Chapter 1

Introduction

Consider the unfortunate situation of falling down a mountain. Subject to the inexorable effect of gravity and friction, the hiker will roll downhill until they reach a certain valley, a spot at which they will finally terminate their unlucky dynamics. This final state is called an attractor. Now, consider a landscape like the one in Fig. 1.1A. The mountain has several valleys, separated by peaks. An example of this separation is shown in Fig. 1.1B. Consider then the even more unfortunate situation of *two* people falling down a mountain. If they start very close together, on the same side of a peak, they will fall down to the same valley. If, however, they were separated by a peak when the fall started, then they will fall into distinct valleys. This is shown by the green and red trajectories in Figs. 1.1A-B. Again, each valley is an attractor. An attractor is chosen by the initial condition - where the person was and how fast they were moving when they started to fall. All initial conditions that lead to the same attractor form a set called the basin of attraction of that attractor. All the red trajectories in Fig. 1.1A belong to the same basin. Trajectories are typically separated by peaks in the landscape (green and red of Fig. 1.1B), so the peaks usually form the boundaries between basins of attraction.

The example of the hiking disaster serves as a good introduction to the notion of *multistability* - the simultaneous coexistence of different ending states, different attractors, in a dynamical system with constant parameters (notice that the mountain landscape does not change in time in the example!). This phenomenon is present in a wide variety of notable systems, with important real-world consequences [1, 2, 3]. In biology, multistability can explain how genetically identical cells can exist in multiple metabolically distinct stable states [4, 5]. Similarly, there has been evidence, and models, suggesting that multistability in the gut microbiome can explain microbiome shifts, which are changes in the composition of the microbiome in the gut [6]. On a technological side, power grids - networks of connected generators and consumers of electrical energy - need to operate on an attractor in which all units have their frequencies synchronized in the 50-60Hz range [7]. Multistability in the grids can be dangerous, as perturbations can switch the system out of the operating state, potentially leading to blackouts. Studies on models try to look for conditions that make the desired state as stable as possible [7, 8]. Multistability can also be a powerful mechanism in brain dynamics. Some models for long-term memory consider that each memory corresponds to an attractor in the system [9, 10], and some models of large-scale brain dynamics exhibit multistability [11]. There are many more examples of multistability, such as in artificial neural networks [12], models for ice sheets [13], mechanical systems [14], and in tissue repair [15].

The examples in neural networks and power grids in particular highlight the ubiquitous presence of multistability in networked systems - systems formed by the interactions of smaller subunits, such as neurons or electric generators. Another phenomenon in networks that can coexist with multistability is synchronization [16, 17]. In a synchronized network, the different subunits have similar activity - for instance, frequency synchronization occurs when individual oscillators with different natural frequencies spontaneously lock into a common frequency [18]. A perhaps more technically relevant example has been mentioned before for power grids, in which all the units must have their frequencies synchronized at the same level, such as 50 Hz [7]. When
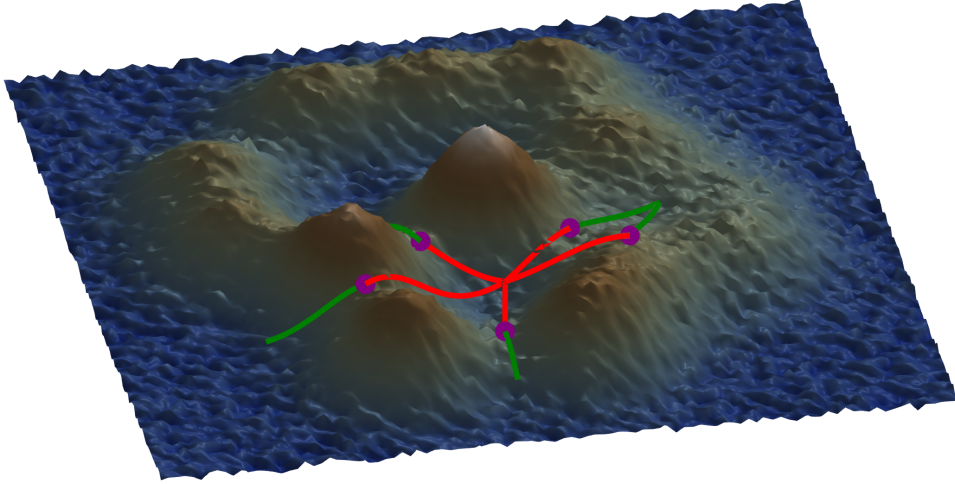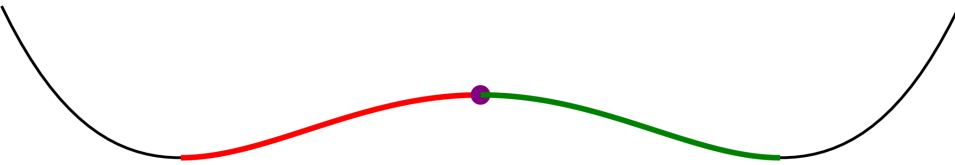
Figure 1.1: **Landscape with valleys and peaks constitutes an example of multistability for an unfortunate falling person.** Panels A and B respectively show a 3D and 2D example of a landscape, with red trajectories converging onto the same attracting region, and green trajectories, which start next to the red trajectories but on the other side of the peak, converge onto other attracting regions.

