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▶ To cite this version:

Sébastien Orange, Nathalie Verdière, Loïs Naudin. Target observability of nonlinear complex networks with linear and nonlinear couplings. 2023. hal-04008773

HAL Id: hal-04008773 https://hal.science/hal-04008773

Preprint submitted on 28 Feb 2023

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1	Target observability of nonlinear complex networks with
2	linear and nonlinear couplings
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February 28, 2023

Abstract

Many real-life systems can be modeled as a complex network made up of nodes whose 10 dynamics are governed by nonlinear differential equations. Observability on such networks 11 is one fundamental problem consisting in the capability of inferring the states of all/some 12 target nodes from the knowledge of some node states. In this paper, we present a new ap-13 proach for studying the full and the target observability in networks of nonlinear systems 14 with linear and/or nonlinear couplings. The proposed method is based on a mathematical 15 result ensuring the existence of specific local relations obtained from equations of each node. 16 Two consequences in terms of observability are deduced from this theoretical result and are 17 used to elaborate an algorithm. This algorithm, named TargetObservability, determines 18 sets of nodes ensuring the observability of a given target set. We exemplify our approach on 19 a biological neural network of C. elegans, made up of Hodgkin-Huxley type models coupled 20 through linear and nonlinear terms. This provides a testable hypothesis that is likely to 21 accelerate the discovery and analysis of the biological circuitry in C. elegans. 22

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Keywords: Observability; complex networks; nonlinear couplings; algorithm; neurons.

²⁵ 1 Introduction

Many real-life systems can be modeled as a complex network, made up of nodes connected through 26 edges (Newman, 2018). In such a configuration, each node has its own dynamics governed by a set 27 of differential equations, and the edges describe the interactions between the nodes. A neuronal 28 network is an example of complex network in which the nodes represent the neurons, and the edges 29 represent the synaptic connections. The best way to monitor the state of a complex network would 30 be to measure the state of all its nodes separately. However, in practice, we are often restricted to 31 a limited set of measurements due to technical and experimental impediments. Therefore, we can 32 ask which nodes of the system can contain sufficient information about the other nodes to retrieve 33 the network complete state, making the system full observable. 34

However, in many applications, the full observability is not the right concept since retrieving 35 the state of *all* the nodes in the network is not expected. Indeed, we might want to infer the 36 state of only a subset of nodes, called *target* nodes, since only their states would describe a desired 37 property of the network. As an example, in neuroscience, muscle states form the basis of the 38 locomotor behavior, and are modulated by the activity of neurons in the nervous system. In this 39 case, we might be interested in identifying an optimal set of neurons from which we can infer 40 the state of the muscles, without having to retrieve the state of all neurons in the entire nervous 41 system. 42

There is a long tradition and a substantial literature that deal with the observability and its 43 dual concept, the controllability, of *linear* complex systems (Meng et al., 2023; Aguirre and Letel-44 lier, 2016; Wang et al., 2014; Gao et al., 2014; Leitold et al., 2017; Czeizler et al., 2018; Montanari 45 et al., 2022). In such a case, the nodal dynamics and couplings are considered linear, despite the 46 fact that they are fundamentally nonlinear in nature. If these simplifications facilitate the mathe-47 matical studies of systems, they are not without consequences (Aguirre et al., 2018). Indeed, some 48 recent works demonstrate the irrelevance of the linear observability and controllability to nonlinear 49 dynamical networks. First, the linearized system could be not controllable, while the original non-50 linear system is actually controllable (Liu and Barabási, 2016). Also, linear controllability theory 51 tends to generate information that is not useful for nonlinear control of many complex systems. 52 For instance, linear controllability may give great importance to some nodes for the controllability 53 of the system while these nodes are theoretically unimportant (Jiang and Lai, 2019). Last, linear 54 observability can highly underestimate the number of sensors necessary to retrieve the state of the 55 variables of the original nonlinear system (Letellier et al., 2018b). Taken together, these evidences 56 urged the development of mathematical tools capable of dealing with the nonlinear observability. 57 In this context, some approaches dealing with the nonlinear observability have emerged from 58 different perspectives. Liu et al. (2013) proposed a graph-theoretic approach, based on an inference 59

diagram, that only yields a strict lower bound for the size of the minimum sensor set, which still 60 tend to severely underestimate their number to get a good observability (Letellier et al., 2018a). 61 Therefore, Letellier et al. (2018a) slightly modified the inference diagram from Liu et al. (2013) by 62 removing all the nonlinear couplings, thus taking into account only the linear ones. If this approach 63 proved to be efficient in some particular cases, it turns out to be inapplicable for complex systems 64 with only or mostly nonlinear connections. Another approach is based on the symbolic formalism 65 (Bianco-Martinez et al., 2015; Letellier and Aguirre, 2009; Letellier et al., 2018b) that suffers 66 from a high computational cost: the number of variable combinations to investigate increases 67 exponentially with the system dimension. 68

