Evaluation of French motorway network in relation to slime mould transport networks

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Abstract
France has developed a high quality motorway system that has been rapidly rationalised and matured in the late 20th century yet has been founded on ancient, Roman infrastructures. The development of the motorway system is thus an iterative method associated with hierarchical ‘top-down’ processes taking into consideration factors such as population density, network demand, location of natural resources, civil engineering challenges and population growth. At the opposite extreme to this approach is the development of transport networks within simple biological systems which are typically decentralised, dynamic and emerge from simple, local and ‘bottom-up’ interactions. We examine the notion, and to what extent, that the structure of a complex motorway network could be predicted by the transport network of the single-celled slime mould Physarum polycephalum. This comparison is explored through its ability to ‘deduce’ the French motorway network in a series of analogue and digital experiments. We compare Physarum network and motorway network topology in relation to proximity graphs and assess the trade-off between connectivity and minimal network length with a bottom-up model of a virtual plasmodium. We demonstrate that despite the apparent complexity of the challenge, Physarum can successfully apply its embodied intelligence to rationalise the motorway topology. We also demonstrate that such calculations prove challenging in the face of significant obstacles such as, mountainous terrain and may account for the missing route between Nice, Grenoble, Avignon and Lyon. Finally, we discuss the topological findings with respect to circle and spoke city planning infrastructures and certain species of web-building spiders.

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Introduction: The French motorway network

The French motorway network is the fourth largest in the world comprising 11,882 km length of motorways, including 9048 km of toll highway (see data from ASFA, 2014). It takes almost 25% of the national traffic while accounting for only 1% of French roads in linear distance (Gandil, 2005). Underpinning the success of these motorways is that some regions like Corsica and a large part of Brittany do not have highways but expressways. Only two French territories are not served by any highway namely, Ardèche and Hautes-Alpes. This is in part due to the mountainous terrain which provides a significant engineering obstacle and there is therefore no direct highway connecting the two major cities Nice and Lyon.

France’s motorway system has ancient origins – the first Roman roads of northern Gaul were established by Emperor Augustus (63 B.C. to 14 A.D.), who entrusted this task to his son-in-law Agrippa (62 B.C. to 12 B.C.). He started then the creation of a vast hub-and-spoke network centred on Lyon, the new capital of Gaul, thus joining the confines of the Empire to the north, west and south. Only 25 years after the end of the Gallic Wars, Rome was connected to the English Channel by a route for the military and commercial operation of its new conquests. Yet, the initial plan was not fully completed until the middle of the 1st century A.D. During the four centuries that followed, new important towns were connected to this infrastructure, or re-routed to bypass unsafe or poorly maintained roads.

However, even the Roman roads have more ancient origins that rationalised a dense, heterogeneous and well maintained Gallic network of roads that were shaped by independent trading routes between hundreds of local territories. This refined network enabled Roman armies to move more efficiently and communicate more effectively with its imperial power centres. In peacetime, the network promoted the development of trade and civilian communications between different parts of the Roman Empire. The roads were particularly useful for grain supply of the large urban centres, which were swelling significantly during antiquity. The disappearance of the imperial administration in late antiquity led, among other things, to termination of road maintenance. After the ravages of the Hundred Years’ War (1337–1453), the creation of a powerful monarchy allowed the reconstruction of the country with Paris as the centre and the rehabilitation of roads and land routes. The road network became a priority of the state during the 18th century with the ‘Ponts et Chaussées’ (‘Bridges and Roads’) service being created in 1716 to develop the road network with the support of the Ministers of War. Up until the French Revolution around 30,000 km of roads were created under the Royal Chore. This made incumbent French regimes responsible for their maintenance – initially royal, then imperial under Napoleon, and finally the duty of national government in the 20th century that has been underpinned by a stable form of private/public financing (Gandil, 2005).