units have the same frequencies and the phases of their oscillations are also the same, we talk of phase synchronization. This has also been proposed as an important mechanism in brain circuits [19, 20, 21]. Interestingly, lack of phase synchrony can also play an important role, e.g. in the flight pattern of fruit flies [22].

The real-world relevance of such systems has stimulated a lot of research into their dynamics [1]. An approach taken by several works has been to study simple models that capture some essential properties of real world systems. A particularly important example, which has become paradigmatic in the synchronization literature, is that of Kuramoto oscillators (see Sec. 2.4). They constitute quite a beautiful example of how units with very simple dynamics can generate complex behavior when interacting together. Each unit in the model is described by a phase (angle) variable that by itself just varies linearly according to its own natural frequency. The interesting dynamics comes from the nonlinear coupling, done via the sin of the phase difference between coupled units, cf. Eq. 2.34. The model is simple enough to allow for analytic treatment but still complex enough to show relevant dynamics [18, 23]. In particular, it displays a continuous phase transition from desynchronization to frequency and phase synchronization as the strength of the inter-unit coupling is increased. Roughly, if the natural frequencies are spread too widely compared to the coupling between them, the units oscillate incoherently; if instead the coupling

becomes large enough, the units start to oscillate with the same frequency - they become phase-locked. As the coupling increases, the phases also become more clustered together, although complete phase synchronization does not occur.

The Kuramoto model is also generic in the sense that it can be derived as an approximation of general limit cycle oscillators under weak coupling [17]. In this case, one considers units that oscillate on a periodic orbit. If the coupling between the units is weak enough, the amplitude of their oscillation is not significantly affected, only the phase along the limit cycle. Then, the interplay between the differences in frequency and the coupling determines the time evolution of the phases. The Kuramoto model is a somewhat more specific case of this phase reduction, in that one chooses a purely sinusoidal coupling [18]. Still, the combination of simplicity and complexity leading to a synchronization transition, and this argument of genericity, incited a lot of research and inspired new concepts [23, 24, 18].

This also inspired us to translate results we had from spiking neural networks [25]. In those networks we described a phenomenon we called *dynamical malleability*, the sensitivity of a whole network's dynamics to changes in parameters of single components, usually changes in parameters of single units. Similarly to the Kuramoto oscillator networks, the spiking neural networks we studied also present a transition to synchronization, in particular to phase synchronization, when the coupling strength is increased. They also present a transition to synchronization as the topology changes: as the connections in the system are changed from being restricted only to k-nearest neighbors to being randomly allocated, the neurons also start to synchronize their phases. Types of topologies are described in more detail in Sec. 2.3. In the neighborhood of both of these transitions, we showed that the network's dynamical malleability increases considerably. As we see in Chap. 3, this phenomenology generalizes for Kuramoto networks with heterogeneous frequencies. In fact, it occurs very strongly: changing the parameter of a single unit can drastically alter the behavior of the whole network in a very sensitive manner [26], which was until then not known.