In this paper, we propose a work on the target observability in network of nonlinear systems 69 with non linear couplings avoiding such a high computationnal cost. Further, this paper has a two-70 fold contribution. The first is a theoretical result: from the differential equations corresponding 71 to one node, this result ensures the existence of relations involving only one state variable of the 72 node, the coupling terms and eventual controls. Two observability properties propagating in the 73 network are deduced from this result. These two properties constitute the basis of the second 74 contribution which consists in an algorithm, called TargetObversability, that determines sets of 75 nodes which should be observed to deduce the state of a given target set of nodes. Many models 76 fall within the scope of the present work in neuroscience (Hodgkin and Huxley, 1952; FitzHugh, 77 1969; Hindmarsh and Rose, 1984; Naudin et al., 2022b,a). 78

To show the suitability of our approach, we apply it for the target observability of *C. elegans* muscles involved in a chemotaxis behavior (Costalago-Meruelo et al., 2018). The *C. elegans* worm is a well-known model organism in neuroscience due to its simple nervous system and its fully mapped connectome (White et al., 1986; Varshney et al., 2011). In particular, we determine a set of neurons from which the state of *C. elegans* muscles can be inferred.

The remainder of the paper is organized as follows. In Section 2, we define the problem of the target observability in mathematical terms. Section 3 presents a theoretical result centered on local differential algebraic relations from which two corollaries giving observability conditions are deduced in Section 4. These corollaries form the basis of the TargetObservability algorithm developed in Section 5. Finally, this algorithm is applied in Section 6 on a *C. elegans* neuronal network, and the perspectives are drawn in Section 7.

⁹⁰ 2 Problem statement

In this paper, we consider directed complex networks formed of N nonlinear nodes coupled through linear and nonlinear terms. Some nodes can be controlled using inputs u_i and the other nodes are ⁹³ coupled between them and to the controlled ones (Figure 4.A). Here the coupling acts on a single ⁹⁴ variable of the node, the one characterizing the node dynamics. Moreover, the dynamics of each ⁹⁵ node are governed by a nonlinear dynamical system described by a set of differential equations. ⁹⁶ These differential systems are not necessarily identical. The state variable $X_i = (x_{i,1}, \ldots, x_{i,n})^T$ of ⁹⁷ the *i*th node $(i = 1, \ldots, N)$ takes the form:

$$\begin{cases} \dot{x}_{i,1} = f_{i,1}(X_i, \Theta_i) + \sum_{j \in \mathcal{N}_i^-} c_j(x_{i,1}, x_{j,1}) + u_i \\ \dot{x}_{i,2} = f_{i,2}(X_i, \Theta_i), \\ \vdots \\ \dot{x}_{i,n} = f_{i,n}(X_i, \Theta_i), \end{cases}$$
(1)

98 where

• $f_{i,j}(X_i, \Theta_i)$ are linear combinations of the state variables $x_{i,2}, \ldots, x_{i,n}$ whose coefficients are analytical functions in $\Theta_i, x_{i,1}$ and its derivatives^A;

• the initial states $X_i(t_0)$, i = 1, ..., N, of the network are supposed to be known at time t_0 ;

• $\sum_{j \in \mathcal{N}_i^-} c_j(x_{i,1}, x_{j,1})$ is a coupling term with \mathcal{N}_i^- the in-neighbors set of the node *i* (that is, the nodes whose edge comes into the node *i*), and $c_j : \mathbb{R}^2 \to \mathbb{R}$ is an infinitely differentiable such that, for all $x_{i,1} \in \mathbb{R}, x_{j,1} \to c_j(x_{i,1}, x_{j,1})$ is a one to one function.

Figure 4.B illustrates the full complex network presented in Figure 4.A with the set of differential equations associated with each node, and the intra- and inter-node couplings.

It is worth noting that System (1) describes a large class of models in real-life problems. In this paper, we emphasize on the neuroscience field in which most of neuron models describe the dynamics of the neuron voltages following a system of the form (1). Some examples are the large class of conductance-based models that use the Hodgkin–Huxley formalism (Hodgkin and Huxley, 1952), the Hindmarsh–Rose model (Hindmarsh and Rose, 1984), the Fitzhugh–Nagumo model (FitzHugh, 1969), or the phenomenological non-spiking models (Naudin et al., 2022b,c).

Now, we aim to study the observability of a set of nodes of the network, called *target* afterwards.
To do this, from the solutions of some nodes, we set the following target observability definition.

Definition 2.1. Let \mathcal{N} and \mathcal{T} be two sets of nodes of the network, the second one being the target. The set of nodes \mathcal{T} is \mathcal{N} -observable if there exists a surjective function on the solution set of $(X_i)_{i\in\mathcal{N}}$ in the solution set of $(X_i)_{i\in\mathcal{T}}$.

