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# Target observability of nonlinear complex networks with linear and nonlinear couplings

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## Abstract

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

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

# 1 Introduction

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

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

There is a long tradition and a substantial literature that deal with the observability and its dual concept, the controllability, of *linear* complex systems (Meng et al., 2023; Aguirre and Letellier, 2016; Wang et al., 2014; Gao et al., 2014; Leitold et al., 2017; Czeizler et al., 2018; Montanari et al., 2022). In such a case, the nodal dynamics and couplings are considered linear, despite the fact that they are fundamentally nonlinear in nature. If these simplifications facilitate the mathematical studies of systems, they are not without consequences (Aguirre et al., 2018). Indeed, some recent works demonstrate the irrelevance of the linear observability and controllability to nonlinear dynamical networks. First, the linearized system could be not controllable, while the original nonlinear system is actually controllable (Liu and Barabási, 2016). Also, linear controllability theory tends to generate information that is not useful for nonlinear control of many complex systems. For instance, linear controllability may give great importance to some nodes for the controllability of the system while these nodes are theoretically unimportant (Jiang and Lai, 2019). Last, linear observability can highly underestimate the number of sensors necessary to retrieve the state of the variables of the original nonlinear system (Letellier et al., 2018b). Taken together, these evidences urged the development of mathematical tools capable of dealing with the nonlinear observability.

In this context, some approaches dealing with the nonlinear observability have emerged from different perspectives. Liu et al. (2013) proposed a graph-theoretic approach, based on an inference

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

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

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

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

## 90 2 Problem statement

91 In this paper, we consider directed complex networks formed of  $N$  nonlinear nodes coupled through  
92 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  $X_i = (x_{i,1}, \dots, x_{i,n})^T$  of  
 97 the  $i$ th node ( $i = 1, \dots, N$ ) takes the form:

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

98 where

- 99 •  $f_{i,j}(X_i, \Theta_i)$  are linear combinations of the state variables  $x_{i,2}, \dots, x_{i,n}$  whose coefficients are  
 100 analytical functions in  $\Theta_i$ ,  $x_{i,1}$  and its derivatives<sup>A</sup>;
- 101 • the initial states  $X_i(t_0)$ ,  $i = 1, \dots, N$ , of the network are supposed to be known at time  $t_0$ ;
- 102 •  $\sum_{j \in \mathcal{N}_i^-} c_j(x_{i,1}, x_{j,1})$  is a coupling term with  $\mathcal{N}_i^-$  the in-neighbors set of the node  $i$  (that is, the  
 103 nodes whose edge comes into the node  $i$ ), and  $c_j : \mathbb{R}^2 \rightarrow \mathbb{R}$  is an infinitely differentiable such  
 104 that, for all  $x_{i,1} \in \mathbb{R}$ ,  $x_{j,1} \rightarrow c_j(x_{i,1}, x_{j,1})$  is a one to one function.

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

107 It is worth noting that System (1) describes a large class of models in real-life problems. In  
 108 this paper, we emphasize on the neuroscience field in which most of neuron models describe the  
 109 dynamics of the neuron voltages following a system of the form (1). Some examples are the large  
 110 class of conductance-based models that use the Hodgkin–Huxley formalism (Hodgkin and Huxley,  
 111 1952), the Hindmarsh–Rose model (Hindmarsh and Rose, 1984), the Fitzhugh–Nagumo model  
 112 (FitzHugh, 1969), or the phenomenological non-spiking models (Naudin et al., 2022b,c).

113

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

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

---

<sup>A</sup>An 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  $x_{i,3}$ .

