

DEPARTMENT OF MATHEMATICS

# Synchronization of Oscillators

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#### Abstract

In this thesis we consider a system of coupled oscillators: 'cells' that progress through a cycle and neither reproduce nor die. The cycle the oscillators progress through is divided into a region in which oscillators can send signals and a region in which they can receive and react to those signals by speeding up or slowing down their progression, as a generalisation of the integrate-and-fire model of Mirollo & Strogatz.

We say oscillators are synchronized if they have identical phase and we are interested in the stability of the synchronized population. Does a population that is split in two return to the synchronized state or not. Instead of solving a system of coupled ODE's exactly, we analyse the dynamics of the oscillators by a Poincaré-like map on the unit interval, called full cycle map, that gives the position of a group when the other has completed one cycle.

Since the synchronized state corresponds to the two boundary fixed points of the full cycle map, we can analyse the (local) stability of the synchronized state by considering the derivative of the full cycle map. Also conjectures can be made about the full cycle map itself. In this way we investigate the influence of the sign and amount of feedback on the stability of synchronization and the existence and stability of cycle phase-locked configurations: two oscillators that neither converge nor diverge after one cycle completion.

Another approach focuses on the result of feedback on oscillators going from signalling to receiving or vice versa. This method gives intuitive results on synchronization that can easily be generalized to any number of oscillators, but lacks the precision to calculate the existence and stability of cycle phase-locked configurations.

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## 1 Introduction

Synchronization of oscillators manifests itself in many natural phenomena, partly because of the broad interpretation of the words oscillator and synchrony. Anything that progresses periodically through a cycle can be called an oscillator and communication between oscillators can lead to the creation of synchronized cohorts (groups of oscillators with identical phase).

Biological examples of oscillators are fireflies, that congregate in trees and flash in unison: "one of the most spectacular examples of synchronization in nature", according to Renato Mirollo and Steven Strogatz [2], or crickets chirping and listening to other crickets, see [6]. Also groups of bacteria may show synchronized oscillatory behaviour when coupled via signalling molecules [7], and in yeast populations periodic-like oxygen consumption oscillations can be seen [8], [4]. In human beta pancreas cells, oscillations are seen due to increasing population density [9], and size-structured population models can exhibit cohort-synchronization [10].

Also in physics we find examples of synchronizing oscillators: neutrino oscillations in the early universe, or the synchronization of metronomes placed on a freely moving base [11]. Better known may be the impulsive coupling of spiking neurons [12].

The integrate-and-fire oscillators from [2] or [3], originally proposed by Peskin [5] in 1975, progress through the complete cycle and fire a pulse before starting over. The oscillators evolve according to an evolution function defined on the unit interval and receiving a pulse causes an instantaneous increment of the state of the oscillators, or pulls them up to the endpoint, which results in firing. Both authors prove that a monotonically increasing concave down evolution function with excitatory coupling leads to synchronization.

For this thesis we developed a generalization of the model from [2], in a way that the firing is no longer pulse-like. The cycle through which the oscillators in this thesis progress is divided into a region in which oscillators can send signals and a region in which they can receive and react to those signals; also we allow neutral zones in which the oscillators neither send nor receive. The regions mentioned have no common interior points (at most two common boundary points), so oscillators cannot receive signals while they are sending and vice versa. If we let the sending region contract to one point, the model becomes strictly integrate-and-fire.

The division of the cycle into different regions comes from [4]. The authors consider two identical oscillators that progress through a cycle with unit speed. Receiving signals causes a constant increase in progression speed. Their key observation is that, under their assumptions, positive feedback typically leads to synchrony, while negative feedback systems tend to phase-locked behaviour.

Receiving signals results in this thesis in changes of the cycle speed, either positive or negative, depending on the position of the oscillator in the cycle. The question in this thesis is how assumptions on the feedback translate to conclusions about the dynamics of the oscillators.

Instead of solving the system of differential equations and investigating the occurrence of synchrony we define the full cycle map, that gives a stroboscopic view of the dynamics. The main goal of our analysis is to determine the stability of a population of synchronized oscillators with respect to the full cycle map, i.e. what has happened to different oscillators after they completed one cycle. Also we want to know if other cycle phase-locked steady states occur, either stable or unstable, and how the existence and the stability of these steady states depend on the feedback and possibly the strength of the signals sent.

### 1.1 Outline of the text

First we will develop the mathematical model and introduce the necessary notations. We make precise what is meant by synchrony and how the oscillators evolve. In the second section we introduce the half cycle and full cycle map which are used to translate the continuous dynamical system to a discrete one. In this way the synchronized state corresponds to the boundary fixed points of the full cycle map. After the first two sections a motivated preview will follow, with a recap on the notation and hints of the results: conditions for the stability of the synchronized state in Section 5. Here we emphasize the differences between the circle and the interval.

Section 6 covers the effect of a reflection of the feedback function on the cycle maps and in Theorem 6.4 we prove a relation that gives the cycle maps if the position dependence of the feedback in the receiving region is reflected. This theorem can be used to find interior fixed points in Section 7. Interior fixed points correspond to oscillators that, in the stroboscopic view, progress in a phase-locked manner. In this section we will prove that monotonic feedback drastically restricts the behaviour of the oscillators.

Having obtained results by analysing the full cycle map, we follow a different approach to generalize the results to the case of a cluster of arbitrarily many oscillators. This is done without the cycle maps or linearisation, but by considering the effect of the feedback on the width of the cluster of oscillators.

After conclusions three appendices will follow. A more thorough comparison with the article of Todd Young, which was the inspiration for this thesis, shows the major differences and similarities. The last two appendices will compare our model with that of [2] and [3], where we first introduce a limit procedure to arrive at the integrate-and-fire oscillators.

## 1.2 Acknowledgements

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Also Sebastiaan Janssens deserves my gratitude, for giving inspiration and correcting errors. Prof. Yuri Kuznetsov agreed to read my thesis and examine it, which I appreciate a lot. His comments helped me to improve the structure and presentation of this thesis.

## 2 The model

Mathematically we view the oscillators as moving with a positive speed on a circle or equivalently on the unit interval [0, 1], with the endpoints identified. Although the latter view requires some remarks later on, we will describe the oscillators by a phase (indicated by  $\theta$ ,  $\psi$  or  $\phi$ )<sup>1</sup> in [0, 1] where we need to reset the phase of an oscillator to  $\theta = 0$  as soon as it reaches  $\theta = 1$ .

While moving through the interval the oscillators can either send or receive signals and accordingly we distinguish two regions <sup>2</sup>: a receiving region  $[0, 1 - \eta]$  and a signalling region  $(1 - \eta, 1)$ , for some  $0 < \eta < 1$ . The two oscillators have different signal strengths which add up to one. The relative signal strength is indicated by  $\alpha$  so  $\alpha_1 = 1 - \alpha$  and  $\alpha_2 = \alpha$ , for some  $\alpha \in [0, 1]$ . Note that we can view an oscillator as a cohort of oscillators moving simultaneously. The signal strength of a cohort then reflects its size, i.e. the number of cells in a cohort.

#### Definition 2.1.

Denote the position of group i after a time t by  $\Psi_i(t; \psi_{01}, \psi_{02}, \alpha_i)^3$ , where  $\psi_{0j}$  describes the initial position of the jth group. The dynamics of the two oscillators is described by:

$$\frac{d\Psi_1}{dt}(t) = 1 + \alpha \ h(\Psi_1(t)) \ w(\Psi_2(t)) \qquad \text{with } \Psi_1(0) = \psi_{01}$$

$$\frac{d\Psi_2}{dt}(t) = 1 + (1 - \alpha) \ h(\Psi_2(t)) \ w(\Psi_1(t)) \qquad \text{with } \Psi_2(0) = \psi_{02}$$
(1)

We will call  $h : [0,1] \to \mathbb{R}$  the sensitivity function and  $w : [0,1] \to \mathbb{R}^+$  the impact function. The following assumptions will be used:

Sending region: 
$$w = 1_{(1-\eta,1)}$$
 (A1)

No self-excitation: 
$$h(\phi) = 0$$
 for  $\phi \notin [0, 1 - \eta]$  (A2)

**Positive bounded speed:** there exists an  $M \in \mathbb{R}$  s.t.  $-1 < h(\phi) \le M \ \forall \phi$  (A3)

so 
$$0 < 1 + \alpha h(\phi) \le 1 + M \ \forall \ \alpha \in [0, 1]$$
 and all  $\phi$ .

**Continuity:** The restriction of h to the receiving regions is (A4) Lipschitz.<sup>4</sup>

Note that although h and w are defined on the unit interval, we can easily extend them to the real line by periodic continuation.

We see from Definition 2.1 that the system is equivariant with respect to T, where  $T : [0,1] \times [0,1] \times [0,1] \mapsto [0,1] \times [0,$ 

Using Definition 2.1 we can define the synchronized state as follows.

#### Definition 2.2.

Two oscillators  $\Psi_1$  and  $\Psi_2$  move in synchrony if there exists a  $T \ge 0$  such that

$$\Psi_1(t;\psi_{01},\psi_{02},1-\alpha) = \Psi_2(t;\psi_{01},\psi_{02},\alpha) \tag{2}$$

for all  $t \geq T$ .

<sup>&</sup>lt;sup>1</sup>We will use capital letters to denote the phase as a function (of time), and lower case letters for coordinates.

 $<sup>^2 \</sup>mathrm{The}$  open interval assures that the signalling and receiving region are disjoint.

<sup>&</sup>lt;sup>3</sup>We will abbreviate this to  $\Psi_i(t)$  whenever the risk of confusion is negligible.

<sup>&</sup>lt;sup>4</sup>We allow  $h(0) \neq 0$  and  $h(1-\eta) \neq 0$ .

We call the configuration with two oscillators with identical phase moving in synchrony the synchronized state.

Notice that the 'for all  $t \ge T$ -part' in Definition 2.2 is in fact redundant. Indeed from Assumptions (A1) and (A2) it follows that once the two oscillators have identical phase, they keep identical phase and both move forward with unit speed, since the receiving region and signalling region are disjoint. Therefore synchronized oscillators will remain synchronized.

Note that, if we start with two oscillators with non-identical phase, we will not reach the synchronized state in finite time. Indeed the synchronized state is the limit of two oscillators converging to each other and although the difference between converging oscillators will become negligible, it will never become zero. If oscillators close to each other converge to the synchronized state we say the synchronized state is asymptotically stable.

Instead of simultaneous movement of the oscillators as in Definition 2.2, we could also consider movement of the oscillators with a fixed phase difference between them as synchronisation. We will call this phase-locked behaviour and discuss it later on.

Motivated by the idea of a Poincaré map we consider from now on the case where  $\psi_{01} = 0$  and  $\psi_{02} = \phi$ , as illustrated in Figure 1. A more detailed description of the model can be found in [1].



**Figure 1:** The oscillators move along the interval [0, 1], sending out signals in the interval  $(1 - \eta, 1)$ .

## 3 Definition of cycle maps

To study the dynamics of the system we will introduce the half cycle map, which 'interchanges' the oscillators. Notice first that always at least one group is moving with speed 1, since a group only receives signals if another group is firing and self-excitation is impossible. Second, note that  $\Delta t = 1 - \phi$  is the time the group with  $\psi_{02} = \phi$  needs to reach the endpoint of the interval, since it isn't influenced by any signals. Therefore restricting the system from Definition 2.1 to the time domain  $[0, 1-\phi]$ , gives:  $\frac{d\Psi_2}{dt}(t) = 1$  for all  $t \in [0, 1-\phi]$ . This leads to the following statement:

#### Assertion 3.1.

The system described in Definition 2.1 corresponds to

$$\begin{cases} \frac{d\Psi_1}{dt}(t) &= 1 + \alpha \ h(\Psi_1(t))w(\phi + t) \\ \Psi_1(0) &= 0 \end{cases}$$
(3)

for all  $t \in [0, 1 - \phi]$ , together with  $\Psi_2(t; 0, \phi, \alpha) = \phi + t$ .

Since this simplification is only justified for  $t \in [0, 1 - \phi]$ , we have to extend it to larger time domains by relabelling the oscillators. The idea is that after  $\Delta t = 1 - \phi$  we have  $\Psi_2(1 - \phi; 0, \phi, \alpha) = 1$  and  $\Psi_1(1 - \phi; 0, \phi, \alpha) < 1$ . We will then 'reset' the oscillator at  $\theta = 1$  to  $\theta = 0$  and then specify the position of the other oscillator by the Poincaré-like half cycle map  $f_{\alpha}$ , which we define now:

#### Definition 3.2.

We define the half cycle map  $f_{\alpha} : [0,1] \mapsto [0,1]$  by

$$f_{\alpha}(\phi) = \Psi_1(1-\phi; 0, \phi, \alpha)$$

where  $\Psi_1$  satisfies Equation (3). Next we define the **full cycle map**  $F_{\alpha}: [0,1] \mapsto [0,1]$  by

$$F_{\alpha} = f_{1-\alpha} \circ f_{\alpha}$$

After application of  $f_{\alpha}$  we can again use Assertion 3.1 but now with  $1 - \alpha$  instead of  $\alpha$  and  $f_{\alpha}(\phi) = \Psi_1(1 - \phi; 0, \phi, \alpha)$  instead of  $\phi$ . This gives the full cycle map  $F_{\alpha}$ , as in the definition above. It gives the new position  $\Psi_2$  of group 2 when the initial order of the two oscillators is restored and group 1 has returned to  $\theta = 0$ .

The synchronized state is fixed under the full cycle map, since synchronized oscillators stay synchronized during their cycle. We can translate the continuous dynamical system on the circle to a discrete dynamical system generated by the full cycle map on the interval. In this setting the synchronized state corresponds to the boundary points  $\theta = 0$  and  $\theta = 1$ . Note that, on the interval,  $\theta = 0$  can only be approached from the right (and  $\theta = 1$  only from the left). More on this is discussed in Remark 5.2 below.

We will see later that the full cycle map  $F_{\alpha}$  can have interior fixed points, i.e.  $\phi \in (0, 1)$  such that  $F_{\alpha}(\phi) = \phi$ . If that is the case, then the non-zero distance between the oscillators has not changed after one cycle. We then say that the oscillators are cycle phase-locked, which differs slightly from the usual definition of phase-locked behaviour. Indeed note that the distance between the oscillators can change during the cycle progression, but that the net change after completion of the cycle is zero.