^AAn example of such a system is given by System (5). A system in which function $f_{i,2}(X_i, \theta_i) = \dot{x}_{i,1}x_{i,2} + x_{i,1}x_{i,3}^2$ does not belong to the framework of the present work since it is not linear in $x_{i,3}$.



Figure 1: (A) Example of a complex network composed of 4 nodes (N = 4) coupled through directed edges, and controlled through the first node. (B) Full complex network presented in (A) with the set of dynamical systems associated with each node, and the intra-node (in black) and inter-node (in orange) couplings. This representation highlights the inter-node couplings through the first variable x_{i1} , i = 1, ..., N, and the heterogeneity of dynamical systems governing the behavior of nodes of the network.

From the known solutions of the set of nodes \mathcal{N} , our goal is to determine whether it is possible to infer the solutions of the set of nodes \mathcal{T} . Our approach is based on specific relations linking the first state variable of a node and the first variables of its in-neighbors. More precisely, we deduce an ordinary differential equation ensuring that the first variable of System (1) can be inferred from its in-neighbor nodes and vice versa. This is the subject of the following section.

¹²⁴ 3 Analytical redundancy relations of nodes

The result presented in this section gives the general form of the differential equation linking the node *i* to the nodes $j \in \mathcal{N}_i^-$. In the literature, these relations linking the parameters, the outputs, and the inputs (and their derivatives) of the system are classically called Analytical Redundancy Relations (ARR) (Staroswiecki and Comtet-Varga, 2001; Travé-Massuyes et al., 2006; Verdière et al., 2015). **Proposition 3.1.** Let $i \in [1, N]$ and X_{-i} be the vector $(x_{j,1})_{j \in \mathcal{N}_i^-}$. There exists an ARR of the form

$$\tilde{P}_{i}(x_{i,1}, X_{-i}, \Theta_{i}) = P_{i}(x_{i,1}, \Theta_{i}) + \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_{i})u_{i}^{(k)} + \sum_{j \in \mathcal{N}_{i}^{-}} \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_{i})c_{j}(x_{i,1}, x_{j,1})^{(k)} = 0$$
(2)

131 where

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• $h_{i,k}$ are analytical functions in Θ_i , $x_{i,1}$ and its derivatives;

• $\alpha < n$ with n the dimension of System (1).

Proof. To simplify the proof, let us set $w_i = \sum_{j \in \mathcal{N}_i^-} c_j(x_{i,1}, x_{j,1}) + u_i$. Under the hypotheses of Section 2, System (1) can be written

$$(3) \begin{cases} \dot{x}_{i,1} = g_{i,1,1}(x_{i,1},\Theta_i) + g_{i,1,2}(x_{i,1},\Theta_i)x_{i,2} + \dots + g_{i,1,n}(x_{i,1},\Theta_i)x_{i,n} - w_i \end{cases}$$
(3a)

$$(\dot{x}_{i,j} = g_{i,j,1}(x_{i,1},\Theta_i) + g_{i,j,2}(x_{i,1},\Theta_i)x_{i,2} + \dots + g_{i,j,n}(x_{i,1},\Theta_i)x_{i,n}, \quad j = 2, \dots, n,$$
 (3b)

with $g_{i,j,k}$ analytical functions in Θ_i , $x_{i,1}$ and its derivatives.

Using Equation (3b), the successive derivatives of

$$w_{i} = -\dot{x}_{i,1} + g_{i,1,1}(x_{i,1},\Theta_{i}) + g_{i,1,2}(x_{i,1},\Theta_{i})x_{i,2} + \dots + g_{i,1,n}(x_{i,1},\Theta_{i})x_{i,n} \text{ (see Equation 3a)}$$

134 can be expressed as linear combinations of $x_{i,2}, \ldots, x_{i,n}$:

$$w_i^{(l)} = m_{1,l}(x_{i,1},\Theta_i) + m_{2,l}(x_{i,1},\Theta_i)x_{i,2} + \dots + m_{n,l}(x_{i,1},\Theta_i)x_{i,n}, \quad l \in \mathbb{N}$$

$$\tag{4}$$

We have $(w_i, \dot{w}_i, \dots, w_i^{(n-1)})^T = M(1, x_{i,2}, \dots, x_{i,n})^T$ where $M = (m_{j,l})_{1 \le j \le n, \ 0 \le l \le n-1}$. If det(M) = 0 then a linear combination of the rows of M is null. The last equality shows that the same linear combination of the $(w_i, \dot{w}_i, \dots, w_i^{(n-1)})^T$ is null.