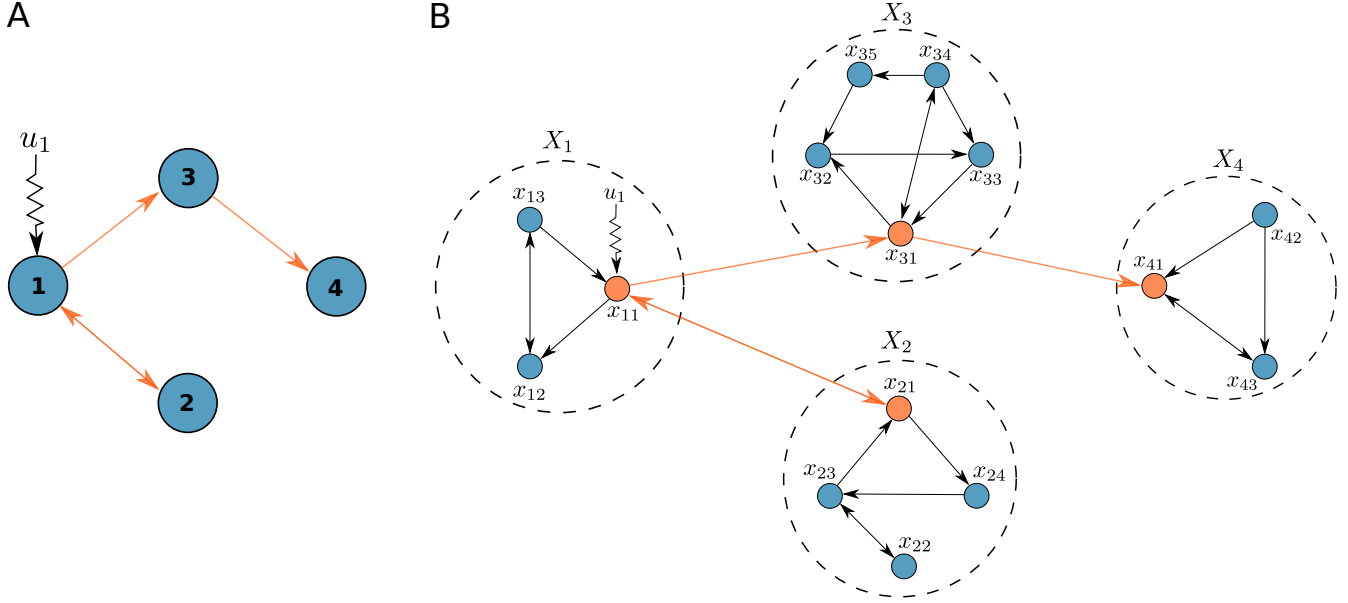


Figure 1: **(A)** Example of a complex network composed of 4 nodes ( $N = 4$ ) coupled through directed edges, and controlled through the first node. **(B)** Full complex network presented in (A) with the set of dynamical systems associated with each node, and the intra-node (in black) and inter-node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

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

### 124 3 Analytical redundancy relations of nodes

125 The result presented in this section gives the general form of the differential equation linking the  
 126 node  $i$  to the nodes  $j \in \mathcal{N}_i^-$ . In the literature, these relations linking the parameters, the outputs,  
 127 and the inputs (and their derivatives) of the system are classically called Analytical Redundancy  
 128 Relations (ARR) (Staroswiecki and Comtet-Varga, 2001; Travé-Massuyes et al., 2006; Verdière  
 129 et al., 2015).

130 **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

$$\tilde{P}_i(x_{i,1}, X_{-i}, \Theta_i) = P_i(x_{i,1}, \Theta_i) + \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_i) u_i^{(k)} + \sum_{j \in \mathcal{N}_i^-} \sum_{k=0}^{\alpha} h_{i,k}(x_{i,1}, \Theta_i) c_j(x_{i,1}, x_{j,1})^{(k)} = 0 \quad (2)$$

131 where

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

133 •  $\alpha < n$  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

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

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

Using Equation (3b), the successive derivatives of

$$w_i = -\dot{x}_{i,1} + g_{i,1,1}(x_{i,1}, \Theta_i) + g_{i,1,2}(x_{i,1}, \Theta_i)x_{i,2} + \cdots + g_{i,1,n}(x_{i,1}, \Theta_i)x_{i,n} \quad (\text{see Equation 3a})$$

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

$$w_i^{(l)} = m_{1,l}(x_{i,1}, \Theta_i) + m_{2,l}(x_{i,1}, \Theta_i)x_{i,2} + \cdots + m_{n,l}(x_{i,1}, \Theta_i)x_{i,n}, \quad l \in \mathbb{N} \quad (4)$$

We have  $(w_i, \dot{w}_i, \dots, w_i^{(n-1)})^T = M(1, x_{i,2}, \dots, x_{i,n})^T$  where  $M = (m_{j,l})_{1 \leq j \leq n, 0 \leq l \leq n-1}$ .

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

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

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

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

138 in place since it requires the inversion of a formal matrix leading to complex calculus even in simple  
 139 examples. When the functions  $f_{i,j}$  of System (1) are differential polynomials in the components of  
 140  $X_i$ , ARR can be found in using the Rosenfeld-Groebner elimination algorithm implemented in the  
 141 package Differential Algebra of Maple (Boulier, 1994; Verdière et al., 2015; Verdière and Orange,  
 142 2018). Let us see with the FitzHugh-Nagumo model how to obtain the ARR of Proposition 3.1 by  
 143 this kind of procedure.