**Figure 2:** The half cycle map  $f_{\alpha}$ .

It is clear that the speed of an oscillator may change abruptly when it crosses  $\theta = 1 - \eta$ . Notice that if  $\phi < 1 - \eta$ , then both oscillators move with unit speed for a time  $1 - \eta - \phi$ . We can eliminate the impact function w from equation (3) which leads to the following corollary.

#### Corollary 3.3.

The half cycle map  $f_{\alpha}$  can be represented as

$$f_{\alpha}(\phi) = \begin{cases} \Phi(\eta; 1 - \eta - \phi, \alpha) & \text{if } \phi \in [0, 1 - \eta] \\ \Phi(1 - \phi; 0, \alpha) & \text{if } \phi \in [1 - \eta, 1] \end{cases}$$
(4)

where  $\Phi(t) = \Phi(t; \phi_0, \alpha)$  is the solution to

$$\begin{cases} \frac{d\Phi}{dt}(t) &= 1 + \alpha \ h(\Phi(t)) \\ \Phi(0) &= \phi_0 \end{cases}$$
(5)

Therefore we have

$$\eta = \int_{1-\eta-\phi}^{f_{\alpha}(\phi)} \frac{\mathrm{d}s}{1+\alpha \ h(s)} \ for \ \phi \in [0, 1-\eta]$$
(6)

$$1 - \phi = \int_0^{f_\alpha(\phi)} \frac{\mathrm{d}s}{1 + \alpha \ h(s)} \text{ for } \phi \in (1 - \eta, 1)$$

$$\tag{7}$$

*Proof.* Using Assertion 3.1 and the definition of the impact function  $w = 1_{(1-\eta,1)}$  in (A2) we obtain Equation (4). The integrals (6) and (7) follow from (4) since integration of the inverse of the travelling speed from begin- to endpoint gives the time a group needs to travel.

Note that it is possible that the lagging group reaches  $\theta = 1 - \eta$  before the heading group reaches  $\theta = 1$ . In that case Assumption (A2) gives that after that both oscillators move with unit speed until the heading group reaches  $\theta = 1$ .

Using Assumption (A2) and the periodic continuation of h we find that  $h(\phi) = 0$  for  $\phi \in (-\eta, 0)$ . Therefore we have that

$$\int_{1-\eta-\phi}^{0} \frac{\mathrm{d}s}{1+\alpha \ h(s)} = \phi - (1-\eta)$$

holds for  $\phi \in (1 - \eta, 1)$ . If we add the integral above to both sides of Equation (7), we get that Equation (6) also holds for  $\phi \in (1 - \eta, 1)$ . Although Equation (6) is therefore in a sense universal, we will still use both equations if that is convenient.

#### Lemma 3.4.

 $f_{\alpha}: [0,1] \to [0,1]$  is a continuous function with  $f_{\alpha}(0) = 1$  and  $f_{\alpha}(1) = 0$ . Furthermore we have that  $f_{\alpha}$  is strictly decreasing and  $F_{\alpha}$  is strictly increasing for all  $\alpha$ .

#### Proof.

Using Corollary 3.3 we see that  $f_{\alpha}(0) = \Phi(\eta; 1 - \eta, \alpha) = 1$ , since h = 0 on  $(1 - \eta, 1)$  and that  $f_{\alpha}(1) = \Phi(0; 0, \alpha) = 0$ .

Both cases in the definition of  $f_{\alpha}$  in Corollary 3.3 coincide for  $\phi = 1 - \eta$ , so to prove continuity of  $f_{\alpha}$  we need to prove that  $(t, \phi_0) \mapsto \Phi(t; \phi_0, \alpha)$  is continuous for all  $t \in [0, \eta]$  and  $\phi_0 \in [0, 1 - \eta]$ .

Assumption (A4) gives Lipschitz continuity for h on  $[0, 1 - \eta]$ , and because h is also Lipschitz continuous (identically zero) on  $[1 - \eta, 1]$  while  $\theta = 1 - \eta$  is crossed with positive speed, according to Assumption (A3), we get that there exists a unique solution  $\Phi$  to (5) that depends continuously on time t and on its initial condition  $\phi_0$ . Therefore  $f_{\alpha}$ , represented by Corollary 3.3, is continuous.

From the uniqueness of solutions also follows that for solutions of (3) we have for all t > 0 and for all  $\theta$ , that

If 
$$x > y$$
, then  $\Psi_1(t; x, \theta, \alpha) > \Psi_1(t; y, \theta, \alpha)$ 

so it is impossible for oscillators to pass each other (except for the reset at the boundary points.

Assume then that  $\phi_1 < \phi_2$  and define  $\check{\phi} = \Psi_1(\phi_2 - \phi_1; 0, \phi_1, \alpha)$ , where  $\check{\phi}$  is positive since any group has positive speed. Hence, by Definition 3.2,

$$f_{\alpha}(\phi_{1}) = \Psi_{1}(1 - \phi_{1}; 0, \phi_{1}, \alpha)$$
  
=  $\Psi_{1}(1 - \phi_{2}; \check{\phi}, \phi_{2}, \alpha)$   
>  $\Psi_{1}(1 - \phi_{2}; 0, \phi_{2}, \alpha) = f_{\alpha}(\phi_{2})$ 

from which we conclude that  $f_{\alpha}$  is monotonically decreasing. Since  $F_{\alpha}$  is the composition of two monotonically decreasing functions, it is monotonically increasing.

Note that since  $f_{\alpha}$  is monotonically decreasing, it is differentiable almost everywhere. Since h is piecewise Lipschitz continuous with in general  $h(1-\eta) \neq 0$  or  $h(0) \neq 0$ ,  $f_{\alpha}$  fails to be differentiable at  $\phi = 1 - \eta$  and at  $\phi = \psi$  with  $f_{\alpha}(\psi) = 1 - \eta$ .

We can also view  $f_{\alpha}$  and  $F_{\alpha}$  as a function of its parameter  $\alpha$ .



Figure 3: The picture shows  $f_{0.2}$  and  $f_{0.5}$  for monotone sensitivity functions  $h(\phi) = \pm (0.9 - \phi)$ , both positive  $f_{\alpha}^+$  (above the anti-diagonal) and negative  $f_{\alpha}^-$  (below the anti-diagonal). We used  $\eta = 0.2$ .

#### Lemma 3.5.

The map  $\alpha \mapsto f_{\alpha}(\phi)$  is continuous for all  $\phi \in [0, 1]$ .

Next assume that h is either strictly positive or strictly negative. If h is positive, then  $\alpha \mapsto f_{\alpha}(\phi)$  is strictly increasing for  $\phi \in (0, 1)$ . Therefore  $\alpha \mapsto F_{\alpha}$  is strictly decreasing. If h is everywhere negative,  $\alpha \mapsto f_{\alpha}$  is strictly decreasing for  $\phi \in (0, 1)$ , and thus  $\alpha \mapsto F_{\alpha}$  is strictly increasing for  $\phi \in (0, 1)$ .

*Proof.* The continuity of  $\alpha \mapsto f_{\alpha}(\phi)$  follows directly from Corollary 3.3.

We prove the second statement for positive h, the proof for negative h is similar. Assume  $\alpha_1 > \alpha_2$  for some

 $\alpha_1, \alpha_2 \in [0, 1]$ . Then as h is positive, we have, using the integrals from Corollary 3.3,

$$\begin{split} \alpha_1 > \alpha_2 \Rightarrow 1 + \alpha_1 h(s) > 1 + \alpha_2 h(s) \\ \Rightarrow \frac{1}{1 + \alpha_1 h(s)} < \frac{1}{1 + \alpha_2 h(s)} \\ \Rightarrow \eta = \int_{1-\eta-\phi}^{f_{\alpha_1}(\phi)} \frac{\mathrm{d}s}{1 + \alpha_1 h(s)} < \int_{1-\eta-\phi}^{f_{\alpha_1}(\phi)} \frac{\mathrm{d}s}{1 + \alpha_2 h(s)} \text{ for } \phi \in (0, 1-\eta] \text{ and} \\ 1 - \phi = \int_0^{f_{\alpha_1}(\phi)} \frac{\mathrm{d}s}{1 + \alpha_1 h(s)} < \int_0^{f_{\alpha_1}(\phi)} \frac{\mathrm{d}s}{1 + \alpha_2 h(s)} \text{ for } \phi \in [1-\eta, 1) \end{split}$$

Therefore, since the integration to  $f_{\alpha_1}$  on the right hand side is larger than integration to  $f_{\alpha_2}$ , we see by Assumption (A3) that

$$\Rightarrow f_{\alpha_1}(\phi) > f_{\alpha_2}(\phi) \ \forall \ \phi \in (0,1)$$

so  $f_\alpha$  is increasing, and since this implies that

$$\Rightarrow f_{1-\alpha_1}(f_{\alpha_1}(\phi)) < f_{1-\alpha_1}(f_{\alpha_2}(\phi)) < f_{1-\alpha_2}(f_{\alpha_2}(\phi))$$

we conclude that  $F_{\alpha}$  is decreasing. Note that the boundary points are excluded since these are fixed points for all values of  $\alpha$ .

## 4 Motivated preview

In the first two sections we introduced the model and its ingredients: a sensitivity function h, a signal strength splitting  $\alpha$  and the length of the signalling region  $\eta$ . A remark has to be made about the case  $\alpha = \frac{1}{2}$ . This can either be interpreted as the two oscillators having equal signal strengths, or as the irrelevance of the strength of the signal. In the last case only the presence of a signal influences the movement of an oscillator, independently of the strength of the incoming signal. The special character of  $\alpha = \frac{1}{2}$  will be more evident later.

Using the three ingredients we defined the half cycle map  $f_{\alpha}$  and the full cycle map  $F_{\alpha}$ . As we are interested in synchronization, the aim is to determine how qualitative behaviour of the cycle map depends on the ingredients, the sensitivity function h and the signal strength  $\alpha$  in particular.

The synchronized state, where all oscillators have identical phase, corresponds to the boundary fixed points  $\theta = 0$  and  $\theta = 1$ , which can be identified at the cost of having to pay attention to one-sided stability. Focussing on the most simple situations, we distinguish for a fixed  $\alpha$  four different graphs of the full cycle map  $F_{\alpha}$ , depicted in Figure 4.



Figure 4: Four different full cycle maps.

The stability of fixed points under iteration of the full cycle map  $F_{\alpha}$  can be determined by looking at the



Figure 5: Scenarios on the circle corresponding to Figure 4. Note that in the lower two figures an interior fixed point has to exist.

derivative of the map at these fixed points. We will find that

$$DF_{\alpha}(0) = \frac{1 + (1 - \alpha)h(0)}{1 + \alpha h(1 - \eta)}$$

and

$$DF_{\alpha}(1) = \frac{1 + \alpha h(0)}{1 + (1 - \alpha)h(1 - \eta)}.$$

which are related by the transformation  $\alpha \mapsto 1 - \alpha$ .

We will show that a strictly monotone h leads to one of these four cases, for all  $\alpha$ . A more elaborate computation shows that if h is symmetric, i.e.  $h(1 - \eta - \theta) = h(\theta) \ \forall \theta \in [0, 1 - \eta]$ , then the full cycle map  $F_{\alpha}$  is excitable for all  $\alpha$ 's except  $\alpha = \frac{1}{2}$ , with  $F_{\frac{1}{2}}$  equal to the identity.

On the other hand, it is possible to create full cycle maps with as many fixed points as we want, by choosing h to be highly non-injective. This will be shown in the section with numerical results.

Lastly, after considering models from other literature, we generalise the results for two oscillators to any number of oscillators. We prove, under certain relatively mild assumptions, that the synchronized state is stable no matter how we perturb it.

## 5 Fixed points and stability

We already saw that  $f_{\alpha}(0) = 1$  and  $f_{\alpha}(1) = 0$ , so 0 and 1 are 'period-two' points of the dynamical system corresponding to alternately applying  $f_{\alpha}$  and  $f_{1-\alpha}$  and therefore fixed points of the full cycle map. This is



**Figure 6:** The full cycle map in case of symmetric h and  $\alpha = \frac{1}{2}$ .

as expected because synchronized oscillators will remain synchronized.

A look at the definition of  $F_{\alpha}$  gives us a relation between not only the boundary points, but also other (interior) fixed points.

#### Lemma 5.1.

The full cycle map  $F_{\alpha}$  is topologically conjugate to the full cycle map  $F_{1-\alpha}$ . In particular we know that the full cycle map  $F_{\alpha}$  has a fixed point  $\phi \in [0,1]$ , i.e.  $F_{\alpha}(\phi) = \phi$ , if and only if  $F_{1-\alpha}$  has a fixed point  $f_{\alpha}(\phi)$ .

*Proof.* The topological conjugacy follows from

$$F_{\alpha} = f_{\alpha}^{-1} \circ F_{1-\alpha} \circ f_{\alpha}$$

Using this relation we see that  $F_{\alpha}(\phi) = \phi$ , i.e.  $f_{1-\alpha}(f_{\alpha}(\phi)) = \phi$ , is by the monotonicity of  $f_{\alpha}$  equivalent to  $f_{\alpha}(f_{1-\alpha}(f_{\alpha}(\phi))) = f_{\alpha}(\phi)$ , i.e.  $F_{1-\alpha}(f_{\alpha}(\phi)) = f_{\alpha}(\phi)$ .

Since  $F_{\alpha}$  is topologically conjugate to  $F_{1-\alpha}$  it is in a sense sufficient to investigate the dynamics of only one of them, since the dynamics of the other will then follow by the conjugation.