In the literature for Kuramoto oscillators we found some works related to this phenomenon. In a series of papers, Hong and colleagues studied it from the point of view of statistical mechanics [27, 28], where dynamical malleability is often called sample-to-sample (STS) fluctuations. There, they say that the STS fluctuations increase near a phase transition. Changing the parameters of a single unit leads to a different network, which is termed to be a different sample. In this case, one shows that the finite size of the networks leads only to an approximate phase transition, whose critical parameter varies depending on the sample. These studies, however, did not look closely at the dynamics of these finite networks. One work that looks at this more closely for all-to-all topologies was Ref. [29], where they propose that the kurtosis of the natural frequency distribution correlates with the critical coupling strength of the transition. Therefore, changing the frequency of the units changes the kurtosis and thus changes the critical coupling strength. However, they did not explore how this also interacted with more complex topologies. As we then showed in our work, their mechanism alone does not explain the malleability we describe: networks with shuffled natural frequencies have the same kurtosis but still can vary significantly. The malleability does come in part from the sample-to-sample fluctuations described for instance in works by Hong et al. [27]. But it also comes from multistability, which is another behavior we then analyzed.

We looked at multistability in the networks as a function of the coupling strength and topology, and showed the emergence of a large number of coexisting attractors at the transition to phase synchronization. This therefore means that the networks we studied are very sensitive to perturbations in the state variables (which can lead the system to switch to other attractors, due to multistability) and in the parameters (which can change the attractor considerably, due to malleability). This was another contribution from our work. Naturally, there have been studies on multistability in Kuramoto networks. In the case of heterogeneous frequencies, Tilles et al. studied multistability arising in nearest-neighbor rings [30]. In a related Kuramoto model, which has an inertial term, some studies have shown the coexistence of multiple attractors in random topologies [31], and in power grid topologies [7, 8]. Ref. [32] looks at how properties of power grid topologies relate to the dynamics of first-order Kuramoto models, but do not report multistability.

Multistability has been studied in detail for units with homogeneous frequencies (which are then identical) and which are coupled in k-nearest-neighbor topologies. In this case, the network can be written as a gradient system, meaning its only attractors are equilibria, which are single points in state space (cf., Secs. 2.1.2-2.1.3). This considerably simplifies their study. The networks can have multiple stable equilibria, each being characterized by neighboring units having a fixed and constant phase relationship. These equilibria are called twisted states [33], and their stability depends on the relationship between the number of nearest neighbors k and the size N of the network [33] - see Sec. 2.4.2 for more.

For these networks there have been studies looking at the effect of the topology [34], showing a minimum coupling strength that guarantees complete synchronization globally. Another important contribution has looked at the basins of attraction for these networks: Zhang and Strogatz have shown that the basins behave like octopuses - the head of the octopus contains the attractor, an equilibrium. The head is relatively small compared to the tentacles: most of the volume of the basins is not concentrated around the equilibrium, but spread around in tentacle-like structures in state space [35].

In both the case of heterogeneous and of homogeneous frequencies, we are unaware of any systematic study on the emergence of multistability and effect of changing topology, in particular for first-order Kuramoto models. Inspired by this, we have started to study more deeply how exactly these attractors emerge and how their basins behave. This is subject for future work, but its basis is found in our study on malleability. In general, therefore, our work served to bridge two gaps in the Kuramoto literature: the dynamics of malleability and that of multistability, both of which contribute to understanding the sensitivity of these networks.