French motorways are therefore both imprints of history and the logical consequence of network optimisation. Generally, they have been built in parallel with many national roads and in some cases they allow for more direct routes to major cities – including the displacement of the centre of gravity from Lyon to Paris. A further complexification of the French motorway network is conferred by its connection to sparsely populated cities, which is due to geographic, economic or historical reasons and makes the reading of the French network more complex.

Keywords
Agent-based modelling (ABM), planning theory, self-organisation
The modern rationalisation of French motorways began in the late 20th century. Between 1960 and 1970, the network grows from Paris to Lille, in the north, Paris to Marseille-Toulon, in the south and bypasses Dijon, Lyon and Avignon. Paris-Lyon-Marseille is a major structural axis in France. The motorway linking Paris to Rouen, to the west, is also built during the 60s. During the 70s and the 80s, the network extends radially from Paris to cities of Strasbourg in the east, Nantes and Bordeaux in the southwest, Le Havre in the west and Clermont-Ferrand in the centre of France. During this time, the Paris-Marseille motorway is extended westward to Toulouse via Montpelier. Between 1990 and 2000, these axes leaving Paris are extended from the cities in the centre of France to the major southern cities. The concentric orbits around Paris that form its current, striking ‘spider-web’ configuration (Figure 1) begin in 2000 and are ongoing, where radial axes join the major French cities without passing through Paris, such as the Lyon-Bordeaux and Nantes-Bordeaux motorways.

Figure 1. Motorway network in mainland France (Réseau des Sociétés Concessionnaires d’Autoroutes et d’ouvrages d’art) is reminiscent of spider-web structure. Colored (online) bold lines are motorways and thin black lines are national roads.
Slime mould transport networks

The emerging influence of centralised large scale planning, coordination and control of the motorway network is in contrast to the construction of transport networks employed by a wide range of simple organisms (Bebber et al., 2007). Like human constructs, these networks are used to transport material (for example, nutrients, metabolites) about the organism (Fricker et al., 2008) or population (Garnier et al., 2009). In this article, we concentrate on transport networks formed by an extremely simple single-celled organism.

Over a range of theoretical and experimental works the true slime mould *Physarum polycephalum* has demonstrated that it can be manipulated and used in an 'unconventional' (Adamatzky et al., 2007) computational context to solve mazes (Nakagaki et al., 2000), 'remember' environmental details (Reid et al., 2012; Saigusa et al., 2008) and also find the shortest routes between spatially separated points (Adamatzky, 2010, 2012; Shirakawa et al., 2009).

*Physarum polycephalum* is a macroscopic protist belonging to the phylum mycetozoa. It is visible to the naked eye and typically grows to over 10 cm². The organism consists of a giant single cell containing myriad nuclei, during its vegetative stage, which is able to move via contractile protein-induced oscillations in its gel-sol core (Durham and Ridgway, 1976). Under hydrostatic pressure from these contractions, the active growth front of the organism streams forward, attracted by nearby nutrient gradients. Behind the densely ramified growth front, the structure of the plasmodium adapts and coarsens, forming a protoplasmic tube connecting the growth front and previously engulfed nutrients. These tubes are used to distribute nutrients throughout the entire organism. In this state, it has been considered capable of demonstrating ‘intelligent behaviour’ although it lacks any typical centrally organised structure to coordinate these tasks such as, a brain, or formally organised nervous system. Such an information processing system may be regarded as a form of embodied intelligence (Adamatzky, 2012) that is able to resolve internal and external cues through morphology.

It’s ability to compute transport network topologies resides in plasmodium’s ability to construct and adapt its self-made and self-organised transport network when presented with a choice of food sources (typically oat flakes in experimental conditions). As it forms a set of communicating tubes to distribute nutrients and links its initial and final destination. Consequently, an optimised network of tubes is formed when several food sources are presented. In this manner, *Physarum* exhibits a basic form of decision making when establishing the distribution of these tubes. Typically the plasmodium body will engulf smaller obstacles but spread around larger ones and effectively perform a complex set of manoeuvres that calculate the most efficient network topology for the organism and approximates man-made travel routes (Adamatzky, 2014; Adamatzky and Jones, 2010). Corresponding city locations can be represented on a nutrient medium using food sources, which are typically provided by natural bacterial colonies that grow on oat flakes.

