The uncoupling limit of identical Hopf bifurcations with an application to perceptual bistability

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Abstract We study the dynamics arising when two identical oscillators are coupled near a Hopf bifurcation where we assume a parameter $\epsilon$ uncouples the system at $\epsilon = 0$. Using a normal form for $N = 2$ identical systems undergoing Hopf bifurcation, we explore the dynamical properties. Matching the normal form coefficients to a coupled Wilson-Cowan oscillator network gives an understanding of different types of behaviour that arise in a model of perceptual bistability. Notably, we find bistability between in-phase and anti-phase solutions that demonstrates the feasibility for synchronisation to act as the mechanism by which periodic inputs can be segregated (rather than via strong inhibitory coupling, as in existing models). Using numerical continuation we confirm our theoretical analysis for small coupling strength and explore the bifurcation diagrams for large coupling strength, where the normal form approximation breaks down.

Keywords Synchrony · Perceptual Bistability · Bifurcation Analysis · Normal Form · Neural Competition · Hopf Bifurcation.

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List of abbreviations

IP  In-phase
AP  Anti-phase
FP  Fixed Point
LC  Limit Cycle
PD  Period Doubling
PF  Pitchfork
TR  Torus Bifurcation
LA  Low Amplitude
HA  High Amplitude

1 Introduction

The Hopf bifurcation is a generic and well-characterized transition that a nonlinear system can undergo to create temporal patterns of behaviour on changing a parameter. At such a bifurcation, an equilibrium of an autonomous smooth dynamical system develops an oscillatory instability and emits a small amplitude periodic orbit that, when followed, may be used to understand a wide variety of oscillatory phenomena. This includes many problems that appear in Neuroscience applications [6].

For larger network systems composed of similar subsystems that undergo oscillatory instability, when coupled together this can lead to the formation of non-trivial spatio-temporal patterns. Notably there is a large literature on coupled oscillators, viewed from a wide variety of theoretical view points, and from the point of view of applications, e.g. [31]. Much of this theory either considers very specific models, or makes an assumption of weak coupling which allows a reduction to a phase oscillator description such as that of Kuramoto [1], suitable for answering a lot of questions about synchronization of system oscillations.

In this paper we consider identical subsystems undergoing a Hopf bifurcation that have an uncoupling limit. This approach gives a natural setting of two parameters that allows a thorough and generic analysis of the low-dimensional dynamics of coupled oscillator systems, by means of normal form theory. We use this analysis to understand the behaviour of a pair of Wilson-Cowan oscillators that arise in a model of perceptual bistability, which complements the results in [10].

The phenomenon of perceptual bistability motivates this study of oscillatory dynamics in a coupled dynamical system. For certain static but ambiguous sensory stimuli, two distinct perceptual interpretations (percepts) are possible, but only one can be held at a time. Not only can the initial percept be different from one short presentation of the stimulus to the next, but for extended presentations, the percept can switch dynamically. Perceptual bistability has been investigated in a number of different visual paradigms e.g. ambiguous figures [30,38], binocular rivalry [24,8,9], random-dot rotating spheres [44], motion plaids [16] and multistable barber-pole illusion [26]. Such ambiguous stimuli provide an opportunity to gain insights about the computations underlying perceptual competition in the brain. Whilst synchrony of oscillatory activity is known to play a role in the encoding of perceptually ambiguous stimuli [12], this mechanism has been widely overlooked.

Further background and motivation for the study of coupled oscillatory instabilities close to the uncoupling limit is given in Section 1.1, whilst further background and motivation for the study of oscillatory dynamics in the context of perceptual competition is given in Section 1.2 (not required reading if primarily interested in this paper’s mathematical results).
1.1 Coupled oscillatory instabilities

As noted by several authors, networks of oscillators near Hopf bifurcation allow one to explore not just the collective phase dynamics but also amplitude behaviour [14] and this allows one to use many of the tools of generic bifurcation theory with symmetry (in particular, the consequence of group actions on normal forms and the phase space) to understand the creating and properties of many oscillator patterns that may arise, biological applications including, for example, animal gaits and visual hallucination patterns [14].

A recent paper [7] explored coupled Hopf bifurcations in a two parameter setting where one of the parameters results in uncoupling of the systems. In that setting, they found that it is possible to find not only a reduction to Kuramoto-like oscillators in a weak coupling close to threshold limit, but also to find the next order corrections that include multiple oscillator interactions. The setting also allows study of patterns where only part of the system is oscillating. More precisely, [7] considers \( N \) identical and identically interacting smooth \((C^\infty)\) vector fields on \( x_i \in \mathbb{R}^d (d \geq 2)\) and present the normal form near a Hopf bifurcation.

In this paper we explore the dynamical properties of the special case \( N = 2 \) with \( d = 2 \). We give a dimension reduction via group-invariant coordinates in order to simplify dynamics. In the 2D normal form we look at the effects of coupling beyond the weak limit. A similar analysis was performed in [5] for the case of a linear coupling term, thus considering a particular sub-case of the normal form studied here. We then apply this theory to understand the appearance of a variety of oscillatory patterns in a model of perceptual bistability.

1.2 Oscillatory models of perceptual bistability

Perceptual bistability can also arise with stimuli that change periodically. Apparent motion can be observed when a dot on a screen present at one location disappears and spontaneously reappears at a nearby location, as if travelling smoothly across the screen [20,2]. Figure 1A shows two frames of such an apparent motion display\(^1\), where a black square to the left of a fixation point might reappear on the right of the fixation point. If two such frames alternate every, say 200 ms, as in the schematic Fig. 1B, this can be perceived as a single square moving from side to side (“percept 1” in Fig. 1C). However, another interpretation is possible, of distinct squares blinking on and off either side of the fixation point (“percept 2” in Fig. 1C). Watching such a display, perception switches between percept 1 and percept 2 every few seconds; see [3,33], references within and more recently [13,29]. Perceptual bistability also occurs for the so-called auditory streaming paradigm [42,4,32]\(^2\). The stimulus consists of interleaved sequences of tones A and B, separated by a difference in tone frequency \( \Delta f \), and repeating in an “ABABAB...” pattern (Fig. 1D). This can be perceived as one stream, integrated into an alternating rhythm (“percept 1” in Fig. 1E) or as two segregated streams (“percept 2” in Fig. 1E); see recent reviews [27,41]. There are commonalities between these visual and auditory paradigms, in percept 1 (Fig. 1C and E) the stimulus elements are linked into a single percept. In percept 2, the stimulus elements are separated into their distinct parts in space or in frequency. In both cases the stimulus alternates rapidly (in the range at 2–5 Hz for the visual stimulus [3]; in the range 5–10 Hz for the auditory stimulus [42]), whilst the perceptual interpretations are stable on the order of several seconds (over many cycles of the rapidly alternating stimuli).

\(^{1}\) More complex example than the one we’re interested in: https://open-mind.net/videomaterials/kohler-motion-quartet.mp4/view

\(^{2}\) https://auditoryneuroscience.com/scene-analysis/streaming-alternating-tones
Models of perceptual bistability have successfully captured the dynamics of perceptual switching [21, 46, 47], the dependence of these dynamics on stimulus parameters [21, 28, 39, 36], mechanisms for attention [25], entrainment to slowly varying stimuli [19] and the effects of stimulus perturbations [35]. Generally models are based on competition between abstract, percept-based units [46, 40, 15, 25], but more recently models with a feature-based representation of competition have been developed [21, 17, 34, 36]. Some percept-based models have explored how rapidly alternating inputs (>2 Hz) can still give rise to stable perception over several seconds [47, 43, 25]. The models described above have considered competition directly between populations encoding different percepts, or between populations separated on a feature space. In general model studies of perceptual bistability have not explored how synchrony properties of oscillations entrained at the rate of a rapidly alternating stimulus could be the mechanism by which different perceptual interpretations emerge and coexist as bistable states (although see [45] for a large network approach to this problem). We hypothesise that oscillations play a key role in perceptual integration (like “percept 1”) and perceptual segregation (like “percept 2”). Towards exploring this hypothesis in future modelling studies of perceptual bistability, this paper lays the mathematical groundwork for studying the encoding perceptual states similar to those described above. An aim of the study is to identify regions of parameter space where such states coexist for a suitable neural oscillator model (but not transitions between these states).

Matching the normal form coefficients to a coupled Wilson-Cowan oscillator network allows for an understanding of the parameters in the model that govern different types of behaviour. Numerical continuation is used to confirm our theoretical analysis and to complete bifurcation diagrams for large coupling strength demonstrating where the normal form approximation breaks down. Finally, our analysis is extended with numerics to demonstrate that coexisting states akin to “percept 1” and “percept 2” persist in the presence of symmet-
tical periodic inputs. These coexisting states persist with low coupling strengths (down to the uncoupling limit) thus removing the need for the assumption of strong mutual inhibition between neural populations encoding different perceptual interpretations.

1.3 Outline

The structure of the paper is as follows: in Section 2 we use recent theoretical results in [7] to write the normal form of a system of two weakly coupled identical oscillators near a Hopf bifurcation. In Section 3 we perform a dynamical analysis of the system given by the dominant terms of the normal form. In particular, we study how the solutions for the uncoupled system persist for weak coupling. In Section 4 we identify different dynamical regimes depending on specific coefficients of the normal form and study the bifurcation diagrams. In Section 5 we write the equations for two mutually inhibiting Wilson-Cowan oscillators near a Hopf bifurcation and we perform a change of coordinates to put the system in the normal form discussed in Section 2. For this example, we compare the theoretical predictions given by the normal form analysis with a bifurcation diagram computed numerically. Finally, we note that the results are of broad interest, extending beyond the study of neural oscillators and perceptual bistability to the study of any system involving two coupled oscillators.

2 Two identical Hopf bifurcations with an uncoupling limit

We will study systems consisting of two identically coupled oscillators of the form:

\[
\frac{dx_1}{dt} = H_\lambda(x_1) + c h_{\lambda,\epsilon}(x_1; x_2), \quad (x_1, x_2) \in \mathbb{R}^2, \quad \epsilon, \lambda \in \mathbb{R} \tag{1}
\]

\[
\frac{dx_2}{dt} = H_\lambda(x_2) + c h_{\lambda,\epsilon}(x_2; x_1),
\]

having \( S_2 \) permutation symmetry, that is \( h_{\lambda,\epsilon}(x_1; x_2) = h_{\lambda,\epsilon}(x_2; x_1) \). We assume that when system (1) is uncoupled (\( \epsilon = 0 \)), each system undergoes a Hopf bifurcation at the origin when the parameter \( \lambda \) crosses zero.

More concretely, we assume that the uncoupled system for \( x \in \mathbb{R}^2 \) given by

\[
\frac{dx}{dt} = H_\lambda(x)
\]

has a stable focus at \( x = 0 \) for \( \lambda < 0 \) that undergoes a supercritical Hopf bifurcation for \( \lambda = 0 \) which gives rise to a small amplitude stable limit cycle for \( \lambda > 0 \). For simplicity we assume that the eigenvalues of \( DH_\lambda(0) \) are \( \lambda \pm i\omega \) with \( \omega \neq 0 \). Moreover, without loss of generality, we assume that \((x_1, x_2) = (0, 0)\) is an equilibrium point for \((\lambda, \epsilon)\) in some neighbourhood of \((0, 0)\) for system (1).

