Neural Codes and Neural Rings: Topology and Algebraic Geometry

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Geometry of Neuroscience

References for this lecture:

- Curto, Carina; Itskov, Vladimir; Veliz-Cuba, Alan; Youngs, Nora, *The neural ring: an algebraic tool for analyzing the intrinsic structure of neural codes*, Bull. Math. Biol. 75 (2013), no. 9, 1571–1611.
- Nora Youngs, *The Neural Ring: using Algebraic Geometry to analyze Neural Codes*, arXiv:1409.2544
- Yuri Manin, *Neural codes and homotopy types: mathematical models of place field recognition*, Mosc. Math. J. 15 (2015), no. 4, 741–748
- Carina Curto, Nora Youngs, *Neural ring homomorphisms and maps between neural codes*, arXiv:1511.00255
- Elizabeth Gross, Nida Kazi Obatake, Nora Youngs, *Neural ideals and stimulus space visualization*, arXiv:1607.00697
- Yuri Manin, *Error-correcting codes and neural networks*, preprint, 2016

Basic setting

- set of neurons $[n] = \{1, \dots, n\}$
- *neural code* $\mathcal{C} \subset \mathbb{F}_2^n$ with $\mathbb{F}_2 = \{0, 1\}$
- *codewords* (or "codes") $\mathcal{C} \ni c = (c_1, \dots, c_n)$ describe activation state of neurons
- support $\mathrm{supp}(c) = \{i \in [n] \, : \, c_i = 1\}$

  $$\mathrm{supp}(\mathcal{C}) = \cup_{c \in \mathcal{C}} \mathrm{supp}(c) \subset 2^{[n]}$$

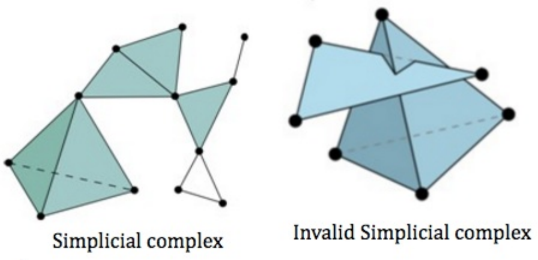
  $2^{[n]}$ = set of all subsets of $[n]$
- neglect information about timing and rate of neural activity: focus on combinatorial neural code

Simplicial complex of the code

- $\Delta \subset 2^{[n]}$ simplicial complex if when $\sigma \in \Delta$ and $\tau \subset \sigma$ then also $\tau \in \Delta$
- neural code $\mathcal{C}$ simplicial if $\mathrm{supp}(\mathcal{C})$ simplicial complex
- if not, define simplicial complex of the neural code $\mathcal{C}$ as

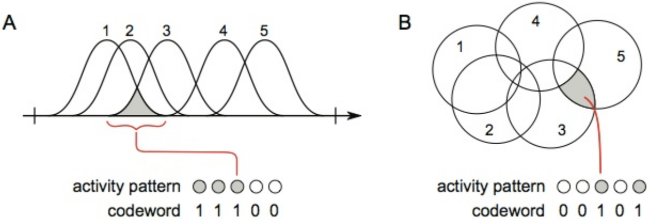
$$\Delta(\mathcal{C}) = \{\sigma \subset [n] \,:\, \sigma \subseteq \mathrm{supp}(c), \quad \text{for some } c \in \mathcal{C}\}$$

smallest simplicial complex containing $\mathrm{supp}(\mathcal{C})$



Receptive fields

- patterns of neuron activity
- maps $f_i : X \to \mathbb{R}_+$ from space X of stimuli: average firing rate of i-th neuron in $[n]$ in response to stimulus $x \in X$
- open sets $U_i = \{x \in X \ : \ f(x) > 0\}$ (receptive fields) usually assume *convex*
- *place field* of a neuron $i \in [n]$: preferred convex region of the stimulus space where it has a high firing rate (orientiation-selective neurons: tuning curves, preference for particular angle, intervals on a circle)
- code words from receptive fields overlap