While such maps have been produced for some countries (Adamatzky, 2012) and individual cities (Tero et al., 2010), no such biologically inspired adaptive network modelling of the French motorway exists. French motorways offer a particularly intriguing challenge for the network rationalisation powers of *Physarum* since they have a complex origin established during Roman times that has been rationalised over the late 20th century.

In this article, we will examine the established ability (Adamatzky, 2012; Adamatzky et al., 2013) of the plasmodium to map transport routes between hubs of activity that represent cities. In these instances, iterative exchanges between the *Physarum* body and complex factors in the environment provide a model through which it is possible to find the shortest route
between two points to generate network topologies with comparable efficiency, fault tolerance and cost to those of real-world infrastructure networks (Tero et al., 2010).

Specifically, we will compare the structure of slime mould Physarum networks connecting analogues of major urban areas of mainland France with the French motorway network connecting the same areas. We will compare the similarity and differences of Physarum networks and motorway networks. The structure of the article progresses as follows: Experimental methods section describes the experimental methods to construct Physarum networks. Results of laboratory experiments section describes the process of statistically quantifying the Physarum network structure from the experimental results. The Physarum networks are statistically compared to the motorway network in Comparative analysis with mainland France motorway network section and both Physarum and motorway networks are compared to proximity graph structures in Slime mould networks and motorway networks versus proximity graphs section. A modelling approach using the bottom-up network adaptation processes seen in slime mould is described in Computer modelling of slime mould transport networks section. Finally, a discussion of the findings is given in Discussion section.

**Experimental methods**

Plasmodium of *P. polycephalum* is cultivated in plastic container, on paper kitchen towels moistened with still water, and fed with oat flakes. For experiments we use 220 mm × 220 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 continental (mainland) France.

We selected the 15 most populated major urban areas of France (see configuration in Figure 2, which roughly corresponds to distribution of population densities). The size of each oat flake was approximately equal (5 mm) and did not directly correspond to the relative size of the selected urban areas.

To represent the set of major urban areas, denoted by \( U \), we place oat flakes in the positions of agar plate corresponding to the areas. At the beginning of each experiment an oat flake colonised by plasmodium is placed in the Paris area. We undertook 12

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**Figure 2.** Outline map of France with major urban areas \( U \) shown by encircled numbers.
experiments. The Petri dishes with plasmodium are kept in darkness, at temperature 22–25°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 an experimental Petri dish is shown in Figure 3.

**Results of laboratory experiments**

**Formation of protoplasmic networks**

In a few hours after inoculation in Paris, the plasmodium recovers from initial shock, starts exploring its substrate, detects gradients of chemo-attractants emitted by virgin oat flakes placed in major urban areas U and starts propagating along gradients of chemo-attraction. A typical scenario of plasmodium development is shown in Figure 4.

On the first day of such a typical scenario the slime mould propagates from its inoculation site in Paris to Rouen and Lille (Figure 4(a)). The second day shows growth from Lille to Strasbourg and Lyon, and then from Strasbourg to Grenoble and from Lyon to Grenoble. These are followed by further propagation towards Toulon and Nice (Figure 4(c)). After colonising Nice and Toulon – on the third day of the experiment – the slime mould connects cluster of urban areas Grenoble, Avignon, Marseille, Toulon, Nice and then moves from Avignon to Toulouse, from Montpellier to Toulouse, from Toulouse to Bordeaux, from Bordeaux to Nantes and from Nantes to Rennes (Figure 4(c)). On the fourth day of the experiment, the slime mould returns to its original site of inoculation by propagating from Rennes to Rouen to Paris (Figure 4(d)).

