for 3-sparse codes, closed convexity is not equivalent to avoiding local obstructions to convexity. Finally, we disprove a conjecture of Goldrup and Phillips, and then present an example of a code that is neither open convex nor closed convex.

Keywords  Neural code · Place cell · Convex · Simplicial complex

1 Introduction

Place cells are neurons that fire (are active) when an animal is in specific locations [1]. The resulting subsets of neurons that fire together, called a neural code, can be used by the brain to form a mental map of an animal’s environment. Place cells were discovered by John O’Keefe in 1971, earning him a joint Nobel Prize in Physiology or Medicine in 2014.

The specific location where a place cell fires is called its place field, and this set is typically convex. Thus, neural codes arising from place cells describe the regions cut out by intersecting convex sets. This motivates the following question: Which neural codes arise from open convex sets in some Euclidean space? (Each set is required to be open to account for the fact that place fields are full dimensional.) Many investigations into this question have been made in recent years (for instance, [2] [3] [4] [5] [6] [7] [8] [9] [10]). A distinct, but closely related topic is that of intersection patterns of convex sets (see [11] for an overview).

In this work, we consider the above question, and also, following [2] [6], the analogous question for closed convex sets. Additionally, we ask how these two classes of codes — open convex and closed...
convex codes – are related. Which codes are open convex but not closed convex (or vice-versa)? Which codes are neither open convex nor closed convex?

One starting point of our work is a recent “monotonicity” result of Cruz et al. [2]: If two codes \( \mathcal{C} \) and \( \mathcal{C}' \), with \( \mathcal{C} \subset \mathcal{C}' \), generate the same simplicial complex, and \( \mathcal{C} \) is open convex, then so is \( \mathcal{C}' \) (see Proposition 2.10). Hence, as open convexity is “inherited” from \( \mathcal{C} \) to \( \mathcal{C}' \), this result greatly simplifies the analysis of open convex codes. However, Cruz et al. did not know whether the analogous result holds for closed convexity [2], and here we show that, somewhat surprisingly, it does not (Theorem 3.2).

Next, we use the same counterexample code to resolve the closed-convex version of a question posed in [12] (Theorem 3.7). This question concerns \( k \)-sparse codes, those where at most \( k \) neurons fire simultaneously. We also disprove a conjecture of Goldrup and Phillipson [6] concerning the relationship between open convex and closed convex codes (Theorem 3.9). Finally, we give the first example of code on 8 neurons that has no “local obstructions” to (open or closed) convexity, but in fact is neither open convex nor closed convex (Theorem 3.10).

The outline of our work is as follows. Section 2 provides relevant definitions and prior results. In Section 3, we prove our main results, and then we end with a Discussion in Section 4.

### 2 Background

This section introduces definitions and notation related to neural codes.

#### 2.1 Neural codes and convexity

In what follows, we use the notation \([n] := \{1, 2, ..., n\}\).

**Definition 2.1.** A neural code on \( n \) neurons is a set \( \mathcal{C} \subset 2^{[n]} \). Each \( \sigma \in \mathcal{C} \) is a codeword, and \( \sigma \) is a maximal codeword of \( \mathcal{C} \) if it is a maximal element of \( \mathcal{C} \) with respect to inclusion.

For example, the codeword \( \sigma = \{1, 3, 4\} \) indicates that neurons 1, 3, and 4 are active, while all other neurons are silent. For brevity, we will write codewords without brackets or commas; for instance, \( \sigma = 134 \). Also, when we list the codewords of a code, all maximal codewords will be in boldface.

**Example 2.2.** The following is a neural code on 6 neurons, with 12 codewords:

\[
\mathcal{C} = \{\emptyset, 1, 2, 12, 13, 14, 23, 24, 123, 124, 135, 236\}.
\]

The focus of this work is open convex and closed convex codes, defined below. Recall that a set \( V \subset \mathbb{R}^d \) is convex if the line segment joining any two points in \( V \) is contained entirely within \( V \). Also, given subsets \( U_1, U_2, \ldots, U_n \) of some \( \mathbb{R}^d \) and a nonempty \( \sigma \subset [n] \), we use the notation \( U_\sigma := \cap_{i \in \sigma} U_i \).

