Schlauschleimer in Reichsautobahnen:  
Slime mould imitates motorway network in Germany

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Final version is published in  
Andrew Adamatzky, Theresa Schubert, (2012) "Schlauschleimer in Reichsautobahnen: Slime mould imitates motorway network in Germany", Kybernetes, Vol. 41 Iss: 7/8, pp.1050–1071.

Abstract. The German motorway, or ‘autobahn’, is characterised by long traditions, meticulous state planning, historical misbalance between West and East Germany’s transport networks, and highest increase in traffic in modern Europe, posing a need for expansion and/or restructuring. We attempt to evaluate the structure of autobahns using principles of intrinsic optimality of biological networks in experiments with slime mould of Physarum polycephalum. In laboratory experiments with living slime mould we represent major urban areas of Germany with sources of nutrients, inoculate the slime mould in Berlin, wait till the slime mould colonises all major urban areas and compare the statistical structure of protoplasmic networks with existing autobahn network. The straightforward comparative analysis of the slime mould and autobahn graphs is supported by integral characteristics and indices of the graphs. We also study the protoplasmic and autobahn networks in the context of planar proximity graphs.

Keywords: biological transport networks, unconventional computing, slime mould

1 Introduction

In contrast to other countries, motorways in Germany are not just means of transportation but a pivotal part of citizens’ mentality. The history of the German motorway network dates back to 1926 when the so-called Hafabra association was formed to build a motorway linking Hamburg with Basel via Frankfurt. The project was dormant till Hitler’s National Socialist Party came to power and made the whole idea of free-flowing vehicular transport networks a revolutionary driving force — Reichsautobahnen, dictatorship of motorways
of the miraculous economical and technological progress of pre-war Germany and an instrument for propaganda. After the Second World War the ‘Hitler Autobahns’ were re-interpreted as means of reconstruction of West German democracy [43]. The ‘Green Nazi’ environmentally oriented approach towards the construction of autobahns and the aesthetics and design of surrounding landscapes was — at different stages of history — propagandised, mythologised, refuted, dismissed [43] but then partially ‘resurrected’ in 1990s and now actively considered by specialists in the context of transport network integrative development in Germany.

German motorways, or ‘autobahns’, are a unique road system because it is amongst earliest state planned transport networks; it was planned precisely and meticulously yet possesses a wide range of quality; and, it has the highest traffic load in Europe. Peculiar features of German motorways are based on long-standing traditions of car ownership, the wide range of roads quality and the absence of speed limits in some parts of the motorways [14]. Germany occupies central geographical position in Europe. This leads to a dramatic increase of traffic on autobahns, which in turns leads to increase in number of traffic accidents. Expansion of the autobahn network is amongst many possibilities of solving the traffic problem [15]. However the possibilities for adding new autobahn routes are very limited.

How would the autobahn network develop from scratch under the current configuration of urban areas in Germany? Are autobahns optimal from primitive living creatures point of view? Does the topology of autobahns satisfy any principle of natural foraging behaviour and fault tolerance? Are there any matches between German transport networks and basic planar proximity graphs? All these are — at least partially — answered in the present paper by physically imitating the autobahns development in laboratory experiments with slime mould *Physarum polycephalum*.

*Physarum polycephalum* is an acellular slime mould [38]. It inhabits forests in many parts of the world, and can be found in under logs and decayed tree branches. Its vegetative stage — the *plasmodium* — is a single cell, visible by an unaided eye, with myriad of nuclei. The plasmodium feeds on a wide range of microorganisms. During its development and foraging behaviour the plasmodium makes blob-like colonies on sources of nutrients. The colonies are connected in a single organism by a network of protoplasmic tubes. The network is considered to be optimal [26,28] in terms of efficiency of nutrients spanning, sensorial inputs and cost-efficient transportation of nutrients and metabolites in the plasmodium’s body. In his pioneering works Toshiyuki Nakagaki and his colleagues demonstrated that the plasmodium’s foraging behaviour can be interpreted as a computation [26,28]. In slime mould ‘computers’ [6] data are represented by spatial configurations of attractants and repellents. The computation is implemented during the slime mould’s propagation and colonisation of nutrients. The results of the computation are represented by the structure of the plasmodium’s protoplasmic network as developed on a data set of nutrients [26,28,6]. The problems solved by plasmodium of *P. polycephalum* include shortest path [26,28].
implementation of storage modification machines [3], Voronoi diagram [35], Delaunay triangulation [6], logical computing [42], and process algebra [34].