**Physarum graphs**

To generalise our experimental results we constructed a Physarum graph with weighted-edges. A Physarum graph is a tuple $P = (U, E, w)$, where $U$ is a set of urban areas, $E$ is a set edges, and $w : E \to [0, 1]$ associates each edge of $E$ with a probability (or weights). For every two regions

![Figure 3. A typical image of slime mould Physarum polycephalum growing on a non-nutrient substrate and connecting oat flakes, which represent major urban areas U by a network of protoplasmic tubes. a: site of inoculation; b: virgin oat flakes; c: active zone, propagating part of plasmodium in a search for nutrients; d: oat flake occupied by plasmodium’s active zone; e: protoplasmic tube.](image-url)
For example, if we observed a protoplasmic tube connecting areas \(a\) and \(b\) in 7 experiments, the weight of edge \((a, b)\) will be \(w(a, b) = \frac{7}{12}\). We do not take into account the exact configuration of the protoplasmic tubes but merely their existence. Furthermore, we will be dealing with threshold \(\text{Physarum}\) graphs \(P(\theta) = (U, T(E), w, \theta)\). The threshold \(\text{Physarum}\) graph is obtained from \(\text{Physarum}\) graph by the transformation: 

\[ T(E) = \{e \in E : w(e) \geq \theta\} \]

That is, all edges with weights less than \(\theta\) are removed. Examples of threshold \(\text{Physarum}\) graphs for various values of \(\theta\) are shown in Figure 5.

In analysing the thresholded results we can see that the \(\text{Physarum}\) graph undergoes the following critical transformations with increase of \(\theta\):

- \(\theta = 3\): The graph becomes planar.
- \(\theta = 6\): Leaves (nodes of degree one) appear, for example Lille becomes a leaf.

Figure 4. Experimental laboratory example of slime mould propagation guided by shape of France and configuration of urban areas \(U\). Petri dishes with slime mould were scanned every 24 h. (a) 24 h (b) 48 h (c) 72 h (d) 96 h.
\[ (\theta = 7) \text{: Isolated nodes appear, for example Strasbourg loses connections to the rest of } U; \]
\[ (\theta = 8) \text{: The graph splits into four disconnected components. The components are chains } \]
\[ \text{Lille – Paris – Rouen, Lyon – Grenoble, Nice – Toulon – Marseille, Avignon – Montpellier – Toulouse – Bordeaux – Nantes – Rennes.} \]

The strongest components of the graph are links Nantes – Rennes, Toulouse – Bordeaux, Marseille – Avignon, Nice – Toulon. They remain in the graph up to \( \theta = 11 \).

### Comparative analysis with mainland France motorway network

To quantify any similarity between Physarum networks and the Motorway network the generalised Physarum graph was compared with the motorway map \( H \). The motorway graph is derived as follows. Let \( U \) be a set of urban regions/cities; for any two regions \( a \) and \( b \) from \( U \), the nodes \( a \) and \( b \) are connected by an edge \( (ab) \) if there is a highway starting in vicinity of \( a \), passing in vicinity of \( b \), and not passing in vicinity of any other urban area \( c \in U \). In the case of branching – that is, a highway 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 \( H \). The highway graph is planar (Figure 6).

Intersection of Physarum graph for several values of \( \theta \) and the motorway graph is shown in Figure 7. As we can see, strong components of the Physarum graph are the subgraphs of the France motorway graph.
We can define a degree of approximation of $H$ by $P(\theta/12)$ as a percentage of edges of $H$ represented by edges of $P(\theta/12)$. Then the exact value $(\theta/12) 100\%$ characterises the accuracy of approximation. The plot of the degree of approximation $\delta$ versus accuracy of approximation $\alpha$ is shown in Figure 8. It fits well a linear approximation $\delta = 79 - 0.62 \cdot \alpha$, with coefficient of determination $R^2 = 0.96$. One of the outcome of the approximation is that Physarum successfully approximates over half of motorway links in over half of the laboratory experiments.

