A NOTE ON SHAPLEY RATINGS IN BRAIN NETWORKS

By

M. Musegaas, B.J. Dietzenbacher, P.E.M. Borm

11 July 2016

ISSN 0924-7815
ISSN 2213-9532
A note on Shapley ratings in brain networks

M. Musegaas*† B.J. Dietzenbacher* P.E.M. Borm*

July 7, 2016

Abstract

We consider the problem of computing the influence of a neuronal structure in a brain network. Abraham, Kötter, Krummack, and Wanke (2006) computed this influence by using the Shapley value of a coalitional game corresponding to a directed network as a rating. Kötter, Reid, Krummack, Wanke, and Sporns (2007) applied this rating to large-scale brain networks, in particular to the macaque visual cortex and the macaque prefrontal cortex. We introduce an alternative coalitional game that is more intuitive from a game theoretical point of view. We use the Shapley value of this game as an alternative rating to analyze the macaque brain networks and corroborate the findings of Kötter et al. (2007). Moreover, we show how missing information on the existence of certain connections can readily be incorporated into this game and the corresponding Shapley rating.

Keywords: brain networks, coalitional games, Shapley value

1 Introduction

In this paper we study the influence of a single neuronal structure on the connectivity structure of the whole brain network. The aim is to contribute to the methodology proposed by Abraham et al. (2006) from a game theoretical perspective. Cooperative game theory analyzes the importance of players in a joint collaboration structure by taking into account the possibility of cooperation in subgroups or coalitions. Von Neumann and Morgenstern (1944) introduced the model of a coalitional game, in which each coalition is assigned a worth reflecting what this coalition can achieve if it acts on its own. In the context of brain networks, the Shapley value (cf. Shapley (1953)) can be applied to measure the influence of each neuronal structure in a brain network. This measure depends on the corresponding coalitional game.

In the coalitional game proposed by Abraham et al. (2006) the worth of a coalition of vertices (neuronal structures) is defined by the number of strongly connected components in its induced subnetwork (within the whole brain network). We will illustrate that this coalitional game is counter-intuitive from a game theoretical point of view as it does not satisfy the two basic properties of superadditivity and monotonicity. Moreover,

*CentER and Departement of Econometrics and Operations Research Tilburg University, P.O. Box 90153, 5000 LE Tilburg, The Netherlands
†Correspondence to: m.musegaas@tilburguniversity.edu
the Shapley value of this game does not specify the relative influence of the neuronal structures.

In this paper we introduce an alternative coalitional game which resolves these issues.
We discuss specific features of this game in small networks and apply our model to the large-scale brain networks considered by Kötter et al. (2007). Generally speaking, our results corroborate the findings of Kötter et al. (2007). Besides, since missing information on possible connections in a brain network is a common problem (cf. Kötter and Stephan (2003)), we illustrate how our new approach allows for a direct incorporation of probabilistic considerations.

2 Shapley ratings in brain networks

A brain network is a directed graph \((N, A)\) where \(N\) is a set of vertices, representing a set of neuronal structures, and \(A\) is a set of arcs, representing the connections between the neuronal structures. Let \(\overline{A}\) denote all ordered pairs \((i, j)\) of vertices in \(N\) for which there exists a directed path from \(i\) to \(j\) in \((N, A)\). A graph \((N, A)\) is called strongly connected if for every two vertices \(i\) and \(j\) in \(N\) there is a directed path from \(i\) to \(j\) and from \(j\) to \(i\) in \((N, A)\), i.e., if \(\overline{A}\) contains all ordered pairs in \(N\). The induced subgraph \((S, A[S])\) is a graph where a subset \(S \subseteq N\) is the set of vertices and \(A[S]\) is the set of arcs consisting of any arc in \(A\) whose starting and end point are both in \(S\). A strongly connected component is a maximal induced subgraph which is strongly connected, i.e., there is no other strongly connected subgraph containing this strongly connected component. Let \(\text{SCC}(N, A)\) denote the number of strongly connected components in graph \((N, A)\).

Example 2.1. Consider the brain network \((N, A)\) with \(N = \{1, 2, 3, 4\}\) illustrated below.1

\[
\begin{align*}
&1 \\
&\downarrow \\
&2 \\
&\downarrow \\
&3 \\
&\downarrow \\
&4 \\
&\downarrow \\
&1
\end{align*}
\]

Note that \((N, A)\) is strongly connected because for every vertex in the graph there exists a directed path to every other vertex. However, the subgraph induced by \(\{1, 2, 3\}\) is not strongly connected and we have

\[
\overline{A}[^{\{1, 2, 3\}}] = \{(1, 2), (1, 3), (2, 1), (2, 3)\}.
\]

Note that \(\text{SCC}(\{1, 2, 3\}, A[^{\{1, 2, 3\}}]) = 2\) because the subgraph induced by \(\{1, 2, 3\}\) consists of two strongly connected components: the subgraphs induced by \(\{1, 2\}\) and \(\{3\}\).