2.1 Truncated Normal Form in Complex Coordinates

In [7], it is shown that systems as in (1), having \( S_2 \) symmetry and undergoing a supercritical Hopf bifurcation for \( \lambda = 0 \), can be written in the following normal form

\[
\frac{dz_1}{dt} = U_\lambda(z_1) + c F_N(z_1, z_2, \epsilon) + \mathcal{O}_{N+1}(z_1, z_2), \quad (z_1, z_2) \in \mathbb{C} \tag{2}
\]

\[
\frac{dz_2}{dt} = U_\lambda(z_2) + c F_N(z_2, z_1, \epsilon) + \mathcal{O}_{N+1}(z_2, z_1),
\]
where $F_N$ is a $N$-degree polynomial function that is equivariant under the rotational symmetries
\[ F_N(z_1e^{i\phi}, z_2e^{i\phi}, \epsilon) = e^{i\phi} F_N(z_1, z_2, \epsilon). \]

If we consider the normal form up to order three and ignore the $O_4(z)$ terms, we obtain the truncated normal form
\[
\begin{align*}
\frac{dz_1}{dt} &= z_1 \left( \lambda + i\omega + \alpha_{01}|z_1|^2 \right) + \epsilon \left[ z_1 \left( \alpha_{00} + \alpha_{11}|z_1|^2 + \alpha_{22}|z_2|^2 + \alpha_{33}\bar{z}_1z_2 \right) \\
&\quad + z_2 \left( \beta_{01} + \beta_{21}|z_2|^2 + \beta_{31}\bar{z}_2z_1 \right) \right], \\
\frac{dz_2}{dt} &= z_2 \left( \lambda + i\omega + \alpha_{01}|z_2|^2 \right) + \epsilon \left[ z_2 \left( \alpha_{00} + \alpha_{11}|z_2|^2 + \alpha_{22}|z_1|^2 + \alpha_{33}\bar{z}_1z_2 \right) \\
&\quad + z_1 \left( \beta_{01} + \beta_{21}|z_1|^2 + \beta_{31}\bar{z}_1z_2 \right) \right],
\end{align*}
\]
(3)

where the constants $\alpha_{01}, \alpha_{11}, \beta_{01} \in \mathbb{C}$ with the restriction $\text{Re}(\alpha_{01}) < 0$ because the Hopf bifurcation is supercritical.

Next section is devoted to analyse the dynamics of system (3). In particular, we will analyse its oscillatory solutions.

### 2.2 Truncated Normal Form in Polar Coordinates

We use polar coordinates to simplify the analysis of the oscillatory solutions. To express the normal form in (2) up to $N = 3$ in polar coordinates we write $z_n = r_ne^{i\phi_n}$ with $r_n > 0$ and $\phi_n \in \mathbb{T}$, so that
\[
\dot{z}_n = (\dot{r}_n + i\dot{r}_n\phi_n)e^{i\phi_n} = U_\lambda(r_n e^{i\phi_n}) + \epsilon F_3(r_n e^{i\phi_n}, r_3 - n e^{i\phi_3}, \epsilon) \quad n = 1, 2.
\]
(4)

and matching imaginary and real parts in (4), we obtain the following set of equations for $r_n$ and $\phi_n$
\[
\begin{align*}
\dot{r}_1 &= r_1 \left( \lambda + \alpha_{01}R^2 \right) + \epsilon f_r(r_1, r_2, \Delta \phi), \\
\dot{r}_2 &= r_2 \left( \lambda + \alpha_{01}R^2 \right) + \epsilon f_r(r_2, r_1, -\Delta \phi), \\
\dot{r}_1\phi_1 &= r_1 \left( \omega + \alpha_{01}R^2 \right) + \epsilon f_{\phi}(r_1, r_2, \Delta \phi), \\
\dot{r}_2\phi_2 &= r_2 \left( \omega + \alpha_{01}R^2 \right) + \epsilon f_{\phi}(r_2, r_1, -\Delta \phi),
\end{align*}
\]
(5)

where $\Delta \phi = \varphi_2 - \varphi_1$ and the subscript $X = R, I$ in $\alpha_{01}$ refers to its real and imaginary parts, respectively. The expression for the functions $f_r$ and $f_{\phi}$ can be found in Eq. (56) in the Appendix. System (5) can be also written using the variable $\Delta \phi$:
\[
\begin{align*}
\dot{r}_1 &= r_1 \left( \lambda + \alpha_{01}R^2 \right) + \epsilon f_r(r_1, r_2, \Delta \phi), \\
\dot{r}_2 &= r_2 \left( \lambda + \alpha_{01}R^2 \right) + \epsilon f_r(r_2, r_1, -\Delta \phi), \\
\Delta \phi &= \alpha_{01}(R^2 - \bar{r}_1^2) + \epsilon f_{\Delta \phi}(r_1, r_2, \Delta \phi), \\
\dot{\phi}_1 &= \omega + \alpha_{01}R^2 + \frac{\epsilon}{r_1} f_{\phi}(r_1, r_2, \Delta \phi),
\end{align*}
\]
(6)

where the expression for the function $f_{\Delta \phi}$ can be found in Eq. (57) in the Appendix.
3 Dynamical analysis of the truncated normal form

This section is devoted to analyse the dynamics of system (3) (or its equivalent expressions (5) or (6) in polar coordinates) taking \((\lambda, \epsilon)\) as bifurcation parameters.

3.1 The uncoupled system \((\epsilon = 0)\)

Let us start by considering system (6) in the uncoupled case \((\epsilon = 0)\),

\[
\begin{align*}
\dot{r}_1 &= r_1 \left( \lambda + \alpha_{01} R r_1^2 \right), \\
\dot{r}_2 &= r_2 \left( \lambda + \alpha_{01} R r_2^2 \right), \\
\Delta \varphi &= \alpha_{01} (r_2^2 - r_1^2), \\
\dot{\varphi}_1 &= \omega + \alpha_{01} r_1^2.
\end{align*}
\]

As we consider two identical systems having a supercritical Hopf bifurcation for \(\lambda = 0\), the solutions of system (7) for \(\lambda > 0\) will correspond to the product of solutions of each 2-dimensional system. We observe that, even if the solutions \(r_1 = 0\) or \(r_2 = 0\) are admissible for system (7), they will be singular when we consider the whole system (6). For this reason, when we deal with these solutions, we refer to system (3). Thus, the solution \(r_1 = r_2 = 0\) \((\forall \varphi_2, \varphi_1 \in \mathbb{T})\) will be denoted by \(S_0\) and corresponds to the fixed point of system (3)

\[
S_0 = \left\{ z_1 = z_2 = 0 \right\},
\]

the eigenvalues of the linearization of system (3) at \(S_0\) are \(\lambda \pm i\omega\) with multiplicity 2. Therefore, the origin will be a stable focus for \(\lambda < 0\) and an unstable focus for \(\lambda > 0\).

As \(\alpha_{01} R < 0\), for \(\lambda > 0\), we have \(\forall \varphi^0_2, \varphi^0_1 \in \mathbb{T}, \)

\[
S_1(\varphi^0_2) = \left\{ r_1 = r_2 = \sqrt{-\frac{\lambda}{\alpha_{01} R}}, \quad \Delta \varphi = \varphi^0_2 - \varphi^0_1, \quad \varphi_1(t) = \varphi^0_1 + (\omega - \lambda \frac{\alpha_{01} I}{\alpha_{01} R}) t \right\}
\]

is a solution of system (7), corresponding to the periodic orbit

\[
\begin{align*}
z_1 &= \sqrt{-\frac{\lambda}{\alpha_{01} R}} e^{i\varphi_1(t)} = \sqrt{-\frac{\lambda}{\alpha_{01} R}} e^{i(\varphi^0_1 + (\omega - \lambda \frac{\alpha_{01} I}{\alpha_{01} R}) t)}, \\
z_2 &= \sqrt{-\frac{\lambda}{\alpha_{01} R}} e^{i(\varphi_1(t) + \Delta \varphi)} = \sqrt{-\frac{\lambda}{\alpha_{01} R}} e^{i(\varphi^0_2 + (\omega - \lambda \frac{\alpha_{01} I}{\alpha_{01} R}) t)}
\end{align*}
\]

of system (3).

Moreover, the union of these periodic orbits fills a stable 2-dimensional torus \(T_0\)

\[
T_0 = \bigcup_{\varphi^0_2 \in \mathbb{T}} S_1(\varphi^0_2) = \left\{ r_1 = r_2 = \sqrt{-\frac{\lambda}{\alpha_{01} R}}, \quad \varphi_1, \varphi_2 \in \mathbb{T}^2 \right\},
\]

whose characteristic exponents are the eigenvalues of the fixed point \(r_1 = r_2 = \sqrt{-\frac{\lambda}{\alpha_{01} R}}\) associated to the two first equations of system (7), which are \(-2\lambda\) double. Therefore, \(T_0\) is a normally hyperbolic attracting torus of system (3) for \(\lambda > 0\).
There exists another periodic solution of system (3), denoted by \( S^2 \), corresponding to 
\[ r^2 = \sqrt{\frac{-\lambda}{\alpha_{01}^2}}, r^2 \equiv 0, \]
\[ S^2 = \left\{ z_1 = \frac{-\lambda}{\alpha_{01}^2} e^{i\varphi_2(t)}, \quad z_2 = 0, \quad \varphi_1(t) = \varphi_1^0 + (\omega - \lambda \frac{\alpha_{11}}{\alpha_{01}^2}) t \right\}, \tag{11} \]
which has characteristic exponents \(-2\lambda, \lambda \pm i\omega\). Therefore, it is an unstable periodic orbit of saddle type.

Because of the permutation symmetry of system (3), it follows that we have another periodic solution
\[ S^3 = \left\{ z_1 = 0, \quad z_2 = \frac{-\lambda}{\alpha_{01}^2} e^{i\varphi_2(t)}, \quad \varphi_2(t) = \varphi_2^0 + (\omega - \lambda \frac{\alpha_{11}}{\alpha_{01}^2}) t \right\}, \tag{12} \]
which is also of saddle type having characteristic exponents \( \lambda \pm i\omega, -2\lambda \).

As the torus \( T_0 \) and the periodic orbits \( S^2 \) and \( S^3 \) are hyperbolic for \( \lambda > 0 \), we have the following result thanks to Fenichel’s theorem [11]:

**Lemma 1**  For a fixed value of \( \lambda > 0 \), there exists \( \epsilon_0 = \epsilon_0(\lambda) \), such that for any \( 0 \leq \epsilon \leq \epsilon_0 \), system (3) has a stable 2-dimensional torus \( T_\epsilon \) and two periodic orbits of saddle type \( S_\epsilon^2 \) and \( S_\epsilon^3 \) which are \( \epsilon \)-close to \( T_0 \), \( S^2 \) and \( S^3 \), respectively. Moreover, the origin \( S_0 \) also persists.

### 3.2 Hopf bifurcations of the origin

In the previous Section we have shown that the uncoupled system (7) has 4 solutions which we expect to exist for a small enough coupling \( \epsilon \) thanks to Fenichel’s theorem. Let us start by analysing the stability of the origin \( S_0 \) given in (8). The Jacobian matrix of system (3) evaluated at the origin is
\[
\begin{pmatrix}
\lambda + i\omega + \epsilon\alpha_0 & 0 & \epsilon\beta_0 & 0 \\
0 & \lambda - i\omega + \epsilon\alpha_0 & 0 & \epsilon\beta_0 \\
\epsilon\beta_0 & 0 & \lambda + i\omega + \epsilon\alpha_0 & 0 \\
0 & \epsilon\beta_0 & 0 & \lambda - i\omega + \epsilon\alpha_0
\end{pmatrix}, \tag{13}
\]
and its eigenvalues are given by
\[ \mu_+ = \lambda + i\omega + \epsilon(\alpha_0 + \beta_0), \quad \mu_- = \lambda + i\omega + \epsilon(\alpha_0 - \beta_0), \tag{14} \]
and its complex conjugate pairs \((\mu_+, \mu_-)\). Therefore, the origin of system (3) can undergo two independent Hopf bifurcations, given by \( Re(\mu_+) = 0 \) and \( Re(\mu_-) = 0 \). These conditions define the following Hopf bifurcation curves \( C^\pm_{HB} \) in the \((\lambda, \epsilon)\) parameter space
\[
C^+_{HB} = \left\{ Re(\mu_+) = 0 \right\} \quad \text{or equivalently} \quad \bar{\alpha}^+ := \lambda + \epsilon(\alpha_{0R} + \beta_{0R}) = 0, \\
C^-_{HB} = \left\{ Re(\mu_-) = 0 \right\} \quad \text{or equivalently} \quad \bar{\alpha}^- := \lambda + \epsilon(\alpha_{0R} - \beta_{0R}) = 0. \tag{15}\]

At each curve \( C^\pm_{HB} \), a limit cycle is born, that will be denoted by \( S^\pm_{osc} \).