**Definition 2.3.** Let \( \mathcal{U} = \{U_1, U_2, \ldots, U_n\} \) be a family of sets in a stimulus space \( X \subset \mathbb{R}^d \). Then \( \text{code}(\mathcal{U}, X) \) is the code on \( n \) neurons given by:

\[
\sigma \in \text{code}(\mathcal{U}, X) \iff U_\sigma \setminus \bigcup_{j \notin \sigma} U_j \neq \emptyset,
\]

where \( U_\emptyset := X \). A code \( \mathcal{C} \) on \( n \) neurons is realized by a family of sets \( \mathcal{U} = \{U_1, U_2, \ldots, U_n\} \) in a stimulus space \( X \subset \mathbb{R}^d \) if \( \mathcal{C} = \text{code}(\mathcal{U}, X) \).

**Definition 2.4.** A code \( \mathcal{C} \) on \( n \) neurons is open convex (respectively, closed convex) if there exists a stimulus space \( X \subset \mathbb{R}^d \) (for some \( d \)) and a family of open (respectively, closed) convex sets \( \mathcal{U} = \{U_1, U_2, \ldots, U_n\} \) in \( X \) such that \( \mathcal{C} = \text{code}(\mathcal{U}, X) \).

**Remark 2.5.** For the codes in this work, we always take the stimulus space \( X \) to be \( \mathbb{R}^d \).
Figure 1: Open-convex realization of the code in Example 2.2.

Example 2.6 (Example 2.2 continued). Consider again the code $C$ in (1). First, $C$ is open convex: an open-convex realization is shown in Figure 1 (more precisely, each set $U_i$ is the interior of the union of all closures of regions labeled by some codeword containing $i$). Also, $C$ is closed convex. Indeed, by replacing each $U_i$ in Figure 1 by its closure, we obtain a closed-convex realization of $C$.

Definition 2.7. A code $C$ is $k$-sparse if every codeword $\sigma \in C$ has size at most $k$.

Definition 2.8. A code $C$ is max-intersection complete if all intersections of its maximal codewords are in $C$. Otherwise, $C$ is max-intersection incomplete.

If a code is max-intersection complete, then it is both open convex and closed convex [2]. The converse, however, is not true. For instance, the code $C$ in (1) is open convex and closed convex (see Example 2.6), but not max-intersection complete ($135 \cap 236 = 3$ is not in $C$).

2.2 Simplicial complexes and mandatory codewords

An (abstract) simplicial complex on $[n]$ is a subset of $2^{[n]}$ that is closed under taking subsets.

Definition 2.9. For a neural code $C$ on $n$ neurons, the simplicial complex of $C$ is the smallest simplicial complex containing $C$:

$$\Delta(C) := \{\sigma \subset [n] : \exists \alpha \in C, \sigma \subset \alpha\}.$$

The following result, due to Cruz et al. [2], states that for codes having the same simplicial complex, open-convexity is a monotone property with respect to inclusion:

Proposition 2.10 (Monotonicity property for open convex codes [2]). Let $C$ and $C'$ be codes with $C \subset C'$ and $\Delta(C) = \Delta(C')$. If $C$ is open convex, then $C'$ is also open convex.

In Proposition 2.10, can “open” be replaced by “closed”? Below we answer this question in the negative (Theorem 3.2).

Definition 2.11. Let $\Delta$ be a simplicial complex on $[n]$ and let $\sigma \in \Delta$. Then the link of $\sigma$ in $\Delta$ is:

$$\text{Lk}_\sigma(\Delta) := \{\tau \subset [n] : \exists \sigma \cup \tau \in \Delta\}.$$

Recall that a contractible set is homotopy-equivalent to a single point.

Definition 2.12. Let $\Delta$ be a simplicial complex. A nonempty word $\sigma \in \Delta(C)$ is a mandatory codeword of $\Delta$ if (the geometric realization of) $\text{Lk}_\sigma(\Delta)$ is non-contractible. Otherwise, $\sigma$ is non-mandatory.

The following definition, pertaining to codes without certain “local obstructions” to convexity, is equivalent to the original definition [4].

Definition 2.13. A code $C$ is locally good if it contains every mandatory codeword of $\Delta(C)$.

If a code is open convex or closed convex, then it is locally good [2, 5].
3 Results

Our main results are as follows. First, closed convex codes do not possess the same monotonicity property that open convex codes have (Theorem 3.2). Next, even for 3-sparse codes, being locally good is not equivalent to closed convexity (Theorem 3.7). We also disprove a conjecture on the relationship between open convexity and closed convexity (Theorem 3.9). Finally, we give an example of code on 8 neurons that is locally good, but neither open convex nor closed convex (Theorem 3.10), and then conjecture that there are no such codes on fewer neurons.