If $det(M) \neq 0$ then $\tilde{M}(w_i, \dot{w}_i, \dots, w_i^{(n-1)})^T = det(M)(1, x_{i,2}, \dots, x_{i,n})^T$ where \tilde{M} is the transposed comatrix of M. This last equality shows, in particular, that a linear combination of $w_i, \dot{w}_i, \dots, w_i^{(n-1)}$ is equal to det(M).

In both cases, we obtain an ARR of the form

$$P_i(x_{i,1}, X_{-i}, \Theta_i) = P_i(x_{i,1}, \Theta_i) + \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_i) w_i^{(k)} = 0 \text{ with } \alpha < n.$$

Equation (2) is then a direct consequence of this last equality and of the definition of w_i .

Proof of Proposition 3.1 gives a way to obtain such ARRs and the expression form (2) will permit
 to define criteria for the target observability. However, the proposed method can be difficult to put

in place since it requires the inversion of a formal matrix leading to complex calculus even in simple examples. When the functions $f_{i,j}$ of System (1) are differential polynomials in the components of X_i , ARRs can be found in using the Rosenfeld-Groebner elimination algorithm implemented in the package Differential Algebra of Maple (Boulier, 1994; Verdière et al., 2015; Verdière and Orange, 2018). Let us see with the FitzHugh-Nagumo model how to obtain the ARR of Proposition 3.1 by this kind of procedure.

Example 1. Consider a complex network made up of three neurons whose dynamics are governed by the FitzHugh–Nagumo (FHN) model (FitzHugh, 1969). In this network, the first two nodes are controlled by a constant input current I_i that models a sensory information (see Figure 2). The entire system of the complex network, noted Γ , is then given by

$$\Gamma \begin{cases}
\Gamma_{1} \begin{cases}
\dot{x}_{1,1} = x_{1,1} - \frac{x_{1,1}^{3}}{3} - x_{1,2} + I_{1}, \\
\dot{x}_{1,2} = \frac{1}{\tau} (x_{1,1} + a - bx_{1,2}). \\
\Gamma_{2} \begin{cases}
\dot{x}_{2,1} = x_{2,1} - \frac{x_{2,1}^{3}}{3} - x_{2,2} + I_{2}, \\
\dot{x}_{2,2} = \frac{1}{\tau} (x_{2,1} + a - bx_{2,2}). \\
\Gamma_{3} \begin{cases}
\dot{x}_{3,1} = x_{3,1} - \frac{x_{3,1}^{3}}{3} - x_{3,2} + e_{31}(x_{1,1} - x_{3,1}) + e_{32}(x_{2,1} - x_{3,1}), \\
\dot{x}_{3,2} = \frac{1}{\tau} (x_{3,1} + a - bx_{3,2}).
\end{cases}$$
(5)

where $x_{1,1}$, $x_{2,1}$ and $x_{3,1}$ represent the membrane potential of the neuron 1, 2 and 3 respectively. Moreover, assume that $x_{3,1}$ is the output of the system Γ , and denote $\Theta \coloneqq (a, b, \tau)$.

For System Γ_3 , $x_{1,1}$ and $x_{2,1}$ can be considered as inputs. The Gröbner-Rosenfeld algorithm applied to System Γ_3 with the elimination order $[\Theta] < [x_{3,1}, x_{1,1}, x_{2,1}] < [x_{3,2}]$ (that consists in eliminating first the state variable $x_{3,2}$ then $x_{2,1}$ and $x_{1,1}$) returns:

$$\tilde{P}_{3}(x_{3,1}) = P_{3}(x_{3,1}) + e_{31}\left(3b(x_{1,1} - x_{3,1}) + 3\tau(\dot{x}_{1,1} - \dot{x}_{3,1})\right) + e_{32}\left(3b(x_{2,1} - x_{3,1}) + 3\tau(\dot{x}_{2,1} - \dot{x}_{3,1})\right) = 0$$
(6)

153 with $P_3(x_{3,1}) = -3 \tau x_{3,1}^2 \dot{x}_{3,1} + 3 \tau \dot{x}_{3,1} - 3 \tau \ddot{x}_{3,1} - 3 x_{3,1} - b x_{3,1}^3 + 3 b x_{3,1} - 3 b \dot{x}_{3,1} - 3 a.$

Identifying (2) and (6) leads to set $h_{3,0} = 3b$, $h_{3,1} = 3\tau$, $c_1(x_{3,1}, x_{1,1}) = e_{31}(x_{1,1} - x_{3,1})$ and $c_2(x_{3,1}, x_{2,1}) = e_{32}(x_{2,1} - x_{3,1})$,

¹⁵⁶ 4 Consequences on target observability

In this section, the ARR (2) is used to present consequences on the target observability from a given set of nodes \mathcal{N} . The ARR, \tilde{P}_i is a differential equation linking $x_{i,1}$ and $x_{j,1}$ for $j \in \mathcal{N}_i^-$ and is



Figure 2: Coupling of three neurons governed by the FitzHugh–Nagumo (FHN) model, where the first two nodes are controlled by constant input currents I_1 and I_2 .