To study the stability of the origin of system (3), we analyse the sign of the real part of its eigenvalues \( \mu^+ \) and \( \mu^- \) given in (14) at the Hopf bifurcation curves \( C^\pm_{HB} \) defined in (15). Thus, if
\[
(\lambda, \epsilon) \in C^+_{HB} \Rightarrow Re(\mu_+) = 0, \quad Re(\mu_-) = -2\epsilon\beta_{0R},
\]
and if
\[
(\lambda, \epsilon) \in C^-_{HB} \Rightarrow Re(\mu_+) = 2\epsilon\beta_{0R}, \quad Re(\mu_-) = 0. \tag{16}
\]

Therefore, we conclude that (see Fig. 2):
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- If $\beta_0 R > 0$, for $(\lambda, \epsilon) \in C^+_H$ the solution $S_0$ changes from a stable-stable focus to an unstable-stable focus and a stable limit cycle $S_{\text{osc}}^+$ emerges from $C^+_H$. Moreover, when $(\lambda, \epsilon) \in C^-_H$, the solution $S_0$ changes from an unstable-stable focus to an unstable-unstable focus and an unstable limit cycle $S_{\text{osc}}^-$ appears.

- If $\beta_0 R < 0$, for $(\lambda, \epsilon) \in C^+_H$ the solution $S_0$ changes from a stable-stable focus to an unstable-stable focus and a stable limit cycle $S_{\text{osc}}^-$ emerges from $C^+_H$. Moreover, when $(\lambda, \epsilon) \in C^-_H$, the solution $S_0$ changes from a stable-unstable focus to an unstable-unstable focus and an unstable limit cycle $S_{\text{osc}}^+$ appears.

- If $\beta_0 R = 0$, for $(\lambda, \epsilon) \in C^+_H = C^-_H$, the solution $S_0$ changes from a stable-stable focus to an unstable-unstable focus and two stable limit cycles $S_{\text{osc}}^+$ and $S_{\text{osc}}^-$ appear.

3.3 The Oscillating Solutions $S_{\text{osc}}^\pm$

For the coupled case, we have shown the existence of two periodic orbits $S_{\text{osc}}^\pm$ arising at the Hopf bifurcation curves $C^\pm_H$. Furthermore, Lemma 1 ensures that the attracting torus $T_0$, which was foliated by the periodic orbits $S_1(\varphi_0^2)$, persists as a torus $T_{\epsilon}$ when $\epsilon > 0$. The aim of this section is to relate the existence of the torus $T_{\epsilon}$ and the limit cycles $S_{\text{osc}}^\pm$ in the coupled case.

To simplify the analysis we exploit the $S_2$ permutation symmetry of the system. Let us define the following permutation map

$$K : (r_1, r_2, \Delta \varphi) \rightarrow (r_2, r_1, -\Delta \varphi) \quad \text{and} \quad K^2 = Id,$$

which in the variables $s = r_1 + r_2$, $d = r_1 - r_2$, $\Delta \varphi$, with $s, d \in \mathbb{R}^+ \times \mathbb{R}$ writes as

$$\tilde{K}(s, d, \Delta \varphi) \rightarrow (s, -d, -\Delta \varphi),$$
so it becomes diagonal. Thus, we take advantage of this symmetry and express system (6) in the variables $(s, d, \Delta \varphi)$ obtaining

\begin{align}
\dot{s} &= s \left( \lambda + \frac{\alpha_{01}}{4} (s^2 + 3d^2) \right) + \epsilon g_s(s, d, \Delta \varphi), \\
\dot{d} &= d \left( \lambda + \frac{\alpha_{01}}{4} (d^2 + 3s^2) \right) + \epsilon g_d(s, d, \Delta \varphi), \\
\dot{\Delta \varphi} &= -\alpha_{01} I_{sd} + \epsilon g_{\Delta \varphi}(s, d, \Delta \varphi). 
\end{align}

System (19), which will be referred to as the reduced system, considers only the first three equations of system (6) as they are independent of the variable $\varphi_1$. The expressions for functions $g_s$, $g_d$ and $g_{\Delta \varphi}$ are given in Eq. (58) in the Appendix.

### 3.3.1 Dynamical analysis of the reduced system for $\epsilon = 0$

Let us start by analysing system (19) in the uncoupled case ($\epsilon = 0$). That is,

\begin{align}
\dot{s} &= s \left( \lambda + \frac{\alpha_{01}}{4} (s^2 + 3d^2) \right), \\
\dot{d} &= d \left( \lambda + \frac{\alpha_{01}}{4} (d^2 + 3s^2) \right), \\
\dot{\Delta \varphi} &= -\alpha_{01} I_{sd}.
\end{align}

Notice that in this case, the first two equations uncouple from the third one and can be studied independently. As the variables $(s, d)$ are defined in $\mathbb{R}^+ \times \mathbb{R}$, the fixed points of the two first equations of system (20) are given by

\begin{align}
(0, 0), \quad \left( \sqrt{-4\lambda \alpha_{01}}, 0 \right), \quad \left( + \sqrt{-\lambda \alpha_{01}}, -\sqrt{-\lambda \alpha_{01}} \right), \quad \left( + \sqrt{-\lambda \alpha_{01}}, +\sqrt{-\lambda \alpha_{01}} \right).
\end{align}

Then, as the Jacobian matrix for the two first equations of system (20) is given by

\begin{align}
\begin{pmatrix}
\lambda + \frac{3\alpha_{01}}{4 \alpha_{01} R} (s^2 + d^2) \\
\frac{\alpha_{01} R}{4} 6ds \\
\lambda + \frac{3\alpha_{01}}{4 \alpha_{01} R} (s^2 + d^2)
\end{pmatrix},
\end{align}

it is straightforward to see that the eigenvalues of (22) for $(s, d) = (0, 0)$ are $\lambda$ (double), for $(s, d) = \left( \sqrt{-\lambda \alpha_{01}}, 0 \right)$ are $-2\lambda$ (double) and for $(s, d) = \left( \sqrt{-\lambda \alpha_{01}}, \pm \sqrt{-\lambda \alpha_{01}} \right)$ are $\lambda$ and $-2\lambda$.

Thus, when $\lambda = 0$ the origin undergoes a bifurcation and changes from stable to unstable while three new fixed points appear: one stable corresponding to $(s, d) = \left( \sqrt{-\lambda \alpha_{01}}, 0 \right)$ plus two unstable corresponding to $(s, d) = \left( \sqrt{-\lambda \alpha_{01}}, \pm \sqrt{-\lambda \alpha_{01}} \right)$. 


Now let us study the solutions of system (20) obtained from the fixed points (21) when consider the variable $\Delta \varphi$. The (singular) solution

$$S_0 = \left\{ s = d = 0, \quad \Delta \varphi \in T \right\},$$

(23)

corresponds to the origin of system (3), which is a focus, with eigenvalues $\lambda \pm i\omega$ (double).

For any value of $\Delta \varphi_0$, the solution

$$S_1(\Delta \varphi_0) = \left\{ s = \sqrt{-\frac{4\lambda}{\alpha_{01} R}}, \quad d = 0, \quad \Delta \varphi = \Delta \varphi_0 \right\},$$

(24)

is a fixed point of system (20) with eigenvalues $-2\lambda$ (double) and 0. The fixed points fill up the invariant curve

$$T_0 = \left\{ s = \sqrt{-\frac{4\lambda}{\alpha_{01} R}}, \quad d = 0, \quad \Delta \varphi \in T \right\},$$

(25)

whose characteristic exponents are $-2\lambda$ (double). Then, the fixed points $S_1(\Delta \varphi_0)$ and the invariant curve $T_0$ correspond in the system (3) to the periodic orbits $S_1(\varphi_0^i)$ and the invariant torus $T_0$, respectively.

The other two fixed points give rise to the following periodic orbits

$$S^2 = \left\{ s = d = \sqrt{-\frac{\lambda}{\alpha_{01} R}}, \quad \Delta \varphi = \Delta \varphi_0 - \frac{\alpha_{11}}{\alpha_{01} R} \lambda t \right\},$$

$$S^3 = \left\{ s = -d = \sqrt{-\frac{\lambda}{\alpha_{01} R}}, \quad \Delta \varphi = \Delta \varphi_0 + \frac{\alpha_{11}}{\alpha_{01} R} \lambda t \right\},$$

(26)

whose characteristic exponents are $\lambda$ and $-2\lambda$, so they are unstable. These solutions correspond to solutions $S^2$ and $S^3$ of system (3).

In conclusion, the phase space for system (20) has two invariant curves filled with fixed points, $S_0$ and $T_0$, and two unstable periodic orbits, $S_2$ and $S_3$ (see Fig. 4).
Fig. 4 Phase space for the unperturbed system (20) for $\lambda > 0$. There are two invariant curves, $\bar{S}_0$ (which is unstable) and $\bar{T}_0$ (which is stable), filled with fixed points. Moreover there exist two unstable limit cycles $\bar{S}_2$ and $\bar{S}_3$.

3.3.2 Dynamical analysis of the reduced system in the coupled case ($\epsilon > 0$)

We can take advantage of the $S_2$ symmetry of system (19) to look for solutions which remain invariant under the application of the permutation map $\tilde{K}$ in (18). Notice that by denoting $r_1 = r_2 = r^*$, the curves $(r^*, r^*, 0)$ and $(r^*, r^*, \pi)$ are invariant for system (19). Then, if we write these curves in the $(s, d)$ coordinates

$$\Xi^+ = \{(s, d, \Delta \varphi) = (s, 0, 0)\}, \quad \Xi^- = \{(s, d, \Delta \varphi) = (s, 0, \pi)\},$$

the dynamics for system (19) when restricted to $\Xi^\pm$ reduces to

$$\dot{s} = \lambda s + \frac{s^3}{4} \alpha_{0R} + \epsilon \left[ \alpha_{00} R \pm \beta_{00} R \right] s + \frac{s^3}{4} \left( \alpha_{2R} + \alpha_{1R} \pm \beta_{1R} + \alpha_{3R} \right) \left( \alpha_{c2R} + \alpha_{c1R} \pm \beta_{c1R} + \alpha_{c3R} \right) \Delta \varphi,$$

$$\dot{d} = 0,$$

$$\dot{\Delta \varphi} = 0,$$

where the $\pm$ sign corresponds to $\Delta \varphi = 0, \pi$, respectively.

It is straightforward to check that the equation for $s$ in (28) has three steady solutions, namely, $s = 0$ (which corresponds to the solution $\bar{S}_0$ studied before) and $s_{osc}^\pm$ given by

$$s_{osc}^\pm = \sqrt{-4 \left( \frac{\lambda + \epsilon (\alpha_{00} R \pm \beta_{00} R)}{\alpha_{01} R + \epsilon K_{stb}} \right)}.$$

Notice that since $s \in \mathbb{R}^+$ we have discarded the negative solutions for the square root.