The mechanisms that give rise to multistability in networks in general are still not fully understood. In particular, during my PhD we started to study multistability in a network of bursting neurons coupled diffusively, looking to explain results from previous publications [36]. The neurons, which follow the Hindmarsh-Rose equations [37], have individually a stable periodic orbit as an attractor. By changing parameters of the neurons, one can make a certain region of this periodic orbit very slow, but without going through a bifurcation. Preliminary results showed that multistability only emerges in the coupled networks when the neurons have this slow region. To better understand this, we looked at a simpler conductance-based neuronal model [38] which also has regions of slow flow. We focused on the case when this model has excitable dynamics. The isolated neuron then has only one attractor, a stable equilibrium. And it also has two unstable equilibria, which force some trajectories to go on long excursions before converging to that attractor. These excursions are called excitations, and correspond to the neuron spiking. One of these unstable equilibria also slows down trajectories passing near it. By coupling two such neurons diffusively we show the emergence of different types of oscillating attractors, which can all coexist. We show the bifurcations giving rise to these attractors. Furthermore, we describe a qualitative mechanism for how they occur. The idea is that the diffusive coupling acts to repeatedly reinject the trajectories of each neuron into the region responsible for the excitations, thereby effectively *trapping the trajectories in the previously transient region* - see Chap. 5 for more. The slowness near one the equilibria plays an important role in this mechanism, which might help to explain the original problem we started on. For two units, it can happen that both are trapped in this excitability region, or just one is, generating in total three possible combinations. For more units, the number of possible combinations increases, and therefore so does the number of coexisting attractors. The emerging attractors are all oscillating, and can do so periodically, quasiperiodically, or chaotically - all despite the individual units having only equilibria! This mechanism is also a simple example of how coupling can interact with transients to generate attractors, an idea that has been studied in the literature under different circumstances. In particular, Medeiros et al. studied units which have a periodic attractor and a chaotic saddle, an unstable chaotic set, in their state space. They showed that diffusive coupling between them can counteract the divergence tendency near the chaotic saddle, effectively trapping the units in its neighborhood, and creating a chaotic attractor which coexists with the units' periodic attractor [39, 40]. However, the authors did not observe multiple attractors emerging from the trapping in the chaotic saddle. Therefore, the coupled excitable neurons, with their trapping mechanism, constitutes a simple yet powerful mechanism for generating a

rich multistability in networks, which had not been described previously in the literature, to our knowledge.

This line of investigation on multistability also contributes to the study of how oscillations arise in non-oscillating units interacting via diffusive coupling. As discussed in Chap. 5, this line of work has a rich history, with an early work by Smale showing that Hopf bifurcations can give rise to oscillations [41] - see Sec. 2.2 for bifurcations. Later works showed the possibility of chaos, and also the emergence of multistability in repulsive coupling. Our contribution in this case has been to show a rich multistability, with the possible coexistence of periodic, quasiperiodic, and also chaotic solutions - with repulsive or attracting coupling.

These studies on multistability require efficient and reliable algorithms to identify the co-existing attractors of a system. To this end, I have contributed to creating Attractors.jl, an open-source package in the Julia programming language that collects such algorithms. In particular, George Datseris and Alexander Wagemakers had already introduced an algorithm to find attractors based on recurrences in state space [42], from an idea by Nusse and Yorke [43]. I then contributed to implementing and refining another algorithm, proposed in Refs. [44, 31], based on finding attractors by grouping trajectories with similar features. These algorithms are described more in Sec. 2.1.7. Together with Datseris and Wagemakers, we built a continuation framework that allows one to use either of these two methods across a parameter range. This idea is similar to linear continuation analysis, but generalizes to any type of attractor, including chaotic attractors. This led to a publication [45]. On top of the novelty of the continuation algorithm, and the improvements made to the state of the art algorithms for finding attractors, our contribution here was also to provide a package that is free and easy to use.

Going back now to the excitable neurons, the multistability seen there is remarkable: stable states arise from the interaction with transient behavior (the excitations). Often in the literature we are preocupied with the final states of the system - usually justifiably so - but anyone who asks the falling hikers in our initial example will probably find out that transients should not be disregarded so easily. In particular for neuroscience, transient dynamics has been the object of a lot of recent work. For instance, transients can be harnessed to perform computations [46], particularly when they are long-lived [47]. Ref. [47] proposes that long-lived transients, particularly in the form of ghosts of saddle-node bifurcations, offer some distinct computational advantages, such as maintaining a dynamical memory of a signal. See Sec. 2.2 for more on ghosts. For instance, Ref. [48] studied a simple model for how cells respond to changing chemical signals and use them to move. Without any signal, the cell operates on a stable equilibrium. A signal causes a saddle-node bifurcation that leads it to another stable equilibrium. As the signal is removed, the inverse bifurcation happens, and the cell eventually converges back to the original equilibrium. But before returning, the cell stays for a while visiting the ghost of the second equilibrium. Biologically, this means that cell keeps the memory of the signal for a while [48, 47]. Indeed, long-lived transients are an ubiquitous phenomenon observed in neural activity [49, 50], and are often referred to as *metastable*. One interesting example comes from studies measuring how mice encode for tastants fed to them. The study measured the firing rate activity in the gustatory cortex of the mice as a response to different tastants [51]. They identified that the stimulus elicits a sequence of distinct long-lived but transient regimes. By regime here we mean an epoch of the time series with some unique properties - in their case, the configuration of the average firing rate across the ensemble of neurons. Each tastant evoked a specific sequence of such metastable regimes. The duration of these regimes varies across trials, but the sequence itself is consistent [52, 50].