Whether or not interior fixed points of  $F_{\alpha}$  exist is not immediately clear but will be investigated in later sections. For now we notice that  $F_{\frac{1}{2}}$  is a special case since  $\frac{1}{2} = 1 - \frac{1}{2}$  so we do know, since  $F_{\frac{1}{2}} = f_{\frac{1}{2}}^2$ , that  $F_{\frac{1}{2}}$  has at least one interior fixed point  $\phi_{\frac{1}{2}}$ , given by the condition

$$f_{\frac{1}{2}}(\phi_{\frac{1}{2}}) = \phi_{\frac{1}{2}} \tag{8}$$

From the fact that  $f_{\frac{1}{2}}$  is strictly decreasing with  $f_{\frac{1}{2}}(0) = 1$  and  $f_{\frac{1}{2}}(1) = 0$ , it follows that  $\phi_{\frac{1}{2}}$  is uniquely defined. If we apply Lemma 5.1 to  $\alpha = \frac{1}{2}$ , we see that the full cycle map  $F_{\frac{1}{2}}$  can in general not have an even number of fixed points, since fixed points of  $F_{\frac{1}{2}}$  come in pairs  $(\phi, f_{\frac{1}{2}}(\phi))$ . These two points only coincide at

 $\phi = \phi_{\frac{1}{2}}$  which makes the number of fixed points of  $F_{\frac{1}{2}}$  odd.

For the rest of this section we will focus on the boundary points,  $\theta = 0$  and  $\theta = 1$ . To determine their stability, and therefore the stability of the synchronized state on the circle (see Remark 5.2), we will compute the derivative of the full cycle map. From classical theory we know that a derivative smaller than one (in absolute value) implies the fixed point  $\bar{\phi}$  is an attractor, a larger derivative implies the fixed point  $\bar{\phi}$  is a repellor. Since  $F_{\alpha}$  is monotonically increasing, its derivative is always positive so we can ignore the absolute value signs.

#### Remark 5.2.

When talking about stability (in terms of derivatives), the difference between the circle and the interval is more subtle. Recall that, viewing the boundary points as elements of the interval,  $\theta = 0$  can only be approached from the right and  $\theta = 1$  only from the left. Therefore derivative has to be read as right-derivative for  $\theta = 0$  and left-derivative for  $\theta = 1$ , with the same remark for (in)stability. We illustrate this by the following example:

If  $F'_{\alpha}(0) > 1$  and  $F'_{\alpha}(1) < 1$ , the boundary point  $\theta = 0$  is unstable w.r.t. minor perturbations, i.e. application of  $F_{\alpha}$  to a  $\phi$  slightly bigger than zero will lead to an increase of the distance between the two oscillators, while  $\theta = 1$  is stable. If no other fixed points exist on the circle, the synchronized state on the circle behaves like a homoclinic loop: stable from the left, unstable from the right. As perturbations of  $\theta = 0$  can only be to the right, and perturbations of  $\theta = 1$  only to the left, our synchronized state is globally stable, but locally unstable.

Recall that we defined  $h(\phi) = 0$  for all  $\phi \notin [0, 1 - \eta]$ . In both the following lemma and the theorem derived from it, it is important to recall that h can be periodically continued to define  $h(\phi)$  for e.g. negative  $\phi$ . In particular,  $h(\phi) = 0$  if  $\phi \in (-\eta, 0)$  or  $(1 - \eta, 1)$ .

#### Lemma 5.3.

The derivative of the half cycle map  $f_{\alpha}(\phi)$  w.r.t.  $\phi$  is given by:

$$Df_{\alpha}(\phi) = -\frac{1 + \alpha h \left(f_{\alpha}(\phi)\right)}{1 + \alpha h \left(1 - \eta - \phi\right)} \tag{9}$$

Proof.

Differentiation with respect to  $\phi$  on both sides of equation (6) in Corollary 3.3 gives:

$$0 = \frac{1}{1 + \alpha h(f_{\alpha}(\phi))} Df_{\alpha}(\phi) + \frac{1}{1 + \alpha h(1 - \eta - \phi)} \text{ so } Df_{\alpha}(\phi) = -\frac{1 + \alpha h(f_{\alpha}(\phi))}{1 + \alpha h(1 - \eta - \phi)}$$

Then we consider the case that  $\phi > 1 - \eta$ , and after differentiation of equation (7) w.r.t.  $\phi$  we have

$$-1 = \frac{1}{1 + \alpha \ h\left(f_{\alpha}(\phi)\right)} \ Df_{\alpha}(\phi) \text{ so } Df_{\alpha}(\phi) = -\left(1 + \alpha \ h\left(f_{\alpha}(\phi)\right)\right)$$

which gives the same result since  $\phi > 1 - \eta \Rightarrow h(1 - \eta - \phi) = 0$ .

Recall the fact that  $f_{\alpha}$  fails to be differentiable at  $\phi = 1 - \eta$  and at  $\phi = \psi$  with  $f_{\alpha}(\psi) = 1 - \eta$  and notice that at those points  $Df_{\alpha}$  is not continuous, unless resp. h(0) = 0 and  $h(1 - \eta) = 0$ .

By assumption (A3), both the numerator and denominator of the derivative are positive, so the  $f_{\alpha}$  has negative derivative. This is consistent with Lemma 3.4. From Lemma 5.3 we can deduce the derivatives in  $\theta = 0$  and  $\theta = 1$ . Namely:

$$DF_{\alpha}(0) = Df_{1-\alpha}(f_{\alpha}(0)) \cdot Df_{\alpha}(0) = \frac{1 + (1-\alpha)h(0)}{1 + \alpha h(1-\eta)},$$
(10)

$$DF_{\alpha}(1) = Df_{1-\alpha}(f_{\alpha}(1)) \cdot Df_{\alpha}(1) = \frac{1 + \alpha h(0)}{1 + (1 - \alpha)h(1 - \eta)},$$
(11)

Notice that  $DF_{\alpha}(0) = DF_{1-\alpha}(1)$  for all  $\alpha$ . A similar computation gives the derivative of the full cycle map for other values of  $\phi$  using

$$DF_{\alpha}(\phi) = Df_{1-\alpha} \left( f_{\alpha}(\phi) \right) Df_{\alpha}(\phi)$$

#### Theorem 5.4.

The derivative of the full cycle map  $F_{\alpha}(\phi)$  w.r.t.  $\phi$  is given by:

$$DF_{\alpha}(\phi) = \frac{1 + (1 - \alpha)h(F_{\alpha}(\phi))}{1 + (1 - \alpha)h(1 - \eta - f_{\alpha}(\phi))} \cdot \frac{1 + \alpha h(f_{\alpha}(\phi))}{1 + \alpha h(1 - \eta - \phi)}$$
(12)

Recall that the numerators of the derivatives are positive due to Assumption (A3).

We are interested in the stability of the boundary points as a function of  $\alpha$ , i.e. we consider  $\alpha$  as a bifurcation parameter. Recall that  $DF_{\alpha}(0) = \frac{1+(1-\alpha)h(0)}{1+\alpha h(1-\eta)}$  and  $DF_{\alpha}(1) = \frac{1+\alpha h(0)}{1+(1-\alpha)h(1-\eta)}$  so

$$DF_{\alpha}(0) = 1 \Leftrightarrow (1 - \alpha)h(0) = \alpha h(1 - \eta)$$
$$DF_{\alpha}(1) = 1 \Leftrightarrow \alpha h(0) = (1 - \alpha)h(1 - \eta)$$

Solving for  $\alpha$  leads to the following definition:

#### Definition 5.5.

If  $h(0) + h(1 - \eta) \neq 0$ , we define  $\bar{\alpha} = \frac{h(0)}{h(0) + h(1 - \eta)}$ .

Note that  $|h(0)| \leq |h(1-\eta)|$  implies that  $\bar{\alpha} \leq 1-\bar{\alpha}$ , so  $\bar{\alpha} < \frac{1}{2}$ . We defined  $\bar{\alpha}$  such that  $DF_{\bar{\alpha}}(0) = DF_{1-\bar{\alpha}}(1) = 1$ . 1. This statement only makes sense in our context whenever  $\bar{\alpha} \in [0, 1]$ .

If  $h(0) + h(1 - \eta) = 0$  with h(0) < 0, then  $DF_{\alpha}(0) < 1$  and  $DF_{\alpha}(1) < 1$  for all  $\alpha$ , while if  $h(0) + h(1 - \eta) = 0$ with h(0) > 0, then  $DF_{\alpha}(0) > 1$  and  $DF_{\alpha}(1) > 1$  for all  $\alpha$ . If  $h(0) = h(1 - \eta) = 0$ , then  $DF_{\alpha}(0) = 1 = DF_{\alpha}(1)$  for all  $\alpha$ .

Because  $DF_{\alpha}(\phi)$  is a continuous function of  $\alpha$  for all  $\phi$ , the boundary points change stability while  $\alpha$  moves from 0 to 1 if  $\bar{\alpha} \in (0, 1)$ . If  $\bar{\alpha} \notin [0, 1]$ , then  $DF_{\alpha}(0) - 1$  and  $DF_{\alpha}(1) - 1$  are sign definite for  $\alpha \in [0, 1]$ , so the boundary points have for  $\alpha \in [0, 1]$  a fixed stability character, independent of  $\alpha$ .

Using the values of h(0) and  $h(1-\eta)$  and the formulas above, we can determine the stability of the boundary points. If for example  $0 < h(0) \le h(1-\eta)$ , then  $DF_{\alpha}(0) < 1 \Leftrightarrow \alpha > \bar{\alpha}$  with  $\bar{\alpha} < \frac{1}{2}$ , as can be seen in the left plot in the left-upper corner of Table 1. If on the other hand  $h(0) \le h(1-\eta) < 0$ , then  $DF_{\alpha}(0) < 1 \Leftrightarrow \alpha < \bar{\alpha}$ with  $\bar{\alpha} > \frac{1}{2}$  as in the right plot of the middle of Table 1. Note that we can use the relation

$$DF_{\alpha}(0) = DF_{1-\alpha}(1)$$

to determine the stability of  $\theta = 1$  from the stability of  $\theta = 0$ . Indeed the plots in Table 1 are symmetric around the middle of the square.

In Table 1 we summarized the results of the linearisation of the full cycle map in the boundary fixed points, so it shows the stability of the synchronized state. We do not know what happens for the interior points, so the plots need to be completed. This will be done in later sections where interior fixed points will appear



**Table 1:** Incomplete bifurcation diagrams for the boundary fixed points with  $\alpha$  on the horizontal axis and  $\phi$  on the vertical axis. The representation (dotted or solid) of the lines indicate the stability of the boundary points  $\theta = 0$ , the lower line, and  $\theta = 1$ , the upper line. In some cases we need more information to determine the value of  $\bar{\alpha}$ :  $\bar{\alpha} \leq \frac{1}{2}$  (left of the two sub-diagrams) if  $|h(0)| \leq |h(1 - \eta)|$ , while  $\bar{\alpha} > \frac{1}{2}$  (right of the two sub-diagrams) otherwise. The vertical bar denotes the position of  $\bar{\alpha}$  if in [0, 1].

The stability of the boundary points depends on  $\alpha$ , h(0) and  $h(1 - \eta)$ . For each combination of these ingredients, oscillators close to synchrony behave as they do in Figure 5 from Section 4.

as solid or dotted lines in the interior of the squares. In Section 9 we will consider the stability of the synchronized state without linearising the full cycle map.

In Figures 4 from Section 4 we plotted four graphs for the full cycle map  $F_{\alpha}$ , corresponding to scenarios in Figure 5. Using Table 1 we can determine which scenario will (locally) occur for a given combination of the ingredients  $h(0), h(1 - \eta)$  and  $\alpha$ .

## 6 Reflection

We will now investigate the effect on the full cycle map of reflecting the sensitivity function h in the midpoint of  $[0, 1-\eta]$ . This leads to interesting results which we can use later on to prove more about the (non-)existence of interior fixed points. First we will prove a helpful lemma.

#### Lemma 6.1.

Define  $\tilde{h}$  as the reflection of the sensitivity function h in the midpoint  $\frac{1-\eta}{2}$  of the receiving region  $[0, 1-\eta]$ , i.e.  $\tilde{h}(\theta) = h(1-\eta-\theta)$ . Then for  $0 \le q \le p \le 1$  we have:

$$\int_{q}^{p} \frac{\mathrm{d}s}{1+\alpha \ h(s)} = \int_{1-\eta-p}^{1-\eta-q} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)}$$

Proof.

The statement follows directly from the definition of  $\tilde{h}$  in terms of h (see Figure 7 for a visual hint).





#### Notation 6.2.

Let H be the set of functions<sup>4</sup>  $h : [0,1] \to \mathbb{R}$  that satisfy assumptions (A2) - (A4) and define the map  $Q: H \to H$  as  $Q(h) = \tilde{h}$ , which maps the set H to itself.<sup>5</sup> By definition we then have  $Q^2 = I$ .

For any function  $S(\cdot;h)$  with h as a parameter, we will write

 $\tilde{S}(\cdot;h) = S(\cdot;Q(h)).$ 

Note that for any function S depending on h we have  $\tilde{\tilde{S}} = S$ . Indeed  $\tilde{\tilde{S}}(\cdot; h) = \tilde{S}(\cdot; Q(h)) = S(\cdot; Q^2(h)) = S(\cdot; h)$ .

Note that both the half cycle map  $f_{\alpha}$  and the full cycle map  $F_{\alpha}$  are functions that parametrically depend on the sensitivity function h. Because in most cases it is clear which h determines the half or full cycle map we will omit the parameter notation  $f_{\alpha}(\cdot;h)$  and write  $f_{\alpha}(\cdot)$ , with the same convention for  $F_{\alpha}$ . Therefore  $\tilde{f}_{\alpha}$  is short for  $f_{\alpha}\left(\cdot;\tilde{h}\right)$  and  $\tilde{F}_{\alpha}$  for  $F_{\alpha}\left(\cdot;\tilde{h}\right) = f_{1-\alpha}\left(f_{\alpha}\left(\cdot;\tilde{h}\right);\tilde{h}\right)$ . We consider the composition of  $\tilde{f}_{\alpha}$  and  $f_{\alpha}$ .

Theorem 6.3.

For all  $\alpha \in [0,1]$  we have

$$\tilde{f}_{\alpha} \circ f_{\alpha} = I$$

And since  $\tilde{\tilde{f}}_{\alpha} = f_{\alpha}$  we also have  $f_{\alpha} \circ \tilde{f}_{\alpha} = I$ .

<sup>&</sup>lt;sup>4</sup>Recall once more Assumption (A2) and the periodic continuation of h. These imply that, although  $\frac{1-\eta}{2}$  is not the middle of the interval on which h is originally defined, the reflection of h in  $\frac{1-\eta}{2}$  is well defined.