Taking into account that $\alpha_{01} R < 0$, solutions $s_{osc}^\pm$ in (29) are only admissible when $\bar{\alpha}^\pm = \lambda + \epsilon (\alpha_{00} R \pm \beta_{00} R) > 0$. This restriction defines the following conditions for the bifurcation

$$\bar{\alpha}^+ = \epsilon (\alpha_{00} R + \beta_{00} R) + \lambda = 0 \quad \text{for} \quad \Delta \varphi = 0,$$

$$\bar{\alpha}^- = \epsilon (\alpha_{00} R - \beta_{00} R) + \lambda = 0 \quad \text{for} \quad \Delta \varphi = \pi,$$

which are exactly the conditions defining the curves $C_{HB}^\pm$ in (15) corresponding to the Hopf bifurcations of the origin.
Therefore, for \((\lambda, \epsilon)\)-values on the right-hand-side of curves \(C_{HB}^{\pm}\) we can define, respectively, the following fixed points of system (19)

\[
\begin{align*}
\bar{S}_{osc}^+ &= (s, d, \Delta \varphi) = (s_{osc}, 0, 0), \\
\bar{S}_{osc}^- &= (s, d, \Delta \varphi) = (s_{osc}, 0, \pi),
\end{align*}
\]

which appear across a pitchfork bifurcation (whose character will be discussed below) of the origin in the \(s\) direction. Fixed points in (31) correspond to the periodic orbits \(S_{osc}^{\pm}\) of system (3) that appear at the Hopf bifurcation curves. Next, we will study its stability and possible bifurcations by using the reduced system (19).

The Jacobian matrix evaluated at the fixed points \(\bar{S}_{osc}^{\pm}\) is block diagonal

\[
\begin{pmatrix}
c_s & 0 & 0 \\
0 & c_d & c_d \\
0 & c_d & c_{\Delta \varphi}
\end{pmatrix},
\]

where the terms \(c_s, c_d, c_{\Delta \varphi}\) and \(c_{\Delta \varphi}\) are different from zero, and their precise expressions are given in Eq. (59) in the Appendix.

Because of the block diagonal form of the Jacobian matrix, it is straightforward to check the stability in the \(s\) direction as it corresponds to the 1x1 block. Thus, the eigenvalue \(\bar{\mu}^{\pm}_1\) takes the form

\[
\bar{\mu}^{\pm}_1 = c_s = -2(\epsilon(\alpha \epsilon_0 + \beta \epsilon_0) + \lambda),
\]

and therefore, the solutions \(\bar{S}_{osc}^{\pm}\) are always stable in the \(s\) direction as they appear for \(\bar{\alpha}^{\pm} = \epsilon(\alpha \epsilon_0 + \beta \epsilon_0) + \lambda > 0\). Therefore, the pitchfork bifurcations of the origin are supercritical (see Fig. 5).

As the solutions \(S_{osc}^{\pm}\) are always stable in the \(s\) direction, one has to consider the eigenvalues of the 2x2 block, corresponding to the transverse directions, in order to study possible bifurcations of the symmetric solutions \(\bar{S}_{osc}^{\pm}\). The trace \((Tr^{\pm})\) and the determinant \((Det^{\pm})\) of the 2x2 block of (32) at \(\bar{S}_{osc}^{\pm}\) are given up to order 2 in \(\lambda, \epsilon\) by:

\[
\begin{align*}
Tr^{\pm}(\lambda, \epsilon) &= c_d + c_{\Delta \varphi} = -2(\lambda + \epsilon(\alpha \epsilon_0 + 3 \beta \epsilon_0)), \\
Det^{\pm}(\lambda, \epsilon) &= \pm4(\lambda + \epsilon(\alpha \epsilon_0 + \beta \epsilon_0))(C_{det} + \beta \epsilon_0) + 4\epsilon^2(\beta_{01}^2 + \beta_{0R}^2),
\end{align*}
\]

where

\[
C_{det} := \frac{\beta_{0110}}{\alpha \epsilon_0 \beta_{01}^2}.
\]

So, computing the discriminant

\[
\Delta^{\pm} = (Tr^{\pm})^2 - 4Det^{\pm} = (\lambda + \epsilon(\alpha \epsilon_0 + \beta \epsilon_0))(\lambda + \epsilon(\alpha \epsilon_0 + \beta \epsilon_0) + 4C_{det}) - 4\epsilon^2 \beta_{01}^2.
\]
we find that the eigenvalues of the 2x2 block of the Jacobian matrix (32) write as,
\[
\begin{align*}
\bar{\mu}_1^\pm &= -\left(\lambda + \epsilon (\alpha_{c0R} \pm \beta_{c0R})\right) - \sqrt{\xi}, \\
\bar{\mu}_2^\pm &= -\left(\lambda + \epsilon (\alpha_{c0R} \pm \beta_{c0R})\right) + \sqrt{\xi},
\end{align*}
\]
where
\[
\xi = \left(\lambda + \epsilon (\alpha_{c0R} \pm \beta_{c0R})\right)\left(\lambda + \epsilon (\alpha_{c0R} \pm \beta_{c0R}) \mp 4\epsilon C_{det}\right) - 4\epsilon^2 \beta_{c0I}^2.
\]

Next, we study the stability of the solutions $S_{osc}^\pm$ given in (31) when the parameters $\lambda, \epsilon$ lie in the areas
\[
\mathcal{A}^\pm := \{(\lambda, \epsilon) \in \mathbb{R}^2 \mid \bar{\alpha}^\pm \geq 0, \ \epsilon > 0\},
\]
which correspond to the region on the right hand side of curves $C_{HB}^\pm$ and above the horizontal axis (see Fig. 2 left).

In particular, for $\bar{\alpha}^\pm = 0$, that is $(\lambda, \epsilon) \in C_{HB}^\pm$, the eigenvalues of the Jacobian matrix (32) at the fixed points $S_{osc}^\pm$ are given by
\[
\begin{align*}
\bar{\mu}_1^\pm &= 0, \\
\bar{\mu}_2^\pm &= \mp 2\beta_{c0R} - i2\epsilon \beta_{c0I}, \\
\bar{\mu}_3^\pm &= \mp 2\beta_{c0R} + i2\epsilon \beta_{c0I}.
\end{align*}
\]
Therefore, when the parameters $(\lambda, \epsilon)$ cross the curves $C_{HB}^\pm$ from left to right, if $\beta_{c0R} > 0$, $S_{osc}^\pm$ is a stable focus whereas $S_{osc}$ is a saddle-focus with a 1-dimensional unstable manifold (corresponding to the $s$ dimension which is always stable) and vice versa if $\beta_{c0R} < 0$.

For $\epsilon$ small and $\bar{\alpha}^\pm \geq 0$ the eigenvalues of the Jacobian matrix (32) at the fixed points $S_{osc}^\pm$ are given by
\[
\begin{align*}
\tau^\pm_1 &= -2\lambda + O(\epsilon), \\
\tau^\pm_2 &= -2\lambda + O(\epsilon), \\
\tau^\pm_3 &= \mp 2\epsilon (\beta_{c0R} + C_{det}) + O(\epsilon^2),
\end{align*}
\]
which are $O(\epsilon)$-close to the ones of the uncoupled case, $-2\lambda$ (double) and 0. In particular, depending on the sign of $(\beta_{c0R} + C_{det})$, one fixed point is a stable node whereas the other is a saddle with a 1-dimensional unstable manifold. We remark that consistently with Fenichel’s theory we can show that the invariant curve $\mathcal{T}$ persists for $\epsilon$ small as a perturbation of the unperturbed one $\mathcal{T}_0$ in (25). Indeed, by using the variables $(s, d, \Delta \varphi)$, we show that for $\beta_{c0R} > 0$, $\mathcal{T}_0$ consists of the union of the saddle point $S_{osc}^-$, its unstable 1-dimensional manifold and the stable node $S_{osc}^+$ (and vice versa if $\beta_{c0R} < 0$), so $S_{osc}^\pm \in \mathcal{T}_c$ for $\epsilon > 0$ small (see Fig. 6).

To conclude, we link the results for the reduced 3D system (19) with the full system (3). We have shown that fixed points $S_{osc}^\pm$ of system (19) correspond to the periodic orbits $S_{osc}^\pm$ of the full system (5) and, for $\epsilon$ small, they are contained in the invariant curve $\mathcal{T}_c$. Therefore, the 4D system has an invariant torus $\mathcal{T}_c$ that contains two periodic orbits, $S_{osc}^\pm$ and $S_{osc}$ with $\Delta \varphi = 0$ and $\Delta \varphi = \pi$, respectively, whose stability depends on the sign of $\beta_{c0R} + C_{det}$. Furthermore, these periodic orbits collapse to a fixed point at different Hopf bifurcation curves $C_{HB}^\pm$ and $C_{HB}^\pm$ given in (15), and the stability of these periodic orbits before the bifurcation depends on the sign of $\beta_{c0R}$.

In the next Section we will study the evolution of fixed points $S_{osc}^+$ and $S_{osc}^-$ in the area $\mathcal{A}^\pm$ defined in (39) for different combinations of the signs of $\beta_{c0R} + C_{det}$ and $\beta_{c0R}$.
The uncoupling limit of identical Hopf bifurcations with an application to perceptual bistability

Fig. 6 Phase space of system (19) for $\epsilon \neq 0$, $\beta_{0R} + C_{\text{det}} > 0$ and $\lambda + \epsilon(\alpha_{0R} \pm \beta_{0R}) > 0$. There exist two fixed points $\bar{S}_{\text{osc}}^\pm$, a stable node and a saddle point, respectively, which together with the unstable invariant manifold of the saddle point form the invariant curve $\mathcal{T}_\epsilon$. Due to the coupling term there are only two fixed points on $\mathcal{T}_\epsilon$ whereas we had an infinite number in the unperturbed case. Notice that the dynamics on the $s$ direction is always attracting.

4 Bifurcation diagrams of the reduced system

In the previous Sections we have shown that when $\epsilon$ is small and $\bar{\alpha}^\pm > 0$ there exist two critical points $\bar{S}_{\text{osc}}^\pm$ of system (19) belonging to the curve $\mathcal{T}_\epsilon$ which disappear at the curves $C_{\text{HB}}^\pm$. The points $\bar{S}_{\text{osc}}^\pm$ undergo several bifurcations in the parameter regions $A_\pm$ defined in (39). Table 1 shows the values of the trace $\text{Tr}^\pm$ in (34), the determinant $\text{Det}^\pm$ in (35) and the discriminant $\Delta^\pm$ in (37) of the Jacobian matrix of system (19) at $\bar{S}_{\text{osc}}^\pm$ near the curves $C_{\text{HB}}^\pm$ (given by the condition $\bar{\alpha}^\pm = 0$) and for $\bar{\alpha}^\pm > 0$ and $\epsilon$ small. Notice that the sign of the constants $\beta_{0R}$ and $C_{\text{det}} + \beta_{0R}$ is relevant to determine the local dynamics around the fixed points. In particular,

- $\beta_{0R}$ determines which of the two solutions $\bar{S}_{\text{osc}}^\pm$ can have a null trace. For $\beta_{0R} > 0$, is $\bar{S}_{\text{osc}}^+$, whereas for $\beta_{0R} < 0$ is $\bar{S}_{\text{osc}}^-$. 