**Slime mould networks and motorway networks versus 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. 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.

**GG** Points $a$ and $b$ are connected by an edge in the Gabriel Graph $GG$ if disc with diameter $\text{dist}(a, b)$ centred in middle of the segment $ab$ is empty (Gabriel and Sokal, 1969; Matula and Sokal, 1980) (Figure 9(a)).

**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 $\text{dist}(a, b)$ (Toussaint, 1980) (Figure 9(b)).

**MST** The Euclidean minimum spanning tree (MST) (Nešetřil et al., 2001) is a connected acyclic graph which has minimum possible sum of edges’ lengths (Figure 9(c) and (d)). Strictly speaking, the tree rooted in Paris (Figure 9(c)) is not the minimum tree however it is just 1.082 longer than the minimum spanning tree rooted in Toulouse (Figure 9(d)), see Table 1.

In general, the graphs relate as $\text{MST} \subseteq \text{RNG} \subseteq \text{GG}$ (Jaromczyk and Toussaint, 1992; Matula and Sokal, 1980; Toussaint, 1980) this is called the Toussaint hierarchy.
Figure 7. Intersection of motorway graph $H$ and Physarum graphs $P(\theta)$ for (a) $\theta = \frac{1}{12}$, (b) $\theta = \frac{3}{12}$, (c) $\theta = \frac{5}{12}$, (d) $\theta = \frac{6}{12}$, (e) $\theta = \frac{7}{12}$, (f) $\theta = \frac{8}{12}$.

Figure 8. Plot of the accuracy of approximation of France motorway edges by edges of Physarum graphs versus the degree of approximation.
Table 1. Lengths of spanning trees rooted in $\mathbf{U}$.

| Root | Length |
|------|--------|
| 1    | 1.082  |
| 2    | 1.138  |
| 3    | 1.149  |
| 4    | 1.000  |
| 5    | 1.084  |
| 6    | 1.004  |
| 7    | 1.149  |
| 8    | 1.110  |
| 9    | 1.205  |
| 10   | 1.110  |
| 11   | 1.138  |
| 12   | 1.088  |
| 13   | 1.149  |
| 14   | 1.149  |
| 15   | 1.149  |

Figure 9. Proximity graphs constructed on sites of $\mathbf{U}$. (a) Gabriel graph, (b) relative neighbourhood graph, (c) spanning tree rooted in Paris, (d) minimum spanning tree rooted in Toulouse.

Figure 10. Intersection of highways graph $\mathbf{H}$ with (a) relative neighbourhood graph, (b) Gabriel graph, (c) spanning tree rooted in Nantes, (c) spanning tree rooted in Rennes.
Intersections of the motorway graph with the proximity graphs is shown in Figure 10. Neither GG nor RNG are subgraphs of H however, 15 of 17 edges of GG are included in H and 13 of 14 edges of RNG. The missing links are Grenoble – Avignon and Nice – Grenoble in case of GG and Grenoble – Avignon in case of RNG. Only spanning trees rooted in Nantes and Rennes are completely subgraphs of H, intersections of trees rooted in all sites with H consist of two disconnected components.

We now compare proximity graphs with Physarum graphs P. In Figure 11, we compare proximity graphs with P(1/12) (because this graph represents all links developed in laboratory experiments) and P(6/12) (because this graph shows links occurred in over half of the laboratory experiments, and therefore represents the highest accuracy of approximation yet still connected graph).

We find that relative neighbourhood graph RNG, Gabriel graph GG and spanning tree routed in Paris are subgraphs of P(1/12) (Figure 11(a) to (c)). This indicates that the Physarum graph includes all principal proximity graphs and thus represents an optimal covering of the configuration of major urban areas of France. In contrast, the motorway graph H does not represent several edges of the proximity graphs, see Figure 10.