 $<sup>{}^{5}</sup>Q$  maps H into itself since the reflection of a function that satisfies assumptions (A2) - (A4) also satisfies assumptions (A2) - (A4).

*Proof.*  $^{6}$  Using Lemma 6.1 we rewrite the identities (6) and (7) from Corollary 3.3 as follows:

$$\int_{1-\eta-\phi}^{f_{\alpha}(\phi)} \frac{\mathrm{d}s}{1+\alpha \ h(s)} = \eta \qquad = \int_{1-\eta-f_{\alpha}(\phi)}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \qquad \text{if } \phi \in [0, 1-\eta] \tag{13}$$

$$\int_{0}^{f_{\alpha}(\phi)} \frac{\mathrm{d}s}{1+\alpha \ h(s)} = 1-\phi = \int_{1-\eta-f_{\alpha}(\phi)}^{1-\eta} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \qquad \text{if } \phi \in [1-\eta, 1] \tag{14}$$

Also we write, now using the reflected versions of equations (6) and 7 with  $\phi$  replaced by  $f_{\alpha}(\phi)$ , that

$$\eta = \int_{1-\eta-f_{\alpha}(\phi)}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \text{if } f_{\alpha}(\phi) \in [0, 1-\eta] \qquad (15)$$
$$-f_{\alpha}(\phi) = \int_{0}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \text{if } f_{\alpha}(\phi) \in [1-\eta, 1] \qquad (16)$$

Now assume  $\phi \in [0, 1 - \eta]$  and  $f_{\alpha}(\phi) \in [0, 1 - \eta]$ , then using equation (13) and (15) we see that

$$\int_{1-\eta-f_{\alpha}(\phi)}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = \eta = \int_{1-\eta-f_{\alpha}(\phi)}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)}$$

1

Secondly, for  $\phi \in [1 - \eta, 1]$  and  $f_{\alpha}(\phi) \in [0, 1 - \eta]$  we get, using equation (14) in the second step, that

$$\int_{1-\eta-f_{\alpha}(\phi)}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = \int_{1-\eta-f_{\alpha}(\phi)}^{1-\eta} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} + \phi - (1-\eta) \qquad \left[ \text{since } \tilde{h}(s) = 0 \text{ for } s > 1-\eta \text{ and } \phi > 1-\eta \right]$$
$$= 1-\phi + \phi - (1-\eta) = \eta = \int_{1-\eta-f_{\alpha}(\phi)}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \left[ \text{by (15)} \right]$$

Thirdly we see that for  $\phi \in [0, 1 - \eta]$  and  $f_{\alpha}(\phi) \in [1 - \eta, 1]$ , we have

 $^{6}\mathrm{Comments}$  to improve readability are placed between brackets,

Lastly  $\phi \in [1 - \eta, 1]$  and  $f_{\alpha}(\phi) \in [1 - \eta, 1]$  give

$$\int_0^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = \int_0^{1-\eta} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} - (1-\eta) + \phi$$
$$= \int_0^{f_{\alpha}(\phi)} \frac{\mathrm{d}s}{1+\alpha \ h(s)} - f_{\alpha}(\phi) + \phi$$

since h(s) = 0 for  $s > 1 - \eta$  and both  $\phi > 1 - \eta$  and  $f_{\alpha}(\phi) > 1 - \eta$ , so

$$\int_{0}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = 1 - \phi - f_{\alpha}(\phi) + \phi \qquad \qquad \left[ \text{by Equation (14)} \right]$$
$$= 1 - f_{\alpha}(\phi) = \int_{0}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \qquad \left[ \text{again by (16)} \right]$$

To summarize we have now proved that

$$\int_{1-\eta-f_{\alpha}(\phi)}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = \eta = \int_{1-\eta-f_{\alpha}(\phi)}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \text{if } f_{\alpha}(\phi) \in [0, 1-\eta]$$
$$\int_{0}^{\phi} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} = 1 - f_{\alpha}(\phi) = \int_{0}^{\tilde{f}_{\alpha}(f_{\alpha}(\phi))} \frac{\mathrm{d}s}{1+\alpha \ \tilde{h}(s)} \qquad \text{if } f_{\alpha}(\phi) \in [1-\eta, 1]$$

which leads since the integrals are equal and the integrand is positive by Assumption (A3) to

$$f_{\alpha}(f_{\alpha}(\phi)) = \phi \text{ for all } \phi \in [0,1]$$

This strong result gives us the following theorem.

## Theorem 6.4.

 $\tilde{F}_{\alpha} = F_{1-\alpha}^{-1} \text{ for all } 0 \leq \alpha \leq 1.$ 

#### Proof.

The full cycle map is defined as  $F_{\alpha} = f_{1-\alpha} \circ f_{\alpha}$ . Using the above theorem and the fact that  $\tilde{\tilde{h}} = h$  we see that

$$f_{\alpha} \circ f_{\alpha} = I = f_{1-\alpha} \circ f_{1-\alpha}$$

since we didn't specify any value of  $\alpha$  in the analysis above. Therefore

$$\tilde{F}_{\alpha} \circ F_{1-\alpha} = \tilde{f}_{1-\alpha} \circ \tilde{f}_{\alpha} \circ f_{\alpha} \circ f_{1-\alpha} = I = f_{\alpha} \circ f_{1-\alpha} \circ \tilde{f}_{1-\alpha} \circ \tilde{f}_{\alpha} = F_{1-\alpha} \circ \tilde{F}_{\alpha}$$

So we have  $\tilde{F}_{\alpha} = F_{1-\alpha}^{-1}$ 

In Figure 8 both  $\tilde{F}_{\alpha}$  and  $F_{1-\alpha}$  are plotted for  $h(\theta) = 0.9 - \theta$  and  $\alpha = 0.4$ . We see that the plots are reflections of each other in the diagonal, as is described in Corollary 6.5.



Figure 8:  $\tilde{F}_{.4}$  and  $F_{.6}$  for  $h(\theta) = 0.9 - \theta$ . Note that the fixed points of  $\tilde{F}_{.4}$  and  $F_{.6}$  coincide, but have opposite stability character.

#### Corollary 6.5.

A point q is a fixed point of  $\tilde{F}_{\alpha}$  if and only if it is a fixed point of  $F_{1-\alpha}$ . If q is stable as a fixed point of  $F_{1-\alpha}$ , then it is unstable as a fixed point of  $\tilde{F}_{\alpha}$ , and vice versa. Furthermore we have that the graph of  $\tilde{F}_{\alpha}$  is the reflection in the diagonal of the graph of  $F_{1-\alpha}$ .

*Proof.* The first statement follows from Theorem 6.4 and the observation that  $F_{1-\alpha}$  and  $F_{1-\alpha}^{-1}$  have equal fixed points. By looking at the orbits of  $F_{1-\alpha}$  and  $\tilde{F}_{\alpha}$  respectively:

$$\cdots, F_{1-\alpha}^{-2}(\phi), F_{1-\alpha}^{-1}(\phi), \phi, F_{1-\alpha}^{1}(\phi), F_{1-\alpha}^{2}(\phi), \cdots$$

and

$$\cdots, F_{1-\alpha}^2(\phi), F_{1-\alpha}^1(\phi), \phi, F_{1-\alpha}^{-1}(\phi), F_{1-\alpha}^{-2}(\phi), \cdots$$

we see that the orbits are equal upon time reversal. Time reversal results in a stability change of the fixed points, because fixed points which are generically attracting for positive time will be repelling for negative time. Since  $F_{1-\alpha}$  is a 1D-map, its fixed points are either attracting or repelling so we conclude that the equal fixed points of  $F_{1-\alpha}$  and  $\tilde{F}_{\alpha}$  have opposite stability. Taking the inverse of a (monotone so one-to-one) map on [0, 1] corresponds graphically to the reflection of the graph in the diagonal, which also reveals the stability change.

If a sensitivity function h is **symmetric**, i.e.  $h = \tilde{h}$ , then  $\tilde{f}_{\alpha} = f_{\alpha}$  and  $\tilde{F}_{\alpha} = F_{\alpha}$  for all  $\alpha$ . Therefore if h is symmetric,  $F_{\alpha}$  is topologically equivalent to  $F_{\alpha}^{-1}$ .

The following result is an elementary observation we will use in the proof of Theorem 6.7.

#### Lemma 6.6.

Any continuous function g on [a, b] with  $g(g(x)) = x \forall x$  and g(a) = a, g(b) = b equals the identity.

*Proof.* Since  $g(x) = g(y) \Rightarrow g(g(x)) = g(g(y)) \Rightarrow x = y$ , we see that g is one-to-one. Since g(a) < g(b) we know by the intermediate value theorem and the fact that g is one-to-one that g(a) < g(c) < g(b) for all a < c < b. Because g is one-to-one we must have for any  $x < y \in [a, b]$  that g(x) < g(y), so g is monotonically increasing.

If there would exist a  $u \in [a, b]$  such that g(u) > u, then the monotonicity gives u = g(g(u)) > g(u) which is a contradiction. The same reasoning shows that g(u) < u is impossible, so we conclude that g(u) = u for all  $u \in [a, b]$ .

From Theorem 6.4 and Lemma 6.6 we deduce the following:

#### Theorem 6.7.

If h is symmetric,  $F_{\frac{1}{2}} = I$  and therefore every  $\phi \in [0, 1]$  is a period-two-point of  $f_{\frac{1}{2}}$ . The family of period two orbits has exactly one 'degenerate' element<sup>7</sup>  $\phi_{\frac{1}{2}}$ , for which both period two points  $\phi_{\frac{1}{2}}$  and  $f_{\frac{1}{2}}(\phi_{\frac{1}{2}})$  coincide to form a fixed point.

Proof.

Using Theorem 6.4, we conclude that

$$F_{\frac{1}{2}}^{-1}(\phi) = \tilde{F}_{\frac{1}{2}}(\phi) = F_{\frac{1}{2}}(\phi)$$

Since  $F_{\frac{1}{2}}(0) = 0$  and  $F_{\frac{1}{2}}(1) = 1$  Lemma 6.6 gives that  $F_{\frac{1}{2}}$  is the identity, so  $F_{\frac{1}{2}}(\phi) = \phi$  for all  $\phi \in [0, 1]$ . Note that the point  $\phi_{\frac{1}{2}}$  is a fixed point of  $f_{\frac{1}{2}}$  so  $\phi_{\frac{1}{2}}$  and  $f_{\frac{1}{2}}(\phi_{\frac{1}{2}})$  coincide.

Note that a symmetric h gives  $h(0) = h(1 - \eta)$ , so by Definition 5.5, we have  $\bar{\alpha} = \frac{h(0)}{h(0) + h(1 - \eta)} = \frac{1}{2}$ , so  $DF_{\frac{1}{2}}(0) = 1 = DF_{\frac{1}{2}}(1)$ . We therefore see that the boundary fixed points of  $F_{\alpha}$  indeed change stability when  $\alpha$  crosses  $\frac{1}{2}$ .

Theorem 6.7 can be explained from a more fundamental point of view. Note that the feedback a group receives depends on its phase. Therefore the feedback from opposite sides of the sensitivity region is equal. Since the half cycle map switches the order, and for  $\alpha = \frac{1}{2}$  the signal strengths are equal, the effect of feedback on the full cycle map cancels out. We will use and explain this reasoning further in Section 9.

## 7 Interior fixed points

Apart from the boundary fixed points corresponding to the synchronized state, also interior fixed points can exist. Their existence, location and stability depend on the shape of the sensitivity function h, as we saw in Table 1. The goal of this section is to complete the diagrams given in Table 1, and to determine what happens between the boundary fixed points. To find interior fixed points we can use Theorem 7.1.

#### Theorem 7.1.

A point  $q \in (0,1)$  is a fixed point<sup>8</sup> of  $F_{\alpha}$  if and only if  $\tilde{f}_{1-\alpha}(q) = f_{\alpha}(q)$ .

Proof. Applying  $\tilde{f}_{1-\alpha}$  to  $F_{\alpha}(q) = f_{1-\alpha}(f_{\alpha}(q))$  and using Theorem 6.3, we see that  $F_{\alpha}(q) = q \Leftrightarrow \tilde{f}_{1-\alpha}(F_{\alpha}(q)) = \tilde{f}_{1-\alpha}(q) \Leftrightarrow f_{\alpha}(q) = \tilde{f}_{1-\alpha}(q)$ , since  $\tilde{f}_{1-\alpha} \circ f_{1-\alpha} = I$  so  $\tilde{f}_{1-\alpha}(F_{\alpha}(q)) = f_{\alpha}(q)$ .

Before we continue we need to introduce some notation.

<sup>&</sup>lt;sup>7</sup>As introduced in Equation (8) in Section 5.

<sup>&</sup>lt;sup>8</sup>Note that the statement trivially holds for q = 0 and q = 1.

#### Notation 7.2.

We write

$$W(a,b,\alpha) = \int_{a}^{b} \frac{(1-\alpha)h(1-\eta-s) - \alpha h(s)}{(1+\alpha h(s))(1+(1-\alpha)h(1-\eta-s))} ds$$
(17)

In case h is symmetric, W simplifies to

$$W_s(a, b, \alpha) = \int_a^b \frac{(1 - 2\alpha)h(s)}{(1 + \alpha \ h(s))(1 + (1 - \alpha)h(s))} \mathrm{d}s$$
(18)

This notation allows us to give another existence criterion for interior fixed points.

#### Lemma 7.3.

A point  $q \in (0, 1 - \eta]$  is an interior fixed point of  $F_{\alpha}$  if and only if  $W(1 - \eta - q, f_{\alpha}(q), \alpha) = 0$ . A point  $q \in [1 - \eta, 1)$  is an interior fixed point of  $F_{\alpha}$  if and only if  $W(0, f_{\alpha}(q), \alpha) = 0$ .

