A fixed point theorem for Boolean networks expressed in terms of forbidden subnetworks

Adrien Richard

University of Nice - France

CNRS

I3S Laboratory

Contents

An n-dimensional **Boolean network** is a function

$$f : \mathbb{B}^n \to \mathbb{B}^n \qquad (\mathbb{B} = \{0, 1\})$$

$$x = (x_1, \ldots, x_i, \ldots, x_n) \mapsto f(x) = (f_1(x), \ldots, \underset{\substack{\uparrow \\ \text{local transition function}}}{f_i(x)}, \ldots, f_n(x))$$

The **interaction graph** of f is the directed graph $G(f)$ with vertex set $\{1, \ldots, n\}$ and arcs defined by

$$j \to i \in G(f) \iff f_i \text{ depends on } x_j$$

Example : $f : \mathbb{B}^3 \to \mathbb{B}^3$ is defined by :

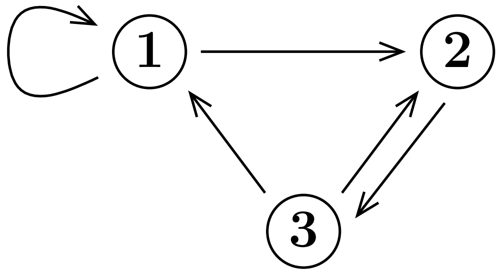
x	$f(x)$
000	100
001	000
010	101
011	001
100	100
101	110
110	101
111	111

$\Leftrightarrow$

$$\begin{aligned} f_1(x) &= x_1 \vee \overline{x_3} \\ f_2(x) &= x_1 \wedge x_3 \\ f_3(x) &= x_2 \end{aligned}$$

The interaction graph of f is :

$G(f)$

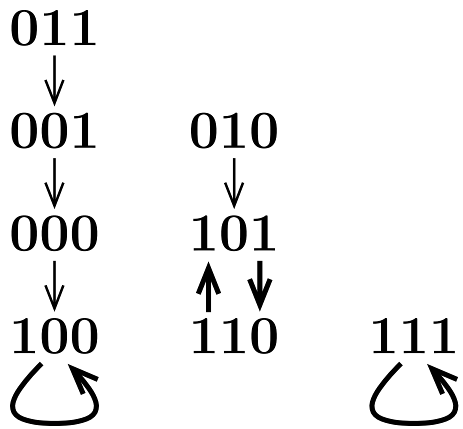


A network f with an **update schedule** (parallel, sequential, block-sequential, asynchronous...) defines a **discrete dynamical system**.

With the parallel update schedule : $x^{t+1} = f(x^t)$

$$
\begin{aligned}
f_1(x) &= x_1 \vee \overline{x_3} \\
f_2(x) &= x_1 \wedge x_3 \\
f_3(x) &= x_2
\end{aligned}
$$

Parallel dynamics



For all update schedules : **fixed points of f = stable states**.

Simple definitions, but complex behaviors : several attractors, long limit cycles, long transient phases...

Many applications : biology, sociology, computer science...

In particular, from the seminal works of Thomas and Kauffman (60's), Boolean networks are extensively used to model gene networks.

In this context :

- $G(f)$ is "known" but f is "unknown"
- fixed points of $f \simeq$ cell types

What can be said on fixed points of f according to $G(f)$?

Contents

THEOREM (Robert 1980)

If $G(f)$ has no cycle, then f has a unique fixed point.

More precisely, if $\boldsymbol{G}(\boldsymbol{f})$ has no cycle, then $\boldsymbol{f}$ has a unique fixed point $\boldsymbol{\xi}$, and *the system converges toward* $\boldsymbol{\xi}$ (for all update schedules).

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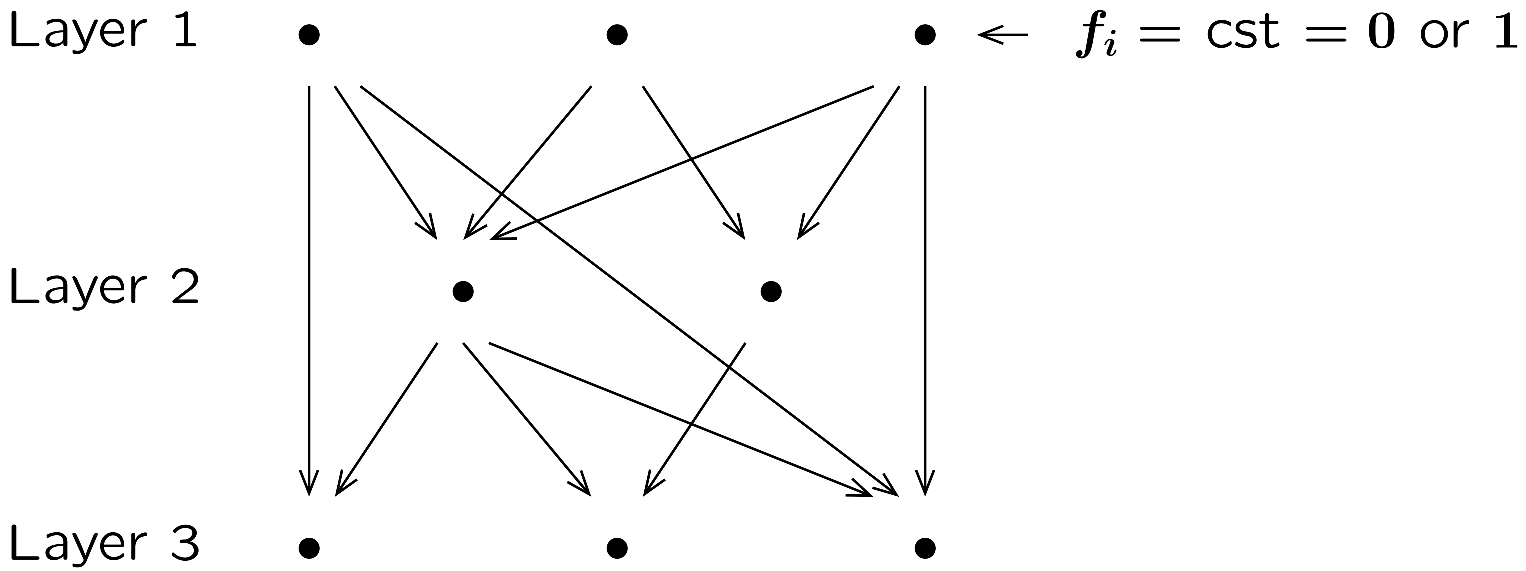