A coalitional game is a pair \((N, v)\) where \(N\) denotes a non-empty, finite set of players and \(v\) is a function which assigns a number to each subset \(S \subseteq N\) (also called a coalition). By convention, \(v(\emptyset) = 0\). Abraham et al. (2006) introduced a coalitional game \((N, w^A)\) corresponding to a brain network \((N, A)\) defined by

\[
w^A(S) = \text{SCC}(S, A[S]),
\]

1This instance of a brain network is also used in Example 1 in Section 3.1 of Moretti (2013).
for all $S \subseteq N$. Hence, the worth of a coalition in $w^A$ is defined by the number of strongly connected components in its induced subgraph.

Alternatively, we define the brain network game $(N, v^A)$ corresponding to $(N, A)$ by

$$v^A(S) = |A[S]|,$$

for all $S \subseteq N$. Hence, the worth of a coalition $S$ in $v^A$ is defined by the number of ordered pairs $(i, j)$ of vertices in $S$ for which there exists a directed path from $i$ to $j$ in $(S, A[S])$.

Two basic properties for coalitional games are superadditivity and monotonicity. A coalitional game is called monotonic if the worth of a coalition increases when the coalition grows, and called superadditive if breaking up a coalition into parts does not pay. From a game theoretical perspective it is desirable that coalitional games satisfy these two basic properties since they provide a clear incentive for cooperation in the grand coalition and thus provide a motivation to focus on fairly allocating the worth of the grand coalition. Unfortunately, these properties are not satisfied by the coalitional game $(N, w^A)$. In contrast, the brain network game $(N, v^A)$ does satisfy monotonicity and superadditivity. This is illustrated in the following example.

**Example 2.2.** Reconsider the brain network $(N, A)$ presented in Example 2.1. The worth of every coalition in the games $(N, w^A)$ and $(N, v^A)$ is presented below.

<table>
<thead>
<tr>
<th>$S$</th>
<th>{1}</th>
<th>{2}</th>
<th>{3}</th>
<th>{4}</th>
<th>{1,2}</th>
<th>{1,3}</th>
<th>{1,4}</th>
<th>{2,3}</th>
<th>{2,4}</th>
<th>{3,4}</th>
<th>{1,2,3}</th>
<th>{1,2,4}</th>
<th>{1,3,4}</th>
<th>{2,3,4}</th>
<th>{1,2,3,4}</th>
</tr>
</thead>
<tbody>
<tr>
<td>$w^A(S)$</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>$v^A(S)$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>6</td>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>

Note that $(N, w^A)$ is not monotonic since $\{3, 4\} \subset \{2, 3, 4\}$ but nevertheless

$$w^A(\{3, 4\}) = 2 > 1 = w^A(\{2, 3, 4\}).$$

Note that $(N, w^A)$ is also not superadditive since, e.g.,

$$w^A(\{1, 2\}) + w^A(\{3, 4\}) = 3 > 1 = w^A(\{1, 2, 3, 4\}).$$

It is readily checked that $(N, v^A)$ is both monotonic and superadditive. △

The Shapley value (cf. Shapley (1953)) of a coalitional game $(N, v)$ is for all $i \in N$ defined by

$$\Phi_i(v) = \sum_{S \subseteq N \setminus \{i\}} p_S (v(S \cup \{i\}) - v(S)),$$

where $p_S = \frac{|S|!|N| - |S| - 1|!}{|N|!}$. Hence, the Shapley value looks at the marginal contributions of a player to all possible coalitions. The weight $p_S$ is such that all marginal contributions are weighted adequately to obtain an efficient allocation of the worth of the grand coalition.

In the context of coalitional games corresponding to brain networks, the Shapley value can be interpreted as a measure for the influence of a neuronal structure. Abraham et al. (2006) considered the Shapley value $\Phi(w^A)$ as a rating for the neuronal structures in a brain network. Similarly, we consider the Shapley value $\Phi(v^A)$ as a rating.
Example 2.3. Reconsider the coalitional games \((N, w^A)\) and \((N, v^A)\) of Example 2.2. The Shapley rating \(\Phi(w^A)\) is given by
\[
\Phi(w^A) = \left(\frac{1}{2}, -\frac{1}{6}, \frac{1}{3}, \frac{1}{3}\right),
\]
while the Shapley rating \(\Phi(v^A)\) is given by
\[
\Phi(v^A) = \left(2\frac{1}{6}, 4\frac{1}{6}, 2\frac{5}{6}, 2\frac{5}{6}\right),
\]
both determining a ranking \((2, 3, 4, 1)\) or \((2, 4, 3, 1)\) (there is a tie for the second highest ranking). We note that a lower Shapley rating in \(w^A\) indicates a higher influence in a brain network. On the contrary, a higher Shapley rating in \(v^A\) indicates a higher influence.