- ¹⁵⁹ supposed to be determined for each node of the network. Recall that the initial condition $X_i(t_0)$,
- i = 1, ..., N is assumed to be known in System (1) and also the derivatives of X_i at t_0 at any order.
- ¹⁶¹ The following corollaries are deduced from these ARRs and the initial condition. They give con-
- ditions ensuring the \mathcal{N} -observability of a given node from a set of nodes \mathcal{N} -observable.

¹⁶³ These corollaries are illustrated by Figure 3.A and 3.B.

Corollary 4.1. Let \mathcal{N} a given set of nodes. If, for all $j \in \mathcal{N}_i^-$, the j^{th} node is \mathcal{N} -observable, then the *i*th node is \mathcal{N} -observable.

Proof. By hypothesis, there exists a surjection from the set of solutions of $(X_j)_{j \in \mathcal{N}}$ on the set of solutions of $(X_j)_{j \in \mathcal{N}_i^-}$. The Picard-Lindelöf theorem, applied to Equation (2), ensures the existence of a surjection from $(X_j)_{j \in \mathcal{N}_i^-}$ to X_i . Consequently, there exists a surjection from the set of solutions of $(X_j)_{j \in \mathcal{N}}$ to X_i .

Example 2. Let take again Example 1. The initial value problem formed of polynomial P_3 (see Equation (6)) and initial conditions $x_{3,1}(t_0)$, $\dot{x}_{3,1}(t_0)$ admits a unique solution $x_{3,1}$ according to the Picard-Lindelöf theorem.

Corollary 4.2. Let \mathcal{N} be a given set of nodes and $j_0 \in \mathcal{N}_i^-$. If the *i*th node and all the *j*th nodes for $j \in \mathcal{N}_i^- \setminus \{j_0\}$ are \mathcal{N} -observable then the j_0^{th} node is \mathcal{N} -observable.

175 Proof. By isolating terms depending on j_0 , the ARR (2) can be rewritten

$$Q(x_{i,1}, X_{-i}, \Theta_i) + \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_i) z^{(k)} = 0$$
(7)

where $z = c_{j_0}(x_{i,1}, x_{j_0,1})$. Equation (7) can be solved with respect to z and z is \mathcal{N} -observable. Since $x_{j_0,1} \rightarrow c_{j_0}(x_{i,1}, x_{j_0,1})$ is a one to one function, X_{j_0} is also \mathcal{N} -observable.

Consequently, there exists a surjection from the set of solutions of $(X_j)_{j \in \{i\} \cup \mathcal{N}_i^- \setminus \{j_0\}}$ to X_{j_0} . As in the proof of Corollary 4.1, we can construct a surjection from the set of solution $(X_j)_{j \in \mathcal{N}}$ to X_{j_0} . **Remark 4.1.** Note that ARR (2) may not depend explicitly on x_{j_0} for $j_0 \in \mathcal{N}_i^-$. In this case, there exists a differential equation linking x_{j_0} and $x_{i,1}$. Consequently, it stays possible to infer the set of solutions of X_{j_0} from the solutions of X_i and the initial condition.

Example 3. Consider again Example 1. Let i = 3 and $j_0 = 2$ and suppose that nodes 1 and 3 are N-observable. The initial value problem composed of the differential equation \tilde{P}_3 and the known initial conditions $x_{2,1}(t_0)$ and $\dot{x}_{2,1}(t_0)$ admits a unique solution $x_{2,1}$.



Figure 3: (A) Illustration of Corollary 4.1. The \mathcal{N} -observability of node *i* is deduced from the one of its in-neighbors (\mathcal{N}_i^-). (B) Illustration of Corollary 4.2. The \mathcal{N} -observability of node j_0 is deduced from the \mathcal{N} -observability of the node *i* and of its in-neighbors, \mathcal{N}_i^- (except the j_0 th).

From any set \mathcal{N} , Corollaries 4.1 and 4.2 are used to define the function ObservableNodes which computes the set of \mathcal{N} -observable nodes. This function is used in the TargetObservability algorithm presented in the next section.

¹⁹⁰ 5 Target observability algorithm

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¹⁹¹ In this section, in order to simplify the notation, the nodes are identified to their indexes.

¹⁹² The algorithm TargetObservability, presented afterwards, is based on Corollaries 4.1 and 4.2.

¹⁹³ This algorithm determines sets of nodes from which the state of a set of target nodes can be ¹⁹⁴ inferred.