An early evaluation of the road-modelling potential of *P. polycephalum* in 2007 [2] came to no definite conclusion. However, significant progress has been made since that time; such as has been reported in our recent papers on approximation of highways systems in the United Kingdom [7], Mexico [8], the Netherlands [11], Iberia [9] and Brazil [12]. For all of these countries we found that the network of protoplasmic tubes developed by *P. polycephalum* matches, at least partly, network of human-made transport systems; though the closeness of fit varies from country to country. A variable that likely plays an important role in determining the closeness of fit is the constraint that each country’s government design policies place on their unique highway transport networks. This is why we are in the process of collecting data on the development of plasmodium networks in all major countries, in preparation toward undertaking a final comparative analysis. In the present paper we imitate the development of German transport networks with the slime mould. We believe the result possesses a particular value due to the unique history of autobahns and relatively precise planning of the transport system by German governments over last eighty years.

The paper is structured as follows. We outline our experimental techniques and methods of analysis of the slime mould and autobahn graphs in Sect. 2. Particulars of foraging behaviour of the slime mould on sources of nutrients, representing major urban areas of Germany, are discussed in Sect. 3. Analysis of protoplasmic networks, developed by *P. polycephalum*, and their comparison with German motorway network are undertaken in Sects. 4 and 5. The slime mould and autobahn graphs are considered in terms of planar proximity graphs in Sect. 6. And finally, in Sect. 7 we study a response of protoplasmic network to imitate large-scale contamination.

## 2 Experimental and methods

Plasmodium of *P. polycephalum* is cultivated in a plastic container, on paper kitchen towels moistened with still water, and fed with oat flakes. For experiments we use 120 × 120 mm polystyrene square Petri dishes and 2% agar gel (Select agar, by Sigma Aldrich) as a substrate. Agar plates, about 2-3 mm in depth, are cut in a shape of Germany.

We selected 21 most populated major urban areas listed below (see configuration of the areas in Fig. 1a, which roughly corresponds to distribution of population densities by 2009 [36]):

1. Berlin
2. Hamburg
3. Munich
4. Cologne, including Dusseldorf, Bonn
5. Frankfurt, including Wiesbaden
6. Stuttgart
7. Dortmund area
8. Bremen
9. Dresden
10. Hanover
11. Leipzig
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1. Berlin
2. Hamburg
3. Munich
4. Cologne, Dusseldorf, Bonn
5. Frankfurt, Wiesbaden
6. Stuttgart
7. Ruhrgebiet (Dortmund, Essen, Duisburg, Bochum, Wuppertal, Gelsenkirchen, Mönchengladbach, are not included because it is very close to 4 and 7)
8. Bremen
9. Dresden
10. Hanover
11. Leipzig
12. Nuremberg
13. Bielefeld
14. Mannheim
15. Karlsruhe
16. Münster
17. Augsburg
18. Aachen
19. Chemnitz
20. Braunschweig
21. Kiel

Due to scale, they are grouped in 21 urban areas.

Fig. 1. A map of Germany with major urban areas shown by encircled numbers.
Fig. 2. A typical image of slime mould *P. polycephalum* growing on a non-nutrient substrate and connecting oat flakes, which represent major urban areas by a network of protoplasmic tubes.