Since a Shapley rating in \(w^A\) can be negative, as is the case in this example, it is not possible to determine the relative influence of two vertices on the basis of \(\Phi(w^A)\). On the other hand, a Shapley rating in \(v^A\) can not be negative by definition. Therefore, using \(\Phi(v^A)\), we can say that the influence of vertex 2 in the brain network \((N, A)\) is almost twice as large as the influence of vertex 1. △

A common problem in the analysis of brain networks is the fact that it is not known whether some specific connections (arcs) are present or not (cf. Kötter and Stephan (2003)). Using a certain probabilistic knowledge about these unknown connections, this lack of information can readily be incorporated in the brain network game.

We assume that each possible arc \((i, j)\) is present with probability \(p_{ij} \in [0, 1]\). Clearly, for each present arc we set \(p_{ij} = 1\) and for each absent arc we set \(p_{ij} = 0\). All probabilities are summarized into a vector \(p\). Given such a vector \(p\), we define the \textit{stochastic brain network game} \((N, v^p)\) in which the worth of a coalition equals the expected (in the probabilistic sense) number of ordered pairs for which there exists a directed path in its induced subgraph.

Example 2.4. Reconsider the brain network presented in Example 2.1. Only now suppose that the arcs \((1, 4)\) and \((3, 1)\) are present with probability \(p_{14}\) and \(p_{31}\), respectively. The complete corresponding vector \(p\) can be found below.

<table>
<thead>
<tr>
<th>(i, j)</th>
<th>(1, 2)</th>
<th>(1, 3)</th>
<th>(1, 4)</th>
<th>(2, 1)</th>
<th>(2, 3)</th>
<th>(2, 4)</th>
<th>(3, 1)</th>
<th>(3, 2)</th>
<th>(3, 4)</th>
<th>(4, 1)</th>
<th>(4, 2)</th>
<th>(4, 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(p_{ij})</td>
<td>1 0</td>
<td>(p_{14})</td>
<td>1 1 0</td>
<td>(p_{31})</td>
<td>0 1 0 1 0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In total there are four possible brain networks. These different brain networks are illustrated below and the corresponding probabilities for those networks are \(p_{14}p_{31}\), \((1-p_{14})p_{31}\), \(p_{14}(1-p_{31})\) and \((1-p_{14})(1-p_{31})\) for (a), (b), (c), and (d), respectively.

\footnote{Because of a mistake in the worth of \(w^A(\{1, 2, 3\})\), the Shapley value is incorrectly stated by Moretti (2013).}
In order to calculate the worth of coalition \( \{1, 3, 4\} \) in the corresponding stochastic brain network game \((N, v^p)\) we take the following weighted averages

\[
v^p(\{1, 3, 4\}) = p_{14}p_{31} \cdot v^{A1}(\{1, 3, 4\}) + (1 - p_{14})p_{31} \cdot v^{A2}(\{1, 3, 4\}) \\
+ p_{14}(1 - p_{31}) \cdot v^{A3}(\{1, 3, 4\}) + (1 - p_{14})(1 - p_{31}) \cdot v^{A4}(\{1, 3, 4\}) \\
= p_{14}p_{31} \cdot 3 + (1 - p_{14})p_{31} \cdot 2 + p_{14}(1 - p_{31}) \cdot 2 + (1 - p_{14})(1 - p_{31}) \cdot 1 \\
= 1 + p_{14} + p_{31}.
\]

The worth of every coalition is presented below.

\[
\begin{array}{cccccccccccc}
S & \{1\} & \{2\} & \{3\} & \{4\} & \{1, 2\} & \{1, 3\} & \{1, 4\} & \{2, 3\} & \{2, 4\} & \{3, 4\} & \{1, 2, 3\} & \{1, 2, 4\} & \{1, 3, 4\} & \{2, 3, 4\} & \{1, 2, 3, 4\} \\
\hline
v^p(S) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & p_{31} & p_{14} & 1 & 1 & 1 & 1 & 1 \n+ 2p_{31} & 4 + 2p_{14} & 1 + p_{14} + p_{31} & 6 & 12
\end{array}
\]