*Proof.* In general we have that

$$\tilde{f}_{1-\alpha}(q) = f_{\alpha}(q) \Leftrightarrow \int_{1-\eta-q}^{\tilde{f}_{1-\alpha}(q)} \frac{\mathrm{d}s}{1+(1-\alpha)\tilde{h}(s)} = \int_{1-\eta-q}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1+(1-\alpha)\tilde{h}(s)} \tag{(\star)}$$

If we assume that  $q \in (0, 1 - \eta]$ , then the left integral is by (6) equal to  $\eta$ , so we see, using (6) once more, that

$$(\star) \Leftrightarrow \int_{1-\eta-q}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1+\alpha h(s)} = \int_{1-\eta-q}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1+(1-\alpha)\tilde{h}(s)}$$
$$\Leftrightarrow W\left(1-\eta-q, f_{\alpha}(q), \alpha\right) = 0$$

by definition of W. In general we also have that

$$\tilde{f}_{1-\alpha}(q) = f_{\alpha}(q) \Leftrightarrow \int_{0}^{\tilde{f}_{1-\alpha}(q)} \frac{\mathrm{d}s}{1 + (1-\alpha)\tilde{h}(s)} = \int_{0}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1 + (1-\alpha)\tilde{h}(s)} \tag{(*)}$$

so if  $q \in [1 - \eta, 1)$ , then the left integral is by (7) equal to  $1 - \phi$ , so we see, using (7) once more, that

$$* \Leftrightarrow \int_{0}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1 + \alpha h(s)} = \int_{0}^{f_{\alpha}(q)} \frac{\mathrm{d}s}{1 + (1 - \alpha)\tilde{h}(s)}$$
$$\Leftrightarrow W(0, f_{\alpha}(q), \alpha) = 0$$

which proves the statement

Looking at the definition of W we observe a property that will be useful later. Lemma 7.4 holds for both W and  $W_s$ .

#### Lemma 7.4.

Fix any  $\alpha \in [0,1]$  and assume  $(1-\alpha)\tilde{h} - \alpha h$  is either strictly positive or strictly negative on  $(0,1-\eta)$ . Then the function W (and so  $W_s$ ) satisfies:

$$W(a, b, \alpha) = 0 \text{ if and only if either } [a, b] \cap (0, 1 - \eta) = \emptyset \text{ or } a = b$$
(19)

*Proof.* The integrand in Equation (19) is sign-definite in the interval  $(0, 1 - \eta)$  by the assumption in the statement so  $W(a, b, \alpha) = 0$  is equivalent with either integration over an interval disjoint with  $(0, 1 - \eta)$  or over an integration interval of zero length.

If we combine Lemma 7.3 and Lemma 7.4, we can conclude that interior fixed points do not always exist.

#### Theorem 7.5.

If  $(1-\alpha)\tilde{h}-\alpha h$  either strictly positive or strictly negative on  $(0,1-\eta)$ , then  $F_{\alpha}$  has no interior fixed points.

Proof. Assume q is an interior fixed point of  $F_{\alpha}$ , so  $F_{\alpha}(q) = q$  and assume first that  $q \in (0, 1 - \eta]$ . Recall that the group starting at  $\theta = 0$  first moves with unit speed for a time  $1 - \eta - q$  before it receives any signals. So  $f_{\alpha} > 1 - \eta - q$ , because oscillators always move forward, regardless of h. Note that the intersection  $[1 - \eta - q, f_{\alpha}(q)] \cap (0, 1 - \eta)$  is non-empty because  $0 \le 1 - \eta - q < 1 - \eta$  and  $1 - \eta - q < f_{\alpha}(q) < 1$ . Since  $(1 - \alpha)\tilde{h} - \alpha h$  is either strictly positive or strictly negative on  $[0, 1 - \eta]$ , we can use Lemma 7.4 to conclude that  $W(1 - \eta - q, f_{\alpha}(a), \alpha) \ne 0$ . This is, according to Lemma 7.3, in contradiction with the assumption that q is an interior fixed point of  $F_{\alpha}$ .

If we assume q to be in  $[1 - \eta, 1)$ , then we get, using Lemma 7.3, Lemma 7.4 and the fact that  $f_{\alpha}(q) > 0$ , that  $W(0, f_{\alpha}(q), \alpha) \neq 0$ , which is in contradiction with the assumption that q is an interior fixed point of  $F_{\alpha}$ . Therefore  $F_{\alpha}$  has no interior fixed points if  $(1 - \alpha)\tilde{h} - \alpha h$  is either strictly positive or strictly negative on  $(0, 1 - \eta)$ .

Having prepared some more general theorems and criteria, we will now look at some specific types of sensitivity functions and try to complete the diagrams from Table 1.

#### 7.1 Symmetric feedback

In Theorem 6.7 we proved that  $F_{\frac{1}{2}} = I$  for symmetric sensitivity functions h. If we combine this with what we know from Table 1 we obtain the bifurcation diagram in Figure 9. In this section we prove Theorem 7.6, about the full cycle map for values of  $\alpha \neq \frac{1}{2}$ . Theorem 7.6 states that Figure 9 provides the complete bifurcation diagram for sensitivity functions of a fixed sign.



Figure 9: Incomplete bifurcation diagram for symmetric positive h.

#### Theorem 7.6.

If  $\alpha \neq \frac{1}{2}$ , and h is symmetric and either strictly positive or strictly negative, then  $F_{\alpha}$  has no interior fixed points. An interchange of  $\alpha$  and  $1 - \alpha$  corresponds to inversion of  $F_{\alpha}$  and hence to a switch in stability of the synchronized states.

#### Proof.

Let  $\alpha \neq \frac{1}{2}$ . Since *h* is symmetric,  $\tilde{h} = h$  and therefore  $(1 - \alpha)\tilde{h} - \alpha h = (1 - 2\alpha)h$  which is either strictly positive or strictly negative whenever *h* is. Therefore we conclude using Theorem 7.5 that  $F_{\alpha}$  has no interior fixed points.

The fact that h is symmetric leads with Theorem 6.4 to the last result.

#### 7.2 Monotone Feedback

In Table 1 we saw that it is possible for the two boundary fixed points to have the same stability character. In that case there must exist (at least) one interior fixed point that separates the domains of attraction or repulsion. We will prove that the bifurcation diagrams are as simple as possible, whenever h is monotone.

Recall from Definition 5.5 that for  $\bar{\alpha} = \frac{h(0)}{h(0)+h(1-\eta)}$  we have  $DF_{\bar{\alpha}}(0) = 1 = DF_{1-\bar{\alpha}}(1)$ . We also saw that when h(0) and  $h(1-\eta)$  have different sign, then  $\bar{\alpha} \notin [0, 1]$  and when h is positive then  $h(0) < h(1-\eta) \Leftrightarrow \bar{\alpha} < 1-\bar{\alpha}$  while when h is negative then  $h(0) < h(1-\eta) \Leftrightarrow \bar{\alpha} > 1-\bar{\alpha}$ .



Figure 10: Bifurcation diagram for positive strictly increasing h. For values of  $\alpha \in [\bar{\alpha}, 1 - \bar{\alpha}]$  the boundary fixed points have the same stability character.

The central assumption in this subsection is, as the title says, the monotonicity of h on  $[0, 1 - \eta]$ . So h is either strictly increasing or strictly decreasing. To complete the plots from Table 1, see also Figure 10, we will use the following lemma, which proves no interior fixed points exist in the most left region (separated by the vertical dotted lines).

#### Lemma 7.7.

Assume that h is sign definite (either strictly positive or strictly negative) and monotone (either strictly increasing or strictly decreasing) on  $[0, 1-\eta]$ . Then for all  $\alpha < \min(\bar{\alpha}, 1-\bar{\alpha}) F_{\alpha}$  has no interior fixed points.

#### Proof.

Assume h is strictly positive. Then for  $\alpha < \min(\bar{\alpha}, 1 - \bar{\alpha})$ , we have  $DF_{\alpha}(0) > 1$  and  $DF_{\alpha}(1) < 1$ , as indicated in Figure 10. This is equivalent with  $(1 - \alpha)h(0) > \alpha h(1 - \eta)$  and  $\alpha h(0) < (1 - \alpha)h(1 - \eta)$ .

Assume that h is strictly increasing on  $[0, 1 - \eta]$ . Then we have using the first inequality that for all  $s \in [0, 1 - \eta]$ 

$$(1-\alpha)h(1-\eta-s) \ge (1-\alpha)h(0) > \alpha h(1-\eta) \ge \alpha h(s)$$

so there is no interior fixed point by Theorem 7.5.

If on the other hand h is strictly decreasing on  $[0, 1 - \eta]$ , we see using the second inequality that for all  $s \in [0, 1 - \eta]$  we have

$$\alpha h(s) \le \alpha h(0) < (1-\alpha)h(1-\eta) \le (1-\alpha)h(1-\eta-s)$$

so there is no interior fixed point by Theorem 7.5. In both cases we therefore have that  $F_{\alpha}$  has no interior fixed points.

If h is strictly negative we have  $DF_{\alpha}(0) < 1$  and  $DF_{\alpha}(1) > 1$  so  $(1 - \alpha)h(0) < \alpha h(1 - \eta)$  and  $\alpha h(0) > (1 - \alpha)h(1 - \eta)$ . Using the reversed inequalities from above and Theorem 7.5 we conclude  $F_{\alpha}$  has no interior fixed points.

By Lemma 5.1 we know that the assumptions in Lemma 7.7 also imply that no interior fixed points exist for  $\alpha > \max(\bar{\alpha}, 1 - \bar{\alpha})$ , since this would imply the existence of fixed points of  $F_{\alpha}$  for  $\alpha < \min(\bar{\alpha}, 1 - \bar{\alpha})$ .

In Figure 10 we see that for intermediate values of  $\alpha$ , both boundary fixed points have the same stability character. Therefore at least one interior fixed point has to exist. Lemma 7.8 shows this is the only interior fixed point as long as h is monotone, since the existence of multiple interior fixed points would require at least one of them being stable.



Figure 11: Two half cycle maps  $f_{0.2}$  corresponding to  $h(\phi) = 20 - \phi$  and  $h(\phi) = 2 - \phi$  with for both  $\eta = 0.2$ . Note that for the red curve  $f_{0.2}(1-\eta) \in (1-\eta, 1]$ . In the region  $(1-\eta, 1] \times (1-\eta, 1]$ , the red curve  $f_{0.2}$  has a derivative of minus one.

First notice that the graph of  $f_{\alpha}$ , see Figure 11, when plotted in the square  $[0, 1] \times [0, 1]$  either has a part in the region  $[0, 1-\eta] \times [0, 1-\eta]$  or in the region  $(1-\eta, 1] \times (1-\eta, 1]$ . Part of the graph is in the first region if  $f_{\alpha}(1-\eta) \in [0, 1-\eta]$  and in the second if  $f_{\alpha}(1-\eta) \in (1-\eta, 1]$ . If  $f_{\alpha}(1-\eta) \in (1-\eta, 1]$ , the group starting in

 $\theta = 0$  is pulled through the complete sensitivity region and enters the signalling region in less than  $\Delta t = \eta$  time. This requires a high positive feedback, but is possible.

A second remark is that we only need to prove Lemma 7.8 for strictly increasing h. Indeed once we proved Lemma 7.8 for strictly increasing h, we also proved the lemma for the reflection of h, using Corollary 6.5, which is strictly decreasing. Note that Lemma 7.8 makes no assumptions on the sign of h.

#### Lemma 7.8.

Assume that h is strictly increasing. If  $f_{\alpha}(1-\eta) \in [0, 1-\eta]$ , then any interior fixed point of  $F_{\alpha}$  is unstable<sup>9</sup>. If  $f_{\alpha}(1-\eta) \in (1-\eta, 1]$ , then for  $\alpha \neq \frac{1}{2}$  any interior fixed point of  $F_{\alpha}$  is unstable. The full cycle map  $F_{\frac{1}{2}}$  has an interval of (neutral) interior fixed points from  $\phi = 1 - \eta$  until  $f_{\frac{1}{2}}(\phi) = 1 - \eta$ , but this interval is repelling.

*Proof.* We first prove the following two statements.

- (i) If  $\phi \in (0, 1 \eta]$  and  $f_{\alpha}(\phi) \in (1 \eta, 1)$ , then  $F_{\alpha}(\phi) = \phi$  implies  $D^2 F_{\alpha}(\phi) > 0$ .
- (ii) If  $\phi \in (1 \eta, 1)$  and  $f_{\alpha}(\phi) \in (0, 1 \eta]$ , then  $F_{\alpha}(\phi) = \phi$  implies  $D^2 F_{\alpha}(\phi) < 0$

Assume that  $\phi$  satisfies the conditions in statement (i). Then, from Theorem 5.4 and the fact that  $f_{\alpha}(\phi) \in (1 - \eta, 1]$  we get,  $DF_{\alpha}(\psi) = \frac{1 + (1 - \alpha)h(F_{\alpha}(\psi))}{1 + \alpha h(1 - \eta - \psi)}$  so

$$D^{2}F_{\alpha}(\psi)\Big|_{\substack{\psi=\phi\\F_{\alpha}(\phi)=\phi}} = \frac{(1-\alpha)h'(\phi)DF_{\alpha}(\phi)\left((1+\alpha h(1-\eta-\phi))+\alpha h'(1-\eta-\phi)\left(1+(1-\alpha)h(\phi)\right)\right)}{(1+\alpha h(1-\eta-\phi)))^{2}} > 0$$

since h' > 0,  $DF_{\alpha} > 0$  and  $(1 + \alpha h) > 0$  as well as  $(1 + (1 - \alpha) h) > 0$  according to assumption (A3). Next assume  $\phi$  satisfies the conditions in statement (*ii*). Then, since  $\phi \in (1 - \eta, 1]$ ,  $DF_{\alpha}(\psi) = \frac{1 + \alpha h(f_{\alpha}(\psi))}{1 + (1 - \alpha)h(1 - \eta - f_{\alpha}(\psi))}$ ,

so  $D^2 F_{\alpha}(\phi) \Big|_{\substack{\psi=\phi\\F_{\alpha}(\phi)=\phi}} < 0$ , since  $Df_{\alpha} < 0$  and h' > 0 and  $(1+\alpha h) > 0$  as well as  $(1+(1-\alpha) h) > 0$  according

to assumption (A3). This proves the statements (i) and (ii) above.

