On the convergence of Boolean automata networks without negative cycles

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Gießen, September 19, 2013
Boolean networks

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Finite and heterogeneous CAs on \{0, 1\}
Boolean networks

= Finite and heterogeneous CAs on \{0, 1\}

Classical models for

Neural networks [McCulloch & Pitts 1943]
Gene regulatory networks [Kauffman 1969, Tomas 1973]
Focus on interaction graphs

Question: What can be said on the dynamics of a Boolean network according to its interaction graph?

Application to gene networks: reliable information on the interaction graph only.
Focus on interaction graphs

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What can be said on the dynamics of a Boolean network according to its interaction graph?
Focus on **interaction graphs**

[Diagram of a network with nodes labeled 1 to 11 and arrows indicating interactions.]

[Arabidopsis Thaliana]

**Question**

What can be said on the dynamics of a Boolean network according to its interaction graph?

Application to **gene networks**: reliable information on the interaction graph only.
Definitions
Setting

There are \( n \) components (cells) denoted from 1 to \( n \)

The set of possible states (configurations) is \( \{0, 1\}^n \)

The local transition function of component \( i \in [n] \) is any map

\[
f_i : \{0, 1\}^n \rightarrow \{0, 1\}
\]

The resulting global transition function is

\[
f : \{0, 1\}^n \rightarrow \{0, 1\}^n, \quad f(x) = (f_1(x), \ldots, f_n(x))
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\]

We consider the fully-asynchronous updating

\( \leftrightarrow \) very usual in the context of gene networks [Thomas 73]
Given a map $v : \mathbb{N} \to [n]$, the **fully-asynchronous** dynamics is

$$x_{v(t)}^{t+1} = f_{v(t)}(x^t), \quad x_i^{t+1} = x_i^t \quad \forall i \neq v(t)$$
Given a map $\nu : \mathbb{N} \rightarrow [n]$, the \textbf{fully-asynchronous} dynamics is

$$x^{t+1}_\nu(t) = f_{\nu(t)}(x^t), \quad x^{t+1}_i = x^t_i \quad \forall i \neq \nu(t)$$

In practice, non information on $\nu$... → we regroup all the possible asynchronous dynamics under the form of a directed graph
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In practice, non information on $\nu$... → we regroup all the possible asynchronous dynamics under the form of a directed graph

\textbf{Definition}

The \textbf{asynchronous state graph} of $f$, denoted by $\text{ASG}(f)$, is the directed graph on $\{0, 1\}^n$ with the following set of arcs:

$$\left\{ x \to \bar{x}^i \mid x \in \{0, 1\}^n, \ i \in [n], \ x_i \neq f_i(x) \right\}$$
**Example**

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$ASG(f)$

- Attractor of size one = fixed point
- Attractor of size at least two = cyclic attractor
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The attractors of $ASG(f)$ are its terminal strong components:

- Attractor of size one = fixed point
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A path from a state $x$ to a state $y$ is a direct path if its length $\ell$ is equal to the Hamming distance between $x$ and $y$ (so $\ell \leq n$).
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A path from a state $x$ to a state $y$ is a **direct path** if its length $\ell$ is equal to the Hamming distance between $x$ and $y$ (so $\ell \leq n$).
Definition

The **interaction graph** of $f$, denoted $G(f)$, is the signed directed graph on $\{1, \ldots, n\}$ with the following arcs:

- There is a **positive arc** $j \to i$ iff there is a state $x$ such that
  
  $f_i(x_1, \ldots, x_{j-1}, 0, x_{j+1}, \ldots, x_n) = 0$
  
  $f_i(x_1, \ldots, x_{j-1}, 1, x_{j+1}, \ldots, x_n) = 1$

- There is a **negative arc** $j \to i$ iff there is a state $x$ such that
  
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  \]

\[
  j \rightarrow i \in G(f) \quad \iff \quad f_i(x) \text{ depends on } x_j
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Asynchronous State Graph: $\text{ASG}(f)$

Interaction Graph: $G(f)$

Question: What can be said on $\text{ASG}(f)$ according to $G(f)$?
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Asynchronous State Graph $ASG(f)$

Interaction Graph $G(f)$

Question
What can be said on $ASG(f)$ according to $G(f)$?
Results
Theorem [Robert 1980]

If $G(f)$ has no cycles then

1. $f$ has a unique fixed point
2. $ASG(f)$ has no cycles

⇒ complexity comes from cycles of the interaction graph

Two kinds of cycles have to be considered:
- Positive cycles: even number of negative arcs
- Negative cycles: odd number of negative arcs
Theorem [Robert 1980]

If $G(f)$ has **no cycles** then

1. $f$ has a **unique fixed point**
2. $ASG(f)$ has no cycles
3. $ASG(f)$ has a **direct path** from every state to the fixed point
Theorem [Robert 1980]

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Two kinds of cycles have to be considered:
- **Positive cycles**: even number of negative arcs
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Theorem on positive cycles [Aracena 2004]

If all the positive cycles of $G(f)$ can be destroyed by removing $k$ vertices, then $ASG(f)$ has at most $2^k$ attractors.
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If all the positive cycles of $G(f)$ can be destroyed by removing $k$ vertices, then $ASG(f)$ has at most $2^k$ attractors.