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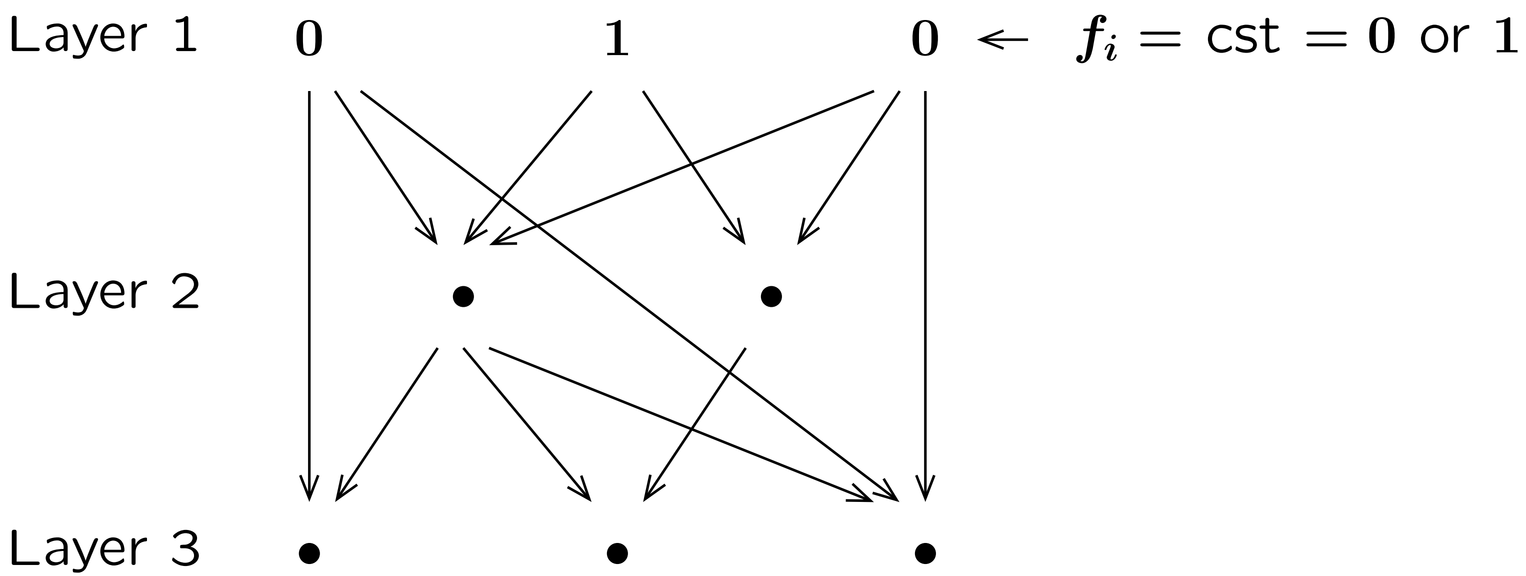