- The sign of $C_{\text{det}} + \beta_{0R}$ determines which of the two solutions $\bar{S}_{\text{osc}}^\pm$ can have a null determinant. For $C_{\text{det}} + \beta_{0R} > 0$, is $\bar{S}_{\text{osc}}^+$, whereas for $C_{\text{det}} + \beta_{0R} < 0$ is $\bar{S}_{\text{osc}}^-$. 

- Moreover, as we increase $\epsilon$ the discriminant always changes from negative to positive. That is, consistently with the eigenvalues obtained in (40) and (41), the fixed points $\bar{S}_{\text{osc}}^\pm$ change from a stable node and a saddle point to a stable focus and a saddle-focus.

Depending on the sign of $\beta_{0R}$ and $C_{\text{det}} + \beta_{0R}$ we consider three different cases: (1) $\beta_{0R} > 0$, $C_{\text{det}} + \beta_{0R} > 0$, (2) $\beta_{0R} < 0$, $C_{\text{det}} + \beta_{0R} < 0$, and (3) $\beta_{0R} = 0$, $C_{\text{det}} > 0$. The cases (i) $\beta_{0R} < 0$, $C_{\text{det}} + \beta_{0R} < 0$, (ii) $\beta_{0R} > 0$, $C_{\text{det}} + \beta_{0R} < 0$, and (iii) $\beta_{0R} = 0$, $C_{\text{det}} < 0$ are analogous to (1), (2) and (3), respectively, just replacing $\bar{S}_{\text{osc}}^\pm$ by $\bar{S}_{\text{osc}}^\mp$. For each case, we study in detail the different bifurcations of the solutions $\bar{S}_{\text{osc}}^\pm$ in the $(\lambda, \epsilon)$ parameter space, we link results obtained for the 3D system (19) with the complete 4D system (3), and we discuss the areas of bistability.
\[ \bar{S}_+^{\text{osc}} \rightarrow 0^+ \quad \bar{\alpha}^+ \geq 0, \quad \epsilon \rightarrow 0^+ \quad \bar{S}_-^{\text{osc}} \rightarrow 0^+ \quad \bar{\alpha}^- \geq 0, \quad \epsilon \rightarrow 0^+ \]

\[
\begin{array}{|c|c|c|}
\hline
& \bar{S}_+^{\text{osc}} & \bar{S}_-^{\text{osc}} \\
\hline
\mathcal{Tr} & -4\epsilon \beta_{0R} & -2\lambda & 4\epsilon \beta_{0R} & -2\lambda \\
\mathcal{Det} & 4\epsilon^2(\beta_{e0I}^2 + \beta_{e0I}^2) & 4\epsilon\lambda(C_{\text{det}} + \beta_{0R}) & 4\epsilon^2(\beta_{e0I}^2 + \beta_{e0I}^2) & -4\epsilon\lambda(C_{\text{det}} + \beta_{0R}) \\
\Delta & -4\epsilon^2 \beta_{e0I}^2 & \lambda^2 & -4\epsilon^2 \beta_{e0I}^2 & \lambda^2 \\
\hline
\end{array}
\]

Table 1 Values for the trace (Tr), the determinant (Det) and the discriminant (\Delta) of the linearisation of system (19) at the fixed points \( \bar{S}_+^{\text{osc}} \) near the curves \( C_{HB}^\mp \) (\( \bar{\alpha}^\pm = 0 \)) and near to the uncoupled case (\( \bar{\alpha}^\pm \geq 0 \) and \( \epsilon \) small).

4.1 Case \( \beta_{0R} > 0 \) and \( C_{\text{det}} + \beta_{0R} > 0 \) (or \( \beta_{0R} < 0 \) and \( C_{\text{det}} + \beta_{0R} < 0 \))

4.1.1 Dynamics of \( \bar{S}_+^{\text{osc}} \)

For \( \bar{\alpha}^+ \geq 0, \lambda \) fixed and \( \epsilon \) small, the fixed point \( \bar{S}_+^{\text{osc}} \) for system (19) is a stable node contained in the invariant curve \( \bar{T}_{\epsilon} \) (region B in Fig. 7), and as \( \epsilon \) increases it becomes a stable focus at the curve \( \Delta^+ = 0 \) (region A in Fig. 7). It disappears at a pitchfork bifurcation of the origin in the \( s \)-direction at \( C_{HB}^+ \).

4.1.2 Dynamics of \( \bar{S}_-^{\text{osc}} \)

The fixed point \( \bar{S}_-^{\text{osc}} \) changes from a saddle-focus with a 1-dimensional stable manifold near \( C_{HB}^- \) to a saddle with a 2-dimensional stable manifold for \( \epsilon \) small and \( \bar{\alpha}^- > 0 \). Moreover, in this case the trace for \( \bar{S}_-^{\text{osc}} \) vanishes. Therefore, if

\[
\beta_{0R} < -C_{\text{det}} + \sqrt{C_{\text{det}}^2 + \beta_{e0I}^2},
\]

(42)
then $T^r = 0$ and $\Delta^- < 0$ and $S_{osc}$ undergoes a Hopf bifurcation.

So, we will distinguish two cases:

1) **Case** $\beta_{oR} < -C_{det} + \sqrt{C_{det}^2 + \beta_{oI}^2}$.

For $\bar{\alpha}^+ > 0$, $\lambda$ fixed and $\epsilon$ small, the fixed point $S_{osc}$ is a saddle point with a 1-dimensional unstable manifold (in the $\Delta\varphi$ direction) contained in the invariant curve $T_c$ (region D in Fig. 7). When crossing the curve $Det^- = 0$ (region C), the point $S_{osc}$ becomes a stable node. As the coupling $\epsilon$ is increased, $S_{osc}$ crosses the curve $\Delta^- = 0$ and $S_{osc}$ becomes a stable focus (region B). When the parameters cross the curve $Tr^- = 0$, $S_{osc}$ undergoes a Hopf bifurcation $\mathcal{H}$ in the $d, \Delta\varphi$ directions and $S_{osc}$ becomes a saddle focus with a 1-dimensional unstable manifold (region A). At this bifurcation there appears or disappears a periodic orbit $\bar{T}^-$ depending whether the Hopf bifurcation is supercritical or subcritical. Finally, the fixed point $S_{osc}$ disappears at a pitchfork bifurcation of the origin in the $s$-direction occurring at the curve $C_{HB}^-$. 

Going back to the original full 4D system (3), for $\epsilon$ small enough, there exists an unstable periodic orbit $S_{osc}$, belonging to the torus $T_e$, which will become stable at the curve $Det^- = 0$. The periodic orbit undergoes a Torus bifurcation and $S_{osc}$ becomes unstable at the curve $T^r = 0$ and a new torus $\bar{T}^-$ appears or disappears depending whether the Torus bifurcation is subcritical or supercritical. Finally, $S_{osc}$ will disappear at a Hopf bifurcation of the origin occurring at $C_{HB}^-$. 

2) **Case** $\beta_{oR} > -C_{det} + \sqrt{C_{det}^2 + \beta_{oI}^2}$.

For $\bar{\alpha}^+ > 0$, $\lambda$ fixed and $\epsilon$ small, the fixed point $S_{osc}$ is a saddle point with a 1-dimensional unstable manifold (in the $\Delta\varphi$ direction) contained in the invariant curve $T_c$ (region C in Fig. 9). As $\epsilon$ increases, $S_{osc}$ becomes a saddle with a 2-dimensional unstable manifold at the curve $Det^- = 0$ (region B). When further increasing the coupling $\epsilon$,
$S_{\text{osc}}^{-}$ becomes a saddle-focus point at the curve $\Delta^{-} = 0$ (region A), which disappears at a pitchfork bifurcation of the origin in the $s$-direction occurring at the curve $C_{HB}^{-}$.

Going back to the original full 4D system (3), for $\epsilon$ small enough, there exists an unstable periodic orbit $S_{\text{osc}}^{-}$ belonging to the torus $\mathcal{T}^{-}$. The periodic orbit undergoes a bifurcation at the curve $Det^{-} = 0$ in which a stable manifold becomes unstable. Finally, $S_{\text{osc}}^{-}$ will disappear at a Hopf bifurcation of the origin occurring at $C_{HB}^{-}$.

### 4.1.3 Areas of bistability

Since $S_{\text{osc}}^{+}$ is always stable, bistability between fixed points will appear in those regions where $S_{\text{osc}}^{-}$ is also stable. As in the case $\beta_{0R} > -C_{det} + \sqrt{C_{det}^2 + \beta_{0I}^2}$, the fixed point $S_{\text{osc}}^{-}$ is never stable, it is not possible to find bistability regions. By contrast, if $\beta_{0R} < -C_{det} + \sqrt{C_{det}^2 + \beta_{0I}^2}$, there exist a region in the $(\lambda, \epsilon)$ parameter space defined as

$$Tr^{-}(\lambda, \epsilon) < 0 \quad \text{and} \quad Det^{-}(\lambda, \epsilon) > 0,$$

in which $S_{\text{osc}}^{-}$ can be either a stable node or a stable focus (see Fig. 8). Thus, the system is bistable in the region (43).

Moreover, in the case $\beta_{0R} < -C_{det} + \sqrt{C_{det}^2 + \beta_{0I}^2}$, the point $S_{\text{osc}}^{-}$ undergoes a Hopf bifurcation $\mathcal{H}$. If the Hopf bifurcation is supercritical, then $S_{\text{osc}}^{-}$ becomes unstable and a stable limit cycle $\mathcal{T}^{-}$ appears, generating bistability between $S_{\text{osc}}^{+}$ and $\mathcal{T}^{-}$. The detailed analysis of this situation is beyond the scope of this paper.

Finally, we remark that the same bistable scenarios can be found in the full system (3) replacing the fixed points $S_{\text{osc}}^{\pm}$ by the limit cycles $S_{\text{osc}}^{\pm}$ and the periodic orbit $\mathcal{T}^{-}$ by the torus $\mathcal{T}^{-}$. 

![Fig. 9](image-url)
4.2 Case $\beta_{0R} < 0$ and $C_{det} + \beta_{0R} > 0$ (or $\beta_{0R} > 0$ and $C_{det} + \beta_{0R} < 0$)

4.2.1 Dynamics of $S_{osc}^+$

In this case the trace for $S_{osc}^+$ vanishes ($\text{Tr}^+ = 0$). Therefore, as

$$\beta_{0R} < -C_{det} < -C_{det} + \sqrt{C_{det}^2 + \beta_{0I}^2},$$

then $\text{Tr}^+ = 0$ and $\Delta^+ < 0$ and $S_{osc}^+$ will always undergo a Hopf bifurcation $H^+$.

For $\bar{\alpha}^+ \geq 0$, $\lambda$ fixed and $\epsilon$ small, the fixed point $S_{osc}^+$ is a stable node (region C in Fig. 10) and becomes a stable focus when the parameters cross the curve $\Delta^+ = 0$ (region B). For larger values of $\epsilon$, the fixed point $S_{osc}^+$ undergoes a Hopf bifurcation $H^+$ at the curve $\text{Tr}^+ = 0$ and becomes a saddle-focus point (region A). At this bifurcation there appears or disappears a limit cycle $T^+$ depending whether this Hopf bifurcation is subcritical or supercritical. For larger values of $\epsilon$, the fixed point $S_{osc}^+$ disappears at a pitchfork bifurcation of the origin in the $s$-direction at the curve $C_{HB}^+$.

\[ \text{Fig. 10} \] Phase space for $S_{osc}^+$ in the case $\beta_{0R} < 0$ and $C_{det} + \beta_{0R} > 0$. The fixed point $S_{osc}^+$ appears at a supercritical pitchfork bifurcation of the origin in the $s$ direction occurring at the curve $C_{HB}^+$, and undergoes a Hopf bifurcation $H^+$ at the curve $\text{Tr}^+ = 0$.