Delving into the metastability literature, we found that a general conceptual framework was lacking. First, the very definition of metastability varied between works, leading to apparent inconsistencies, as explained in more details in Chap. 4. Second, the mechanisms proposed for metastability also varied. Some works propose ghost of saddle-node bifurcations [49] while others propose noise [50], with few works attempting to compare different proposals [53]. In our work, we drew from from tools of dynamical systems theory to provide such a conceptual framework. We provide a simple definition of metastable regimes as long-lived transients, which encompasses the majority of previous works not only in neuroscience, but also dynamical systems and even ecology. Previous inconsistencies between works can be neatly fit into distinct subtypes

of metastability - for instance, when transitions between metastable regimes are spontaneously or externally driven. Then we use this definition to study general properties of metastability, making use of the concept of almost-invariant sets [54, 55]. We also propose several dynamical mechanisms that can generate metastable regimes. Importantly, we connect these mechanisms to what had been proposed previously in the literature, gathering insights from different literatures.

Taking all of this together, my PhD has been a journey into studying the long-term and the transient dynamics of networked systems - how multistability can emerge and how it affects their robustness - and how long transients (metastability) can arise. This thesis describes this journey and will hopefully reflect the excitement of doing all of this research. In Chap. 2 I introduce in greater depth the fundamental concepts needed for the studies performed in this thesis. These will then follow in Chaps. 3, 5 and 4 in the same order introduced here. Finally, in Chap. 6 I will take all of these results together and reflect on what we learned, what our contributions have been to the literature, and the open questions that lie ahead in the future.

Chapter 6

Conclusions

Science is typically reductionist [265]. We break a hard problem into smaller parts that are easier to understand separately. We have achieved tremendous success with this effort, but we have not solved everything; indeed, we have found out that putting everything back together can be quite complicated: interactions between even simple units can generate complex behavior that is not present in any one of the units alone. The field of complex systems arose from the need to understand this *emergent phenomena* - to (re)construct the full system's behavior from knowledge of its parts. A major challenge still today is to develop tools that allows us to characterize and figure out complicated emergent behavior.

One such complicated behavior is the coexistence of multiple stable solutions to the same equations with the same parameters - *multistability*! How do these solutions come about, where they are situated and how they are they separated in state space - these are all questions under active research [1, 2, 35].

Some of these stable solutions may correspond to synchronized regimes, which brings into light another important phenomenon: *synchronization*. Here again the field of complex systems has to contend with another problem: how individually distinct units can cooperate together and start to operate in unison, in a beautiful example of an emergent phenomenon. The study of synchronization - both frequency and phase synchronization - also has important practical motivations, for instance in the study of power grids. In power grids, and other complex networks, understanding the robustness of solutions, in particular of synchronized solutions has been an object of active research.

Combining these two research areas, Chapter 3 investigated the robustness of solutions in a complex network of Kuramoto oscillators, a paradigmatic model for studies on synchronization phenomena and complex networks in general. The idea was to investigate how the network behaves - how the solutions change - when we alter the parameter of a single unit in the network. We found that the *dynamical malleability* of the network depends on how strongly coupled the units are, and the topology of the connections. Roughly, we showed that for very weak coupling strength the individual tendencies of the oscillators win and most of them oscillate incoherently. For sufficiently strong coupling, most of the oscillators become phase locked - they oscillate at the same frequency. This is the same behavior as in all-to-all networks (see Sec.2.4). The spatial pattern of the phases, which we can measure via the degree of phase synchronization, was then determined by the topology. Networks dominated by short-range connections tended to have short-range patterns (phase desynchronized), while networks dominated by long-range connections tended to have long-range patterns (phase synchronized). These networks typically have multiple attractors coexisting, but most of the attractors, especially the most synchronized attractor, follow this tendency. In parameter space, phase synchronization in these networks lives in the region of sufficiently high coupling strength and number of long-range connections. Changing the parameters toward this region therefore makes the system undergo a transition to phase synchronization. We showed that precisely during this transition their dynamical malleability increases considerably. To the point that changing a single unit radically alters the pattern of phases in the network, potentially changing it from phase synchronized to phase desynchronized.