3.1 Closed convexity is non-monotone

Recall that open convex codes have a monontonicity property (Proposition 2.10). It is natural to ask whether the same is true for closed convexity (indeed, Cruz et al. did not know the answer [2 §3]):

Question 3.1. Let C and C' be codes with C ⊂ C' and Δ(C) = Δ(C'). If C is closed convex, does it follow that C' is also closed convex?

Perhaps surprisingly, we answer Question 3.1 in the negative.

Theorem 3.2 (Closed convexity is non-monotone). Consider the neural codes C = {∅, 4, 5, 12, 23, 45, 123, 124, 235}, and C' = C ∪ {14, 35}. Then Δ(C) = Δ(C'), and C is closed convex, but C' is not closed convex.

Proof. First, checking Δ(C) = Δ(C') is straightforward. Next, we claim that C is closed convex. To see this, relabel the neurons 1, 2, 3, 4, 5 by, respectively, 4, 3, 5, 1, 2. The resulting code is the one Goldrup and Phillipson call C3, and it is closed convex [6 §4.2] (the closed-convex realization is shown in [6 Appendix B]).

We prove that C' is not closed convex by following closely the proof of [2 Lemma 2.9]. Assume for contradiction that C' has a closed convex realization U = {U_i}^5_i=1 in some R^d. As U_{14} ≠ ∅ and U_35 ≠ ∅, but U_{14} ∩ U_35 = ∅, we can pick distinct points x_{14} ∈ U_{14} and x_{35} ∈ U_35. The line segment L_1 := [x_{14}, x_{35}] is compact, and U_{123} is closed and nonempty. So, there exists a closest point on U_{123} to L_1, that is, some x_{123} ∈ U_{123} such that d(x_{123}, L_1) ≤ d(y_{123}, L_1) for all y_{123} ∈ U_{123}.

Next, let L_2 := [x_{14}, x_{123}]. Both x_{14} and x_{123} lie in the convex set U_1, so L_2 ⊂ U_1. Also, U_1 ⊂ U_2 ∪ U_4, as whenever the neuron 1 appears in the code it is always accompanied by either a 2 or a 4 (or both). Thus, L_2 ⊂ U_2 ∪ U_4, and so the (connected and closed) set L_2 is covered by the sets L_2 ∩ U_2 and L_2 ∩ U_4, which are closed and nonempty. Thus, L_2 ∩ U_2 ∩ U_4 is nonempty (and, by above, contained in U_{124}), and so we can now pick a point x_{124} ∈ (L_2 ∩ U_2 ∩ U_4) ⊂ U_{124}.

Similarly, let L_3 := [x_{35}, x_{123}]. Our code C' is unchanged by the permutation on the neurons that swaps neurons 1 and 2, and swaps 4 and 5. So, by this symmetry, and the argument made above for L_2, we conclude that there exists a point x_{235} ∈ (L_3 ∩ U_2 ∩ U_5) ⊂ U_{235}.

Let K := [x_{124}, x_{235}]. We mimic the above argument for L_2, as follows. Both x_{124} and x_{235} are in the convex set U_2, so K ⊂ U_2. Also, U_2 ⊂ U_1 ∪ U_3, as 2 always appears in C' with 1 or 3. Thus, K ⊂ U_1 ∪ U_3, and so K is covered by the closed, nonempty sets K ∩ U_1 and K ∩ U_3. Hence, K ∩ U_1 ∩ U_3 is nonempty (and, we saw, contained in U_{123}). So, there exists y_{123} ∈ (K ∩ U_1 ∩ U_3) ⊂ U_{123}.

Thus, y_{123} ∈ U_{123} is in the interior of the triangle Δ(x_{123}, x_{14}, x_{35}), and so d(y_{123}, L_1) < d(x_{123}, L_1) (see Figure 2). This contradicts the fact that x_{123} is a closest point to L_1 in U_{123}.

Remark 3.3. Theorem 3.2 answered Question 3.1 in the negative, by way of codes C and C' on 5 neurons. We do not know whether such codes exist on 4 or fewer neurons.