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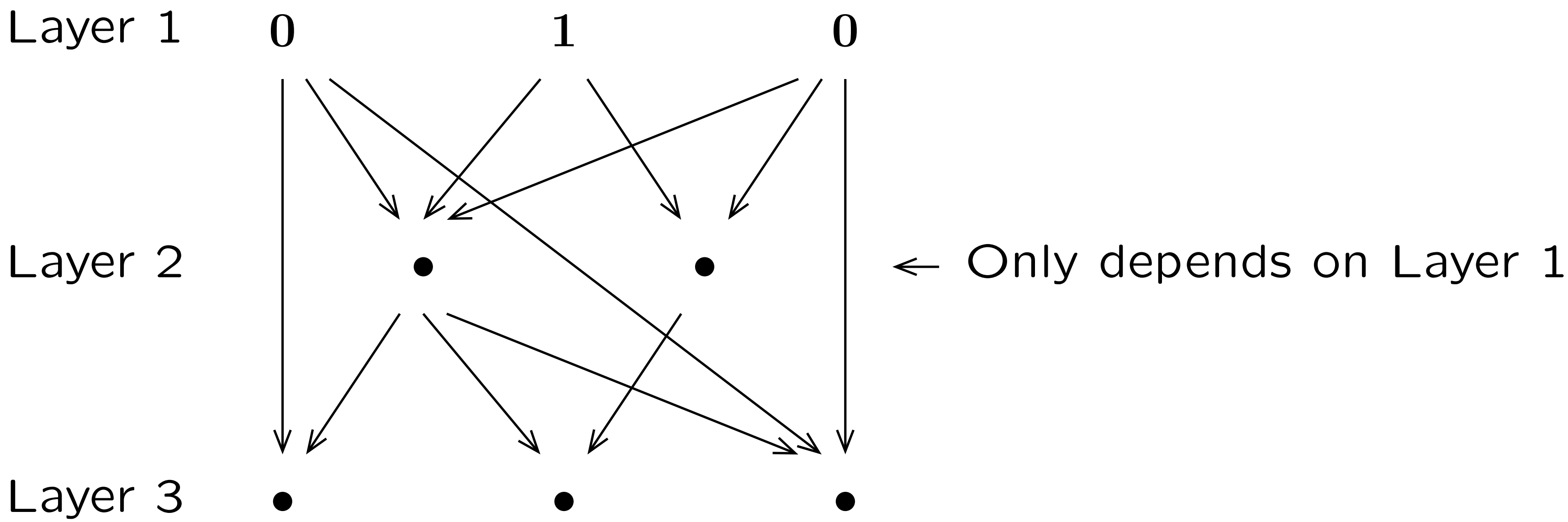

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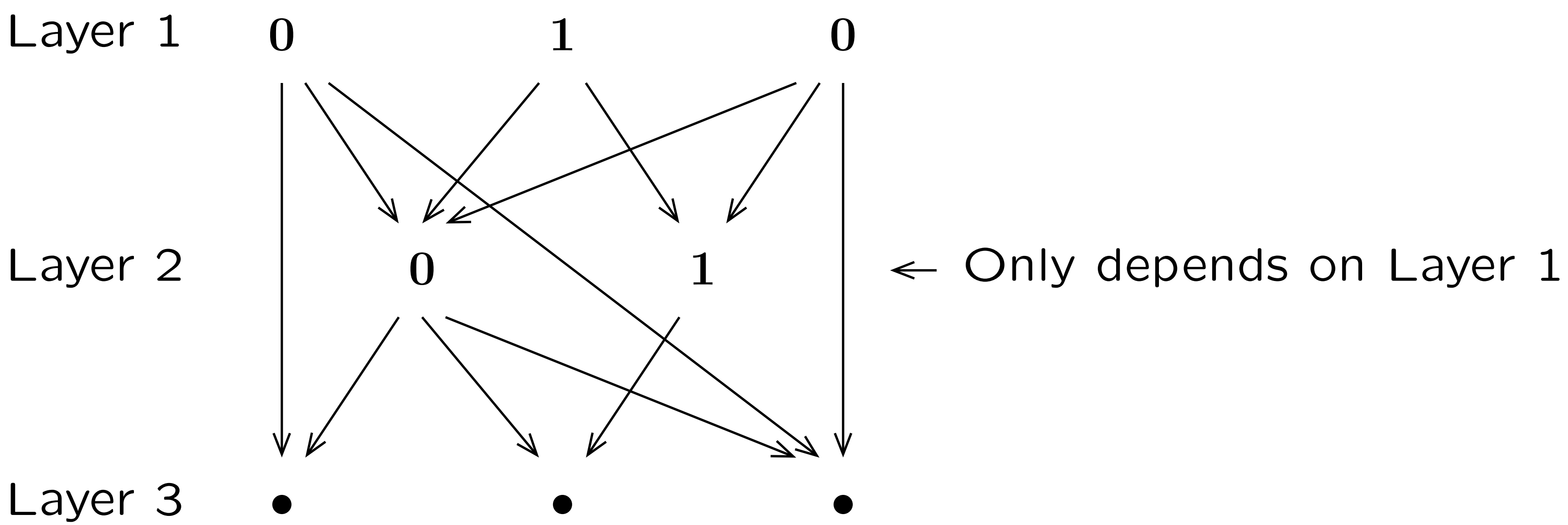