Assume that  $f_{\alpha}(1-\eta) \in [0, 1-\eta]$  and consider  $\phi \in [0, 1-\eta]$  s.t.  $f_{\alpha}(\phi) \in [0, 1-\eta]$  and  $F_{\alpha}(\phi) = \phi$ . Then

$$DF_{\alpha}(\phi)\Big|_{\substack{\psi=\phi\\F_{\alpha}(\phi)=\phi}} = \frac{1+(1-\alpha)h(\phi)}{1+(1-\alpha)h(1-\eta-f_{\alpha}(\phi))} \frac{1+\alpha h(f_{\alpha}(\phi))}{1+\alpha h(1-\eta-\phi)}$$

So, since  $f_{\alpha}(\phi) > 1 - \eta - \phi$  for  $\phi \in [0, 1 - \eta]$  even if  $f_{\alpha}(\phi) \in [0, 1 - \eta]$  and h' > 0, we know that both fractions are larger than 1, so  $DF_{\alpha}(\phi)\Big|_{F_{\alpha}(\phi)=\phi} > 1$ .

If we assume that  $f_{\alpha}(1-\eta) \in (1-\eta, 1]$  then there exist  $\phi \in (1-\eta, 1]$  s.t.  $f_{\alpha}(\phi) \in (1-\eta, 1]$ . For these  $\phi$  we have  $DF_{\alpha}(\phi) = 1$ , by Theorem 5.4. We prove that in this region  $F_{\alpha}(\phi) = \phi \Leftrightarrow \alpha = \frac{1}{2}$ . Indeed  $F_{\alpha}(\phi) = \phi$  implies, using (7) twice, that

$$1 - \phi = \int_0^{f_\alpha(\phi)} \frac{\mathrm{d}s}{1 + \alpha h(s)} \text{ and } 1 - f_\alpha(\phi) = \int_0^{F_\alpha(\phi)} \frac{\mathrm{d}s}{1 + (1 - \alpha)h(s)} = \int_0^{\phi} \frac{\mathrm{d}s}{1 + (1 - \alpha)h(s)}$$

which is equivalent with  $\alpha = 1 - \alpha$  or  $\alpha = \frac{1}{2}$ .

Notice that the existence of any stable fixed point  $\phi_s$  would imply the existence of a smaller and a larger unstable fixed point, because the boundary fixed points are stable. Since this is in all cases clearly impossible, we conclude that if  $F_{\alpha}$  has an interior fixed point it is either unstable, or lies in a repelling interval of interior fixed points, depending on  $\alpha$ ,  $\eta$  and h.

<sup>&</sup>lt;sup>9</sup>In the sense that the derivative  $DF_{\alpha} > 1$  in the fixed point.

The complete bifurcation diagram (numerically generated) is plotted in Figure 12, with a sensitivity function h such that  $f_{\alpha}(1-\eta) \in [0, 1-\eta]$ , where we used  $\eta = 0.2$ . The following theorem describes the full cycle map for strictly positive, increasing h.



Figure 12: The bifurcation diagram for  $h(\phi) = 0.1 + \phi$ . With this sensitivity function, we used  $\eta = 0.2$ , we have  $f_{\alpha}(1-\eta) \in [0, 1-\eta]$ .

#### Theorem 7.9.

Let h be positive, strictly increasing for all  $\phi \in [0, 1 - \eta]$ .

If  $f_{\frac{1}{2}}(1-\eta) \in [0, 1-\eta]$ , then for  $\alpha \leq \bar{\alpha}$  we have  $DF_{\alpha}(0) > 1$  and  $DF_{\alpha}(1) < 1$ , and for  $\alpha \geq 1-\bar{\alpha}$  we have  $DF_{\alpha}(0) < 1$  and  $DF_{\alpha}(1) > 1$ , in both cases without any interior fixed points. For each  $\bar{\alpha} \leq \alpha \leq 1-\bar{\alpha}$  the boundary points are stable and there exists a unique unstable interior fixed point. For  $\alpha = \frac{1}{2}$ , this interior fixed point equals  $\phi_{frac12}$ .

If  $f_{\frac{1}{2}}(1-\eta) \in [1-\eta, 1]$  the same holds for all  $\alpha \neq \frac{1}{2}$ . For  $\alpha = \frac{1}{2}$  there is an interval of unstable fixed points from  $\phi = 1 - \eta$  until  $\phi = \psi$  with  $f_{\frac{1}{2}}(\psi) = 1 - \eta$ , instead of the fixed point  $\phi_{\frac{1}{2}}$ .

*Proof.* Lemma 7.7 proves no fixed points exists for small and large  $\alpha$ . Using Lemma 7.8 we concluded that there is at most one interior fixed point, and since for intermediate values of  $\alpha$  at least one unstable fixed point has to exist we prove there is exactly one fixed point for each  $\alpha$ . The uniqueness follows from Lemma 3.5 since a fixed point of  $F_{\alpha_1}$  cannot be a fixed point of  $F_{\alpha_2}$  if  $\alpha_1 \neq \alpha_2$ .

If  $f_{\frac{1}{2}}(1-\eta) \in [1-\eta, 1]$ , then Lemma 7.8 gives the existence of the interval of fixed points for  $\alpha = \frac{1}{2}$ .

Where small values of  $\alpha$  with positive monotone feedback lead to instability of the  $\theta = 0$  synchronized state, small values of  $\alpha$  lead to stability of  $\theta = 0$  in case of negative monotone feedback. This is as we would expect since the strong signals of the leading group will slow down the group with the smaller signal strength.

For completeness we will state the summarizing theorem for negative monotone feedback.

#### Theorem 7.10.

Let h be negative, strictly increasing for all  $\phi \in [0, 1 - \eta]$ .

For  $\alpha < \bar{\alpha}$  we have  $DF_{\alpha}(0) < 1$  and  $DF_{\alpha}(1) > 1$ , and for  $\alpha \ge 1 - \bar{\alpha}$  we have  $DF_{\alpha}(0) > 1$  and  $DF_{\alpha}(1) < 1$ , in both cases without any interior fixed points. For each  $\bar{\alpha} \le \alpha \le 1 - \bar{\alpha}$  the boundary points are unstable and there exists a unique stable interior fixed point. For  $\alpha = \frac{1}{2}$ , this interior fixed point equals  $\phi_{frac12}$ .

*Proof.* First notice that since h < 0, we have for the half cycle map that  $f_{\alpha}(\phi) < 1 - \phi$  so  $f_{\frac{1}{2}}(1 - \eta) < \eta$ . Therefore the interval of fixed points will not occur.

Lemma 7.7 proves no fixed points exists for small and large  $\alpha$ . Using Lemma 7.8 we concluded that there is at most one interior fixed point, and since for intermediate values of  $\alpha$  at least one stable fixed point has to exist we prove there is exactly one fixed point for each  $\alpha$ . The uniqueness follows from Lemma 3.5 since a fixed point of  $F_{\alpha_1}$  cannot be a fixed point of  $F_{\alpha_2}$  if  $\alpha_1 \neq \alpha_2$ .

Again, a result for strictly decreasing, negative h can be obtained using Corollary 6.5. The bifurcation diagram for negative, strictly decreasing h is plotted in Figure 17c.



Figure 13: Incomplete bifurcation diagrams for mixed feedback. Both boundary fixed points are stable if  $h(0) < 0 < h(1 - \eta)$ , and unstable else.

If h(0) and  $h(1 - \eta)$  have different sign, then  $\bar{\alpha} \notin [0, 1]$ , so both boundary fixed points have a fixed stability character, independent of  $\alpha$ , as can be seen in Figure 13. Since Lemma 7.8 did not use the sign of h we can prove the following.

#### Theorem 7.11.

Let h be strictly increasing and assume  $h(0) < 0 < h(1 - \eta)$ , then there is an interior unstable fixed point  $\phi$  for each  $\alpha \in [0,1]$ . Since  $f_{\alpha}(\phi)$  is a fixed point for  $F_{1-\alpha}$  and  $f_0(\psi) = 1 - \psi$  for all  $\psi$ , the fixed point  $\phi$  moves from some non zero  $\phi_0$  for  $\alpha = 0$  to  $1 - \phi_0$  for  $\alpha = 1$ , passing  $\phi = \phi_{\frac{1}{2}}$  for  $\alpha = \frac{1}{2}$ . If  $f_{\frac{1}{2}}(1 - \eta) \in [1 - \eta, 1]$ , then  $F_{\frac{1}{2}}$  has an interval of fixed points around  $\phi_{\frac{1}{2}}$ , just as in the case of positive feedback.

*Proof.* The assumption  $h(0) < 0 < h(1 - \eta)$  gives that an unstable interior fixed point exists for all  $\alpha \in [0, 1]$  and according to Lemma 7.8 we see that this is the only interior fixed point since h is monotone. Note that we cannot proof uniqueness since Lemma 3.5 only holds for sign definite h.

#### 7.3 Non-monotone feedback

Monotonicity is a big restriction on the sensitivity function h and non-monotonic sensitivity functions could be (biologically) relevant. The following theorem gives a condition about  $F_{\frac{1}{2}}$  for more general h. Recall the definition and properties of  $W(a, b, \alpha)$  from Lemma 7.4. We will consider the case  $\alpha = \frac{1}{2}$  here.

#### Theorem 7.12.

If  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h} - h$  for a certain sensitivity function h, then  $F_{\frac{1}{2}}$  can have only one interior fixed point, namely  $\phi_{\frac{1}{2}}$  determined by  $f_{\frac{1}{2}}(\phi_{\frac{1}{2}}) = \phi_{\frac{1}{2}}$ .

*Proof.* Since the integrand of  $W(a, b, \frac{1}{2})$  is an odd function around  $\theta = \frac{1-\eta}{2}$ , we know that  $W(1-\eta-q, q, \alpha) = 0$ . On the other hand we see that if  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h}-h$  then  $W(a, b, \frac{1}{2}) = 0$  implies that  $a = 1-\eta-b$ .

According to Lemma 7.3, a point  $q \in (0, 1 - \eta)$  is an interior fixed point of  $F_{\frac{1}{2}}$  if and only if

$$W\left(1-\eta-q,f_{\frac{1}{2}}(q),\frac{1}{2}\right)=0$$

which is equivalent with  $1 - \eta - q = 1 - \eta - f_{\frac{1}{2}}(q)$  so  $q = f_{\frac{1}{2}}(q)$ . Since an interior fixed point  $q \in (1 - \eta, 1)$  would imply  $W\left(0, f_{\frac{1}{2}}(q), \frac{1}{2}\right) = 0$ , which is clearly impossible, we conclude that  $F_{\frac{1}{2}}$  can have only one interior fixed point, namely  $\phi_{\frac{1}{2}}$  determined by  $f_{\frac{1}{2}}(\phi_{\frac{1}{2}}) = \phi_{\frac{1}{2}}$ .

As an example we consider piecewise linear sensitivity functions, i.e. functions that satisfy

$$h(\theta) = \begin{cases} a + b\theta & \text{if } 0 \le \theta \le c \\ a + bc + d(\theta - c) & \text{if } c \le \theta \le 1 - \eta \\ 0 & \text{else} \end{cases}$$
(20)

for some  $0 < c < 1 - \eta$  and some  $b, d \neq 0$  with sign (b) = -sign(d). Note that the reflected sensitivity function  $\tilde{h}$  is then also piecewise linear.



Figure 14: Piecewise linear sensitivity functions and their reflections in  $\frac{1-\eta}{2}$  for  $\eta = 0.2$ . Note that for the green graph, we have  $h(1-\eta) < h(0)$ .

So to find fixed points of  $F_{\frac{1}{2}}$  it is useful to consider the roots of  $\tilde{h} - h$ , as we saw before. Linearity helps here and we conclude the following:

#### Lemma 7.13.

Let h be positive and piecewise linear as above defined by (20) and suppose that  $c < \frac{1-\eta}{2}$ . Then we have:

If b < 0, then  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h} - h$  if and only if  $bc + d(1 - \eta - c) > 0$ , while if b > 0, then  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h} - h$  if and only if  $bc + d(1 - \eta - c) < 0$ . For  $c > \frac{1-\eta}{2}$ , we have:

If b < 0, then  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h} - h$  if and only if  $bc + d(1 - \eta - c) < 0$ , while if b > 0, then  $\frac{1-\eta}{2}$  is the only root of  $\tilde{h} - h$  if and only if  $bc + d(1 - \eta - c) > 0$ .

*Proof.* First assume that  $c < \frac{1-\eta}{2}$ . Note that  $\theta = \frac{1-\eta}{2}$  is the only possible root of  $\tilde{h} - h$  in the subinterval  $[c, 1 - \eta - c]$ , since in that interval we have  $h(1 - \eta - \theta) = 1 - \eta - h(\theta)$ . This leads to two possibilities:

If b = h'(0) < 0, then  $h(0) < h(1-\eta)$  gives that  $h(1-\eta-\theta) > h(\theta)$  for all  $\theta \in [0, \frac{1-\eta}{2})$ , so there are no roots of  $\tilde{h} - h$  besides  $\frac{1-\eta}{2}$ . If b = h'(0) > 0, then  $h(0) > h(1-\eta)$  gives that  $h(1-\eta-\theta) < h(\theta)$  for all  $\theta \in [0, \frac{1-\eta}{2})$ , so there are no roots of  $\tilde{h} - h$  besides  $\frac{1-\eta}{2}$ .

Next note that  $c > \frac{1-\eta}{2}$  for h implies that  $c < \frac{1-\eta}{2}$  for  $\tilde{h}$ . Since we are only interested in the roots of  $\tilde{h} - h$  we obtain the inequalities mentioned above, with h(0) and  $h(1-\eta)$  interchanged. This results in reversed inequalities.

The linearity implies that  $h(\theta)$  and  $h(1 - \eta - \theta)$  can only cross once in the interval  $[0, \frac{1-\eta}{2})$ .