Convex Receptive Field Code

- stimulis space X; set of neurons $[n] = \{1, \dots, n\}$; receptive fields $f_i : X \to \mathbb{R}_+$, with convex sets $U_i = \{f_i > 0\}$
- collection of (convex) open sets $\mathcal{U} = \{U_1, \dots, U_n\}$
- *receptive field code*

$$\mathcal{C}(\mathcal{U}) = \{c \in \mathbb{F}_2^n \,:\, (\cap_{i \in \mathrm{supp}(c)} U_i) \smallsetminus (\cup_{j \notin \mathrm{supp}(c)} U_j) \neq \emptyset\}$$

  all binary codewords corresponding to stimuli in X
- with convention: intersection over $\emptyset$ is X and union over $\emptyset$ is $\emptyset$
- if $\cup_{i \in [n]} U_i \subsetneq X$: there are points of stimulus space not covered by receptive field (word $c = (0, 0, \dots, 0)$ in $\mathcal{C}$); if $\cap_{i \in [n]} U_i \neq \emptyset$ word $c = (1, 1, \dots, 1) \in \mathcal{C}$ points where all neurons activated

Main Question

- if know the code $\mathcal{C} = \mathcal{C}(\mathcal{U})$ without knowing X and $\mathcal{U}$ what can you learn about the geometry of X? (to what extent X is reconstructible from $\mathcal{C}(\mathcal{U})$)

- Step One: given a code $\mathcal{C} \subset \mathbb{F}_2^n$ with $m = \#\mathcal{C}$ (number of code words) there exists an $X \subseteq \mathbb{R}^d$ and a collection of (not necessarily convex) open sets $\mathcal{U} = \{U_1, \ldots, U_n\}$ with $U_i \subset X$ such that $\mathcal{C} = \mathcal{C}(\mathcal{U})$
    - list code words $c_i = (c_{i,1}, \ldots, c_{i,n}) \in \mathcal{C}$, $i = 1, \ldots, m$
    - for each code word c_i choose a point $x_{c_i} \in \mathbb{R}^d$ and an open neighborhood $\mathcal{N}_i \ni x_{c_i}$ such that $\mathcal{N}_i \cap \mathcal{N}_j = \emptyset$ for $i \neq j$
    - take $\mathcal{U} = \{U_1, \ldots, U_n\}$ and $X = \cup_{j=1}^m \mathcal{N}_j$ with

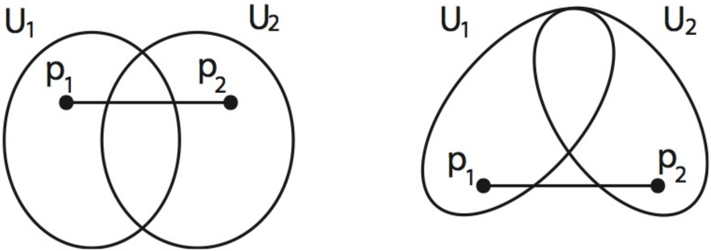
$$U_j = \bigcup_{c_k \,:\, j \in \mathrm{supp}(c_k)} \mathcal{N}_k$$

    - if zero code word in $\mathcal{C}$ then $\mathcal{N}_0 = X \smallsetminus \cup_j U_j$ is set of outside points not captured by code
    - by construction $\mathcal{C} = \mathcal{C}(\mathcal{U})$

Caveat

- can always find a $(X, \mathcal{U})$ given $\mathcal{C}$ so that $\mathcal{C} = \mathcal{C}(\mathcal{U})$ but not always with U_i *convex*