The high accuracy of representation Physarum graph P(6/12) almost includes the proximity (Figure 11(d) to (f)). Namely, the link Lille – Rouen is mixing from the intersection of the graph P(6/12) with RNG, GG and ST. The link Strasbourg – Rouen is missing from the intersection of the Physarum graph with the relative neighbourhood graph and Gabriel graph. The intersection of GG and P(6/12) is also missing the link Paris – Strasbourg.

**Figure 11.** Intersection of Physarum graphs (a, b, c) $P(\frac{1}{12})$ and (d, e, f) $P(\frac{6}{12})$ with (ad) relative neighbourhood graph, (b and e) Gabriel graph, (c and f) spanning tree rooted in Paris.
Computer modelling of slime mould transport networks

Since slime mould is a living system it is subject to limitations of repeatability and unpredictability during its foraging, not to mention the long experimental time to form and adapt the transport networks. To aid the analysis of similarities and differences of the slime mould networks with the motorway network we require a computational mechanism to approximate the evolution of Physarum transport networks. Importantly, however, we must ensure that the networks emerge – as with slime mould – from simple, local and ‘bottom-up’ interactions, as opposed to the ‘top-down’ network constructs formed from classical algorithmic approaches.

We use the multi-agent approach that was introduced in Jones (2010) to approximate the emergent transport networks of slime mould. This approach has been demonstrated to be useful for approximating the biological behaviour of slime mould (Baumgarten et al., 2015; Jones, 2015b) and in developing biologically inspired unconventional computing methods (Jones, 2015a). A population of mobile particles is created and initialised on a 2D lattice configured to the experimental pattern of French cities. The diffusive medium is represented by a discrete two-dimensional floating point lattice. Particle positions are stored on a discrete lattice isomorphic to the diffusive lattice. Particles also store internal floating point representations of position and orientation which are rounded to discrete values to compute movement updates and sensory inputs. A single particle, and an aggregation of particles, are related to the P. polycephalum plasmodium in the following way: the plasmodium is conceptualised as an aggregate of identical components. Each particle represents a hypothetical unit of gel/sol interaction. Gel refers to the relatively stiff sponge-like matrix composed of actin-myosin fibres and sol refers to the protoplasmic solution which flows within the matrix. The structure of the protoplasmic network is indicated by the particle positions and the flux of sol within the network is represented by the movement of the particles. The resistance of the gel matrix to protoplasmic flux of sol is generated by particle movement collisions. For a more detailed description of the model implementation, see Jones (2015a).

The topology of P. polycephalum transport networks is, in part, influenced by unpredictable influences on its formation, for example the initial migration direction of the plasmodium or the presence of previously laid down protoplasmic tubes. This raises the question as to whether the topology of the networks would be more regular under idealised adaptation conditions. In order to minimise this unpredictability, we initialised the simulation model with a uniform distribution of a fully grown virtual plasmodium to solely assess the effect of the spatial arrangement of nutrients (corresponding to city locations) had on the morphological adaptation of the virtual transport network. The results of an example evolution of the virtual plasmodium are shown in Figure 12. Uniform coverage was attained by populating 50% of the habitable area of France with 20,000 particles.

The simulation was started and the collective adapted to the nutrient stimulus by shrinking in size to form a transport network connecting the regions. Twenty runs of the simulation were performed at both fast and slow shrinkage speeds. In the fast shrinkage method, small defects began to form in the material, forming holes which increased in size (Figure 12). This approximates the self-organised formation of P. polycephalum transport networks from a solid initial mass of plasmodium. The model plasmodium maintains its connection to the nutrients (regions) and the transport network adapts its configuration until a stable state is reached. The final networks are typically cyclic (encompassing all regions in a ring structure), with some left-right connectivity between Western and Eastern regions.
In the slower shrinkage method, defects do not form in the virtual plasmodium as it shrinks in size. The final network patterns tend to be as a result of shrinking concave regions in the original shape and approximate Minimum Steiner Trees.