Let \mathcal{N}' be a given set of nodes and \mathcal{T} the set of target nodes. The algorithm TargetObservability

- returns the set E of all the subsets $\mathcal{N} \subset \{1, \ldots, N\} \setminus \mathcal{T}$ containing \mathcal{N}' , minimal for inclusion, such
- ¹⁹⁷ that \mathcal{T} is \mathcal{N} -observable. The sets of E are minimal in the sense that, for any subset \mathcal{N}'' of

198	$\{1,\ldots,N\}$ $\land \mathcal{T}$ such that \mathcal{T} is \mathcal{N}'' -observable, there exists at least an element \mathcal{N} of E contained				
199	in \mathcal{N}'' . In order to compute the set E , the algorithm performs a tree transversal to construct				
200	recursively an increasing sequence of sets $\mathcal{N}' = \mathcal{N}_0 \subset \mathcal{N}_1 \subset \cdots \subset \mathcal{N}_m = \mathcal{N}$ until \mathcal{T} is \mathcal{N} -observable.				
201	Further, the algorithm TargetObservability proceeds as follows. Initially, E is assigned to				
202	the empty set $\{\}$ and the algorithm is called with a set \mathcal{N}' of supposed observed nodes. Now, le				
203	us describe any recursive call performed by the algorithm. From a subset $\tilde{\mathcal{N}}$ of $\{1, \ldots, N\} \setminus \mathcal{T}$, this				
204	algorithm tests whether a set of E is included in $\tilde{\mathcal{N}}$. If it is the case, \mathcal{T} is $\tilde{\mathcal{N}}$ -observable but $\tilde{\mathcal{N}}$ is				
205	not minimal for inclusion and no other computation is performed. Otherwise, the algorithm calls				
206	the function ObservableNodes that determines the set $\mathcal{O} \subset \{1, \ldots, N\}$ of $\tilde{\mathcal{N}}$ -observable nodes.				
207	Note that the computation of \mathcal{O} is based on Corollaries 4.1 and 4.2. Two cases appear:				
208 209	 <i>T</i> ⊂ <i>O</i>. In this case, <i>T</i> is <i>N</i>-observable; <i>N</i> is inserted to <i>E</i> and sets of <i>E</i> that are not minimal for inclusion are removed from <i>E</i>. 				
210	• $\mathcal{T} \notin \mathcal{O}$. In this case, for each of the nodes $i \in \{1, \ldots, N\} \setminus (\mathcal{O} \cup \mathcal{T})^{\mathrm{B}}$, a recursive call of th				
211	algorithm is performed with $\tilde{\mathcal{N}} \cup \{i\}$ as input.				
212	The above description is summarized in the following pseudo-code.				
213	TargetObservability ($ ilde{\mathcal{N}}$)				
214	If $\tilde{\mathcal{N}}$ is not included in one of the set of E Then				
215	$_{5} \qquad \mathcal{O}:= \texttt{ObservableNodes}(ilde{\mathcal{N}});$				
216	If $\mathcal{T} \subset \mathcal{O}$ Then				
217	$E \coloneqq E \cup \{\tilde{\mathcal{N}}\} ;$				
218	Remove sets of E which are not minimal for inclusion ;				
219	Else				
220	for $i \in \{1, \dots, N\} \setminus (\mathcal{O} \cup \mathcal{T})$ do (*)				
221	$\mathrm{E} = \texttt{TargetObservability}\;(ilde{\mathcal{N}} \cup \{i\});$				
222	end do;				
223	end if;				
224	end if;				
225	Return <i>E</i> ;				
226	In the next section, we apply the algorithm TargetObservability described in this section on a				

²²⁷ C. elegans chemotaxis neuronal network.

^BIf $\{1, ..., N\}$ \ ($\mathcal{O} \cup \mathcal{T}$) = Ø then $\tilde{\mathcal{N}}$ can not be completed into a set $\mathcal{N}' \subset \{1, ..., N\}$ \ \mathcal{T} so that \mathcal{T} is \mathcal{N}' -observable. In such a case, the loop (*) is not executed.

$_{228}$ 6 Application on a *C. elegans* chemotaxis network

Here we apply our proposed algorithm TargetObservability for the target observability of mus-229 cles in the C. elegans worm. C. elegans is a well-known model organism in neuroscience due to 230 its simple nervous system, made up of 302 neurons and about 7000 synaptic connections, and its 231 fully mapped connectome (White et al., 1986; Varshney et al., 2011). Despite its simplicity, the 232 nematode surprisingly shares many of the general essential human biological features using similar 233 neurotransmitters, channels, and developmental genes (Altun et al., 2020). Moreover, principles 234 that underlie behaviors in C. elegans may also be similar in more complex animals such as hu-235 mans (Chalasani et al., 2007). For these reasons, C. elegans has become a model of reference to 236 investigate how behavior emerges from its underlying physiological processes (Sarma et al., 2018). 237 Thus, recent efforts have been made to build conductance-based models (Hodgkin and Huxley, 238 1952) that reproduce the experimental dynamics of individual neurons in the worm (Naudin et al., 239 2021, 2022a). These models take the form 240