- Example: $\mathcal{C} = \mathbb{F}_2^3 \smallsetminus \{(1,1,1),(0,0,1)\}$ cannot be realized by a $\mathcal{U} = \{U_1, U_2, U_3\}$ with U_i convex
  - suppose possible: $U_i \subset \mathbb{R}^d$ convex and $\mathcal{C} = \mathcal{C}(\mathcal{U})$
  - know that $U_1 \cap U_2 \neq \emptyset$ because $(1,1,0) \in \mathcal{C}$
  - know that $(U_1 \cap U_3) \smallsetminus U_2 \neq \emptyset$ because $(1,0,1) \in \mathcal{C}$
  - know that $(U_2 \cap U_3) \smallsetminus U_1 \neq \emptyset$ because $(0,1,1) \in \mathcal{C}$
  - take points $p_1 \in (U_1 \cap U_3) \smallsetminus U_2$ and $p_2 \in (U_2 \cap U_3) \smallsetminus U_1$ both in U_3 convex, so segment $\ell = tp_1 + (1-t)p_2$, $t \in [0,1]$ in U_3
  - if ℓ passes through $U_1 \cap U_2$ then $U_1 \cap U_2 \cap U_3 \neq \emptyset$ but $(1,1,1) \notin \mathcal{C}$ (contradiction)
  - or ℓ does not intersect $U_1 \cap U_2$ but then ℓ intersects the complement of $U_1 \cup U_2$ (see fig) this would imply $(0,0,1) \in \mathcal{C}$ (contradiction)



the two cases of the previous example

Constraints on the Stimulus Space

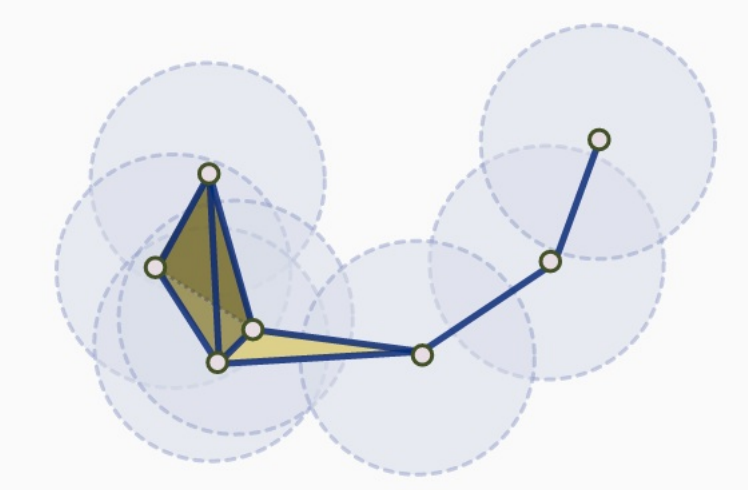
• Codes $\mathcal{C}$ that can be realized as $\mathcal{C} = \mathcal{C}(\mathcal{U})$ with U_i convex put strong constraints on the geometry of the stimulus space X

two types of constraints

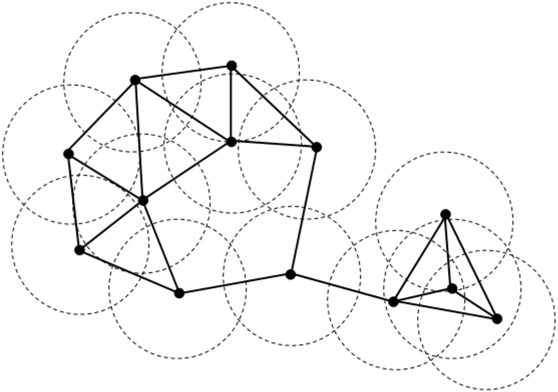
1. constraints from the simplicial complex $\Delta(\mathcal{C})$
2. other constraints from $\mathcal{C}$ not captured by $\Delta(\mathcal{C})$