The mechanism for this dynamical malleability is two-fold. First, it is related to *increased sample-to-sample fluctuations* near a phase transition [27, 28]. This mechanism does not require multistability. In fact, suppose the systems have a single attractor, like the randomly connected networks. Each change to a parameter of a unit leads to a different dynamical system, which may have a different attractor. In particular, the transition to phase synchronization of this attractor may occur at different coupling strength values, earlier or later compared to the system before the change. If we enact this change but keep the coupling strength fixed, we switch to an attractor that has a smaller or larger value of phase synchronization - this is the fluctuation from one sample to another. If the systems have multiple attractors, this effect is still there, but there is the added possibility of switching to other attractors, which might be even more different. The *multistability* increases the possible fluctuations that may occur. This explains our observation that for Watts-Strogatz networks the malleability and multistability seem to go hand in hand. It also explains why these networks have a considerably larger malleability than the distance-dependent networks, which do not seem to be multistable.

An important new concept in the area of complex systems is that of global stability, typically taken to mean the relative size of the basin of attraction of each attractor - attractors that occupy larger regions of state space are more globally stable, in this view [266]. Considering a trajectory on an attractor, bigger basins of attraction mean that bigger perturbations are on average needed in order to kick the trajectory across the basin boundary and into another attractor. This is, of course, a simplification [267], but it highlights the importance given to studying perturbations applied to the state a system. And, in general, more attractors means they are sharing state space more and therefore the global stability is smaller, meaning the system is less robust (or less resilient, depending on terminology [267]). In this work we show that multistability affects the robustness of the system in another way: by affecting its malleability. So not only is it dangerous to kick the state of the system, it is also dangerous to change its parameters - even the parameter of one single unit!

Another important observation was the study of how malleability, and multistability, depend on the topology of the system. Topologies that put the systems in the vinicity of a transition to phase synchronization, which were in the small-world range, made it very malleable. An important question that is left for future work is why these specific topologies lead to a higher number of attractors - which properties do they possess that lead to the emergence of the attractors, compared to, say, the random topologies, which do not induce multistability? The distance-dependent networks also do not seem to be multistable, a factor that would also be interesting to investigate.

A related question is about the generality of these results. Malleability due to sample-to-sample fluctuations is very common, being extensibly described in statistical physics literature [113]. We also described it initially in a network of spiking neurons [25], and observed it in the Kuramoto model under different topologies of distributions of the natural frequency, and under other models, such as a simple model of excitable cells. We believe that the multistability results will also generalize somehow - supported by the available evidence from other works - but this is also object of future research. Understanding better the mechanisms generating the multistability will also help answer this.

In a similar vein, we also investigated how multistability emerges when excitable neurons are coupled diffusively. Excitability in the individual units here occurs due to the presence of a saddle and an unstable equilibrium in state space, which force part of the trajectories to go around on a long excursion before eventually converging to the stable equilibrium. These region where trajectories go through is called the *excitability region*. We showed that the coupling can trap trajectories in this excitability region by repeatedly reinjecting them there. This mechanism underlies all the emergent attractors we observed, even though they arise due to different bifurcations: saddle-node of limit cycles and homoclinic. For two units, it can create three coexisting periodic attractors, and can also create a quasiperiodic attractor. For more units, it can create a larger number of attractors, including potentially a chaotic attractor. Based on the trapping mechanism and preliminary results, we conjecture that the topology of the networks plays a key role in dictating which attrators emerge, and how many. This could be very similar to Kuramoto networks, and a more in-depth comparison is definitely warranted. It would be very interesting

in the future to explore how exactly the size and topology of the networks control the emerging attractors.