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

$$\Gamma \left\{ \begin{array}{l} \Gamma_1 \left\{ \begin{array}{l} \dot{x}_{1,1} = x_{1,1} - \frac{x_{1,1}^3}{3} - x_{1,2} + I_1, \\ \dot{x}_{1,2} = \frac{1}{\tau}(x_{1,1} + a - bx_{1,2}). \end{array} \right. \\ \Gamma_2 \left\{ \begin{array}{l} \dot{x}_{2,1} = x_{2,1} - \frac{x_{2,1}^3}{3} - x_{2,2} + I_2, \\ \dot{x}_{2,2} = \frac{1}{\tau}(x_{2,1} + a - bx_{2,2}). \end{array} \right. \\ \Gamma_3 \left\{ \begin{array}{l} \dot{x}_{3,1} = x_{3,1} - \frac{x_{3,1}^3}{3} - x_{3,2} + e_{31}(x_{1,1} - x_{3,1}) + e_{32}(x_{2,1} - x_{3,1}), \\ \dot{x}_{3,2} = \frac{1}{\tau}(x_{3,1} + a - bx_{3,2}). \end{array} \right. \end{array} \right. \quad (5)$$

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

150 For System  $\Gamma_3$ ,  $x_{1,1}$  and  $x_{2,1}$  can be considered as inputs. The Gröbner-Rosenfeld algorithm  
 151 applied to System  $\Gamma_3$  with the elimination order  $[\Theta] < [x_{3,1}, x_{1,1}, x_{2,1}] < [x_{3,2}]$  (that consists in  
 152 eliminating first the state variable  $x_{3,2}$  then  $x_{2,1}$  and  $x_{1,1}$ ) returns:

$$\tilde{P}_3(x_{3,1}) = P_3(x_{3,1}) + e_{31}(3b(x_{1,1} - x_{3,1}) + 3\tau(\dot{x}_{1,1} - \dot{x}_{3,1})) + e_{32}(3b(x_{2,1} - x_{3,1}) + 3\tau(\dot{x}_{2,1} - \dot{x}_{3,1})) = 0 \quad (6)$$

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

154 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  
 155  $c_2(x_{3,1}, x_{2,1}) = e_{32}(x_{2,1} - x_{3,1})$ ,

## 156 4 Consequences on target observability

157 In this section, the ARR (2) is used to present consequences on the target observability from a  
 158 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



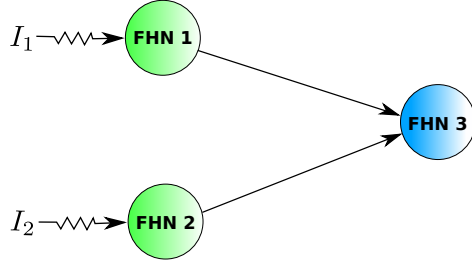


Figure 2: Coupling of three neurons governed by the FitzHugh–Nagumo (FHN) model, where the first two nodes are controlled by constant input currents  $I_1$  and  $I_2$ .

159 supposed to be determined for each node of the network. Recall that the initial condition  $X_i(t_0)$ ,  
 160  $i = 1, \dots, N$  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 ARR and the initial condition. They give con-  
 162 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.

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

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

170 **Example 2.** *Let take again Example 1. The initial value problem formed of polynomial  $\tilde{P}_3$  (see*  
 171 *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*  
 172 *the Picard-Lindelöf theorem.*

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

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

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

176 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  
 177  $x_{j_0,1} \rightarrow c_{j_0}(x_{i,1}, x_{j_0,1})$  is a one to one function,  $X_{j_0}$  is also  $\mathcal{N}$ -observable.

178 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  
 179 in the proof of Corollary 4.1, we can construct a surjection from the set of solution  $(X_j)_{j \in \mathcal{N}}$  to  $X_{j_0}$ .

180 **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  
 181 exists a differential equation linking  $x_{j_0}$  and  $x_{i,1}$ . Consequently, it stays possible to infer the set of  
 182 solutions of  $X_{j_0}$  from the solutions of  $X_i$  and the initial condition.