Simplicial nerve of an open covering

- $\mathcal{U} = \{U_1, \ldots, U_n\}$ convex open sets in $\mathbb{R}^d$ with $d < n$
- *nerve* $\mathcal{N}(\mathcal{U})$ simplicial complex: $\sigma = \{i_1, \ldots, i_k\} \in 2^{[n]}$ is in $\mathcal{N}(\mathcal{U})$ iff $U_{i_1} \cap \cdots \cap U_{i_k} \neq \emptyset$
- $\mathcal{N}(\mathcal{U}) = \Delta(\mathcal{C}(\mathcal{U}))$



convex open sets U_i and simplicial nerve $\mathcal{N}(\mathcal{U})$

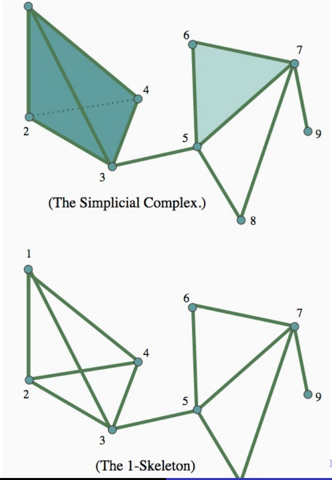


another example of convex open sets U_i and simplicial nerve $\mathcal{N}(\mathcal{U})$

The complex $\mathcal{N}(\mathcal{U})$ is also known as the Čech complex of the collection $\mathcal{U} = \{U_1, \ldots, U_n\}$ of convex open sets

- Topological fact (Helly's theorem): convex $U_1, \ldots, U_k \subset \mathbb{R}^d$ with $d < k$: if intersection of every $d+1$ of the U_i nonempty then also $\cap_{i=1}^k U_i \neq \emptyset$

Consequence: the nerve $\mathcal{N}(\mathcal{U})$ completely determined by its d-skeleton (largest n-complex with that given d-skeleton)



Nerve Theorem

- Allen Hatcher *Algebraic topology*, Cambridge University Press, 2002 (Corollary 4G.3)

- Homotopy types: The homotopy type of $X(\mathcal{U}) = \cup_{i=1}^n U_i$ is the same as the homotopy type of the nerve $\mathcal{N}(\mathcal{U})$

- Consequence: $X(\mathcal{U})$ and $\mathcal{N}(\mathcal{U})$ have the same homology and homotopy groups (but not necessarily the same dimension)

- Note: the space $X(\mathcal{U})$ may not capture all of the stimulus space X if the U_i are not an open covering of X, that is, if $X \smallsetminus X(\mathcal{U}) \neq \emptyset$

Homology groups

• very useful topological invariants, computationally tractable

• simplicial complex $\mathcal{N} \subset 2^{[n]}$; groups of k-chains $C_k = C_k(\mathcal{N})$ abelian group spanned by k-dimensional simplices of $\mathcal{N}$

• boundary maps on simplicial complexes $\partial_k : C_k \to C_{k-1}$

$$\partial_{k-1} \circ \partial_k = 0$$

usually stated as $\partial^2 = 0$

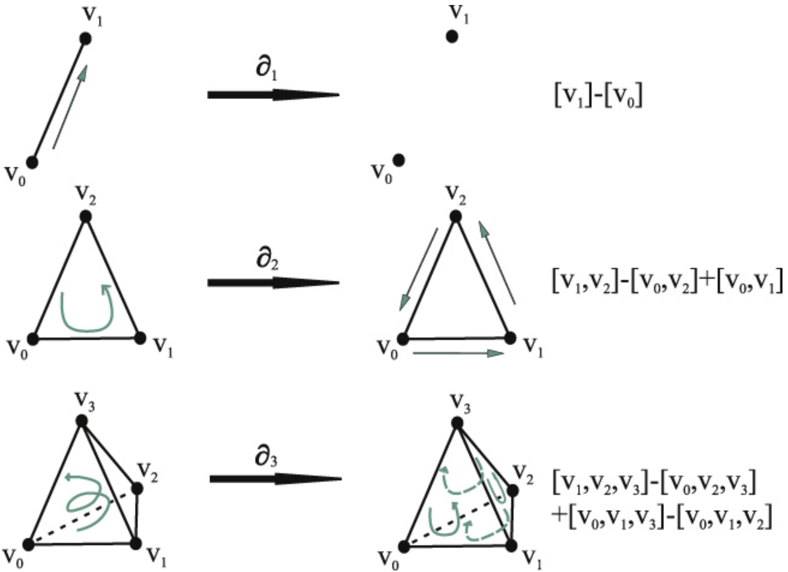
• cycles $Z_k = \mathrm{Ker}(\partial_k) \subset C_k$ and boundaries $B_{k+1} = \mathrm{Range}(\partial_{k+1}) \subset C_k$