12. Nuremberg  
13. Bielefeld  
14. Mannheim  
15. Karlsruhe  
16. Münster  
17. Augsburg  
18. Aachen  
19. Chemnitz  
20. Braunschweig  
21. Kiel

Essen, Duisburg, Bohum, Wuppertale, Gelsenkirchen and Mönchengladbach are not included in the list because they is very close to either Cologne and/or Dortmund.
To represent areas of $\mathbf{U}$ we place oat flakes (each flake weights 9–13 mg and is 5–7 mm in diameter) in the positions of agar plate corresponding to the areas. At the beginning of each experiment an oat flake colonised by plasmodium (25–30 mg plasmodial weight) is placed in Berlin area. We undertook 22 experiments. The Petri dishes with plasmodium are kept in darkness, at temperature 22-25$^\circ$C, except for observation and image recording. Periodically, the dishes are scanned with an Epson Perfection 4490 scanner and configurations of protoplasmic networks analysed. A typical image of experimental Petri dish with Germany-shaped gel plate colonised by $P.\ polycephalum$ is shown in Fig. 2.

To generalise our experimental results we constructed a Physarum graph with weighted-edges. A Physarum graph is a tuple $\mathbf{P} = (\mathbf{U}, \mathbf{E}, w)$, where $\mathbf{U}$ is a set of urban areas, $\mathbf{E}$ is a set of edges, and $w : \mathbf{E} \rightarrow [0, 1]$ associates each edge of $\mathbf{E}$ with a probability (or weights). For every two regions $a$ and $b$ from $\mathbf{U}$ there is an edge connecting $a$ and $b$ if a plasmodium’s protoplasmic link is recorded at least in one of $k$ experiments, and the edge $(a, b)$ has a probability calculated as a ratio of experiments where protoplasmic link $(a, b)$ occurred in the total number of experiments $k = 22$. For example, if we observed a protoplasmic tube connecting areas $a$ and $b$ in 9 experiments, the weight of edge $(a, b)$ will be $w(a, b) = \frac{9}{30}$. We do not take into account the exact configuration of the protoplasmic tubes but merely their existence.

Further we will be dealing with threshold Physarum graphs $\mathbf{P}(\theta) = (\mathbf{U}, T(\mathbf{E}), w, \theta)$. The threshold Physarum graph is obtained from Physarum graph by the transformation: $T(\mathbf{E}) = \{ e \in \mathbf{E} : w(e) > \theta \}$. That is all edges with weights less than or equal to $\theta$ are removed.

To compare slime mould approximation of transport network in Germany with man-made autobahns we compare the generalised Physarum graph with the autobahn graph $\mathbf{H}$. The autobahn graph is derived as follows. Let $\mathbf{U}$ be a set of urban regions/cities; for any two regions $a$ and $b$ from $\mathbf{U}$, the nodes $a$ and $b$ are connected by an edge $(ab)$ if there is an autobahn starting in vicinity of $a$, passing in vicinity of $b$, and not passing in vicinity of any other urban area $c \in \mathbf{U}$. In the case of branching — that is, an autobahn starts in $a$, goes in the direction of $b$ and $c$, and at some point branches towards $b$ and $c$ — we then add two separate edges $(ab)$ and $(ac)$ to the graph $\mathbf{H}$. The autobahn graph is planar (Fig. 3).

We also analyse autobahn and Physarum graphs in a context of planar proximity graphs. A planar graph consists of nodes which are points of the Euclidean plane and edges which are straight segments connecting the points. A planar proximity graph is a planar graph where two points are connected by an edge if they are close in some sense, and no edges intersect. A pair of points is assigned a certain neighbourhood, and points of the pair are connected by an edge if their neighbourhood is empty. Here we consider the most common proximity graph as follows.

- $\mathbf{GG}$: Points $a$ and $b$ are connected by an edge in the Gabriel Graph $\mathbf{GG}$ if disc with diameter $\text{dist}(a, b)$ centred in middle of the segment $ab$ is empty [17][23].
Fig. 3. Autobahn graph $H$ of Germany.
Fig. 4. Illustration of anti-clockwise propagation. Experimental laboratory snapshots of *P. polycephalum* colonising urban areas of U. The snapshots are taken (a) 48 h and (b) 72 h after inoculating the plasmodium in Berlin.

- **RNG**: Points $a$ and $b$ are connected by an edge in the Relative Neighbourhood Graph **RNG** if no other point $c$ is closer to $a$ and $b$ than $\text{dist}(a, b)$ \[11\].
- **MST**: The Euclidean minimum spanning tree (MST) \[29\] is a connected acyclic graph which has minimum possible sum of edges’ lengths.