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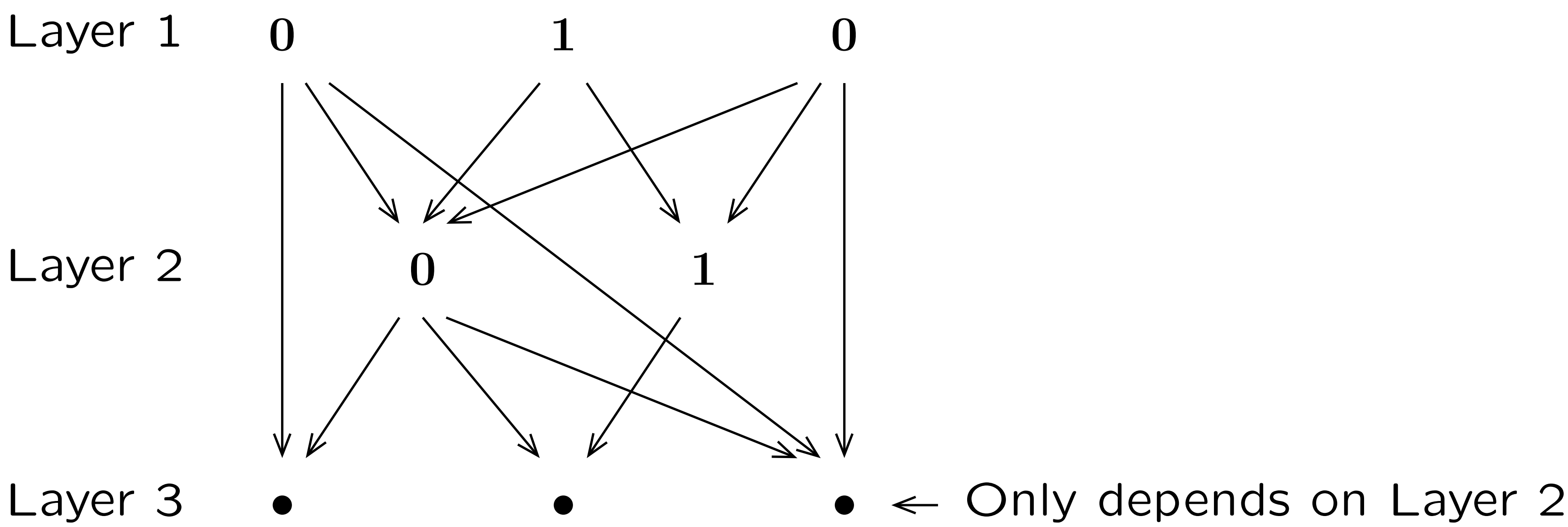

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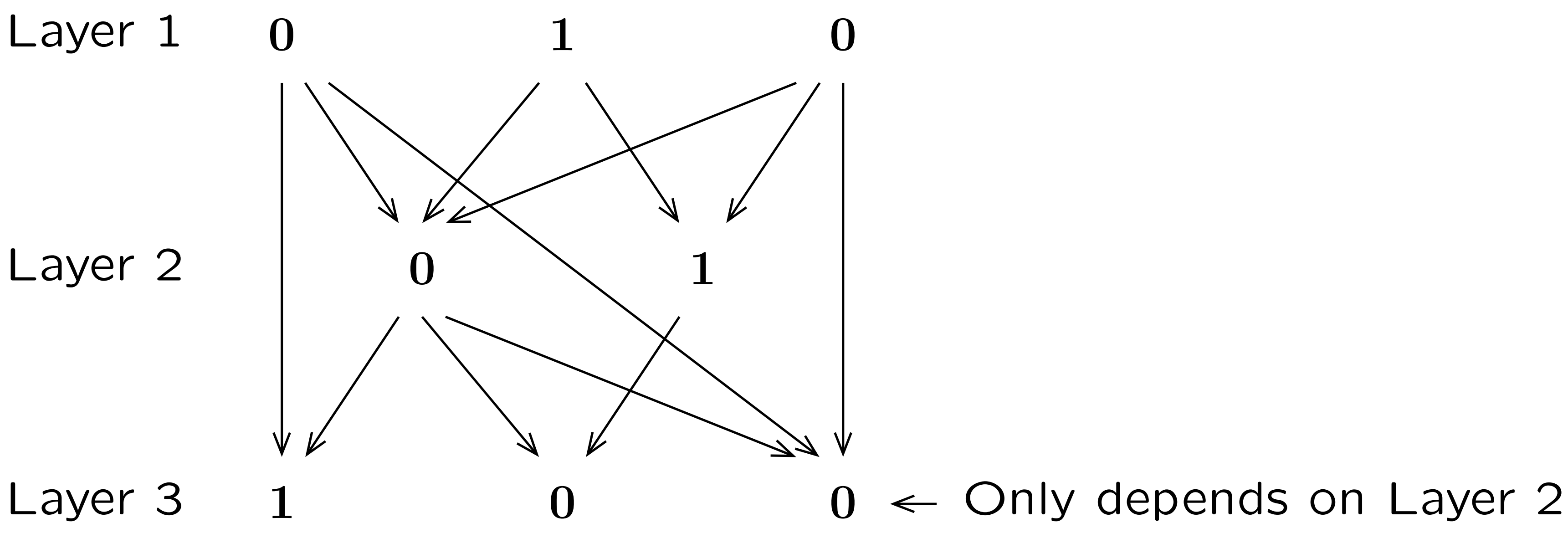

Contents

Notation : $\overline{x}^i = (x_1, \ldots, \overline{x_i}, \ldots, x_n)$

The **local interaction graph** of $f : \mathbb{B}^n \to \mathbb{B}^n$ evaluated at state $x \in \mathbb{B}^n$ is the directed graph $Gf(x)$ with vertex set $\{1, \ldots, n\}$ and such that

$$j \to i \in Gf(x) \;\Leftrightarrow\; f_i(x) \neq f_i(\overline{x}^j)$$

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$$\Downarrow$$

f_i depends on x_j

$$\Updownarrow$$

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$$\Downarrow$$

$$f_i \text{ depends on } x_j$$

$$\Updownarrow$$

$$j \to i \in G(f)$$

Property : $\forall x \in \mathbb{B}^n$, $Gf(x)$ is a subgraph of $G(f)$. More precisely

$$\bigcup_{x \in \mathbb{B}^n} Gf(x) \;=\; G(f)$$

THEOREM (Shih & Dong 2005)

If $Gf(x)$ has no cycle $\forall x \in \mathbb{B}^n$, then f has a unique fixed point.

The proof is more technical. It's an induction on n that uses the notion of *subnetwork* (introduced in few slides).