• because $\partial^2 = 0$ inclusion $B_{k+1} \subset Z_k$

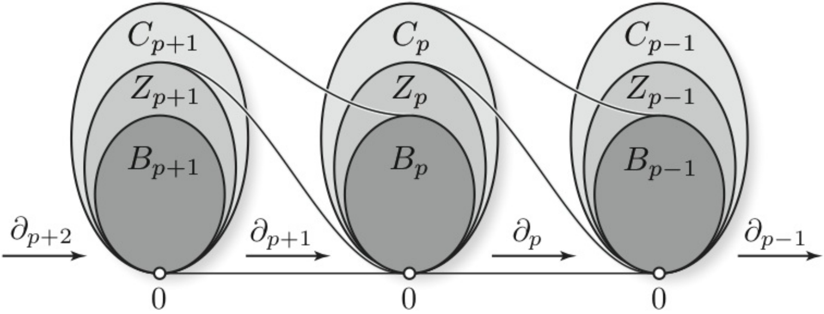
• homology groups: quotient groups

$$H_k(\mathcal{N}, \mathbb{Z}) = \frac{\mathrm{Ker}(\partial_k)}{\mathrm{Range}(\partial_{k+1})} = Z_k / B_{k+1}$$

Boundary maps



Chain complexes and Homology



$$H_p(X,\mathbb{Z}) = \mathrm{Ker}(\partial_p : C_p \to C_{p-1})/\mathrm{Im}(\partial_{p+1} : C_{p+1} \to C_p)$$

What else does $\mathcal{C}$ tells us about X?

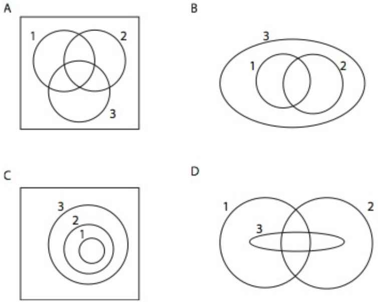


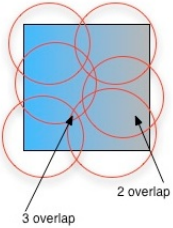
Figure 3: Four arrangements of three convex receptive fields, $\mathcal{U} = \{U_1, U_2, U_3\}$, each having $\Delta(\mathcal{C}(\mathcal{U})) = 2^{[3]}$. Square boxes denote the stimulus space X in cases where $U_1 \cup U_2 \cup U_3 \subsetneq X$. (A) $\mathcal{C}(\mathcal{U}) = 2^{[3]}$, including the all-zeros codeword 000. (B) $\mathcal{C}(\mathcal{U}) = \{111, 101, 011, 001\}$, with $X = U_3$. (C) $\mathcal{C}(\mathcal{U}) = \{111, 011, 001, 000\}$. (D) $\mathcal{C}(\mathcal{U}) = \{111, 101, 011, 110, 100, 010\}$, and $X = U_1 \cup U_2$. The minimal embedding dimension for the codes in panels A and D is $d = 2$, while for panels B and C it is $d = 1$.

all have same $\Delta(\mathcal{C}) = 2^{[3]}$ because $(1, 1, 1)$ code word for all cases

Embedding dimension

• *minimal embedding dimension d*: minimal dimension for which code $\mathcal{C}$ can be realized as $\mathcal{C}(\mathcal{U})$ with open sets $U_i \subset \mathbb{R}^d$