**Corollary**  If $G(f)$ has no positive cycles then $ASG(f)$ has a unique attractor
**Theorem on positive cycles** [Aracena 2004]

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**Corollary** If $G(f)$ has **no positive cycles** then $ASG(f)$ has a unique attractor

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**Theorem on negative cycles** [Richard 2010]

If $G(f)$ has **no negative cycles** then $ASG(f)$ has a path from every state $x$ to a fixed point
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**Theorem on negative cycles** [Richard 2010]
If $G(f)$ has **no negative cycles** then $ASG(f)$ has a path from every state $x$ to a fixed point

**Our contribution**
If $G(f)$ has **no negative cycles** then $ASG(f)$ has a **direct path** from every state $x$ to a fixed point
Sketch of proof
Theorem  If $G(f)$ has no negative cycles then $ASG(f)$ has a direct path from any state $x$ to a fixed point.
**Theorem** If $G(f)$ has no negative cycles then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

It is sufficient to prove the theorem in the case where $G(f)$ strongly connected (the general case follows by decomposition).

So we suppose that $G(f)$ is strong and has no negative cycles.
**Theorem**  If $G(f)$ has no negative cycles then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

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It is well known [Harary 1953] that $G(f)$ has a set of vertices $I$ such that an arc of $G(f)$ is negative iff this arc leaves $I$ or enters in $I$. 
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![Diagram of a graph with vertices I and arcs between them]
Theorem  If $G(f)$ has no negative cycles then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

Let $h$ be the network defined by $h(x) = f(\overline{x^I})^I$ for all $x \in \{0, 1\}^n$. 

In addition, $G(h)$ is obtained from $G(f)$ by changing the sign of every arc that leaves $I$ or enters in $I$. Thus $G(h)$ has only positive arcs.

Conclusion: We can suppose that $G(f)$ has only positive arcs, which is equivalent to say that $f$ is monotonous: $\forall x, y \in \{0, 1\}^n, x \leq y \Rightarrow f(x) \leq f(y)$. 

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**Theorem**  If $G(f)$ has no negative cycles then $ASG(f)$ has a direct path from any state $x$ to a fixed point

Let $h$ be the network defined by $h(x) = f(\overline{x^I})^I$ for all $x \in \{0, 1\}^n$

$ASG(h)$ is isomorphic to $ASG(f)$ and the isomorphism is $x \mapsto \overline{x^I}$

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\forall x, y \in \{0, 1\}^n \quad x \leq y \Rightarrow f(x) \leq f(y)
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**Lemma 1**  $f(0) = 0$ and $f(1) = 1$

Suppose $f(0) \neq 0$, that is, $f_i(0) = 1$ for some $i$.

Then since $f$ is monotonous, $f_i(x) = 1$ for all $x \in \{0, 1\}^n$.

Thus $f_i = cst$, so $i$ has no in-neighbor in $G(f)$.

Thus $G(f)$ is not strong, a contradiction.

We prove similarly $f(1) = 1$. 
Theorem  If $G(f)$ is strong and $f$ is monotonous then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

Lemma 2  The set of states reachable from $x$, denoted by $R(x)$, has a unique maximal element, reachable from $x$ by a direct path.
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Let $P$ be an increasing path from $x$ of maximal length. Let $y$ the last state of $P$, so that $f(y) \leq y$. We prove that $z \leq y$, $\forall z \in R(x)$.
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If not there is a path $x \leadsto z \rightarrow \bar{z}^i$ with $z \leq y$ and $\bar{z}^i \not\leq y$.

Thus $\bar{z}_i^i = 1$ and $y_i = 0$, so $z \rightarrow \bar{z}^i$ increases component $i$.

Thus $f_i(z) = 1$ and since $z \leq y$ and $f_i$ is monotonous, $f_i(y) = 1$. 
**Theorem**  If $G(f)$ is **strong** and $f$ is **monotonous** then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

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Theorem  If $G(f)$ is strong and $f$ is monotonous then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

We prove the theorem by induction on the number of ones in $x$. If $x = 0$ the theorem is true since $f(0) = 0$. Suppose that $x > 0$.
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Maximal element of $R(x)$

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\begin{align*}
    f(z) &\leq f(y) \leq y, \quad \forall z \in R(x)
\end{align*}
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f(z) &\leq f(y) \leq y, \quad \forall z \in R(x) \\
\text{If } f(y) &= y \text{ nothing to prove} \\
\text{Suppose } f_i(y) &< y_i \text{ for some } i
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Maximal element of $R(x)$

$\begin{align*}
  f(z) &\leq f(y) \leq y, \forall z \in R(x) \\
  y_i &= 1
\end{align*}$
Theorem  If $G(f)$ is strong and $f$ is monotonous then $ASG(f)$ has a direct path from any state $x$ to a fixed point.

We prove the theorem by induction on the number of ones in $x$. If $x = 0$ the theorem is true since $f(0) = 0$. Suppose that $x > 0$.

Maximal element of $R(x)$

If $f(y) = y$ nothing to prove
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- $f(z) \leq f(y) \leq y$, $\forall z \in R(x)$
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Maximal element of $R(x)$

- $f_i(x) = 0$
- $x_i = 1$
- $y_i = 1$
- $f(z) \leq f(y) \leq y$, $\forall z \in R(x)$
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Algorithm in $\mathcal{O}(n^2)$
Further results & perspectives
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Suppose that $G(f)$ has no negative cycles.

The set of fixed points reachable from $x$ has a unique maximal element $x^+$ and a unique minimal element $x^-$, which are reachable in at most $2n - 4$ transitions (thigh bound).
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Are all the fixed points of $R(x)$ reachable in at most $2n - 4$ steps?

Can we obtain upper/lower bounds on the number of fixed points reachable from $x$ according to $G(f)$?
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Thank you!