Going back to the original 4D system (3), for $\epsilon$ small enough there exists a stable periodic orbit $S_{osc}^+$. This stable periodic orbit will lose its stability across a torus bifurcation occurring at the curve $\text{Tr}^+ = 0$. At this bifurcation there appears or disappears a torus $T^+$ depending whether the torus bifurcation is subcritical or supercritical. Finally the unstable limit cycle $S_{osc}^+$ collapses to the origin at a Hopf bifurcation occurring at the curve $C_{HB}^+$.

4.2.2 Dynamics of $S_{osc}^-$

For $\bar{\alpha}^- \geq 0$, $\lambda$ fixed and $\epsilon$ small, the fixed point $S_{osc}^-$ of system (19) is a saddle point with a 1-dimensional unstable manifold in the $\Delta\phi$ direction contained in $T_\epsilon$ (region C in Fig. 11), and as $\epsilon$ increases it becomes a stable node when $\epsilon$ crosses the curve $D_{det}^- = 0$ (region B). For larger values of $\epsilon$, the fixed point $S_{osc}$ becomes a stable focus at the curve $\Delta^- = 0$ (region A) and disappears at a pitchfork bifurcation of the origin in the $s$ direction at the curve $C_{HB}^-$. 
Going back to the original 4D system (3), for $\epsilon$ small there exists an unstable periodic orbit $S_{\text{osc}}^-$. This unstable periodic orbit becomes stable at the curve $\text{Det}^- = 0$. Finally, the stable limit cycle $S_{\text{osc}}^-$ collapses to the origin at a Hopf bifurcation occurring at the curve $C_{HB}^-$. 

4.2.3 Bistability Areas

There exist a region in the $(\lambda, \epsilon)$-parameter space given by

$$\text{Tr}^+ (\lambda, \epsilon) < 0 \quad \text{and} \quad \text{Det}^- (\lambda, \epsilon) > 0,$$

in which both fixed points $S_{\text{osc}}^\pm$ are stable. If the Hopf bifurcation is supercritical, then $S_{\text{osc}}^+$ becomes unstable and a stable limit cycle $T^+$ appears, generating bistability between $S_{\text{osc}}^-$ and $T^+$. The detailed analysis of this situation is beyond of the scope of this paper. Finally, we remark that the same bistable scenarios can be found in the full system (3) replacing the fixed points $S_{\text{osc}}^\pm$ by the limit cycles $S_{\text{osc}}^\pm$ and the periodic orbit $T^+$ by the torus $T^+$. 

4.3 The degenerated case $\beta_{0R} = 0$ and $C_{det} > 0$ (or $\beta_{0R} = 0$ and $C_{det} < 0$)

In this case, the curves $C_{HB}^\pm$ coincide. Moreover, the trace in (34) is identically zero for $(\lambda, \epsilon) \in C_{HB}^\pm$. To obtain the sign of $\text{Tr}^\pm$, we compute $\text{Tr}^\pm$ when $\lambda + \epsilon \alpha_{0R} \to 0^+$. We have

$$\text{Tr}(\lambda, \epsilon) = (\lambda + \epsilon \alpha_{0R}) (-2 + O_2(\epsilon)), \quad \text{(46)}$$

so, near the $C_{HB}^\pm$ curves, both fixed points $S_{\text{osc}}^\pm$ are stable.

4.3.1 Dynamics of $S_{\text{osc}}^+$

For $\alpha^+ \geq 0$, $\lambda$ fixed and $\epsilon$ small, the fixed point $S_{\text{osc}}^+$ is a stable node (region B in Fig. 12), and as $\epsilon$ increases it becomes a stable focus when the parameters cross the curve $\Delta^+ = 0$ (region A). For larger values of $\epsilon$, the fixed point $S_{\text{osc}}^+$ disappears at a pitchfork bifurcation of the origin in the $s$ direction at the curve $C_{HB}^+$. 

Fig. 11 Bifurcation diagram for $S_{\text{osc}}$ in the case $\beta_{0R} < 0$ and $C_{det} + \beta_{0R} > 0$. The fixed point $S_{\text{osc}}$ appears at a supercritical pitchfork bifurcation of the origin in the $s$ direction occurring at the curve $C_{HB}^-$, and undergoes a bifurcation at $\text{Det}^- = 0$. 

Going back to the original 4D system (3), for $\epsilon$ small there exists an unstable periodic orbit $S_{\text{osc}}^-$. This unstable periodic orbit becomes stable at the curve $\text{Det}^- = 0$. Finally, the stable limit cycle $S_{\text{osc}}^-$ collapses to the origin at a Hopf bifurcation occurring at the curve $C_{HB}^-$. 

4.2.3 Bistability Areas

There exist a region in the $(\lambda, \epsilon)$-parameter space given by

$$\text{Tr}^+ (\lambda, \epsilon) < 0 \quad \text{and} \quad \text{Det}^- (\lambda, \epsilon) > 0,$$

in which both fixed points $S_{\text{osc}}^\pm$ are stable. If the Hopf bifurcation is supercritical, then $S_{\text{osc}}^+$ becomes unstable and a stable limit cycle $T^+$ appears, generating bistability between $S_{\text{osc}}^-$ and $T^+$. The detailed analysis of this situation is beyond of the scope of this paper. Finally, we remark that the same bistable scenarios can be found in the full system (3) replacing the fixed points $S_{\text{osc}}^\pm$ by the limit cycles $S_{\text{osc}}^\pm$ and the periodic orbit $T^+$ by the torus $T^+$. 

4.3 The degenerated case $\beta_{0R} = 0$ and $C_{det} > 0$ (or $\beta_{0R} = 0$ and $C_{det} < 0$)
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For $\bar{x}$, $\lambda$ fixed and $\epsilon$ small, the fixed point $\bar{S}_{osc}^-$ is a saddle point with a 1-dimensional unstable manifold (region C in Fig. 13), and as $\epsilon$ increases it becomes a stable node when the parameters cross the curve $\text{Det}^- = 0$ (region B). For larger $\epsilon$ values the fixed point $\bar{S}_{osc}^-$ becomes a stable focus at $\Delta^- = 0$ (region A) which collapses at a pitchfork bifurcation of the origin in the $s$ direction at the curve $C_{HB}^-$. Going back to the original 4D system (3), for $\epsilon$ small there exists an unstable periodic orbit $S_{osc}^-$ which changes stability at the curve $\text{Det}^- = 0$. Finally, the stable periodic orbit $S_{osc}^-$ collapses to the origin at a Hopf bifurcation at the curve $C_{HB}^-$. 

Fig. 13 Phase space for the $\bar{S}_{osc}$ fixed point in the case $\beta_{0R} = 0$ and $C_{det} > 0$. The fixed point $\bar{S}_{osc}$ apperas at a supercritical pitchfork bifurcation of the origin in the $s$ direction occurring at the curve $C_{HB}^-$. and undergoes a bifurcation at the curve $\text{Det}^- = 0$. 

Going back to the original 4D system (3), for $\epsilon$ small there exists a stable periodic orbit $S_{osc}$ which collapses to the origin at a Hopf bifurcation occurring at the curve $C_{HB}$. 

Fig. 12 Bifurcation diagram for $\bar{S}_{osc}^+$ in the case $\beta_{0R} = 0$ and $C_{det} > 0$. The fixed point $\bar{S}_{osc}^+$ apperas at a supercritical pitchfork bifurcation of the origin in the $s$ direction occurring at the curve $C_{HB}^+$. 

Going back to the original 4D system (3), for $\epsilon$ small there exists a stable periodic orbit $S_{osc}$, which collapses to the origin at a Hopf bifurcation occurring at the curve $C_{HB}$. 

4.3.2 Dynamics of $\bar{S}_{osc}^-$
4.3.3 Bistability Areas

In the region in the \((\lambda, \epsilon)\)-parameter space given by

\[
\text{Det}^{-1}(\lambda, \epsilon) > 0
\]

(47)

both fixed points \(\bar{S}^+_{osc}\) and \(\bar{S}^-_{osc}\) are stable.

We remark that the same bistability scenarios can be found in the full system (3) replacing the fixed points \(\bar{S}^\pm_{osc}\) by the limit cycles \(S^\pm_{osc}\).

5 Wilson-Cowan models for perceptual bistability

Wilson-Cowan oscillators are biophysically motivated neural oscillators providing a population-averaged firing rate description of neural activity, which have been widely used to study cortical dynamics and cortical oscillations [48,37]. The Wilson-Cowan oscillator (an excitatory \((E)\), inhibitory \((I)\) pair) considered here has dynamics described by

\[
\begin{align*}
\tau \ddot{E} &= -E + S(aE - bI), \\
\tau \ddot{I} &= -I + S(cE - dI),
\end{align*}
\]

(48)

where \(\tau\) is a time constant and the constants \(a, b, c\) and \(d\) are the intrinsic \(E\) to \(E\), \(I\) to \(E\), \(E\) to \(I\) and \(I\) to \(I\) coupling weights, respectively. The function \(S\) is the sigmoidal response function

\[
S(x) = \frac{1}{1 + e^{-\lambda x + \theta}} - \frac{1}{1 + e^\theta},
\]

(49)

which has threshold \(\theta\) and slope \(\lambda\) with the convenient property \(S(0) = 0\). The function \(S\) has the property \(S'(0) = \lambda S_1\), where \(S_1 = \frac{e^\theta}{(1 + e^\theta)^2}\), and \(\lambda\) is treated as a bifurcation parameter playing the equivalent role to \(\lambda\) in previous sections.

The system generically has a steady state \((E, I) = (0, 0)\), which undergoes a Hopf bifurcation at \(\lambda_c = \frac{2(a - d)}{S_1}\). When coupled with a second, identical oscillator the 4-dimensional pair of Wilson-Cowan oscillators (E-I pairs) coupled with strength \(\epsilon\) are given by

\[
\begin{align*}
\tau \ddot{E}_1 &= -E_1 + S(aE_1 - bI_1), \\
\tau \ddot{I}_1 &= -I_1 + S(cE_1 - dI_1 + \epsilon(E_2 - bspI_2)), \\
\tau \ddot{E}_2 &= -E_2 + S(aE_2 - bI_2), \\
\tau \ddot{I}_2 &= -I_2 + S(cE_2 - dI_2 + \epsilon(E_1 - bspI_1)),
\end{align*}
\]

(50)

whose dynamics will be explored in this Section.