• *topological dimension*: minimum d such that any open covering has a refinement such that no point is in more than $d+1$ open sets of the covering



• in previous examples $\Delta(\mathcal{C}) = 2^{[3]}$ same but different *embedding dimension*

Main information carried by the code $\mathcal{C} = \mathcal{C}(\mathcal{U})$:
nontrivial inclusions

• some inclusion relations between intersections and unions always trivially satisfied: example $U_1 \cap U_2 \subset U_2 \cup U_3$ because $U_1 \cap U_2 \subset U_2$

• other inclusion relations are *specific* of the structure of the collection $\mathcal{U}$ of open sets and not always automatically satisfied: this is the *information* encoded in $\mathcal{C}(\mathcal{U})$

• all relations of the form

$$\bigcap_{i \in \sigma} U_i \subseteq \bigcup_{j \in \tau} U_j$$

for $\sigma \cap \tau = \emptyset$, including all empty intersections relations

$$\bigcap_{i \in \sigma} U_i = \emptyset$$

Problem: how to algorithmically extract this information from $\mathcal{C}$ without having to construct $\mathcal{U}$?

- key method: Algebraic Geometry (ideals and varieties)
- Rings and ideals: R commutative ring with unit, $I \subset R$ ideal (additive subgroup; for $a \in I$ and for all $b \in R$ product $ab \in I$)
- set S generators of $I = \langle S \rangle$

$$I = \{r_1 a_1 + \cdots + r_n a_n \; : \; r_i \in R, \, a_i \in S, \, n \in \mathbb{N}\}$$

- *prime ideal*: $\wp \subsetneq R$ and if $ab \in \wp$ then $a \in \wp$ or $b \in \wp$
- *maximal ideal*: $\mathfrak{m} \subsetneq R$ and if I ideal $\mathfrak{m} \subset I \subset R$ then either $\mathfrak{m} = I$ or $I = R$ (geometrically maximal ideals correspond to points)
- *radical ideal*: $r^n \in I$ implies $r \in I$ for all n
- primary decomposition: $I = \wp_1 \cap \cdots \cap \wp_n$ with $\wp_i$ prime ideals

Affine Algebraic Varieties

• polynomial ring $R = K[x_1, \ldots, x_n]$ over a field K; $I \subset R$ ideal $\Rightarrow$ variety $V(I)$

$$V(I) = \{v \in K^n \,:\, f(v) = 0, \forall f \in I\}$$

• ideals $I \subseteq J \Rightarrow$ varieties $V(J) \subseteq V(I)$

• *spectrum* of a ring R: set of prime ideals

$$\mathrm{Spec}(R) = \{\wp \subset R \,:\, \wp \text{ prime ideal } \}$$

• modeling n neurons with binary states on/off, so $K = \mathbb{F}_2 = \{0, 1\}$ and $v = (v_1, \ldots, v_n) \in \mathbb{F}_2^n$ a possible state of the set of neurons

Neural Ring

- given a binary code $\mathcal{C} \subset \mathbb{F}_2^n$ (neural code)
- ideal $I = I_{\mathcal{C}} \subset \mathbb{F}_2[x_1, \ldots, x_n]$ of polynomials vanishing on codewords

$$I_{\mathcal{C}} = \{f \in \mathbb{F}_2[x_1, \ldots, x_n] \,:\, f(c) = 0, \forall c \in \mathcal{C}\}$$

- quotient ring (neural ring)

$$R_{\mathcal{C}} = \mathbb{F}_2[x_1, \ldots, x_n]/I_{\mathcal{C}}$$

• Note: working over $\mathbb{F}_2$ so $2 \equiv 0$, so in $R_{\mathcal{C}}$ all elements idempotent $y^2 = y$ (cross terms vanish): Boolean ring isomorphic to $\mathbb{F}_2^{\#\mathcal{C}}$, but useful to keep the explicit coordinate functions x_i that measure the activity of the i-th neuron