We used the same method of assessing connectivity between cities as in the experimental approach and this resulted in an adjacency matrix containing the frequencies of connected nodes for the 20 experiments in both nutrient conditions. The connectivity graphs at different threshold weights are shown in Figure 13 for fast shrinkage concentrations and Figure 14 for slow shrinkage conditions. The fast shrinkage method has a higher average mean degree over all experiments than the slow shrinkage method (degree 2.75 vs. 2.12). There is a greater connectivity between left and right regions on the map, which persists until the threshold of 14 is reached (above this threshold, the connectivity is similar to the slow method).

A comparison of the connectivity between individual cities is shown in Figure 15 under fast and slow shrinkage conditions. The most highly connected regions in the fast shrinkage method are Paris, Lyon, Bordeaux and Nantes. It is the connectivity from these regions which is responsible for the West-East crossings. In comparison, the most highly connected regions in the slow method are Paris, Lyon, Avignon and Rouen, which are typically connected in a simple path on the Easterly side. The connectivity of Bordeaux and Nantes regions in the fast method (both having mean degree of 3.7) is more than halved (mean degree 1.6) in the slow method, due to the lack of West-East crossings.

Discussion

Using slime mould *P. polycephalum* we produced an unconventional computing model that imitated development of the French transport network through the distribution of its protoplasmic tubes. We found that at least once during laboratory experiments, slime mould represents over 70% of man-made motorways in France. Over half of the motorway links are represented by the slime mould in over half of the laboratory experiments. The transport links represented in over 70% of experiments, that is the
strongest links, are the chain Lyon – Grenoble and the chain Lille – Paris – Rouen – Rennes – Nantes – Bordeaux – Toulouse – Montpellier – Avignon – Marseille – Toulon – Nice. This is a chain of motorways spanning France from the North to South-West to South and South-East.

In comparison to proximity graphs we found that the motorway graphs provide a weak representation of proximity graphs: only spanning trees rooted in Nantes and Rennes are sub-graphs of the motorway graph. Some edges in the relative neighbourhood graph and the Gabriel graph are not included in the motorway graph. In contrast, at least its weakest version, the *Physarum* graph includes all three types of proximity graphs. Moreover, in the strongest *Physarum* graph, only a few edges of the proximity graphs are not included. These findings might demonstrate that while French motorways are lacking the proximity logic typical of engineering projects, their topology is supported by bio-logic of the slime mould.

We must also note that these results can only be an approximation, since only the 15 most populated urban areas have been taken into account for the experiments to simplify the procedure. Notably, none of the hubs of activity are located in the central area of France. For instance in the *Physarum* models, Clermont-Ferrand and Limoges are connected by
motorways to Paris but rank 19th and 37th, respectively in term of population – and Le Havre, ranks 34th but is the 2nd most important harbour in France and therefore has already been connected to Paris by a motorway in the 70s. Perhaps an alternative approach would be to establish a different city ranking for modelling. For example, a more comprehensive selection criteria that takes into account key data such as - population, geographic, historic, tourist and economic criteria – may allow a better representation of the French network without requiring every conurbation to be modelled.

Moreover, limitations were encountered since the experiments were conducted on flat agar plates, where no landscape features (e.g. mountains or lakes) were presented. In future studies, it may be possible to incorporate geographic challenges by cultivating the slime mould on three-dimensional templates of France.

Modelling the experimental setup using similar ‘bottom-up’ local interactions within the virtual plasmodium yielded networks which either retained the central East-West crossing points (fast network adaptation condition) or did not contain the East-West crossing points (slow network adaptation condition). The difference between the two conditions can be interpreted due to the trade-off between network connectivity and network length. Fast shrinkage conditions resulted in defects in the material, causing increased connectivity (and degree) at the ‘expense’ of greater network length (i.e. more network material needed). Slower adaptation resulted in fewer defects and shorter overall networks approximating spanning trees, but at the expense of decreased connectivity. A similar trade-off occurs in human constructed motorway networks. It is technically theoretically feasible to construct motorways where each urban area is connected to all other areas. Of course this would practical problems in terms of expense and construction disruption and would contain many redundant or unnecessary links. At the other extreme it would be possible to construct a minimal distance, spanning tree-like network structure. Such a topology, however, would not account for the relative importance between certain links on the tree and would possess too little network redundancy to cope with network