$$\begin{cases} C\dot{V} = -g_{Ca}m_{Ca}h_{Ca}(V - E_{Ca}) - g_{Kir}h_{Kir\infty}(V)(V - E_{K}) - g_{K}m_{K}(V - E_{K}) - g_{L}(V - E_{L}) + I \\ \dot{m}_{Ca} = \frac{m_{Ca\infty}(V) - m_{Ca}}{\tau_{m_{Ca}}}, \quad m_{Ca\infty}(V) = \left(1 + \exp\left(\frac{V_{1/2}^{m_{Ca}} - V}{k_{m_{Ca}}}\right)\right)^{-1} \\ \dot{h}_{Ca} = \frac{h_{Ca\infty}(V) - h_{Ca}}{\tau_{h_{Ca}}}, \quad h_{Ca\infty}(V) = \left(1 + \exp\left(\frac{V_{1/2}^{h_{Ca}} - V}{k_{h_{Ca}}}\right)\right)^{-1} \\ \dot{m}_{K} = \frac{m_{K\infty}(V) - m_{K}}{\tau_{m_{K}}}, \quad m_{K\infty}(V) = \left(1 + \exp\left(\frac{V_{1/2}^{m_{K}} - V}{k_{m_{K}}}\right)\right)^{-1} \\ h_{Kir\infty}(V) = \left(1 + \exp\left(\frac{V_{1/2}^{h_{Kir} - V}}{k_{h_{Kir}}}\right)\right)^{-1} \end{cases}$$
(8)

²⁴¹ where:

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- V, m_{Ca}, h_{Ca} and m_K are the four state variables of the system. In particular, V is the membrane potential of the neuron, which is the variable that characterizes the behavior of the neuron, and m_{Ca} , h_{Ca} and m_K are the activation and inactivation variables of the ion channels;
- *I* is the control that models a sensory information produced by the environment, or an artificial injection current applied by the experimenter;
- g_{ion} and E_{ion} , $ion \in \{Ca, K, Kir, L\}$, are parameters, as well as τ_x , $V_{1/2}^x$, k_x with $x \in \{m_{Ca}, m_K, h_K, h_{Kir}\}$. The values of these parameters depend on the considered neuron

(Naudin et al., 2021, 2022a).

Chemotaxis network and coupling. Some neuronal networks underlying specific behaviors 251 in C. elegans have been cracked using data from the anatomical connectome (White et al., 1986; 252 Varshney et al., 2011), together with powerful experimental techniques and computational tools. 253 Here, we use a neuronal network associated with a chemotaxis behavior (Costalago-Meruelo et al., 254 2018) (Figure 4). Each neuron is arbitrarily named with three capital letters for convention, and a 255 fourth letter L (left) or R (right) (White et al., 1986). The dynamics of each neuron are governed 256 by a model of the form (8). The electrical and chemical synapses are modeled by coupling terms 257 corresponding to the variable I of the first equation of System (8). The electrical synapses are 258 linear, modeled as ohhmic resistances, while chemical synapses are nonlinear with channels gated 259 in the postsynaptic membrane. Their respective expressions are then given by 260

$$I_{ij}^{gap}(V_i, V_j) = g_{gap}(V_i - V_j)$$
$$I_{ij}^{syn}(V_i, V_j) = g_{syn} s_{\infty}(V_j)(V_i - E_{ij})$$

where *i* and *j* denote a post- and pre-synaptic neuron, respectively; g_{gap} , g_{syn} and E_{ij} are parameters; and s_{∞} is a sigmoid function of the form

$$s_{\infty}(V_j) = \frac{1}{1 + \exp\left(\frac{V_{th} - V_j}{V_{slope}}\right)}$$

with V_{th} and V_{slope} two other parameters.

Therefore, using the notations of System (1), the variable I of System (8) is substituted by the coupling term $\sum_{j \in \mathcal{N}_i^-} c_j(V_i, V_j) + I_i$ with $c_j(V_i, V_j) = I_{ij}^{gap}(V_i, V_j) + I_{ij}^{syn}(V_i, V_j)$, where I_i is an eventual artificial control acting on the node i. The three conditions of System (1) are satisfied by Model (8) with the coupling terms c_j .

Application of the TargetObservability algorithm. Let us suppose that the sensory neurons ASEL and ASER are observed and let $\mathcal{T} = \{Muscle\}$ be the target of the set of this network. The algorithm ObservableNodes applied to $\mathcal{N}' = \{ASEL, ASER\}$ ensures that \mathcal{T} is not \mathcal{N}' -observable.