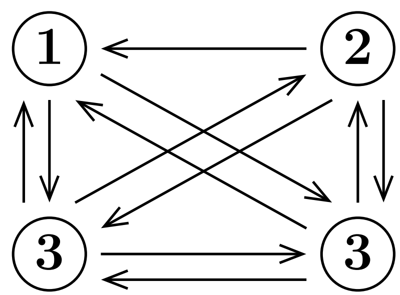
Shih-Dong's theorem generalizes Robert's one :

$$
\begin{gathered}
G(f) \text{ has no cycle} \\
\Downarrow \;\not\Uparrow \\
Gf(x) \text{ has no cycle } \forall x \in \mathbb{B}^n \\
\Downarrow \\
f \text{ has a unique fixed point}
\end{gathered}
$$

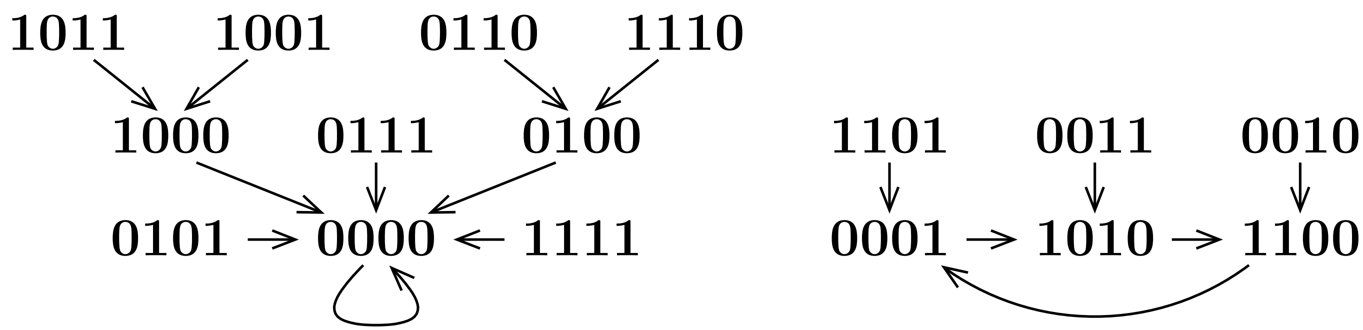
Example : $f : \mathbb{B}^4 \to \mathbb{B}^4$ is defined by :

$$\begin{aligned} f_1(x) &= \overline{x_2} \wedge (x_3 \vee x4) \\ f_2(x) &= x_3 \wedge \overline{x_4} \\ f_3(x) &= \overline{x_1} \wedge \overline{x_2} \wedge x_4 \\ f_4(x) &= x_1 \wedge x_2 \wedge \overline{x_3} \end{aligned}$$

$G(f)$



$G(f)$ has 14 cycles, but $Gf(x)$ **has no cycle** $\forall x \in \mathbb{B}^4$, and f has indeed a unique fixed point :



The condition "$Gf(x)$ has no cycle $\forall x \in \mathbb{B}^n$" *doesn't* imply the convergence toward the unique fixed point.

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A **subnetwork** of $\boldsymbol{f} : \mathbb{B}^{\boldsymbol{n}} \to \mathbb{B}^{\boldsymbol{n}}$ is a network $\tilde{\boldsymbol{f}} : \mathbb{B}^{\boldsymbol{k}} \to \mathbb{B}^{\boldsymbol{k}}$ obtained from $\boldsymbol{f}$ by fixing $\boldsymbol{n} - \boldsymbol{k}$ components to zero or one, with $\boldsymbol{1} \leq \boldsymbol{k} \leq \boldsymbol{n}$.

Remark : $\boldsymbol{f}$ is a subnetwork of $\boldsymbol{f}$

A **subnetwork** of $f : \mathbb{B}^n \to \mathbb{B}^n$ is a network $\tilde{f} : \mathbb{B}^k \to \mathbb{B}^k$ obtained from f by fixing $n-k$ components to zero or one, with $1 \le k \le n$.

Remark : f is a subnetwork of f

Example : $f : \mathbb{B}^3 \to \mathbb{B}^3$ is defined by

$$\begin{aligned} f_1(x_1, x_2, x_3) &= x_1 \vee \overline{x_3} \\ f_2(x_1, x_2, x_3) &= x_1 \wedge x_3 \\ f_3(x_1, x_2, x_3) &= x_2 \end{aligned}$$

The subnetwork $\tilde{f} : \mathbb{B}^2 \to \mathbb{B}^2$ obtained by fixing "$x_3 = 1$" is

$$\begin{aligned} \tilde{f}_1(x_1, x_2) &= x_1 \vee \overline{1} = x_1 \\ \tilde{f}_1(x_1, x_2) &= x_1 \wedge 1 = x_1 \end{aligned}$$

Let $\tilde{\boldsymbol{f}}$ be a subnetwork of $\boldsymbol{f}$ of dimension $\boldsymbol{k} \leq \boldsymbol{n}$.

There exists an *injection* $\boldsymbol{h} : \mathbb{B}^{\boldsymbol{k}} \to \mathbb{B}^{\boldsymbol{n}}$ such that

$$\forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{k}} \qquad \boldsymbol{G}\tilde{\boldsymbol{f}}(\boldsymbol{x}) \subseteq \boldsymbol{G}\boldsymbol{f}(\boldsymbol{h}(\boldsymbol{x}))$$

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As a consequence $\boldsymbol{G}(\tilde{\boldsymbol{f}}) \subseteq \boldsymbol{G}(\boldsymbol{f})$.