Remark 3.4. As noted in the proof of Theorem 3.2 we show that the code C' is not closed convex by closely following the proof of [2 Lemma 2.9]. The authors of [6] also closely followed the
same proof to show that three specific codes are not closed convex. In the future, we would like a general result that gives sufficient conditions precluding closed-convexity, and which proves, as special cases, that the code \( C' \) and the relevant codes in \([2, 6]\) are not closed convex.

### 3.2 Convexity and non-convexity of 3-sparse codes

As noted earlier, if a neural code is open convex or closed convex, then it is locally good \([2, 5]\). The converse, however, is false for codes that are 4-sparse and higher; see \([9]\) for open convex codes, and see \([13, \S 9]\) for both open convex and closed convex codes. Nonetheless, the converse is true for codes that are 2-sparse. Specifically, for 2-sparse codes, the following are equivalent: open convexity, closed convexity, and being locally good \([14]\).

The 3-sparse case therefore remains unresolved, which led the authors of \([12]\) to ask the following question (which we pose as a conjecture):

**Conjecture 3.5.** If \( C \) is a 3-sparse code that is locally good, then \( C \) is open convex.

Conjecture 3.5 holds for codes on up to 5 neurons \([4, 6]\), but is open for 6 or more neurons.

Next, we consider the closed-convex version of Conjecture 3.5.

**Question 3.6.** If \( C \) is a 3-sparse code that is locally good, does it follow that \( C \) is closed convex?

The answer to Question 3.6 is negative: 3 counterexamples, all codes on 5 neurons, can be found in \([6]\) Theorem 4.1. An additional counterexample, a code on 6 neurons, was given in \([2, \S 2.3]\). Yet another counterexample is the code \( C' \) on 5 neurons from the above result, Theorem 3.2.

**Theorem 3.7.** The neural code \( C' = \{\emptyset, 4, 5, 12, 14, 23, 35, 45, 123, 124, 235\} \) is 3-sparse, open convex (thus locally good), and not closed convex.

**Proof.** We already saw that \( C' \) is not closed convex (Theorem 3.2). Additionally, this code can be obtained by adding the codewords 14 and 25 to the open convex code labeled \( C' \) in \([6]\) and then...
permuting the labels of the neurons. So, by Proposition 2.10, \( C' \) is open convex. Alternatively, an open-convex realization of \( C' \) is displayed in Figure 3.

### 3.3 A counterexample to a conjecture of Goldrup and Phillipson

Recently, Goldrup and Phillipson posed the following conjecture as an attempt to distinguish codes that are open convex but not closed convex [6, Conjecture 4.3].

**Conjecture 3.8.** Let \( C \) be a max-intersection incomplete open convex code, where \( \Delta(C) \) has at least two non-mandatory codewords not contained in \( C \). Suppose \( C \) has at least three maximal codewords \( M_1, M_2, M_3 \), and there is \( \sigma \subset M_1 \) with \( \sigma \in C \) such that \( \sigma \cap M_2 \notin C \). Then \( C \) is not closed convex.

We disprove Conjecture 3.8 through a counterexample, namely, the code from Example 2.2.

**Theorem 3.9.** The neural code \( C = \{\emptyset, 1, 2, 12, 13, 14, 23, 24, 123, 124, 135, 236\} \) fulfills the hypotheses of Conjecture 3.8 and is closed convex.

**Proof.** We begin by checking that \( C \) satisfies the hypotheses of Conjecture 3.1. First, we saw that \( C \) is open convex (Example 2.2). Next, \( C \) is max-intersection incomplete, as the intersection of maximal codewords \( 135 \cap 236 = 3 \) is not in \( C \).

We must also show that \( \Delta(C) \) has at least two non-mandatory codewords that are not in \( C \). It is straightforward to check that the links \( \text{Lk}_{\{3\}}(\Delta(C)) \) and \( \text{Lk}_{\{4\}}(\Delta(C)) \) are the following contractible simplicial complexes (respectively):

\[
\begin{array}{cccc}
5 & 1 & 2 & 6 \\
1 & 2 & \\
\end{array}
\]

Therefore, 3 and 4 are non-mandatory codewords. Also, neither 3 nor 4 is in \( C \).