183 □

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

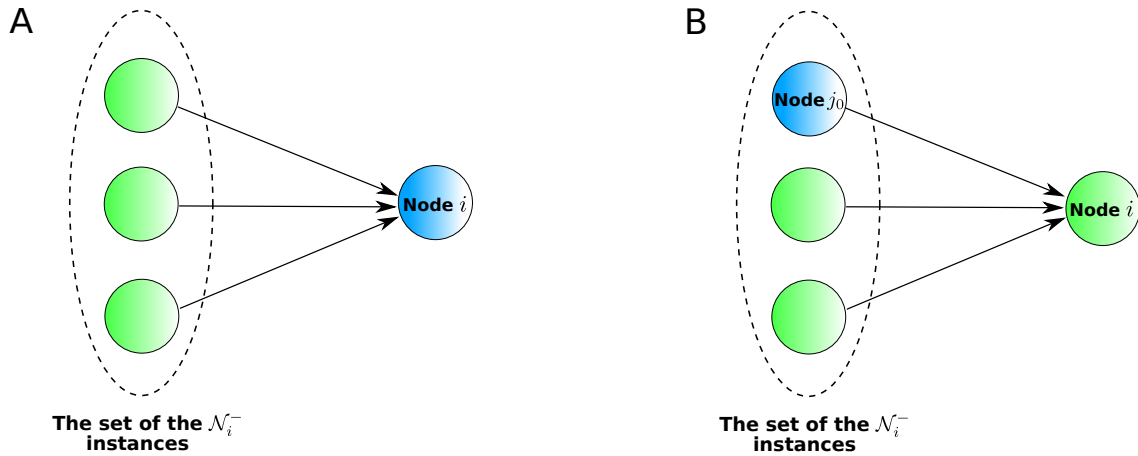


Figure 3: **(A)** Illustration of Corollary 4.1. The  $\mathcal{N}$ -observability of node  $i$  is deduced from the one of its in-neighbors ( $\mathcal{N}_i^-$ ). **(B)** Illustration of Corollary 4.2. The  $\mathcal{N}$ -observability of node  $j_0$  is deduced from the  $\mathcal{N}$ -observability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

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

## 190 5 Target observability algorithm

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.