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As a consequence $\boldsymbol{G}(\tilde{\boldsymbol{f}}) \subseteq \boldsymbol{G}(\boldsymbol{f})$.

PROPERTY OF SUBNETWORKS

If there exists $\boldsymbol{\lambda}$ points $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{k}}$ such that $\boldsymbol{G}\tilde{\boldsymbol{f}}(\boldsymbol{x})$ has a cycle, then there exists $\boldsymbol{\lambda}$ points $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$ such that $\boldsymbol{G}\boldsymbol{f}(\boldsymbol{x})$ has a cycle of length $\leq \boldsymbol{k}$.

Let $\mathcal{C}$ be the set of all **circular networks**, that is, the set of networks f such that $G(f)$ is a cycle.

PROPERTY OF CIRCULAR NETWORKS

If $f : \mathbb{B}^n \to \mathbb{B}^n$ is a circular network, then it has 0 or 2 fixed points, and $Gf(x) = G(f)$ is a cycle for all $x \in \mathbb{B}^n$.

According to Robert's theorem, circular networks are the most simple networks without a unique fixed point.

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QUESTION

If f has no subnetwork in $\mathcal{C}$, then f has a unique fixed point ?

A positive answer would generalize previous results, since :

$$\begin{gathered}\boldsymbol{G(f)} \text{ has no cycle}\\ \Downarrow \\ \boldsymbol{Gf(x)} \text{ has no cycle } \forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}} \\ \Downarrow \\ \boldsymbol{f} \text{ has no subnetwork in } \boldsymbol{\mathcal{C}} \\ \text{¿} \Downarrow \text{?} \\ \boldsymbol{f} \text{ has a unique fixed point}\end{gathered}$$

A positive answer would generalize previous results, since :

$$\boldsymbol{G(f)} \text{ has no cycle}$$
$$\Downarrow$$
$$\boldsymbol{Gf(x)} \text{ has no cycle } \forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$$
$$\Downarrow$$
$$\boldsymbol{f} \text{ has no subnetwork in } \boldsymbol{\mathcal{C}}$$
$$¿\Downarrow ?$$
$$\boldsymbol{f} \text{ has a unique fixed point}$$

Suppose that $\boldsymbol{f}$ has subnetwork $\tilde{\boldsymbol{f}} \in \boldsymbol{\mathcal{C}}$ of dimension $\boldsymbol{k} \leq \boldsymbol{n}$.

By the PROPERTY OF CIRCULAR NETWORKS,
$\boldsymbol{G\tilde{f}(x)} = \boldsymbol{G(\tilde{f})}$ is a cycle for all $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{k}}$,

so, by the PROPERTY OF SUBNETWORKS,
it exists $\boldsymbol{2^k}$ points $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$ such that $\boldsymbol{Gf(x)}$ has a cycle.

A positive answer would generalize previous results, since :

$$\begin{gathered} \boldsymbol{G(f)} \text{ has no cycle} \\ \Downarrow \\ \boldsymbol{Gf(x)} \text{ has no cycle } \forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}} \\ \Downarrow \\ \boldsymbol{f} \text{ has no subnetwork in } \boldsymbol{\mathcal{C}} \\ \text{¿} \Downarrow \text{?} \\ \boldsymbol{f} \text{ has a unique fixed point} \end{gathered}$$

Suppose that $\boldsymbol{f}$ has subnetwork $\tilde{\boldsymbol{f}} \in \boldsymbol{\mathcal{C}}$ of dimension $\boldsymbol{k} \leq \boldsymbol{n}$.

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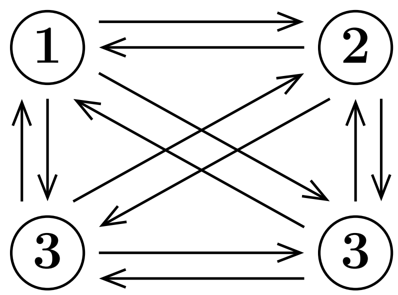
it exists $\boldsymbol{2^k}$ points $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$ such that $\boldsymbol{Gf(x)}$ has a cycle.

However, the answer is negative : counter examples for each $\boldsymbol{n} \geq 4$

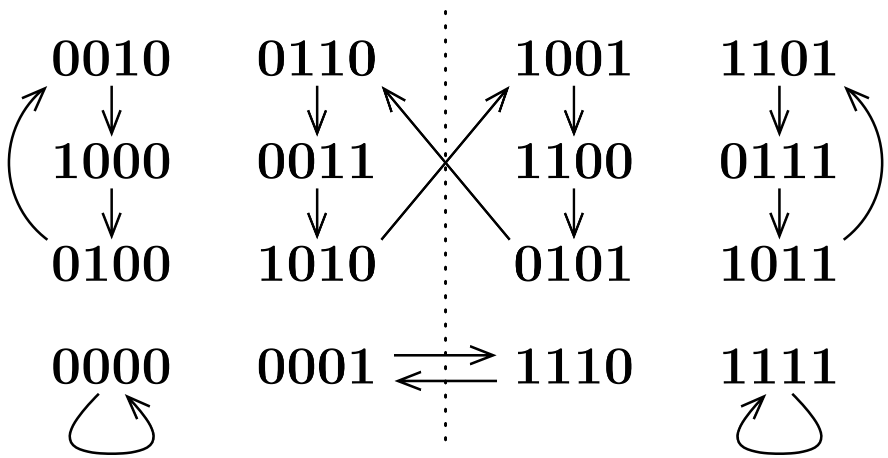
Example : $f : \mathbb{B}^4 \to \mathbb{B}^4$ is defined by :