Next, we must show that \( C \) has three maximal codewords \( M_1, M_2, M_3 \) and a codeword \( \sigma \in C \) such that \( \sigma \subset M_1 \) and \( \sigma \cap M_2 \notin C \). Let \( M_1 = 123, M_2 = 236, M_3 = 124 \), and let \( \sigma = 13 \in C \). Then \( 13 = \sigma \subset M_1 = 123 \). Also, \( 13 \cap 236 = \sigma \cap M_2 = 3 \notin C \).

Finally, we already saw (in Example 2.2) that \( C \) is closed convex.

### 3.4 A locally good code that is neither open convex nor closed convex

Here, we present a code on 8 neurons that, despite being locally good, is neither open convex nor closed convex (Theorem 3.10). As seen in the proof, this code is built by combining two locally good codes, one that is not closed convex and the other not open convex (the one from Theorem 3.7).

**Theorem 3.10.** The following code is locally good, but neither open convex nor closed convex:

\[
C = \{\emptyset, 4, 5, 12, 14, 23, 35, 45, 123, 124, 235\} \cup \{7, 17, 47, 48, 67, 147, 148, 167, 4678\}.
\]

**Proof.** By [4, Theorem 1.3 and Lemma 1.4], being locally good is equivalent to the following: If \( \emptyset \neq \sigma \notin C \) and \( \sigma \) is the intersection of two or more maximal codewords of \( C \), then \( \text{Lk}_\sigma(\Delta(C)) \) is contractible. It is straightforward to check that only 1, 2, and 4 are nonempty intersections of maximal codewords and not in \( C \). Their links in \( \Delta(C) \), respectively, are shown below:

\[
\begin{array}{cccc}
3 & 2 & 4 & 7 & 6 \\
4 & 1 & 3 & 5 & \\
1 & 2 & 5 & \\
\end{array}
\]
Each link is contractible, and so $C$ is locally good.

Next, we show that $C$ is neither open convex nor closed convex. Let $\mathcal{U} = \{U_1, U_2, \ldots, U_8\}$ be a realization of $C$ in some $\mathbb{R}^d$. We must show that some $U_i$ is not open, and some $U_j$ is not closed.

Note that $\{U_1, U_2, U_3, U_4, U_5\}$ is a realization of the restriction of $C$ to the neurons 1,2,3,4,5, which is the code $C'$ from Theorem 3.7. We saw in that theorem that $C'$ is not closed convex, and so at least one of $U_1, U_2, U_3, U_4, U_5$ is not closed.

Similarly, $\{U_1, U_4, U_6, U_7, U_8\}$ realizes the restriction of $C$ to 1,4,6,7,8. This restricted code is – after relabeling neurons 6, 7, and 8, by (respectively) 2, 3, and 5 – the code from $[9$, Theorem 3.1]. This code is not open convex $[9]$, and so at least one of $U_1, U_4, U_6, U_7, U_8$ is not closed.

The code in Theorem 3.10 is on 8 neurons. We want to know whether there is a code with the same properties but on fewer neurons. (For instance, to our knowledge, the codes that Jeffs and Novik show are locally good – in fact, “locally perfect” – but neither open convex nor closed convex, require at least 8 neurons $[13$, §9].)

**Conjecture 3.11.** Every locally good code on at most 7 neurons is open convex or closed convex.

For codes on up to 4 neurons, Conjecture 3.11 is true, as such locally good codes are open convex $[4]$.

4 Discussion

Open convex and closed convex codes share several important properties. For instance, both classes of codes are locally good (and, in fact, “locally perfect” $[14]$). Also, max-intersection complete codes are both open convex and closed convex $[2]$. However, while open convex codes possess a monotonicity property, which greatly simplifies the analysis of all codes with a given simplicial complex, here we showed that this property fails for closed convex codes (Theorem 3.2).

Additional results in our work also address fundamental questions pertaining to open convex and closed convex codes. For instance, even for 3-sparse codes, locally good and closed convex are not equivalent (Theorem 3.7). Also, there is a locally good code on 8 neurons that is neither open convex nor closed convex (Theorem 3.10). These results lead to two open questions. First, for 3-sparse codes, are locally good and open convexity equivalent (Conjecture 3.8)? Second, is there a locally good code on 7 neurons that is neither open convex nor closed convex (Conjecture 3.11)?

Answers to these questions, together with the results we already have on convex codes, will clarify the theories of open convex and closed convex codes. In turn, this knowledge contributes to answering the questions from neuroscience that originally motivated our work. Specifically, we will better understand what types of neural codes allow the brain to represent structured environments.

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