Neural Ring Spectrum

• maximal ideals in polynomial ring $\mathbb{F}_2[x_1, \ldots, x_n]$ correspond to points $v \in \mathbb{F}_2^n$, namely

$$\mathfrak{m}_v = \langle x_1 - v_1, \ldots, x_n - v_n \rangle$$

• in a Boolean ring prime ideal spectrum and maximal ideal spectrum coincide

• for the neural ring $R_{\mathcal{C}}$ spectrum

$$\mathrm{Spec}(R_{\mathcal{C}}) = \{\bar{\mathfrak{m}}_v \,:\, v \in \mathcal{C} \subset \mathbb{F}_2^n\}$$

where $\bar{\mathfrak{m}}_v$ image in quotient ring of maximal ideal $\mathfrak{m}_v$ in $\mathbb{F}_2[x_1, \ldots, x_n]$

• so spectrum of the neural ring recovers the code words of $\mathcal{C}$

Neural ideal

- in general difficult to provide explicit generators for the ideal $I_{\mathcal{C}}$ (problem for practical computational purposes)
- another closely related (more tractable) ideal: neural ideal $J_{\mathcal{C}}$
- given $v \in \mathbb{F}_2^n$ (a possible state of a system of n neurons) take function

$$\rho_v = \prod_{i=1}^{n} (1 - v_i - x_i) = \prod_{i \in \mathrm{supp}(v)} x_i \prod_{j \notin \mathrm{supp}(v)} (1 - x_j)$$

$\rho_v \in \mathbb{F}_2[x_1, \ldots, x_n]$

- binary code $\mathcal{C} \subset \mathbb{F}_2^n \Rightarrow$ ideal $J_{\mathcal{C}}$

$$J_{\mathcal{C}} = \langle \rho_v \; : \; v \notin \mathcal{C} \rangle$$

when $\mathcal{C} = \mathbb{F}_2^n$ have $J_{\mathcal{C}} = 0$ trivial ideal

- ideal of Boolean relations $\mathcal{B} = \mathcal{B}_n$

$$\mathcal{B} = \langle x_i(1 - x_i) \,:\, i \in [n] \rangle$$

- relation between ideals $I_{\mathcal{C}}$ and $J_{\mathcal{C}}$

$$I_{\mathcal{C}} = J_{\mathcal{C}} + \mathcal{B} = \langle \rho_v,\ x_i(1 - x_i) \,:\, v \notin \mathcal{C},\, i \in [n] \rangle$$

Neural Ring Relations

- Notation: given $\mathcal{U} = \{U_1, \ldots, U_n\}$ open sets and $\sigma \subset [n]$

$$U_\sigma := \cap_{i\in\sigma} U_i, \quad x_\sigma := \prod_{i\in\sigma} x_i, \quad (1-x_\tau) := \prod_{j\in\tau}(1-x_j)$$

- interpret coordinates x_i as functions on X:

$$x_i(p) = \begin{cases} 1 & p \in U_i \\ 0 & p \notin U_i \end{cases}$$

- inclusions and relations: $U_\sigma \subset U_i \cup U_j$, then $x_\sigma = 1$ implies either $x_i = 1$ or $x_j = 1$ so relation

$$x_\sigma (1-x_i)(1-x_j)$$

- all inclusion $U_\sigma \subseteq \cup_{i\in\tau} U_i$ correspond to relations $x_\sigma \prod_{i\in\tau}(1-x_i)$
- ideal $I_{\mathcal{C}(\mathcal{U})}$ generated by them (relations defining $R_{\mathcal{C}}$)

$$I_{\mathcal{C}(\mathcal{U})} = \langle x_\sigma \prod_{i\in\tau}(1-x_i) \,:\, U_\sigma \subseteq \cup_{i\in\tau} U_i \rangle$$