$$
\begin{aligned}
f_1(x) &= (\overline{x_2} \wedge x_3 \wedge \overline{x_4}) \vee ((\overline{x_2} \vee x_3) \wedge x_4) \\
f_2(x) &= (\overline{x_3} \wedge x_1 \wedge \overline{x_4}) \vee ((\overline{x_3} \vee x_1) \wedge x_4) \\
f_3(x) &= (\overline{x_1} \wedge x_2 \wedge \overline{x_4}) \vee ((\overline{x_1} \vee x_2) \wedge x_4) \\
f_4(x) &= (x_2 \wedge x_3 \wedge \overline{x_1}) \vee ((x_2 \vee x_3) \wedge x_1)
\end{aligned}
$$

$G(f)$



f has no circular subnetwork, but it has not a unique fixed point :



But all is not lost ! Counter examples are very particular !

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

The network f is **self-dual** : $f(\overline{x}) = \overline{f(x)}$ for all $x \in \mathbb{B}^4$

x	$f(x)$
0000	0000
0001	1110
0010	1000
0011	1010
0100	0010
0101	0110
0110	0011
0111	1011
1000	0100
1001	1100
1010	1001
1011	1101
1100	0101
1101	0111
1110	0001
1111	1111

The network f is **self-dual** : $f(\overline{x}) = \overline{f(x)}$ for all $x \in \mathbb{B}^4$

x	$f(x)$	$x \oplus f(x)$
0000	0000	0000
0001	1110	1111
0010	1000	1010
0011	1010	1001
0100	0010	0110
0101	0110	0011
0110	0011	0101
0111	1011	1100
1000	0100	1100
1001	1100	0101
1010	1001	0011
1011	1101	0110
1100	0101	1001
1101	0111	1010
1110	0001	1111
1111	1111	0000

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x	$f(x)$	$x \oplus f(x)$
0000	0000	0000
0001	1110	1111
0010	1000	1010
0011	1010	1001
0100	0010	0110
0101	0110	0011
0110	0011	0101
0111	1011	1100
1000	0100	1100
1001	1100	0101
1010	1001	0011
1011	1101	0110
1100	0101	1001
1101	0111	1010
1110	0001	1111
1111	1111	0000

The network f is **self-dual** : $f(\overline{x}) = \overline{f(x)}$ for all $x \in \mathbb{B}^4$

And it is **even** : $\{x \oplus f(x)\} = \{x$ with an even number of ones$\}$

x	$f(x)$	$x \oplus f(x)$
0000	0000	0000
0001	1110	1111
0010	1000	1010
0011	1010	1001
0100	0010	0110
0101	0110	0011
0110	0011	0101
0111	1011	1100
1000	0100	1100
1001	1100	0101
1010	1001	0011
1011	1101	0110
1100	0101	1001
1101	0111	1010
1110	0001	1111
1111	1111	0000

CHARACTERIZATION OF CIRCULAR NETWORKS

A network $f : \mathbb{B}^n \to \mathbb{B}^n$ is circular **if and only if** it is

1. **self-dual** : $\forall x \in \mathbb{B}^n$, $f(\overline{x}) = \overline{f(x)}$

2. **even** or **odd** :

$$\{f(x) \oplus x \,|\, x \in \mathbb{B}^n\} = \{x \in \mathbb{B}^n \,|\, x \text{ has an even number of ones}\}$$

or

$$\{x \in \mathbb{B}^n \,|\, x \text{ has an odd number of ones}\}$$

3. **non-expansive** : $\forall x, y \in \mathbb{B}^n$, $d(f(x), f(y)) \leq d(x, y)$

Let $\mathcal{F}$ be the set of even/odd self-dual networks without even/odd self-dual strict subnetworks ($\mathcal{C} \subset \mathcal{F}$).

FORBIDDEN SUBNETWORKS THEOREM

If f has no subnetwork in $\mathcal{F}$, then f has a unique fixed points

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PROPERTY OF CIRCULAR NETWORKS

If $\boldsymbol{f} : \mathbb{B}^{\boldsymbol{n}} \to \mathbb{B}^{\boldsymbol{n}}$ is a circular network, then it has $\mathbf{0}$ or $\mathbf{2}$ fixed points, and $\boldsymbol{Gf}(\boldsymbol{x}) = \boldsymbol{G}(\boldsymbol{f})$ *is a cycle* for all $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$.

Without the non-expansiveness, the property is almost the same :

PROPERTY OF EVEN/ODD SELF-DUAL NETWORKS

If $\boldsymbol{f} : \mathbb{B}^{\boldsymbol{n}} \to \mathbb{B}^{\boldsymbol{n}}$ is an even/odd self-dual network, then it has $\mathbf{0}$ or $\mathbf{2}$ fixed points, and $\boldsymbol{Gf}(\boldsymbol{x})$ *has a cycle* for all $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$.