For this study, we will consider the following set of parameters:

\[
\mathcal{P} = \{a = 7, b = 5.25, c = 5, d = 0.7, \theta = 2, \tau = 1\},
\]

(51)

whereas \(\lambda\) and \(\epsilon\) will be the bifurcation parameters. By considering \(bsp = -0.03, 0.03, 0.0\) we will study different types of dynamics. For each case we will write system (50) in the normal form (3) by numerically computing its corresponding coefficients (see Appendix B). Next, by using numerical continuation we will compute bifurcation diagrams for system (50), so we can check the theoretical predictions in Section 4 and complete the bifurcation diagrams for large values of \(\lambda\) and \(\epsilon\), where the normal form approximation breaks down.
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Table 2 Coefficients of the normal form (3) for the three considered cases, namely \(b_{sp} = -0.03, 0.03\) and 0. These coefficients have been computed using the procedure described in Appendix B.

| \(b_{sp}\) | \(-0.03\) | 0.03 | 0 |
|---|---|---|---|
| \(\alpha_{01R}\) | -21.94 | -21.94 | -21.94 |
| \(\alpha_{01I}\) | -20.94 | -20.94 | -20.94 |
| \(\alpha_{e0R}\) | 0 | 0 | 0 |
| \(\alpha_{e0I}\) | 0 | 0 | 0 |
| \(\alpha_{e1R}\) | 0 | 0 | 0 |
| \(\alpha_{e1I}\) | 0 | 0 | 0 |
| \(\alpha_{e2R}\) | 8.4 | 9.02 | 8.72 |
| \(\alpha_{e2I}\) | 6.34 | 6.8 | 6.57 |
| \(\alpha_{e3R}\) | -24.02 | -22.3 | -23.2 |
| \(\alpha_{e3I}\) | -46.36 | -44.92 | -45.46 |
| \(\omega\) | 1.073 | 1.073 | 1.073 |
| \(\beta_{e0R}\) | 0.0047 | -0.0047 | 0 |
| \(\beta_{e0I}\) | 0.252 | 0.241 | 0.246 |
| \(\beta_{e1R}\) | -12.91 | -13.18 | -13.05 |
| \(\beta_{e1I}\) | 19.36 | 16.76 | 18.06 |
| \(\beta_{e2R}\) | 7.16 | 6.46 | 6.52 |
| \(\beta_{e2I}\) | -5.56 | -5.47 | -5.52 |
| \(\beta_{e3R}\) | 14.29 | 13.33 | 13.81 |
| \(\beta_{e3I}\) | 10.02 | 10.3 | 10.16 |

5.1 Case \(b_{sp} < 0\)

We consider the case \(b_{sp} = -0.03\). The coefficients of the normal form, which were computed using the techniques described in Appendix B, are given in Table 2 and satisfy the conditions \(\beta_{e0R} > 0, C_{det} + \beta_{e0R} > 0\) and \(\beta_{e0R} < -C_{det} + \sqrt{C_{det}^2 + \beta_{e0R}^2}\). Therefore, this case corresponds to the one considered in Section 4.1. Fig. 14 shows the bifurcation diagram of system (50) for \(b_{sp} = -0.03\) obtained numerically. The results match the theoretical predictions obtained in Section 4.1. More precisely, for a fixed \(\epsilon\) value and varying the bifurcation parameter \(\lambda\) we have:

- A stable in-phase (IP) solution corresponding to \(S_{osc}\) will emerge from the Hopf bifurcation at \(C_{HB}^+\). Moreover when varying the bifurcation parameter, the IP solution will maintain its stability (see Fig. 7).
- An unstable anti-phase (AP) solution corresponding to \(S_{osc}\) will emerge from the Hopf bifurcation at \(C_{HB}^-\). For a fixed \(\epsilon\) and varying the bifurcation parameter AP solution gains stability across a Torus bifurcation, but when further increasing the bifurcation parameter it will lose it again across a pitchfork bifurcation (corresponding respectively to the lines \(Tr^- = 0\) and \(Det^- = 0\) in Fig. 8).
5.2 Case $b_{sp} > 0$

We consider the case $b_{sp} = 0.03$. The coefficients of the normal form, which were computed using the techniques described in Appendix B, are given in Table 2 and satisfy the conditions $\beta_{oR} < 0$ and $C_{det} + \beta_{oR} > 0$. Therefore, this case corresponds to the one considered in Section 4.2. Fig. 15 shows the bifurcation diagram of system (50) for $b_{sp} = 0.03$ obtained numerically. The results match the theoretical predictions in Section 4.2. More precisely, for a fixed $\epsilon$ value and varying the bifurcation parameter $\lambda$ we have:

- A stable anti-phase (AP) solution corresponding to $S_{osc}$ will emerge from a Hopf bifurcation at $C^{+}_{HB}$ whereas an unstable in-phase (IP) solution corresponding to $S^{+}_{osc}$ will emerge from the Hopf bifurcation at $C^{+}_{HB}$.

Fig. 14 Bifurcation diagram with parameters $P$ and $b_{sp} = -0.03$ in (50) (corresponding to the case $\beta_{oR} > 0$, $C_{det} + \beta_{oR} > 0$ and satisfying $\beta_{oR} < -C_{det} + \sqrt{C_{det}^2 + \beta_{oR}^2}$ as described in Section 4.1). A: Two-parameter bifurcation diagram in the $(\lambda, \epsilon)$-plane. The legend indicates bifurcations of a fixed point (FP) or a limit cycle (LC) giving rise to or involving the $\Delta \varphi = 0$ in-phase (IP) or $\Delta \varphi = \pi$ anti-phase (AP) solution branches; PD: period doubling; PF: pitchfork; TR: torus bifurcation. Text labels indicate the solutions that are stable in a given region, e.g. ‘IP+AP’ is a region with coexisting, stable IP and AP solutions. B: One-parameter bifurcation diagram at $\epsilon = 0.05$ showing the FP branch, IP branch and AP branch; dashed segments are unstable. The IP and AP branches bifurcate from the FP branch in subsequent Hopf bifurcations (bullet) for $\lambda$ increasing. The IP branch emerges stable and remains stable. For increasing $\lambda$ the AP branch is initially unstable, gains stability at a torus bifurcation (star) and loses stability at a pitchfork bifurcation (diamond). C: Coexisting solutions at $\lambda \approx 3.05$ and $\epsilon = 0.05$ in the $(E_1, E_2)$-plane. Motion on the diagonal (blue) corresponds to in-phase oscillations. D: As C in the $(E_1, I_1)$-plane for one E-I oscillator. E: As C at $\epsilon = 0.5$, where a torus bifurcation (star) is on an unstable branch that gains stability at a Fold of limit cycle (square).
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Fig. 15 Bifurcation diagram with parameters $\mathcal{P}$ and $b_{sp} = 0.03$ in (50) (corresponding to the case $\beta_{a,bR} < 0$ and $C_{det} + \beta_{aR} > 0$, as described in Section 4.2). A: Two-parameter bifurcation diagram in the $(\lambda, \epsilon)$-plane. Legends and labelling as in Fig. 14; TR: torus bifurcation. B: One-parameter bifurcation diagram at $\epsilon = 0.05$ showing the FP branch, IP branch and AP branch; dashed segments are unstable. The AP and IP branches bifurcate from the FP branch in subsequent Hopf bifurcations (bullet) for $\lambda$ increasing. The AP branch loses stability in a pitchfork bifurcation (diamond). The IP branch is initially unstable and gains stability at a torus bifurcation (star).

- The stability of both solutions is reversed as the bifurcation parameter grows. Moreover, the bifurcations giving rise to these stability changes are of the same type as we predicted: IP solution becomes stable across a torus bifurcation (corresponding to the Hopf bifurcation $\bar{H}$ at the $Tr^+ = 0$ line in Fig. 10) whereas the AP solution loses stability across a pitchfork bifurcation of limit cycles (corresponding to the $Det^- = 0$ line in Fig. 11).

5.3 Case $b_{sp} = 0$

We consider the case $b_{sp} = 0.0$. The coefficients of the normal form, which were computed using the techniques described in Appendix B, are given in Table 2 and satisfy the conditions $\beta_{a,bR} = 0$ and $C_{det} > 0$. Therefore, this case corresponds to the “degenerated case” discussed in Section 4.3. Fig. 16 shows the bifurcation diagram of system (50) for $b_{sp} = 0$ obtained numerically. Notice that it matches the theoretical predictions, namely:

- Both Hopf bifurcation curves $C_{HB}^{\pm}$ coincide and give rise to a bistable situation. On one side of the double Hopf curve there exists bistability between the in-phase (IP) solution $\Delta \varphi = 0$ corresponding to $S_{osc}$ and the anti-phase (AP) $\Delta \varphi = \pi$ solution corresponding to $S_{osc}$.

- For $\epsilon$ fixed and increasing the bifurcation parameter $\lambda$, the $S_{osc}$ (AP) solution loses stability across a Pitchfork bifurcation of limit cycles that we found for the 3D system as the line having $Det^- = 0$ (see Fig. 13).

5.4 Dynamics beyond the weak coupling limit

Our numerical bifurcation analysis has revealed the possibility for richer dynamics, whilst noting a wide range of parameters for which the IP and AP solutions are stable and
coexist. Furthermore, a Bautin bifurcation on the AP Hopf branch for $\epsilon_{BT} \approx 0.4$ as seen in Figures 14, 15 and 16 gives rise to a region of parameter space for $\lambda \lesssim \lambda_c$ where a stable AP solution coexists with a stable fixed point. The bifurcation point $\epsilon_{BT}$ separates branches of sub- and supercritical Hopf bifurcations in the parameter space. As we can see, for nearby $\lambda, \epsilon$ parameter values, the system has two limit cycles which collide and disappear via a Fold bifurcation of periodic orbits. Although the analysis done in Sections 3 and 4 is restricted to the weak coupling case, we briefly discuss how the reduced system (19) can provide some insight about this bifurcation.

In the weak coupling regime, the denominator in the formula (29) for the $s^{\pm}_{osc}$ solutions, is given by $\alpha_0R + \epsilon K_{stb}^{\pm}$ and is assumed to be negative. Therefore, $s^{\pm}_{osc}$ solutions appear for $\alpha^{\pm} = \lambda + \epsilon(\alpha_0R \pm \beta_0R) > 0$ at a supercritical pitchfork bifurcation of the origin (see Fig. 5). Nevertheless, writing the equation for $s$ in (28) in the following way

$$\dot{s} = A(\lambda, \epsilon)s + B(\lambda, \epsilon)s^3,$$

we clearly see that at the curve $A(\lambda, \epsilon) = 0$, the origin undergoes a pitchfork bifurcation that is supercritical or subcritical depending on the sign of $B(\lambda, \epsilon)$. Consequently, the point $(\lambda, \epsilon)$ satisfying $A(\lambda, \epsilon) = 0$ and $B(\lambda, \epsilon) = 0$ corresponds to a Bautin bifurcation. Thus, using the expression for $A$ and $B$ (which are known up to first order in $\epsilon$ and $\lambda$), we can estimate that a Bautin bifurcation occurs for

$$\epsilon_{BT} \approx -\frac{\alpha_0R}{K_{stb}^{\pm}},$$

assuming that $K_{stb}^{\pm} > 0$ and for $\lambda_{BT}$ such that $(\lambda_{BT}, \epsilon_{BT}) \in C_{HB}^\pm$. Although an accurate derivation is beyond the scope of this work, this transition from subcritical to supercritical involves the appearance of a curve of saddle-node bifurcations of fixed points for the system (19) for nearby values of the parameters. More precisely, if we consider the exact expression of the determinant of the 2x2 block of Jacobian Matrix (32) given by:

$$Det(s^{\pm}_{osc}) = c^{\phi \phi}_{\pm}c^{\xi \xi}_{\pm} - c^{\xi \phi}_{\pm}c^{\xi \phi}_{\pm}$$

(53)
where the constants are given by Eqs. (59) in the Appendix A with \( s = s_{osc} \) in (29), one can see that it is singular at \( B(\lambda, \epsilon) = 0 \). Therefore, we consider the curve

\[
B(\lambda, \epsilon) \text{Det}(s_{osc}) = 0,
\]

and one can see that the Bautin point \((\lambda_{BT}, \epsilon_{BT})\) belongs to it. Moreover, for \( \epsilon > \epsilon_{BT} \) as \( B(\lambda, \epsilon) > 0 \) this curve corresponds to the saddle-node bifurcations of the solutions \( s_{osc} \) outside the \( C_{HB} \) curve.