In this initial work we decided to focus mainly on the pure dynamics of the system, so we showed most of the results in the case where the coupling is applied to both the x and y directions of the system. In some models, such as ecological models - where the diffusive term would model a migration of species - this might be very sound. For the neuronal case, however, only the x-coupling is biophysically sound. Motivated by this fact, we also investigated how the attractors change when the coupling is applied to only one variable. Interestingly, the mechanism is still present, but the two main types of attractors we observed - with two units trapped in the excitability region or with just one - split up when we split the coupling. The exclusive x-coupling got the former; the exclusive y-coupling got the latter. We confirmed this with a bifurcation analysis and also qualitatively explained it based on the geometry of the attractors and the trapping mechanism. This is important in terms of potential applications. First, it means that adding a gap junction between two otherwise silent neurons could make them bistable, with the possibility of periodic or even quasiperiodic spiking. In fact, there is some evidence that this seems to occur in neurons coupled under gap junctions in the motor cortex of fruit flies [22]. It is also interesting in the ecological direction, if we consider that only some species in an ecological niche might be migrating between patches.

Furthermore, we focused for simplicity on the excitable case, where the trapping mechanism creating the attractors is more easily seen. But attractors still emerge similarly in a bistable regime, where the stable equilibrium coexists with a stable limit cycle. We can achieve this by changing the input current I of the model. A difference in this case is that the uncoupled neuron already has an oscillating attractor. Therefore, when they are diffusively coupled they can also synchronize together in this oscillating attractor. This system thus has the possibility of achieving full synchronization on a periodic attractor. In this case, one could reframe the study in terms of the stability, global and linear, of the synchronized state, and how the coupling might create new attractors and thus reduce the relative size of the basin of the synchronized attractor.

We initially arrived at this this problem when trying to understand the synchronization behavior of a network of bursting neurons [36]. The degree of phase synchronization in that system changes nonmonotonically as a function of the coupling strength: increasing the coupling initially increases the phase synchronization, then actually decreases it in a certain region, before increasing it again for very strong coupling. This is also reminiscent of a behavior observed in networks with chaotic saddles in Ref. [39]. We also studied a network of bursting neurons following another model, and found that a chaotic saddle was important there but also a slow region of system's limit cycle was related to the multistability that emerged. From the work on excitable neurons, we understand that slowness can help generate attractors, at least for the reinjection mechanism we observed. It would be interesting in the future to go back and finish the initial studies.

When working on a project, I believe it is not an uncommon feeling to find an interesting paper, try to replicate its results and not quite manage. Then, to look at the source code that the authors hopefully provided, and to be underwhelmed. While working on a paper, it is often the case that people might want spend as little time as possible implementing the algorithms they need, leading usually to confusing code, which might not be as efficient as it could, and not as well-tested - and thus, more susceptible to errors. One solution to this is to create a unified library that implements efficient code, tests and documents it. And to make it open-source, to share it with the whole community. Then, anyone can scrutinize the code, find improvements and test it further. Also, more importantly, everyone can use it. This saves implementation time, potentially run times due to improved code efficiency, and also re-implementation time for poor students aiming to replicate papers. This is the philosophy of the dynamical systems library [260], started by Dr. George Datseris, written in the Julia programming language. With this idea in mind, we also collaborated to implement algorithms related to finding attractors and their basins. In particular, I worked on the algorithm used in the two multistability works in this thesis. It is a brute-force algorithm that integrates trajectories, converts them into vectors of features, and selects attractors as unique groups of features [31, 44, 45]. Together with Prof. Alexander Wagemakers, we also implemented an algorithm that applies attractor-finding

algorithms across a parameter range, in a continuation manner. The result of this work was the *Attractors.jl* package, also co-developed by more collaborators, and a publication describing this novel algorithm and improvements to previous literature [45].