In general, the graphs relate as **MST** $\subseteq$ **RNG** $\subseteq$ **GG** \[41, 24, 20\]; this is called Toussaint hierarchy.

### 3 Strategies of colonisation

Being inoculated in Berlin slime mould of *P. polycephalum* develops by one of two scenarios: anti-clockwise propagation along boundaries of Germany, in the directions west – south – east – north; and, clockwise propagation, in the directions south – east – north – west. In 13 of 22 experiments plasmodium propagates anti-clockwise, in 9 experiments — clockwise.

Anti-clockwise scenario of colonisation is shown in Fig. 5. The plasmodium is inoculated in Berlin. It propagates to and colonises Leipzig and Dresden simultaneously. Then it builds protoplasmic tubes connecting Dresden and Leipzig with Chemnitz (Fig. 5a). At the same time, the plasmodium grows from Leipzig to Braunschweig, and then occupies almost all urban areas from Bremen in the north to Augsburg in the south (Fig. 5b). By the 3rd day after inoculation the
plasmodium propagates from Augsburg to Munich and Nuremberg, and from Bremen to Hamburg and from Hamburg to Kiel (Fig. 5b).

Clockwise (south-east-north) scenario is illustrated in Fig. 5. The slime mould propagates from Berlin to Leipzig and Dresden simultaneously. Then it colonises Chemnitz, forming protoplasmic tubes (Leipzig–Chemnitz) and (Dresden–Chemnitz). It moves further south and occupies the oat flake corresponding to urban area Nuremberg (Fig. 5a). In its subsequent development, by 48 hr after inoculation in Berlin, the plasmodium develops a chain of protoplasmic tubes linking Nuremberg, Augsburg, Munich in the south, Stuttgart, Karlsruhe, Mannheim and Frankfurt in the south-west, and Aachen, Cologne, Dortmund, Münster, Bielefeld in the west (Fig. 5a). The colonisation of urban areas U is completed by the slime mould by 72 hr after inoculation, when it develops protoplasmic tubes connecting Bremen and Hanover with Hamburg and Kiel (Fig. 5b).

A basic decision-making process implemented by *P. polycephalum* is shown in Fig. 6. In the first two days after being inoculated in Berlin the plasmodium propagates to Leipzig. It then branches from Leipzig to Braunschweig, Chemnitz and Dresden simultaneously (Fig. 6a). At this moment the plasmodium has three options:

1. propagate from Chemnitz to Nuremberg, Augsburg and Munich and then westward and towards north,
2. propagate from Braunschweig westward and then southward,
Fig. 6. Illustration of decision-making by the plasmodium. The snapshots are taken (a) 48 h and (b) 72 h after inoculating the plasmodium in Berlin.
3. implement options 1 and 2 in parallel.

In this particular experimental-laboratory example the plasmodium chooses option 2, because the concentration of nutrients (detected via chemo-attractants) is higher in the region of Braunschweig than around Chemnitz. See scheme of propagation in Fig. 6d. It propagates from Braunschweig to Hanover and Hamburg; from Hamburg to Kiel; from Hamburg to Bremen; from Bremen to Münster and Bielefeld; and, from Münster and Bielefeld to Dortmund (Fig. 6b). On the fourth day after inoculation the plasmodium colonises Cologne and Aachen; builds protoplasmic veins linking Cologne to Frankfurt and Mannheim; Mannheim to Karlsruhe; Karlsruhe to Stuttgart. Snapshot Fig. 6c shows 'moment' when the plasmodium just colonised Munich, Nuremberg and Augsburg and starts to develop growing zones to explore the space around newly occupied areas. The plasmodium also is detecting shortest ways, and evaluating feasibility of propagation, towards Chemnitz.

4 Physarum graphs

Examples of threshold Physarum graphs for some values of \( \theta \), are shown in Fig. 7.