The Shapley rating of the game \((N, v^p)\) is given by

\[
\Phi_1(v^p) = 2\frac{1}{6} + \frac{1}{2}p_{14} + \frac{1}{3}p_{31}, \\
\Phi_2(v^p) = 4\frac{1}{6} - \frac{1}{6}p_{14} - \frac{1}{6}p_{31}, \\
\Phi_3(v^p) = 2\frac{5}{6} - \frac{1}{2}p_{14} + \frac{1}{3}p_{31}, \\
\Phi_4(v^p) = 2\frac{1}{6} + \frac{1}{3}p_{14} - \frac{1}{2}p_{31}.
\]

Fore example, if \(p_{14} = \frac{1}{2}\) and \(p_{31} = \frac{1}{3}\), then

\[
\Phi(v^p) = \left(\frac{2}{3}, \frac{1}{3}, \frac{2}{3}, \frac{2}{3}, \frac{2}{3}\right),
\]

with corresponding ranking \((2, 4, 3, 1)\).

\[\triangle\]

3 Results and discussion

In this section we apply the Shapley rating based on the brain network game \((N, v^A)\) to the two large-scale brain networks considered by Kötter et al. (2007) and we compare the results.

The first large-scale brain network is the macaque visual cortex with thirty neuronal structures as illustrated in Figure 1 of Kötter et al. (2007). The ranking of the five brain regions with the highest Shapley rating obtained by means of the coalitional games \((N, w^A)\) and \((N, v^A)\) can be found below in (a) and (b) respectively.

\[
\begin{array}{ll}
{\text{ Ranking}} & {\text{ Brain region}} \\
1. & V4 \\
2. & FEF \\
3. & 46 \\
4. & V2 \\
5. & Vp
\end{array}
\]

\[
\begin{array}{ll}
{\text{ Ranking}} & {\text{ Brain region}} \\
1. & V4 \\
2. & FEF \\
3. & Vp \\
4. & V2 \\
5. & 46
\end{array}
\]
Note that both ratings agree on the top 5; only with respect to the positions 3 and 5 there are some minor differences.

The entire Shapley rating $\Phi(v^A)$ of the macaque visual cortex can be found in Figure 1 in the appendix. Correspondingly, we can roughly divide the brain regions in five classes based on the relative difference with the brain region with the highest Shapley rating. We consider the following five classes based on the differences in terms of percentage: 0%–5%, 5%–10%, 10%–15%, 15%–20%, 20% and higher. The first class consists of the single brain region V4 with the highest Shapley rating. The second class consists of the brain regions FEF to TF as ordered in Figure 1 that differ 5%–10% with V4. The brain regions in the third class are MSTd to V3, in the fourth class we have MSTI to PITd and in the fifth class we have the single brain region VOT with a relative influence which is 23% lower than that of V4.

The second large-scale brain network is the macaque prefrontal cortex with twelve neuronal structures (as illustrated in Figure 3(a) of Kötter et al. (2007)). In this case there is a lack of information about the presence or absence of nine connections. To get some insight, Kötter et al. (2007) considered two extreme cases. First, they assume that connections with unknown presence are absent. Second, they assume that those connections are present. For both extreme cases the Shapley ratings are calculated separately. Our stochastic brain network game provides a way to incorporate lack of information into one Shapley rating on the basis of probabilistic information. For simplicity, we assume that each connection with unknown presence is absent with probability $\frac{1}{2}$. Note that, in case more information would become available, more adequate probabilities can be readily inserted. Having the complete vector $p$ of arc probabilities, one readily computes the corresponding stochastic brain network game $(N, v^p)$ and the corresponding Shapley rating $\Phi(v^p)$. The ranking based on the Shapley rating $\Phi(v^p)$ can be found below.

<table>
<thead>
<tr>
<th>Ranking</th>
<th>Brain region</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>9</td>
</tr>
<tr>
<td>2.</td>
<td>24</td>
</tr>
<tr>
<td>3.</td>
<td>12</td>
</tr>
<tr>
<td>4.</td>
<td>10</td>
</tr>
<tr>
<td>5.</td>
<td>46</td>
</tr>
<tr>
<td>6.</td>
<td>25</td>
</tr>
<tr>
<td>7.</td>
<td>11</td>
</tr>
<tr>
<td>8.</td>
<td>8B</td>
</tr>
<tr>
<td>9.</td>
<td>13</td>
</tr>
<tr>
<td>10.</td>
<td>8A</td>
</tr>
<tr>
<td>11.</td>
<td>45</td>
</tr>
<tr>
<td>12.</td>
<td>14</td>
</tr>
</tbody>
</table>
References


Figure 1: Shapley rating of the macaque visual cortex.