![Figure 15. Comparison of connectivity degree of cities during fast and slow shrinkage. Cross-hatched bars indicate fast shrinkage, vertical-hatched bars indicate slower shrinkage.](image-url)
disruption or disconnection. Both Physarum networks and the motorway network attempt to resolve the trade-off between network connectivity and network length.

A fundamental assumption underpinning these experiments is that man-made motorway networks still have many things to learn from networks encountered in Nature such as, the striking spider orb-web appearance of the French motorways. This impression is conferred by the radial distribution of central routes that originate from the capital while peripheral motorways appear to be organised around this powerful hub as concentric circles. Moreover, the density of concentric motorways increases as one approaches Paris (Figure 1). However, such analogies may equally well be conferred by other factors such as, the geometry of the environment. This is the most likely explanation for the derived network topologies since the overall geographic region of France is already shaped in an approximately hexagonal configuration – being bounded at the coastal

Figure 16. Idealised city-planning designs such as Ebenezer Howard’s Garden City Howard (1965) also followed spider-web pattern. Source: image from http://upload.wikimedia.org/wikipedia/commons/3/3d/Garden_City_Concept_by_Howard.jpg.
zones and the mountain ranges – and is likely to contribute significantly to the solution produced by the plasmodium network morphology. For a further study, it would be interesting to experiment whether a spider would construct a similar network structure given the same boundary constraints as topographically delineated at the French frontiers. And secondly, it would be interesting to investigate whether slime mould protoplasmic network can converge freely to the same optimised solution given a proper list of French cities and three-dimensional templates of France. This would allow a better understanding of the optimisation process taking place and to improve computer modelling and answer the question: can the spider web and slime mould structures and functions become a fruitful suggestion box for human-made networks?

From an applied perspective Physarum appears to have a deductive, rather than a predictive value in establishing the efficiencies in urban transport routes. Its value in the planning of national highways and motorways therefore is currently limited. Yet, such unconventional computing models may play a role in establishing network optimisations. For example, in developing bypasses – especially if it was demonstrated that replication of 3D topographies can effectively solve the kinds of geographical challenges encountered in this study, that is the presence of a mountain range.

Physarum demonstrates a striking capacity to deduce wheel and spoke architypes that are generated by highly stable circular and radial forms. These are described earlier in this paper as characteristic ‘spider web’ designs but such idealised forms are also recognised in city planning in projects such as, Ebenezer Howard’s Garden City (Howard, 1965) (Figure 16) and are fully operational in places such as, Vienna where wheel and spoke forms of urban organisation and transport organisation have been associated with efficient distribution infrastructures (Cook and Goodwin, 2008). However, drawbacks of this form of organisation include its centralised character that renders day-to-day operations as being relatively inflexible and often requiring two journeys through intersections to reach most destinations. Such an organisation system is prone to bottlenecks and operational congestion. Potentially this may explain why, when an obstacle such as, a mountain range is reached, that no robust alternative transport route is proposed.

Perhaps the ultimate test of a Physarum transport network may be to ask it to deduce a grid structure which is typical of New York or Milton Keynes in the UK. These road structures were designed for maximum navigation and efficiency so, the comparisons between human logic and natural logic in developing transport solutions may be most optimally compared in these systems – particularly as they are driven by geometrical propositions and have comparatively little historical complexity, or ‘organic logic’ in their evolution. Potentially by working at different scales and introducing 3D challenges into the nutrient matrix using 3D printing techniques it may be possible to identify more strategic applications of Physarum in the design of city transport systems that may favour stable network typologies.

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