The raw Physarum graph \( P(\frac{1}{22}) \) is non-planar (Fig. 7). With increase of \( \theta \) — the higher is \( \theta \) of \( P(\theta) \) the more often edges of \( P(\theta) \) appear in laboratory experiments — the threshold Physarum graphs undergo the following transformations:

- \( \frac{1}{22} \leq \theta \leq \frac{4}{22} \): graph \( P(\theta) \) is non-planar and connected (Fig. 7a).
- \( \frac{5}{22} \leq \theta \leq \frac{11}{22} \): graph \( P(\theta) \) is planar and connected (Fig. 7b).
- \( \theta = \frac{12}{22} \): graph \( P(\theta) \) splits into two disconnected components, one consists of urban areas Berlin, Dresden, Leipzig and Chemnitz, another include the remaining areas (Fig. 7c).
- \( \theta = \frac{13}{22} \): Berlin becomes isolated vertex (Fig. 7d).
- \( \theta = \frac{14}{22} \): Berlin, Dresden, Leipzig and Chemnitz become isolated vertices (Fig. 7e).
- \( \theta = \frac{15}{22} \): graph \( P(\theta) \) becomes acyclic (Fig. 7f).

**Proposition 1.** *Slime mould P. polycephalum imitates 1947 year separation of Germany onto East Germany and West Germany.

See Fig. 7f. When we consider only edges represented by protoplasmic tubes in over 41% of laboratory experiments Physarum graph becomes split into two disconnected components. The eastern component is a chain of urban areas Berlin–Leipzig–Chemnitz–Dresden lies exactly in the territory of former Eastern Germany (Fig. 7f). The construction of German transport network was interrupted by the Second World War and resumed only in 1953. Over half of existing autobahns in the West German network had been constructed by 1975 [32] well before fall of the Berlin Wall. The 'weak' fragments, i.e. those which are removed from Physarum graphs with increase of \( \theta \), of motorway network between West and East Germany are the ones which link now territories of East and
Fig. 7. Generalized Physarum graphs $P(\theta)$ for selected values of $\theta$. 
West Germany. Another contributing factor to the weak links exposed in laboratory experiments with *P. polycephalum* could be that car ownership and roads were symbols of freedom and democracy in West Germany, while East Germany characterised with low level of car ownership and poorly maintained roads.

Further increase of $\theta$ to $\frac{16}{22}$ leads to separation of the graph into the following disconnected components: isolated vertices Berlin, Dresden, Leipzig and Chemnitz, two three link chains Kiel–Hamburg–Bremen and Braunschweig–Hanover–Bielefeld, one four link chain Münster–Dortmund–Cologne–Aachen and the five link chain Frankfurt–Mannheim–Karlsruhe–Stuttgart–Augsburg–Munich and the branch Augsburg–Nuremberg.

**Finding 1** Transport links presented in over 68% of laboratory experiments form a connected component consisting of a chain Kiel–Hamburg–Bremen–Hanover–Bielefeld–Münster–Dortmund–Cologne–Frankfurt–Mannheim–Karlsruhe–Stuttgart–Augsburg–Munich with three branches: Hanover–Braunschweig, Cologne–Aachen, Augsburg–Nuremberg.

See Fig. 7f. The slime mould representations reflects thus an ever existing imbalance. Historically the West of Germany has always been richer than the East, the highest concentration of steel and coal-mining industry and engineering was situated in the Ruhrgebiet (Essen, Dortmund etc.).

5 **Autobahns versus protoplasmic networks**

**Finding 2** The only autobahn links presented by *P. polycephalum* in over 90% of laboratory trials are (Hamburg–Bremen), (Hanover–Bielefeld), (Cologne–Dortmund), (Mannheim–Karlsruhe–Münster), and (Augsburg–Munich).

All these links are parts of the so-called Reichsautobahn built by 1940 during Hitler Germany [13]. The only transport link connecting Hanover to Bielefeld is represented by protoplasmic tubes in 95% of all laboratory experiments (Fig. 7h).

**Finding 3** Autobahn links (Frankfurt–Braunschweig), (Frankfurt–Hanover), (Frankfurt–Leipzig) and (Stuttgart–Leipzig) are never represented by protoplasmic tubes of *P. polycephalum*.