Canonical Form pseudomonomial relations

• subsets $\sigma, \tau \subset [n]$: if $\sigma \cap \tau \neq \emptyset$ then $x_\sigma(1 - x_\tau) \in \mathcal{B}$, if $\sigma \cap \tau = \emptyset$ then $x_\sigma(1 - x_\tau) \in J_\mathcal{C}$

• functions of the form $f(x) = x_\sigma(1 - x_\tau)$ with $\sigma \cap \tau = \emptyset$ *pseudomonomial*; ideal J generated by such: *pseudomonomial ideal*

• *minimal pseudomonomial*: $f \in J$ pseudomonomial, no other pseudomonomial g with $\deg(g) < \deg(f)$ and $f = gh$ for some $h \in \mathbb{F}_2[x_1, \dots, x_n]$

• *canonical form* of pseudomonomial ideal $J = \langle f_1, \dots, f_\ell \rangle$ with f_k all the minimal pseudomonomials in J

• ideal $J_\mathcal{C} = \langle \rho_v \, : \, v \notin \mathcal{C} \rangle$ is pseudomonomial (not $I_\mathcal{C}$ because of Boolean relations)

Canonical Form of Neural Ring $J_{\mathcal{C}}$: $CF(J_{\mathcal{C}})$

• given a binary code $\mathcal{C} \subset \mathbb{F}_2^n$ suppose realized as $\mathcal{C} = \mathcal{C}(\mathcal{U})$ with $\mathcal{U} = \{U_1, \dots, U_n\}$ in X (not necessarily convex)

• some $\sigma \subseteq [n]$ minimal for a property P if P satisfied by σ and not satisfied by any $\tau \subsetneq \sigma$

• canonical form $CF(J_{\mathcal{C}})$ of $J_{\mathcal{C}}$ three types of relations:

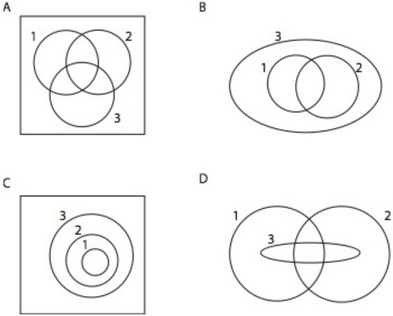
1. x_σ with σ minimal for $U_\sigma = \emptyset$
2. $x_\sigma(1 - x_\tau)$ with $\sigma \cap \tau =$, $U_\sigma \neq \emptyset$ $\cup_{i\in\tau} U_i \neq X$, and σ, τ minimal for $U_\sigma \subseteq \cup_{i\in\tau} U_i$
3. $(1 - x_\tau)$ with τ minimal for $X \subseteq \cup_{i\in\tau} U_i$

• minimal embedding dimension

$$d \geq \max_{\sigma \,:\, x_\sigma \in CF(J_{\mathcal{C}})} \#\sigma - 1$$

• there are efficient algorithms to compute $CF(J_{\mathcal{C}})$ given $\mathcal{C}$ (without passing through $\mathcal{U}$)

Example



A. $CF(J_\mathcal{C}) = \{0\}$. There are no relations here because $\mathcal{C} = 2^{[3]}$.

B. $CF(J_\mathcal{C}) = \{1 - x_3\}$. This Type 3 relation reflects the fact that $X = U_3$.

C. $CF(J_\mathcal{C}) = \{x_1(1 - x_2), x_2(1 - x_3), x_1(1 - x_3)\}$. These Type 2 relations correspond to $U_1 \subset U_2$, $U_2 \subset U_3$, and $U_1 \subset U_3$. Note that the first two of these receptive field relationships imply the third; correspondingly, the third canonical form relation satisfies: $x_1(1 - x_3) = (1 - x_3) \cdot [x_1(1 - x_2)] + x_1 \cdot [x_2(1 - x_3)]$.

D. $CF(J_\mathcal{C}) = \{(1 - x_1)(1 - x_2)\}$. This Type 3 relation reflects $X = U_1 \cup U_2$, and implies $U_3 \subset U_1 \cup U_2$.