So far on the study of dynamical systems we have mostly focused on attractors. The motivation for this is that attractors represent a system's long-term dynamics: after some *transient* time, one just observes the attractors. There is, however, a key assumption here: that the period of time during which we observe the system T_{obs} is longer than the convergence time T_{conv} to the attractor. It is a matter of time-scales: of the observation versus the relaxation to the attractor. Whether this can be guaranteed or not depends on the application. In power grids, for instance, one is generally interested in the long-term dynamics of the system. In the brain, however, changes may be occurring too fast, and there may not be enough time to wait for convergence to an attractor. The time-scales can also vary within the same system: as we saw in the excitable units, trajectories starting on one side of the state space converge rapidly to the attractor, whereas trajectories starting on the excitability region spend a relatively long time performing an excursion in space before reaching the attractor. This problem is made more complicated due to the fact that there are many mechanisms that can generate long - potentially arbitrarily long - transients. An example is chaotic saddles, wherein trajectories can stay indefinitely long [216]. Therefore, the behavior that is actually observed in some studies may be a transient.

And transients can indeed play important roles. One example that illustrates this is the Turing machine, the paradigmatic model for *computations* [268, 269]. It is a simple finite state machine with a head that stores a certain state and can read, write, and move along a tape. The tape is subvided into cells containing symbols (e.g., 0's and 1's). The head represents a modern computer's central processing unit. Accordingly, it follows a set of instructions that take the current state, currently read symbol on the tape and outputs the new state, new symbol it writes on the tape, and the direction it moves. Computations are done by traversing a sequence of such state-symbol combinations. The machine may run forever - it is said to not halt -, in which case the computation is not completed. If the machine does halt, the computation is finished. From this point of view, therefore, the computation is only complete once the machine terminates the previous sequence of states. This sequence can therefore be seen as a transient, which is thus crucial for the computation of the machine. This remark is not just an analogy - dynamical systems can be constructed that implement Turing machines [270].

More concretely, in the brain, transients have been shown to play important roles [160, 139]. There is a plethora of observations showing neural activity going through sequences of distinct states, which are all therefore transient [49, 50]. In several cases, these states are long-lived (i.e., metastable). Understanding the exact roles that *metastable regimes* play in neural circuits is crucial to understanding how they perform computations, a central question in neuroscience and also artificial intelligence [47, 271, 214]. Recent work, based on theoretical and experimental results, has shown that ghosts of saddle-node equilibria, which generate long transients, are a particularly important mechanism [47, 65, 48, 139]. It is expected, however, that other mechanisms are also present in circuits. For instance, a wide literature in neuroscience uses attractors to perform computations, and adds external perturbations to induce changes between regimes [272, 214, 50, 254]. It will be important in the future to contrast these two ideas to see the actual roles played by each of them.

To achieve this advancement, it is important to have both an in-depth as well as a general understanding of metastable dynamics. Under this logic we developed a *general conceptual framework* for metastability, collecting and refining ideas from the neuroscience and dynamical systems literatures. As seen in Chap. 4, we proposed that the main concept behind metastability is that of long-lived transients, and showed many dynamical mechanisms capable of generating this. In the future, one can use this framework to actively compare the different mechanisms, with a view towards experiments - both biological as well as in silico, looking to understand how networks perform computations [47].

Besides the metastable regimes themselves, perhaps the actual *sequences* play an important role. This is the case in the Turing machine, but there is also evidence in biological networks. An important example, already mentioned in the Introduction and in Chap. 4, showed in a series of works that sequences of metastable regimes are elicited when mice are fed tastants [51]. The

sequence of regimes is unique to each tastant, suggesting they play an active role in encoding the stimuli [52]. Sequences of metastable regimes have been linked to computations in other experiments also [139, 52, 272]. In this case, a useful concept coming from dynamical systems theory is that of excitable networks by Ashwin and Postlethwaite [273, 274]. They developed methods that allow one to construct systems with prescribed connections between equilibria states. These connections may be spontaneously activated (as in connected ghosts) or via a perturbation (by perturbing across the basin boundary). This is an example of how the theory of dynamical systems is offering many tools and mechanisms that can be used to model and better understand how circuits are actually solving tasks and performing computations. This is an exciting area for future research.

Taking everything together, the field of complex systems is under intense research, with lots of us aiming to develop theory and tools to understand emergent dynamical phenomena like synchronization, the coexistence of multiple long-term solutions and the (transient) path to them. I believe that during my PhD we managed to provide some timely contributions in these directions, but there is still much to be done - with applications being very significant in biology, technology and even climate. I am very excited to help put all these pieces together.