As we can see in Fig. 8h ‘raw’ Physarum graph, consisting of edges, which are represented by protoplasmic tubes in at least two experiments, is almost a sub-graph of the autobahn graph apart of edges (Frankfurt–Braunschweig), (Frankfurt–Hanover), (Frankfurt–Leipzig) and (Stuttgart–Leipzig). The intersection of Physarum graph, which edges appear in at least eight of 22 experiments, and the autobahn graph remains a connected graph (Fig. 8b). The intersection $H \cap P(\frac{15}{22})$ consists of

- four isolated vertices: Berlin, Dresden, Leipzig, Nuremberg and Chemnitz;
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Fig. 8. Intersection of autobahn graph $H$ with Physarum graphs (a) $P(\frac{1}{22})$, (b) $P(\frac{7}{22})$, (c) $P(\frac{15}{22})$.

- chain Kiel–Hamburg–Bremen–Hanover–Bielefeld with branch Hanover–Braunschweig;
- chain Münster–Dortmund–Cologne–Frankfurt–Mannheim–Karlsruhe–Stuttgart–Augsburg–Munich with branch Cologne–Aachen (Fig. 8).

Let us compare Physarum graph $P(\frac{7}{22})$ with the autobahn graph based on several integral measures listed in Tab. 1. For each measure $\mu$ we calculate a mismatch between the Physarum and autobahn graphs as $1 - \frac{\mu(H)}{\mu(P(\frac{7}{22}))}$. The graphs show very good match in

- Randić index: the index is calculated as $\sum_{ij} C_{ij} \ast \left( \frac{1}{\sqrt{d_i \ast d_j}} \right)$, where $C_{ij}$ is a connectivity matrix [31];
- average link length;
- average degree;
- connectivity: number of edges divided by number of nodes,
- $\Pi$-index;
- average cohesion, which somehow reflects a neighbourhood wholeness.

**Proposition 2.** Slime mould P. polycephalum imitates well the autobahn network in terms of reachability, average travel time between geographically close urban areas and a fault-tolerance.

The reachability is expressed as connectivity (Tab. 1). The average travel time between geographical close urban areas could be measured via average link length. The number of alternative routes is measured via graphs’ branching properties reflected in the Randić index [23]. The slime mould does not represent well the following properties of German transport networks: diameter (longest path between any two vertices, measured in nodes or normalised length of edges), Harary index, and average shortest path between a pair of vertices (Tab. 1).
Table 1. Comparison of autobahn graph H and Physarum graph P(7, 22) using standard measures and indices. Rows are in ascending order of absolute value of mismatch.

| Measure                        | H    | P(7, 22) | Mismatch, 1 − μ(H)/μ(P(7, 22)) |
|--------------------------------|------|----------|---------------------------------|
| Randić index [31]: ∑_{ij} C_{ij} \# \left( \frac{1}{\sqrt{d_i \cdot d_j}} \right), where C_{ij} is a connectivity matrix | 19.88 | 20.06    | -0.01                           |
| Average link length            | 0.44 | 0.45     | 0.02                            |
| Average degree                 | 3.61 | 3.24     | -0.11                           |
| Connectivity: number of edges divided by number of nodes | 1.81 | 1.62     | -0.12                           |
| H-index: The relationship between the total length of the graph L(G) and the distance along its diameter D(d) [15], II = \frac{L(G)}{D(d)} | 85.59 | 74.21    | -0.15                           |
| Average cohesion: let \bar{d} be an average degree of a graph G and ν_{ij} is a number of common neighbours of nodes i and j, and d_i is a degree of node i, then cohesion κ_{ij} between nodes i and j is calculated as κ_{ij} = \frac{ν_{ij} \cdot \bar{d} + \bar{d}_j}{\bar{d}_i + \bar{d}_j} | 0.19  | 0.23     | 0.17                            |
| Average shortest path between any two nodes, in nodes | 2.49 | 4.03     | 0.38                            |
| Harary index [30]: \frac{1}{2} \sum_{ij} \xi(D)_{ij}, where where i and j are indices of a graph nodes, D is a graph distance matrix, where D_{ij} is a length of a shortest path between i and j, \xi(D)_{ij} = D_{ij}^{-1} if i ≠ j and 0, otherwise. | 293.50 | 199.85   | -0.47                           |
| Average shortest path between any two nodes, in normalised lengths | 0.98  | 1.89     | 0.48                            |
| Diameter (longest shortest path between any two nodes), in nodes | 5     | 10       | 0.5                             |
| Diameter (longest shortest path between any two nodes), in normalised lengths | 2.26  | 5.10     | 0.55                            |
6  Slime mould, autobahns and proximity graphs