The forbidden subnetwork theorem generalizes previous results :

$$\boldsymbol{G}(\boldsymbol{f}) \text{ has no cycle}$$
$$\Downarrow \; \not\Uparrow$$
$$\boldsymbol{G}\boldsymbol{f}(\boldsymbol{x}) \text{ has no cycle } \forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$$
$$\Downarrow \; \not\Uparrow$$
$$\boldsymbol{f} \text{ has no subnetwork in } \boldsymbol{\mathcal{F}}$$
$$\Downarrow$$
$$\boldsymbol{f} \text{ has a unique fixed point}$$

Suppose that $\boldsymbol{f}$ has subnetwork $\tilde{\boldsymbol{f}} \in \boldsymbol{\mathcal{F}}$ of dimension $\boldsymbol{k} \leq \boldsymbol{n}$.

By the PROPERTY OF EVEN/ODD SELF-DUAL NETWORKS, $\boldsymbol{G}\tilde{\boldsymbol{f}}(\boldsymbol{x})$ has a cycle for all $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{k}}$,

so, by the PROPERTY OF SUBNETWORKS, it exists $\boldsymbol{2^k}$ points $\boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}}$ such that $\boldsymbol{G}\boldsymbol{f}(\boldsymbol{x})$ has a cycle of length $\leq \boldsymbol{k}$.

The forbidden subnetwork theorem generalizes previous results :

$$\begin{gathered} \boldsymbol{G(f)} \text{ has no cycle} \\ \Downarrow \; \not\Uparrow \\ \boldsymbol{Gf(x)} \text{ has no cycle } \forall \boldsymbol{x} \in \mathbb{B}^{\boldsymbol{n}} \\ \Downarrow \; \not\Uparrow \\ \boldsymbol{f} \text{ has no subnetwork in } \boldsymbol{\mathcal{F}} \\ \Downarrow \\ \boldsymbol{f} \text{ has a unique fixed point} \end{gathered}$$

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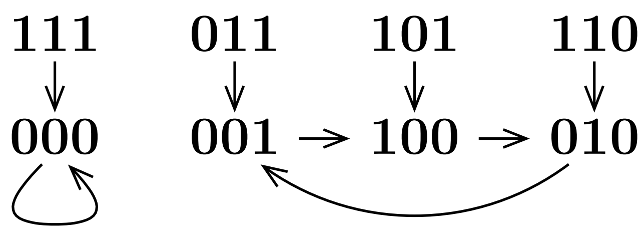
COROLLARY

If for $k = 1, \ldots n$ there is at most $2^k - 1$ points $x \in \mathbb{B}^n$ such that $Gf(x)$ has a cycle of length $\leq k$, then f has a unique fixed point.

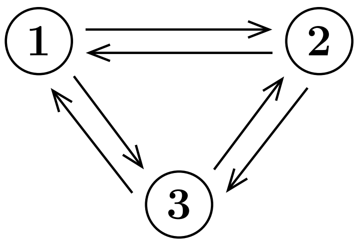
Example : $f : \mathbb{B}^3 \to \mathbb{B}^3$ is defined by :

$$
\begin{aligned}
f_1(x) &= \overline{x_2} \wedge x_3 \\
f_2(x) &= \overline{x_3} \wedge x_1 \\
f_3(x) &= \overline{x_1} \wedge x_2
\end{aligned}
$$

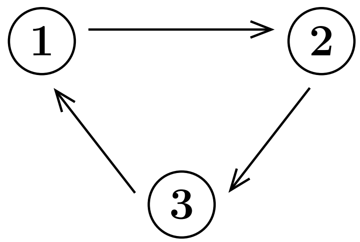


f has no subnetwork in $\mathcal{F}$ (and it has indeed a unique fixed point) but $Gf(x)$ has a cycle for some $x \in \mathbb{B}^3$:

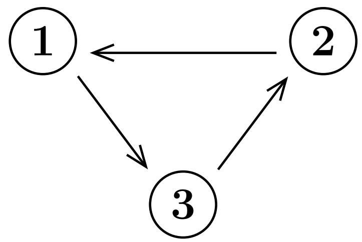
$G(f)$



$Gf(000)$



$Gf(111)$



There is something of optimal in the forbidden subnetwork theorem.

Let us say that a set $\mathcal{H}$ of networks has the **fixed point property** if

1. Every network f without subnetwork in $\mathcal{H}$ has a unique fixed point.
2. No member of $\mathcal{H}$ has a unique fixed point.

We have seen that $\mathcal{F}$ has the fixed point property (but not $\mathcal{C}$).

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So $\mathcal{F}$ is *the* smallest set with the fixed point property.

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Proof : Suppose that $\mathcal{H}$ has the fixed point property.
Suppose, by contradiction, that there exists $f \in \mathcal{F} \setminus \mathcal{H}$.
By the definition of $\mathcal{F}$, f has no strict subnetwork in $\mathcal{F}$.
So if $\tilde{f}$ is a strict subnetwork of f, then $\tilde{f}$ has no subnetwork in $\mathcal{F}$.
By the forb. subnet. theorem, $\tilde{f}$ has a unique fixed point, so $\tilde{f} \notin \mathcal{H}$.
So f has no subnetwork in $\mathcal{H}$, so f has a unique fixed point.
Contradiction.

Problem

Is there exists a class of forbidden subnetworks $\mathcal{H}$ such that :

1. Every network f without subnetwork in $\mathcal{H}$ converges toward a unique fixed point.
2. No member of $\mathcal{H}$ converge toward a unique fixed point.