195 Let  $\mathcal{N}'$  be a given set of nodes and  $\mathcal{T}$  the set of target nodes. The algorithm `TargetObservability`  
 196 returns the set  $E$  of all the subsets  $\mathcal{N} \subset \{1, \dots, N\} \setminus \mathcal{T}$  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  $\{1, \dots, N\} \setminus \mathcal{T}$  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  $\mathcal{N}' = \mathcal{N}_0 \subset \mathcal{N}_1 \subset \dots \subset \mathcal{N}_m = \mathcal{N}$  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, let  
 203 us describe any recursive call performed by the algorithm. From a subset  $\tilde{\mathcal{N}}$  of  $\{1, \dots, N\} \setminus \mathcal{T}$ , 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  $\tilde{\mathcal{N}}$   
 205 is not minimal for inclusion and no other computation is performed. Otherwise, the algorithm calls  
 206 the function `ObservableNodes` that determines the set  $\mathcal{O} \subset \{1, \dots, N\}$  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 •  $\mathcal{T} \subset \mathcal{O}$ . In this case,  $\mathcal{T}$  is  $\tilde{\mathcal{N}}$ -observable;  $\tilde{\mathcal{N}}$  is inserted to  $E$  and sets of  $E$  that are not minimal  
 209 for inclusion are removed from  $E$ .
- 210 •  $\mathcal{T} \not\subset \mathcal{O}$ . In this case, for each of the nodes  $i \in \{1, \dots, N\} \setminus (\mathcal{O} \cup \mathcal{T})^{\text{B}}$ , a recursive call of this  
 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 ( $\tilde{\mathcal{N}}$ ) _____
214 If  $\tilde{\mathcal{N}}$  is not included in one of the set of  $E$  Then
215      $\mathcal{O} := \text{ObservableNodes}(\tilde{\mathcal{N}})$ ;
216     If  $\mathcal{T} \subset \mathcal{O}$  Then
217          $E := E \cup \{\tilde{\mathcal{N}}\}$  ;
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              $E = \text{TargetObservability}(\tilde{\mathcal{N}} \cup \{i\})$ ;
222         end do ;
223     end if ;
224 end if ;
225 Return  $E$  ; _____
  
```

226 In the next section, we apply the algorithm `TargetObservability` described in this section on a  
 227 *C. elegans* chemotaxis neuronal network.

---

<sup>B</sup>If  $\{1, \dots, N\} \setminus (\mathcal{O} \cup \mathcal{T}) = \emptyset$  then  $\tilde{\mathcal{N}}$  can not be completed into a set  $\mathcal{N}' \subset \{1, \dots, N\} \setminus \mathcal{T}$  so that  $\mathcal{T}$  is  $\mathcal{N}'$ -observable. In such a case, the loop (\*) is not executed.

## 6 Application on a *C. elegans* chemotaxis network

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

$$\begin{cases} C\dot{V} = -g_{Ca}m_{Ca}h_{Ca}(V - E_{Ca}) - g_{Kir}h_{Kir\infty}(V)(V - E_K) - g_Km_K(V - E_K) - g_L(V - E_L) + I \\ \dot{m}_{Ca} = \frac{m_{Ca\infty}(V) - m_{Ca}}{\tau_{m_{Ca}}}, \quad m_{Ca\infty}(V) = \left(1 + \exp\left(\frac{V^{m_{Ca}} - V}{k_{m_{Ca}}}\right)\right)^{-1} \\ \dot{h}_{Ca} = \frac{h_{Ca\infty}(V) - h_{Ca}}{\tau_{h_{Ca}}}, \quad h_{Ca\infty}(V) = \left(1 + \exp\left(\frac{V^{h_{Ca}} - V}{k_{h_{Ca}}}\right)\right)^{-1} \\ \dot{m}_K = \frac{m_{K\infty}(V) - m_K}{\tau_{m_K}}, \quad m_{K\infty}(V) = \left(1 + \exp\left(\frac{V^{m_K} - V}{k_{m_K}}\right)\right)^{-1} \\ h_{Kir\infty}(V) = \left(1 + \exp\left(\frac{V^{h_{Kir}} - V}{k_{h_{Kir}}}\right)\right)^{-1} \end{cases} \quad (8)$$

where:

- $V$ ,  $m_{Ca}$ ,  $h_{Ca}$  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  $\tau_x$ ,  $V_{1/2}^x$ ,  $k_x$  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 in *C. elegans* have been cracked using data from the anatomical connectome (White et al., 1986; Varshney et al., 2011), together with powerful experimental techniques and computational tools. Here, we use a neuronal network associated with a chemotaxis behavior (Costalago-Meruelo et al., 2018) (Figure 4). Each neuron is arbitrarily named with three capital letters for convention, and a fourth letter L (left) or R (right) (White et al., 1986). The dynamics of each neuron are governed by a model of the form (8). The electrical and chemical synapses are modeled by coupling terms corresponding to the variable  $I$  of the first equation of System (8). The electrical synapses are linear, modeled as ohmic resistances, while chemical synapses are nonlinear with channels gated in the postsynaptic membrane. Their respective expressions are then given by

$$I_{ij}^{gap}(V_i, V_j) = g_{gap}(V_i - V_j)$$

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

where  $i$  and  $j$  denote a post- and pre-synaptic neuron, respectively;  $g_{gap}$ ,  $g_{syn}$  and  $E_{ij}$  are parameters; and  $s_{\infty}$  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. An application of Algorithm `TargetObservability` returns the following sets of neurons:

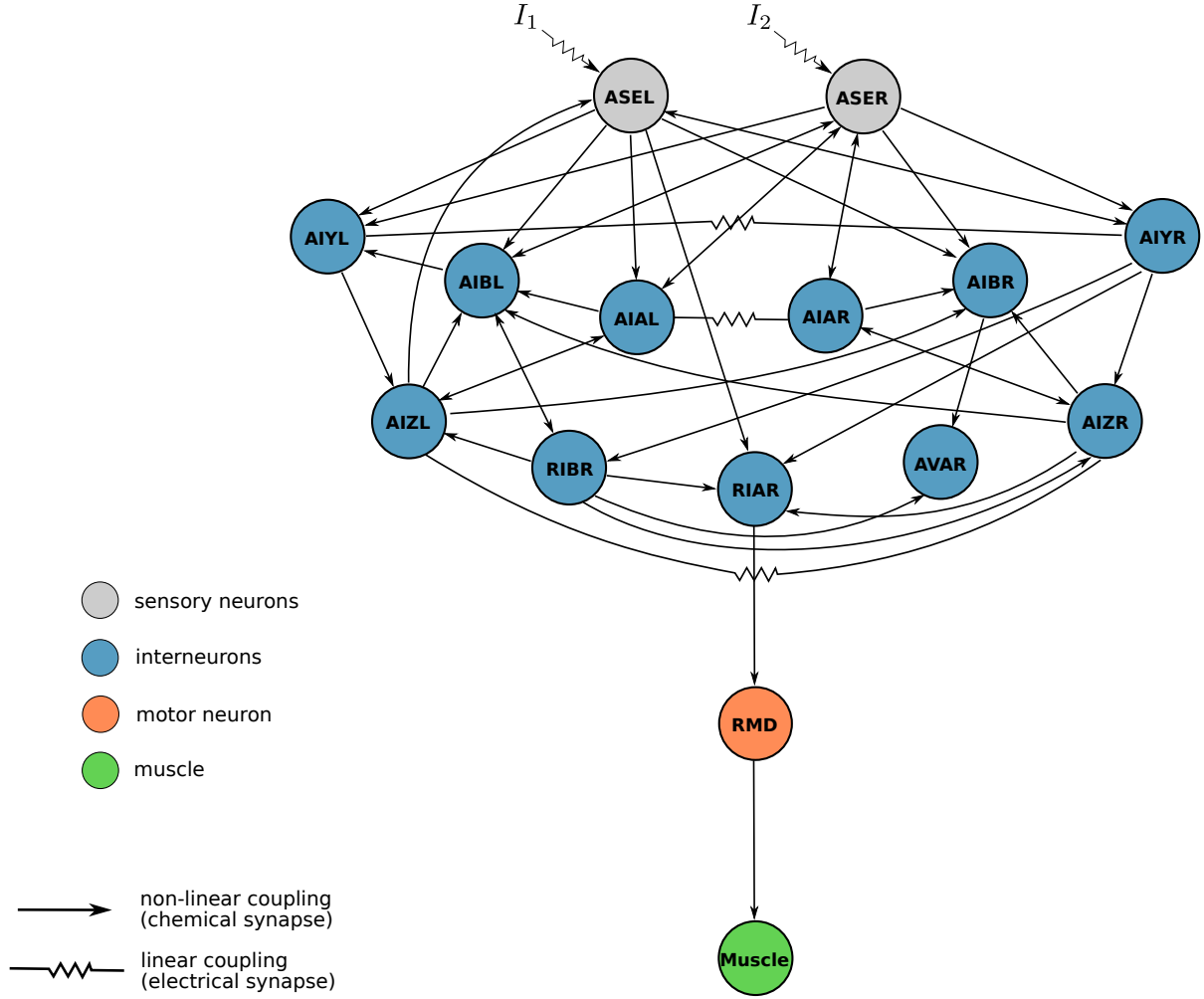


Figure 4: A neural network underlying a chemotaxis behavior in *C. elegans* (Costalago-Meruelo et al., 2018).

$$\begin{aligned}
 E = & \{ \{RIAR\}, \{RMD\}, \{AIAL, AIAR\}, \{AIAL, AIBL\}, \{AIAL, AIYL\}, \{AIAL, AIYR\}, \\
 & \{AIAL, AIZL\}, \{AIAL, AIZR\}, \{AIAR, AIBL\}, \{AIAR, AIYL\}, \{AIAR, AIYR\}, \\
 & \{AIAR, AIZL\}, \{AIAR, AIZR\}, \{AIBR, AIYL, AIZR\}, \{AIBR, AIYR, AIZR\}, \\
 & \{AIBR, AIZL, AIZR\}, \{AIYL, AIZR, AVAR\}, \{AIYL, AIZR, RIBR\}, \\
 & \{AIYR, AIZR, AVAR\}, \{AIYR, AIZR, RIBR\}, \{AIZL, AIZR, AVAR\}, \\
 & \{AIZL, AIZR, RIBR\}, \{AIBL, AIBR, AIZR, AVAR\}, \{AIBL, AIBR, AIZR, RIBR\}, \\
 & \{AIBL, AIZR, AVAR, RIBR\} \}.
 \end{aligned} \tag{9}$$

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

273

<sup>C</sup>Note 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  $E$ .

274 The CPU time needed to obtain this output is approximately 1.07 second with a Maple im-  
 275 plementation of algorithm `TargetObservability` on a Intel Quad Core 2.50GHz Processor with  
 276 8 Go of RAM.

277 **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.  
 279 Let us consider the node  $\mathcal{T} = \{Muscle\}$  which is  $\mathcal{N} = \{ASEL, ASER, AIAL, AIAR\}$ -observable  
 280 (See (9)). By tracking the computations performed by the function `ObservableNodes`, it is possible  
 281 to obtain each of the steps leading to the observability of  $\mathcal{T}$  from the set  $\mathcal{N}$ . In this particular  
 282 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`.

283 **7 Conclusions and perspectives**

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

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

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## 302 **Declaration of competing interests**

303 The authors declare no competing interests.



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