The most common proximity graphs constructed on sites of $U$ are shown in Fig. 9. Seven topologies of spanning trees on $U$ are shown in Fig. 10. Tree rooted in Berlin is not exactly the minimum tree but only 1.02 times longer.

Finding 4  Let $E(G)$ be a number of edges in a graph $G$ and $ST$ be a spanning tree rooted from any node of $U$ then $E(H \cap ST) = E(ST) - 3$.

See illustration Fig. 11.

Finding 5  If RNG was a subgraph of $H$ if $H$ would have edges (Bielefeld–Münster) and (Nuremberg–Augsburg) and RNG would have an edge (Leipzig–Chemnitz).

Finding 6  $H \cap RNG = H \cap ST_{12}$

Relative neighborhood graph RNG, Gabriel graph GG and spanning trees ST are well known species of planar proximity graphs used in geographical variational analysis [17,21], simulation of epidemics [10], and design of ad hoc wireless networks [22,33,37,25]. The proximity graphs, particularly RNG, are invaluable in simulation of human-made, road networks; these graphs are validated in specially interesting studies of Tsukuba central district road networks [45]. The graphs provide a good formal representation of biological transport networks, particularly foraging trails of ants [1]. The fact that just two edges (Bielefeld–Münster) and (Nuremberg–Augsburg) must be removed from RNG and only one edge removed from RNG to make the relative neighbourhood graph a sub-graph of the autobahn graph demonstrates that the autobahn graph fits well into existing concepts of near optimal planar proximity graphs.
Fig. 10. Topological classes of spanning trees, rooted in (a) ST$_1$: Berlin, Leipzig, Chemnitz, Dresden, $l = 1.02$. (b) ST$_2$: Hamburg, Kiel, Bremen, Hanover, $l = 1.07$. (c) ST$_3$: Munich, Augsburg, $l = 1.07$. (d) ST$_4$: Cologne, Aachen, Dortmund, $l = 1$. (e) ST$_5$: Frankfurt, Stuttgart, Mannheim, Karlsruhe, $l = 1.01$. (f) ST$_{12}$: Nuremberg, $l = 1.07$. (g) ST$_{13}$: Bielefeld, Münster, $l = 1.04$. Lengths $l$ of trees are normalised to a length of the minimum spanning tree (d).
Fig. 11. Intersection of autobahn graph $H$ with spanning trees (a) $ST_1$. (b) $ST_2$. (c) $ST_3$. (d) $ST_4$. (e) $ST_5$. (f) $ST_{12}$. (g) $ST_{13}$.

Fig. 12. Intersection of autobahn graph with (a) Gabriel graph and (b) Relative neighbourhood graph.
Fig. 13. Intersection of Physarum graphs (ab) $P(\frac{1}{2^2})$ and (cd) $P(\frac{7}{2^2})$ with (ac) relative neighbourhood graph and (bd) Gabriel graph.

Finding 7 $ST(a) \subset P(\frac{1}{2^2})$ for any $a \in U$.

Namely, in laboratory experiments protoplasmic networks almost always maintain a minimum spanning core as an underlying structure of their topology. This can be demonstrated by direct comparison of graphs presented in Figs. 7 and 10.