Theorem 7.12 gives the behaviour of the full cycle maps when the signal strengths of the oscillators are equal. For other values of  $\alpha$  we cannot rule out the existence of multiple interior fixed points for piecewise linear sensitivity functions. This is confirmed by the graphs of  $F_{\alpha}$  in Figure 15 for

$$h(\phi) = \begin{cases} 2.2 - 3\phi & \text{if } 0 \le \phi \le 0.3\\ 1.3 + (\phi - .3) & \text{if } 0.3 \le \phi \le 1 - \eta \end{cases}$$

#### 7.4 Multiple interior fixed points

From the previous results we can conclude that the injectivity assumption  $(h'(\phi) > 0 \text{ or } h'(\phi) < 0$  for all  $\phi$ ) needs to be violated to obtain multiple (isolated) fixed points. On the other hand we saw in Theorem 7.6 that, whenever h is symmetric, positivity leads to no interior fixed points unless  $\alpha = \frac{1}{2}$ . Therefore a combination of mixed feedback and a non-injective sensitivity function is helpful to have multiple fixed points. In that case we can have a stable interior fixed point while both synchronized states are also stable. An example of this can be found in the next chapter, where we will be looking examples of this.

## 8 Numerical results and bifurcation diagrams

We already saw that if h is symmetric, then  $\alpha = \frac{1}{2}$  is a degenerate case, since the full cycle map is then equal to the identity. We can ask if a (minor) perturbation of the symmetric sensitivity function results in non-degenerate behaviour of the full cycle map.

To model the perturbation we use  $h(t; \omega, \epsilon) = 1 + \epsilon \sin(\omega t)$ , so  $h(t; \omega, 0) = h(t; 0, \epsilon) = 1$ , a symmetric sensitivity function. We want  $\epsilon$  to be small ( $\epsilon < 1$ ), since  $\epsilon$  describes the 'size' of the perturbation. Note that  $h(\cdot; \omega, \epsilon)$  is positive. Using a sine has also disadvantages:  $h\left(t; \frac{10l+5}{4}, \epsilon\right)$  is symmetric for all integers l, since we use  $\eta = \frac{4}{5}$ .

Using the theory from earlier sections we can prove that  $F_{\frac{1}{2}}$  is either the identity or has a unique interior fixed points for all values of  $\omega \in [0, \frac{2\pi}{1-\eta}]$  regardless of the value of  $\epsilon$ . Therefore the degeneracy breaks down because the sensitivity function is no longer symmetric. For bigger values of  $\omega$  other interior fixed points



Figure 15: Full cycle maps for a piecewise linear function for values of  $\alpha \in \{0.47, 0.5, 0.53\}$ . Note that, as proved in Lemma 7.13,  $F_{\frac{1}{2}}$  has a unique interior fixed point, while the full cycle map  $F_{\alpha}$  has multiple interior fixed points for (various) other values of  $\alpha$ . Recall that Lemma 3.5 gives that  $F_{\alpha}$  is a decreasing function of  $\alpha$ .

arise. In Figure 16 the full cycle maps are plotted for  $\omega = 2\pi k$  with  $k \in \{0, 1, 2, 5\}$ .

We can also plot so called bifurcation diagrams for different sensitivity functions h, to extend the results from Table 1. In these diagrams we plot the stable and unstable fixed points of the full cycle map  $F_{\alpha}$  as a function of the bifurcation parameter  $\alpha$ . With bifurcation diagrams we can easily illustrate the results of the research in the previous sections, see Figure 17.



**Figure 16:** Full cycle maps  $F_{\frac{1}{2}}$  for  $h(\theta) = 1 + 0.6 \sin(2k\pi\theta)$ .



Figure 17: Bifurcation diagrams for monotone sensitivity functions.

## 9 More oscillators

Now that we have covered the case with two oscillators, the question arises whether similar results can be obtained if more oscillators are added. To be precise, we want to investigate the stability of the boundary fixed points with respect to a splitting into multiple cohorts.

Instead of considering the linearisation of the full cycle map, or the full cycle map itself, we will argue differently. If all oscillators are in the same region (either signalling or receiving), nothing happens and the oscillators move forward with speed 1. Therefore we can focus on the boundaries of the two regions. There are two boundaries we need to consider, as depicted in Figure 18. For simplicity we assume that the signalling and receiving region are adjacent and partition the circle. Also we assume that the changes are abrupt, so the sensitivity function h is non-zero in the boundary points of the sensitivity region. Lastly we assume the sensitivity function h to be constant in a neighbourhood of the boundary, such that all oscillators in the cluster receive the same feedback.

We use  $\Phi(t, \phi_0)$  to denote the position after a time t of a group which started at  $\phi_0$  influenced by received signals. Note that  $\Phi(t, \phi_0) > t + \phi_0$  if the feedback is positive, since this leads to a higher speed, and  $\Phi(t, \phi_0) < t + \phi_0$  if the feedback is negative, since the group then has a lower speed. We do not care about the exact splitting and the signal strengths corresponding to it, so we left the signal as well as the  $\alpha$ 's out of the notation.



(a) An upcoming passage of a cluster of oscillators from the signalling region to the receiving region, with s as the boundary point. (b) An upcoming passage of a cluster of oscillators from the receiving region to the signalling region, with s as the boundary point.

Figure 18: Passages of boundary points between signalling and receiving regions.

In Figure 18 we see a cluster of oscillators heading to a passage of a boundary. We would like to know how the width of the cluster changes as it passes the boundary. An important remark is that although oscillators in the cluster can move to or from each other, the order of the oscillators remains the same. Indeed, as we have seen in the proof of Lemma 3.4, it is impossible for a group to pass another group (except for the permutation of order by resetting from  $\theta = 1$  to  $\theta = 0$ ).

#### Lemma 9.1.

If a cluster of oscillators passes from the signalling region to the receiving region, the width of the cluster decreases if the feedback is negative, while the width of the cluster increases if the feedback if positive.

*Proof.* The situation in this lemma is the one in Figure 18 (a). Note that the width of the cluster at start of the passage is  $\phi_n - \phi_1$ .

All oscillators in the cluster move with unit speed until group n reaches s (group 1 is then at  $\phi_1 + s - \phi_n$ ). From then on group n (and possible oscillators behind of group n) receive the signals sent by group 1 (and possible oscillators ahead of 1), for a time

$$\Delta t = s - (\phi_1 + s - \phi_n) = \phi_n - \phi_1$$

After time  $\Delta t$  group 1 is at s while group n is at  $\Phi(\phi_n - \phi_1, s)$ . From then on the clusters move with unit speed forward again. The width of the cluster is then

$$\Phi\left(\phi_n - \phi_1, s\right) - s$$

Therefore we see that negative feedback leads to  $\Phi(\phi_n - \phi_1, s) - s < \phi_n - \phi_1$ , which is smaller than the width of the cluster before it passed the region boundary. Positive feedback leads to  $\Phi(\phi_n - \phi_1, s) - s > \phi_n - \phi_1$ , which is an increase of the width of the cluster.

Using the same arguments we get a similar result for the other boundary passage.

#### Lemma 9.2.

If a cluster of oscillators passes the boundary from the receiving region to the signalling region, the length of the cluster increases if the feedback is negative, while the length of the cluster decreases if the feedback if positive.

*Proof.* The situation in this lemma is as in Figure 18 (b). Note that the width of the cluster at start of the passage is  $\phi_n - \phi_1$ .

All oscillators in the cluster move with unit speed until group n reaches s (group 1 is then at  $\phi_1 + s - \phi_n$ ). From then on group n (and later possible oscillators behind of group n) start sending signals which are received by group 1 (and possible oscillators ahead of 1). That means that group 1 reaches s after a time  $\Delta t$ , defined by

$$\Phi\left(\triangle t, \phi_1 + s - \phi_n\right) = s.$$

At that point the heading group n is at  $s + \Delta t$ , so the length of the cluster is now  $\Delta t$ . From then on the cluster moves forward with unit speed.

We see that negative feedback leads to

$$s = \Phi\left(\triangle t, \phi_1 + s - \phi_n\right) < \triangle t + \phi_1 + s - \phi_n,$$

so  $\Delta t > \phi_n - \phi_1$ , i.e. an increase of the cluster width. Positive feedback leads to

$$s = \Phi\left(\triangle t, \phi_1 + s - \phi_n\right) > \triangle t + \phi_1 + s - \phi_n,$$

which gives a decrease of the cluster width.

In Table 1 in Section 5 we saw that whenever the sensitivity function h is negative in a region left from  $\theta = 0$ and positive in a region right from  $\theta = 1 - \eta$ , then both boundary fixed points are stable, independent of the value of  $\alpha$ . Lemmas 9.1 and 9.2 confirm this result, not only for a cluster of two oscillators, but also for clusters of arbitrary size. Indeed, the negative feedback in the region right from  $\theta = 0$  gives according to Lemma 9.1 a decrease of the cluster width. Since the positive feedback in the region left from  $\theta = 1 - \eta$  also gives a decrease of the cluster width by Lemma 9.2, we conclude that the synchronized state is asymptotically stable. Note that in the case of two oscillators this allowed us to conclude the existence of an unstable steady state with two cohorts. Unfortunately we cannot generalize this implication to the case of more oscillators.

If the passage of (a) and (b) leads to an increase of the cluster width in one passage and a decrease in another, then the precise combination of the signal strengths of the oscillators and the increase and decrease

of the cluster width becomes important as we saw in the earlier sections. In that case we have to specify the precise way in which the cluster is split in order to derive conclusions.

In the case of symmetric h, we have that the effect of both passages is equal, so the effect of identical oscillators cancels. Indeed this is what we saw in Section 7. If the oscillators are not identical, it depends again on the ratio of their signal strengths.

## 10 Conclusions

The dynamics of coupled oscillators, described by differential equations that in most cases cannot be solved explicitly, can be very complicated. Therefore following the progression of the oscillators to observe synchronization or de-synchronization will generically be hard or even impossible. By introducing Poincaré-like cycle maps  $f_{\alpha}$  and  $F_{\alpha}$  we can translate the continuous dynamical system to a discrete one, where synchronized or cycle phase-locked cohorts correspond to fixed points of the discrete dynamical system. The synchronized state corresponds to two boundary fixed points of the full cycle map  $F_{\alpha}$ .

On the circle the oscillators synchronize if both boundary fixed points of the interval are stable and we observe de-synchronization on the circle if both boundary fixed points of the interval are unstable. If the boundary points have a different stability character, the synchronized state is excitable. This stability of the boundary points depends on the feedback, in particular on the sign of h(0) and  $h(1 - \eta)$ , and on the signal strength of the oscillators. If the sign of h(0) and  $h(1 - \eta)$  is different, then the boundary points have equal stability character regardless of the signal strength of the oscillators.

Standard theory gives that at least one interior fixed point has to exist if the boundary points have equal stability character, but many more scenarios are thinkable, as we saw in Section 8. If the feedback depends monotonically on the position of the oscillator, then at most one interior fixed point exists.

The results on reflection of the sensitivity function helped to formulate theorems about the (non-)existence of interior fixed points and showed us the highly degenerate behaviour of symmetric sensitivity functions. This degeneracy is understandable because the effect of the feedback is mostly caused by the abrupt changes in speed at the boundaries of the sensitivity region, as discussed in Section 9. Symmetric feedback results in a net zero effect of a cohort staying behind and catching up.

The main result is the fact that monotone feedback results in relative simple behaviour: either global synchronization, global de-synchronization, or excitability. If the sensitivity function is either strictly increasing or strictly decreasing, the values of  $\alpha$ , h(0) and  $h(1 - \eta)$  determine the behaviour. Unfortunately we need an exact specification of the sensitivity function h to calculate the exact location of the interior fixed point, if it exists.

When our main interest is the stability of the synchronized state, it may be advantageous to use a second approach to analyse the dynamics of the oscillators on the circle. As the oscillators progress through the circle, only passages of the boundaries between the receiving and sending region effect the distance between the oscillators. When considering the effect of feedback on the distance between the oscillators, the same results as with the cycle maps can be obtained but in a more intuitive manner. Another advantage of the approach we used in Section 9 is that it not only gives results for two cohorts, but also for a cluster with an arbitrary number of cohorts. A disadvantage of using so called passage maps is that we cannot conclude anything about possible multiple-cohort steady states, as we did in the previous sections using the cycle maps.

Imagine for example that a certain sensitivity function gives a "stable" two-cohort situation, i.e. the synchronized state is unstable, and the single interior fixed point is stable, which is the case when h is negative in a region right from  $\theta = 1 - \eta$  and positive in a region left from  $\theta = 0$ . What we would like to know is if

this situation is stable if we split one of the two cohorts.

Further research needs to be done to figure out if a configuration with multiple oscillators will converge to synchrony or to a stable multiple-cohort solution. Also varying progression speeds in absence of signals would be interesting to look at, as the assumption that all oscillators progress with unit speed is rather limiting. Another simplifying assumptions we made in this thesis is that the impact function w is constant. If the strength of the signals sent varies along the circle, the dynamics become more complicated. We do not know how this might influence our results precisely. We also would like to find out if the result on symmetric sensitivity functions (Theorem 6.7) generalizes to more than two oscillators. The hypothesis is that a symmetric impact function and a symmetric sensitivity function lead to trivial behaviour. Unfortunately time was limited to dive further into these questions.

## Appendix A Response/signalling feedback: comparison with [4]

Todd Young et al. considered two identical oscillators with a cell cycle (seen as an interval) with a signalling and a responsive part with constant feedback a, either positive or negative. To be more precise, they assume oscillators can send signals when in the signalling region S = [0, s) and can receive signals when in the receiving region R = [r, 1). They denote this cell cycle as an RS-system, since  $\theta = 0$  is the boundary point of the receiving region (to the left) and the signalling region (to the right). The oscillators  $x_i$  are described by

$$\frac{dx_i}{dt} = \begin{cases} 1 & \text{if } x_i \notin R\\ 1+a & \text{if } x_i \in R \end{cases} \quad \text{for some } a > 0$$

We will focus on section 6 of the article, where the authors consider the dynamics in the case of two oscillators. Here the similarity is visible, but there's one major difference. In our model  $\theta = 0$  is the boundary point of the signalling region (to the left) and the receiving region (to the right), so we could denote this as an *SR*-system. Also the signalling and receiving region do not partition the interval in [4], but this can be realized in our model if we choose *h* to be zero in some region between S and R.

Figure 19: The system of Young et. al. (RS-model) and the system with S and R reversed (SR-model). Note that the names of the systems correspond to the boundary between the regions that is present.