271 An application of Algorithm TargetObservability returns the following sets of neurons:



Figure 4: A neural network underlying a chemotaxis behavior in *C. elegans* (Costalago-Meruelo et al., 2018).

$$\begin{split} E &= \{\{RIAR\}, \{RMD\}, \{AIAL, AIAR\}, \{AIAL, AIBL\}, \{AIAL, AIYL\}, \{AIAL, AIYR, \}, \\ \{AIAL, AIZL\}, \{AIAL, AIZR\}, \{AIAR, AIBL\}, \{AIAR, AIYL\}, \{AIAR, AIYR\}, \\ \{AIAR, AIZL\}, \{AIAR, AIZR\}, \{AIBR, AIYL, AIZR\}, \{AIBR, AIYR, AIZR\}, \\ \{AIBR, AIZL, AIZR\}, \{AIYL, AIZR, AVAR\}, \{AIYL, AIZR, RIBR\}, \\ \{AIYR, AIZR, AVAR\}, \{AIYR, AIZR, RIBR\}, \{AIZL, AIZR, AVAR\}, \\ \{AIZL, AIZR, RIBR\}, \{AIBL, AIBR, AIZR, AVAR\}, \{AIBL, AIBR, AIZR, RIBR\}, \\ \{AIBL, AIZR, AVAR, RIBR\}\}. \end{split}$$

The union of $\mathcal{N}' = \{ASEL, ASER\}$ and of any of these sets turns \mathcal{T} into an observable node^C.

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^CNote that, by construction of Algorithm TargetObservability, any set \mathcal{N}'' containing nodes ASEL and ASER such that \mathcal{T} is an \mathcal{N}'' -observable contains at least one of the sets of E.

The CPU time needed to obtain this output is approximately 1.07 second with a Maple implementation of algorithm TargetObservability on a Intel Quad Core 2.50GHz Processor with 8 Go of RAM.

An example of the propagation of the observability property through the network.

²⁷⁸ In this paragraph, we focus on the propagation of the observability property in the network.

Let us consider the node $\mathcal{T} = \{Muscle\}$ which is $\mathcal{N} = \{ASEL, ASER, AIAL, AIAR\}$ -observable

(See (9)). By tracking the computations performed by the function ObservableNodes, it is possible to obtain each of the steps leading to the observability of \mathcal{T} from the set \mathcal{N} . In this particular case, a propagation of the observability property can be summed up in Table 1.

Node considered	In-neighbors of the node	Corollary used	Deduced observable node
ASER	{AIBL,AIAL,AIAR}	Cor. 4.2	AIBL
AIAL	$\{ASEL, ASER, AIAR, AIZL\}$	Cor. 4.2	AIZL
AIAR	{ASER,AIAL,AIZR}	Cor. 4.2	AIZR
AIBR	{ASEL,ASER,AIAR,AIZL,AIZR}	Cor. 4.1	AIBR
ASEL	{AIYR.AIZL}	Cor. 4.2	AIYR
AIYR	{ASEL,ASER,AIYL}	Cor. 4.2	AIYL
AIBL	{ASEL,ASER,AIAL,AIZL,AIZR,RIBR}	Cor. 4.2	RIBR
RIBR	{AIBR,AIAL}	Cor. 4.2	AVAR
RIAR	{ASEL,AIYR,AIZR,RIBR,AVAR}	Cor. 4.1	RIAR
RMD	{RIAR}	Cor. 4.1	RMD
Muscle	{RMD}	Cor. 4.1	Muscle

Table 1: Propagation of the {ASEL, ASER, AIAL, AIAR}-observability property in the network to the target $\mathcal{T} = \{Muscle\}$ performed by Algorithm TargetObservability.

7 Conclusions and perspectives

Summary. This paper focuses on the target observability, that consists in determining which nodes are needed to infer the state of a target subset. To that end, we present theoretical results based on specific local analytical redundancy relations. These results lead to two observability properties used to develop the algorithm TargetObservability that automatically identify sets of nodes that can infer the state of target ones. Finally, we apply our algorithm for the target observability of a *C. elegans* muscle involved in a chemotaxis behavior.

Perspectives. The observability property test does not tell us how to numerically reconstruct 290 the states of target nodes and it is well-known that different sets of nodes do not provide the 291 same reconstruction quality (Letellier et al., 1998; Montanari and Aguirre, 2020; Sysoeva et al., 292 2021). Nevertheless, our approach currently returns different sets of nodes from which the target 293 set can be reconstructed. A first extension to this work will be to develop methods quantifying the 294 quality of these sets of nodes by developing metrics to choose the best option to reconstruct the 295 target nodes states. Since this paper provides some building blocks for a practical reconstruction 296 of the nodes states, a second extension of the present work will be the development of a state 297 reconstructor, which is still an open challenge for nonlinear systems (Liu and Barabási, 2016). 298

²⁹⁹ Acknowledgments

This work was supported by the ERDF (XTerm Project), Normandie Region (France) and by The LMAH, FR-CNRS-3335.

³⁰² Declaration of competing interests

³⁰³ The authors declare no competing interests.

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