Finding 8 $GG \subset P(\frac{1}{2^2})$

See Figs. 13. Gabriel graph is a super-graph of relative neighbourhood graph and of minimum spanning tree $41,24,20$. Thus the slime mould $P. polycephalum$ imitates — in its foraging patterns — all three basic planar proximity graphs.
7 Imitating large-scale contamination

To study the effect of a large-scale contamination on a dynamic and structure of transport network, imitated by *P. polycephalum* protoplasmic networks, we placed a grain of sea salt (SAXA Coarse Sea Salt, a crystal weight around 20 mg) in the site of agar plate corresponding to the approximate position of Emsland Nuclear Power Plant [16]. The position is marked by a star in Fig. 14. Inorganic salt is a repellent for *P. polycephalum* therefore the sodium chloride diffusing into
the plasmodium’s growth substrate causes the plasmodium to abandon domains with high level of salinity. As an immediate response to diffusing chloride the plasmodium withdraws from the zone immediate to the epicentre of contamination. Further response usually fits into two types: hyper-activation of transport as an attempt to deal with the situation and migration away from contamination, sometimes even beyond the agar plate, as an attempt to completely avoid the contaminated area.

Typical scenarios of slime mould’s response to contamination are illustrated in Fig. 14. Thus, we observe a substantial increase of foraging activity in Schleswig-Holstein, around Berlin and at the boundary between Thuringia and Upper Franconia.

In example Fig. 14a, transport links are substantially enhanced between Berlin and Hamburg, Braunschweig and Hanover and between Berlin and Leipzig and Dresden. Also, auxiliary transport link from Hamburg and Kiel to Berlin emerges along north-east boundary of the country (Fig. 14a); this link may play a key role in preparation of mass-migration from Germany to north-west Poland. Hyper-activity of transport links connecting Chemnitz and Munich, Nuremberg and Stuttgart, Karlsruhe and Mannheim, and Cologne and Mannheim is recorded in examples shown in (Fig. 14b).

Mass migration is observed from Aachen to Limburg in Belgium, and from Mecklenburg, Western Pomerania inwards north-west Poland (Fig. 14a), from Dessau, Leipzig and Chemnitz areas towards Wrocław in Poland (Fig. 14b), and from Baden-Württemberg area inwards south-east France and Switzerland (Fig. 14c).

8 Discussion

In our experimental laboratory research we represented major urban areas of Germany with oat flakes and inoculated plasmodium of *Physarum polycephalum* in Berlin. The plasmodium propagated from Berlin to nearby urban areas then to fertile urban areas close to already colonised urban areas. Eventually all urban areas were colonised by the plasmodium. We conducted 22 identical experiments. We found that autobahn and protoplasmic networks match each other satisfactorily in many integral characteristics and topological indices, especially connectivity, average link lengths and Randić index. With regards to exact matching between edges of autobahn and Physarum graphs, in 40% of laboratory experiments almost 60% of the autobahn segments are represented by the slime mould’s protoplasmic tubes.

We found that only autobahn links (Frankfurt– Braunschweig) and (Frankfurt– Leipzig) are never represented by protoplasmic tubes of *P. polycephalum* in laboratory experiments. The following transport links are imitated by the slime mould in over 70% of laboratory experiments: (Kiel– Hamburg– Bremen– Hanover– Bielefeld– Münster– Dortmund– Cologne– Frankfurt– Mannheim– Karlsruhe– Stuttgart– Augsburg– Munich), (Hanover– Braunschweig), (Cologne– Aachen), and (Augsburg– Nuremberg). The transport links presented by the plasmod-
ium network in over 90% of laboratory experiments are (Hamburg– Bremen), (Hanover– Bielefeld), (Cologne– Dortmund), (Mannheim– Karlsruhe– Münster), and (Augsburg– Munich). The man-made autobahn links represented in over half of laboratory experiments are the chain (Kiel– Hamburg– Bremen– Hanover– Bielefeld) with the branch (Hanover– Braunschweig) and the chain (Münster– Dortmund– Cologne– Frankfurt– Mannheim– Karlsruhe– Stuttgart– Augsburg– Munich) with the branch (Cologne– Aachen).

We did not aim to give any conclusive answer of weather autobahns are mathematically optimal and environmentally friendly or not. We attempted to find how ‘good’ are autobahns from slime moulds’ point of view, and how the transport network in Germany would develop if it was developed by foraging principles and bio-mechanics of the slime mould from scratch. We demonstrated that the \textit{P. polycephalum} approximates autobahn satisfactory and thus can be considered as a valuable and user-friendly experimental laboratory tool for imitation of man-made transport networks with amorphous living creature.

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