We will use the approach from Section 9 to see how the differences in the system appear in the results. As said, in the RS-system the signalling and receiving region do not partition the interval, as the boundary from the signalling region to the receiving region is not present. To find the stability of the synchronized state, we consider a cluster of oscillators moving through the cycle. By Lemma 9.2 we see that when the cluster passes the boundary from R to S the length of the cluster increases if the feedback is negative, while it decreases when the feedback is positive. Young [4] states that, in the case of two oscillators, an unstable synchronized state leads to either a stable fixed point for the full cycle map, or an interval of neutral fixed points that is an attractor, where a stable synchronized state leads to either an unstable fixed point for the full cycle map, or an interval of neutral fixed points that is a repeller. The interval of neutral fixed points is a consequence of the neutral region where oscillators are insensitive to signals. Therefore a cluster with a large enough length always never has one oscillator in the S-region and while the other is in the R-region.

The fact that the receiving region and the signalling region are not adjacent on one side implies in the RS-system that the boundary from the signalling region to the receiving region is not present. If we would reverse this order, as is sketched in Figure 19, to obtain the SR-system, then the boundary from the receiving region to the signalling region would not be present. Lemma 9.1 then gives the opposite result of the paragraph above: the width of the cluster decreases if the feedback is negative, while it increases when the feedback is positive. In that sense the note of Young et. al. in their first section is justified when they state that: "... in the reversed case, when R follows S, many of our results hold with the roles of positive and negative feedback reversed."

Instead of the analysis used above, we can also construct the full cycle map for the SR-system directly, using Equations (6) and (7) in Corollary 3.3, with the remark that h is zero outside  $R = [0, r) \subset [0, 1 - \eta] = S^c$  since  $s = 1 - \eta$ . If we compare the constructed full cycle map with the results in Appendix B. of [4], we see that indeed the roles of positive and negative feedback are reversed. We find that reversing R and S is equivalent with choosing the constant feedback function h to be equal to  $\frac{-2a}{1+a}$  where a is the constant feedback from [4]. Note that since in [4] the signal strengths of both oscillators are equal, we need to choose  $\alpha = \frac{1}{2}$  here.

Note that if  $h = \frac{-2a}{1+a} \mathbb{1}_{[0,r]}$ , then  $h(1-\eta) = 0$  so indeed a > 0 gives h(0) < 0, which according to Table 1, results in an unstable synchronized state. If a < 0, then h(0) > 0 which gives a stable synchronized state. If we plot  $F_{\frac{1}{2}}$  with a sensitivity function h as above, we obtain Figure 20, which is identical to Fig. 6 in chapter 6 of [4].



**Figure 20:** Plots of  $F_{\frac{1}{2}}$  for various parameter values.

## Appendix B Limit procedure

Motivated by an article of Renato Mirollo and Steven Strogatz, "Synchronization of pulse-coupled biological oscillators", we will consider the limit of our two-group model for  $\eta \to 0$  and  $h \to \infty$ , with their ratio  $\frac{h}{\eta}$  tending to a non-zero limit. The signalling is pulse-like in that limit.

Since we prefer that the support of h does not depend on  $\eta$ , we need to change some assumptions. Instead of defining h to be zero outside of  $[0, 1 - \eta]$ , we will therefore demand  $h : [0, 1] \to \mathbb{R}$  to be continuous on the unit interval and multiply it with a factor  $\frac{(1-H(\cdot-(1-\eta)))}{\eta}$ , where  $H : \mathbb{R} \to \mathbb{R}$  is the Heaviside step function  $H(s) = 1_{[0,\infty)}$ . The scaling with  $\frac{1}{\eta}$  is done to maintain the total boost given. For this limit procedure we need to assume h to be positive, in order not to violate Assumption (A3). A remark about negative feedback follows at the end of this appendix.

Since we will take the limit of  $\eta \to 0$ , we can ignore the case where the cohort 2 starts at  $\phi \in [1 - \eta, 1]$ . So assume at start cohort 1 is at  $\theta = 0$  and cohort 2 is at  $\theta = \phi \in [0, 1 - \eta]$ . Recall from Corollary 3.3 that the position of cohort 1 when cohort 2 hits  $\theta = 1$  is given by  $\Psi(\eta; 1 - \eta - \phi, \alpha)$ , since cohort 1 moves for a time  $\eta$  starting at  $\theta = 1 - \eta - \phi$  receiving signals of strength  $\alpha$ .

We are interested in  $\lim_{\eta\to 0} \Psi(\eta; 1 - \eta - \phi, \alpha)$ , the limit of the half cycle map. After proving its existence we will denote this limit by  $\mathfrak{F}_{\alpha}(\phi)$ .

Recall that  $\Psi(t) = \Psi(t; \psi_0, \alpha, \eta)$ , now also a function of  $\eta$ , satisfies

$$\begin{cases} \frac{d\Psi}{dt}(t) &= 1 + \alpha \frac{h(\Psi(t))}{\eta} \left( 1 - H(\Psi(t) - (1 - \eta)) \right) \\ \Psi(0) &= \psi_0 \end{cases}$$
(21)

We have according to Equation (6) that:

$$\eta = \int_{1-\eta-\phi}^{\Psi(\eta;1-\eta-\phi,\alpha,\eta)} \frac{\mathrm{d}s}{1+\alpha \frac{h(s)(1-H(s-(1-\eta)))}{\eta}}$$

so by dividing both sides by  $\eta$ , we get

$$1 = \int_{1-\eta-\phi}^{\Psi(\eta;1-\eta-\phi,\alpha,\eta)} \frac{\mathrm{d}s}{\eta+\alpha h(s)\left(1-H(s-(1-\eta))\right)}$$

Since the integral on the right hand side depends continuously on  $\eta$ , we can take the limit of  $\eta \to 0$  on both sides of the last equation. Since  $\Psi(\eta; 1 - \eta - \phi, \alpha, \eta) \leq 1$  for all  $\eta \geq 0$ , we can ignore the step function and multiply both sides by  $\alpha$  to obtain

$$\int_{1-\phi}^{\mathfrak{F}_{\alpha}(\phi)} \frac{\mathrm{d}s}{h(s)} = \alpha$$

The identity above will not always be satisfied: if  $\int_{1-\phi}^{1} \frac{ds}{h(s)} < \alpha$ , the increment the oscillators receive due to received signals would cause the oscillator to exceed  $\theta = 1$ . Since we do not allow oscillators to pass each other, the surplus increment vanishes and the oscillator is pulled up to  $\theta = 1$ . This leads to the following definition.

### Definition B.1.

The limit of the half cycle map  $\mathfrak{F}_{\alpha}$  can be characterized by:

$$\begin{cases} \int_{1-\phi}^{\mathfrak{F}_{\alpha}(\phi)} \frac{\mathrm{d}s}{h(s)} = \alpha & \text{if } \int_{1-\phi}^{1} \frac{\mathrm{d}s}{h(s)} < \alpha \\ \mathfrak{F}_{\alpha}(\phi) = 1 & \text{if } \int_{1-\phi}^{1} \frac{\mathrm{d}s}{h(s)} \ge \alpha \end{cases}$$
(22)

In Figure 21 is illustrated that our half cycle map  $f_{\alpha}$  does tend to  $\mathfrak{F}_{\alpha}$  for  $\eta \to 0$  as long as  $\phi \neq 1$ .



Figure 21: A plot of  $f_{\alpha}$  based on the system in Equation 21 with  $\eta \in \{0.2, 0.1, 0.05\}$  and the limit half cycle map  $\mathfrak{F}_{\alpha}$  as defined in Definition B.1. The half cycle maps are based upon  $h(\phi) = 0.4 + \phi$ . We see the half cycle maps indeed tend to their limit.

## Appendix C Continuous signalling versus pulse-like signalling: comparison with [2] and [3]

In this section we will compare the models and results of Mirollo & Strogatz[2] and Alexander Mauroy[3]. Both models consider pulse-signalling, instead of a more continuous signalling like we do here. On the other hand, by taking the limit of  $\eta \to 0$  in our model while increasing the signal strength correspondingly, we obtain a pulse-signalling limit case. In this section we will relate the symbols, formula's and results for the case of two oscillators.

Both [2] and [3] assume the oscillators evolve according to a so called evolution function, that corresponds to the function g we derived in the previous section. When a group reaches the end of the interval, it fires and other oscillators receive this signal. This signal causes an instantaneous increment  $\epsilon > 0$  to the state of all other oscillators, or pulls them up to firing.

Note that both authors consider the two oscillators to be identical at first, while later on they consider oscillators firing in unison allowing different pulse strengths. A second remark is that both authors make a distinction between state space and phase space, where the state-phase relation is given by the evolution function. The distinction is especially clear in [3], as the author uses  $[\underline{x}, \overline{x}]$  for the state and  $\theta \in S^1(0, 2\pi)$  for the phase. The evolution function connects these spaces, since  $[\underline{x}, \overline{x}] \ni x = g(\theta)$  with  $\theta \in S^1(0, 2\pi)$ . Note a difference between [2] and [3] here, the length of the cycle the oscillators progress through is not normalized to unit length.

With the limit cycle map from Definition B.1 we can construct the evolution function for the limit of our model. Notice that  $\mathfrak{F}_{\alpha}$  satisfies

$$\int_0^{\mathfrak{F}_\alpha(\phi)} \frac{\mathrm{d}s}{\hat{h}(s)} = \frac{\alpha}{\int_0^1 \frac{\mathrm{d}s}{\hat{h}(s)}} + \int_0^{1-\phi} \frac{\mathrm{d}s}{\hat{h}(s)}$$

where  $\hat{h} = h \int_0^1 \frac{\mathrm{d}s}{h(s)}$ . This leads to

#### Definition C.1.

Define the evolution function  $g: [0,1] \to [0,1]$  by  $g(x) = \int_0^x \frac{ds}{\hat{h}(s)}$ , which satisfies g(0) = 0 and g(1) = 1. Then we get for the limit cycle map

$$\mathfrak{F}_{\alpha}(\phi) = g^{-1} \left( \hat{\alpha} + g(1 - \phi) \right) \tag{23}$$

where  $\hat{\alpha} = \frac{\alpha}{\int_0^1 \frac{\mathrm{d}s}{h(s)}}$ .

Equation (23) coincides with that of Equation (2.1) in [2].

#### Example C.2.

Consider the monotone sensitivity function  $h(\phi) = \frac{1}{1.2+\gamma\phi}$ ,  $\phi \in [0,1]$ . If we use the above formalism to plot the evolution function  $g(\phi)$  we obtain Figure 22, which can be compared to Figure 2.9 in [3].

The work [3] considers two integrate-and-fire models, monotone and QIF-like oscillators. Monotone oscillators are those whose evolution functions are monotonically increasing and either concave-up or concave-down, i.e. g' > 0 and  $g'' \neq 0$ . Quadratic-Integrate-and-Fire-like oscillators are described in section 2.3.4: they satisfy Property 3 on page 32 of [3]. The author proves that QIF-like oscillators are "concave up/down in the mean" or  $\int_0^{2\pi} g''(\theta) d\theta \neq 0$ .

In Lemma 2.1 in [2], the authors prove, assuming their evolution function g is monotonic increasing and concave down, that the derivative of the full cycle map is smaller than 1. This corresponds to:

$$g' > 0$$
 and  $g'' < 0 \Leftrightarrow h(\phi) > 0$  and  $h'(\phi) > 0$ 



Figure 22: The evolution function g for a monotone sensitivity function  $h(\phi) = \frac{1}{1.2 + \gamma \phi}$ ,  $\phi \in [0, 1]$  with  $\gamma = 2$  (lower blue curve) and  $\gamma = -1$  (upper red curve).

so we can apply Theorem 7.9 with  $\alpha = \frac{1}{2}$  to confirm their statement: there is a unique repelling interior fixed point and the synchronized state is stable. The interval of fixed points is not observed since we took the limit of  $\eta \to 0$ . The same result is stated in Proposition 3.3.1 of [3].

In both works the conclusion is that excitatory monotonically increasing coupling (positive feedback) leads to synchronization, while inhibitory coupling leads to de-synchronization.

## References

[1]	Janssens, Sebastiaan Measure-Valued Integrate-and-Fire Dynamics of Mirollo-Strogatz Type (under construction)
[2]	Mirollo, Renato E. & Strogatz, Steven H. Synchronization of Pulse-Coupled Biological Oscillators SIAM J. Applied Math., 1990, Vol. 50, Iss. 6, pp. 1645-1662
[3]	Mauroy, Alexandre On the dichotomic collective behaviours of large populations of pulse-coupled firing oscillators http://engineering.ucsb.edu/~alex.mauroy/thesis_Mauroy.pdf
[4]	Young, T. et al. Clustering in cell cycle dynamics with general response/signalling feedback J. Theoretical Biology, 2012, Vol. 292, pp. 103-115
[5]	Peskin, C.S. Mathematical Aspects of Heart Physiology Courant Institute of Mathematical Sciences, New York University, 1975, pp. 268-278
[6]	Walker T.J. Acoustic synchrony: two mechanisms in the snowy tree cricket Science, 1969, Vol. 166, Iss. 3907, p. 891-894
[7]	Tinsley M.R. et al. Dynamical quorum sensing and synchronization in collections of excitable and oscillatory catalytic parti- cles Physica D, 2010, Vol. 239, Iss. 11, pp. 785-790
[8]	Boczko E.M., Gedeon T., Stowers C.C., Young T.R. <i>ODE, RDE and SDE models of cell cycle dynamics and clustering in yeast</i> J Biol Dyn., 2010, Vol. 4, Iss. 4, pp. 328-345.
[9]	Cartwright J.H.E. Emergent global oscillations in heterogeneous excitable media: The example of pancreatic beta cells Phys. Rev. E, 2000, Vol. 62, pp. 1149-1154
[10	<ul> <li>Huyer W.</li> <li>On periodic cohort solutions of a size-structured population model</li> <li>J. Math Biol., 1997, Vol. 35, pp. 908-934</li> </ul>
[11	] Pantaleone J. Synchronization of metronomes American J. Physics, 2002, Vol. 70, Iss. 10, pp. 992-1000
[12	] Gouwens N., Zeberg H. ,et al. Synchronization of Firing in Cortical Fast-Spiking Gamma Frequencies: A Phase-Resetting Analysis PLOS Comput. Biol., 2010, Vol. 6, Iss. 9, doi: 10.1371/journal.pcbi.1000951