Using the numerical values given in Table 2, \( K_{stb} > 0 \). Thus, we can estimate from the normal form that the Bautin bifurcation occurs for \( \epsilon_{BT} \approx 0.42, 0.43, 0.42 \) for \( b_{sp} = -0.03, 0.03, 0 \), respectively, which matches the results obtained numerically (see Figures 14, 15 and 16). Recall that in the original 4D system (3) the pitchfork and saddle-node bifurcations correspond to Hopf and fold of limit cycles bifurcations, respectively.

Besides this previous behaviour, we also remark that the IP solution undergoes a period-doubling bifurcation for large \( \epsilon \) and \( \lambda \) leading to richer dynamical behaviour away from the analytically-investigated uncoupling limit.

### 5.5 Periodically Forced Coupled Wilson-Cowan Equations

With the aim of finding coexisting IP and AP solutions (corresponding to “percept 1” and “percept 2” as described in section 1) we now introduce periodic forcing terms to the coupled WC system given by (50). We consider anti-phase inputs with forcing frequency \( f = 2.5 \text{Hz} \) and amplitude \( A \) which will be varied as a bifurcation parameter:

\[
\begin{align*}
\tau \dot{E}_1 &= -E_1 + S(aE_1 - bI_1 + A \sin^{2n}(2\pi ft) + (1 - h)A \cos^{2n}(2\pi ft)), \\
\tau \dot{I}_1 &= -I_1 + S(cE_1 - dI_1 + \epsilon(E_2 - b_{sp}I_2)), \\
\tau \dot{E}_2 &= -E_2 + S(aE_2 - bI_2 + A \cos^{2n}(2\pi ft) + (1 - h)A \sin^{2n}(2\pi ft)), \\
\tau \dot{I}_2 &= -I_2 + S(cE_2 - dI_2 + \epsilon(E_1 - b_{sp}I_1)),
\end{align*}
\]

(54)

where the parameters \( P \) (with the exception of \( \tau \)) and nonlinearity (49) are as above. The input asymmetry parameter \( h \) controls the balance of inputs across the two oscillators; when \( h = 1 \) the oscillators receive exclusive inputs (the case typically considered in competition models [21, 46, 40, 25]) and when \( h = 0 \) the oscillators receive identical inputs (the case considered here). The forcing terms are raised to an even power \( 2n \) with \( n = 5 \) to be positive and sharpened such that the anti-phase inputs do not overlap in time. Noting that the isolated Wilson-Cowan oscillator undergoes a supercritical Hopf bifurcation at \( \lambda = \frac{2}{(n-1)S_{1}} = 3.025 \), we set \( \lambda = 2.6 \), before this bifurcation. Further, noting that the bifurcating branch emerges with period

\[
T = \tau \sqrt{\frac{2\pi}{(n-1)S_{1}}},
\]

and fixing \( T = \frac{1}{f} \) we can set \( \tau = \sqrt{\frac{2\pi}{(n-1)S_{1}}} \) such that the frequencies of oscillations produced at the Hopf match the forcing frequency.

Figure 17 shows a bifurcation diagram for the pair periodically-forced Wilson-Cowan oscillators. Each E-I oscillator receives the same input \( (h = 0) \). Panel A shows regions of the \((\epsilon, A)\) plane in which different types of oscillatory behaviours are stable. For low forcing amplitude there are only low-amplitude oscillations, effectively modulating the FP solution...
Fig. 17 Bifurcation diagram with parameters $\mathcal{P}$ whilst setting $\lambda$ and $\tau$ as described in the text. A: Two-parameter bifurcation diagram in the $(A, \epsilon)$ plane showing locus of bifurcations with legends and labelling as in 16; LA is a symmetric ($\mathcal{E}_1$, $\mathcal{I}_1$) = ($\mathcal{E}_2$, $\mathcal{I}_2$) low-amplitude limit cycle oscillations (following the periodic input) and HA is symmetric high-amplitude limit cycle. The IP and AP solutions co-exist in the region up to the dashed fold curve to the right. B: One-parameter bifurcation diagram at fixed $\epsilon = 0.5$; dashed curve segments are unstable. Diamonds are pitchfork bifurcations and squares are fold bifurcations. The stable IP branch exists between a pitchfork bifurcation to the left and fold to the right. The AP branch emerges unstable and is stable between a secondary pitchfork bifurcation on the left and a fold bifurcation to the right.

in the unforced system. As $A$ is increased, Pitchfork bifurcations give rise to stable IP and AP branches that coexist (see panel B) for small $\epsilon$ approaching the uncoupling limit. For large $\epsilon$ the IP solution persists at intermediate values of $A$. For large $A$ there is a saturated high-amplitude solution.

This bifurcation analysis demonstrates the possibility for coexisting in-phase and anti-phase responses of the coupled Wilson-Cowan oscillators to encode network states corresponding to “percept 1” (IP) and “percept 2” (AP) as described in Section 1. This is possible without strong mutual inhibition (i.e. in the uncoupling limit) between abstract representations of the two possible percepts.

6 Discussion and conclusions

The study of identical coupled oscillators near a Hopf bifurcation is applicable to a wide range of systems where near-identical units undergo oscillatory instability. These systems may in general be represented by very different vector fields. Using the normal form theory of in [7], we are able to predict universal aspects of the mathematical behaviour for such systems. The analysis performed in this work for two oscillators reveals that, as is often the case in normal forms, although (3) involves a big number of parameters, in the weak coupling limit, just a few of them govern and determine the possible bifurcations of the system.

Because of the symmetry of the system, there are usually two oscillating solutions: in-phase ($\Delta \varphi = 0$) and anti-phase ($\Delta \varphi = \pi$). Depending on parameters, we find that all possible combinations between different stabilities of both solutions are possible. Our numerical analysis has shown that away from the coupling limit, richer dynamical behaviour is possible, with secondary bifurcations from the anti-phase branch and regions of coexistence between fixed-point and anti-phase solutions mediated by a fold of cycles. Furthermore, we
find the coexistence of in-phase and anti-phase solutions persists even in the presence of periodic forcing.

6.1 Implications for models of perceptual bistability and neural competition

Models of perceptual bistability are widely based on the assumption of strong mutual inhibition between populations of neurons that encode different perceptual interpretations of ambiguous stimuli. In general, this assumes that populations associated with different percepts are separated in some feature space (e.g. orientation in binocular rivalry) and that these populations enter into competition through mutual inhibition. However, when stimuli are periodic and the two possible perceptual interpretations involve the same features, it is less clear how competition between percepts might arise. For example, for the visual (auditory) stimulus in Fig. 1 both “percept 1” and “percept 2” involve the left spatial location (higher pitch A tone). It is therefore unclear how mutual inhibition between “percept 1” and “percept 2” could be implemented in neural hardware (although see [36] where a population pooling inputs from an intermediate feature location was proposed). Another possibility, proposed and demonstrated to be feasible in this study, involves oscillatory neural activity. Indeed, encoding of perceptual interpretations through oscillations allows for complete synchronisation of the network with all incoming inputs (like “percept 1”) or for partial synchronisation of different parts of a network with separate elements (here in anti-phase). Furthermore, such an encoding mechanism does not rely on strong mutual inhibition, widely assumed between the abstracted percept-based neural populations in competition models with little supporting evidence.

6.2 Future perspectives

An obvious extension of the bifurcation analysis would be to the forced symmetry broken case. If there is no assumed symmetry between percepts 1 and 2. This will result in a separation of the Hopf bifurcations even for the uncoupled limit and unfolding of the degeneracies associated with the symmetry. Finally, one can consider the periodically forced system. Periodic forcing of the oscillators considered here (e.g. [18] for a single oscillator) will bring us to potentially much more complex bifurcation problems.

The study has demonstrated the potential role of oscillations in encoding different interpretations of periodically modulated ambiguous stimuli. It remains to explore the further role of feature space (say spatial location or tone frequency) and its interaction with oscillatory mechanisms. Additionally, as bistable perception involves spontaneous switching between perceptual interpretations, the mechanisms for these switches in the light of oscillatory stimuli remains to be explored.

Perceptual bistability with periodically modulated stimuli is robust over a range of input rates for the stimulus, whereas the simple network motif studied here has a fixed preferred input rate. So-called gradient networks of coupled oscillators have been proposed as a framework to understand many elements of early auditory processing and for perception of musical rhythm and beat [23,22]. Such a framework could be extensible to the study of perceptual bistability, relying in the dynamic mechanisms proposed here in the simple case of only two coupled oscillators.
Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Not applicable

Acknowledgements

This work has been partially funded by the Spanish grants and MTM2015-65715-P (GH, AP, TS), MINECO-FEDER-UE MTM-2015-71509-C2-2-R (GH), the Catalan grant 2017SGR1049 (GH, AP, TS) and the Russian Scientific Foundation Grant 14-41-00044 (TS). GH acknowledges the RyC project RYC-2014-15866. AP acknowledges the FPI Grant from project MINECO-FEDER-UE MTM2012-31714. We thank T. Lázaro for providing us valuable references to compute the normal form coefficients. We also acknowledge the use of the UPC Dynamical Systems group’s cluster for research computing.3 PA and JR acknowledge the financial support of the EPSRC Centre for Predictive Modelling in Healthcare, via grant EP/N014391/1.

Competing Interests

The authors declare they have no competing interests.

Authors’ Contributions

PA, JR, AP formulated the problem. All authors were involved in the theoretical analysis, discussion of the results and writing the manuscript. AP and JR performed numerical simulations. All authors have read and approved the final version.

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\( \Delta \phi \) 

\( r_1, r_2, \Delta \phi \) 

\( f(r_1, r_2, \Delta \phi) = r_1^2 \left[ (\beta_{11} + \alpha_{31}) \cos(\Delta \phi) - (\beta_{11} - \alpha_{31}) \sin(\Delta \phi) \right] + r_2^2 \left[ (\beta_{11} + \alpha_{31}) \cos(2\Delta \phi) - (\beta_{11} - \alpha_{31}) \sin(2\Delta \phi) \right] + r_1 r_2 \alpha_{00} + r_1^2 \alpha_{11} 

\( + r_2^2 \left[ \beta_{22} \sin(\Delta \phi) - \beta_{22} \sin(2\Delta \phi) \right] + r_2 \left[ \beta_{00} \cos(\Delta \phi) - \beta_{00} \cos(2\Delta \phi) \right], \)

\( \Delta \phi \) 

\( f_x (r_1, r_2, \Delta \phi) = r_1^2 \left[ (\beta_{11} + \alpha_{31}) \cos(\Delta \phi) + (\beta_{11} - \alpha_{31}) \sin(\Delta \phi) \right] + r_2^2 \left[ (\beta_{11} + \alpha_{31}) \cos(2\Delta \phi) + (\beta_{11} - \alpha_{31}) \sin(2\Delta \phi) \right] + r_1 r_2 \alpha_{00} + r_1^2 \alpha_{11} 

\( + r_2^2 \left[ \beta_{22} \cos(\Delta \phi) + \beta_{22} \cos(2\Delta \phi) \right] + r_2 \left[ \beta_{00} \cos(\Delta \phi) + \beta_{00} \cos(2\Delta \phi) \right], \)

\( f_\Delta \) 

\( f_\Delta (r_1, r_2, \Delta \phi) = f_x (r_2, r_1, -\Delta \phi) / r_2 - f_x (r_1, r_2, \Delta \phi) / r_1 = \)

\( = \left( r_1^2 - r_2^2 \right) \beta_{11} - \alpha_{11} + \beta_{31} \cos(2\Delta \phi) - 2r_1 r_2 \beta_{11} R \sin(\Delta \phi) \)

\( - \left( r_1^2 + r_2^2 \right) \beta_{31} \sin(2\Delta \phi) + \left( r_1^2 + r_2^2 \right) \beta_{22} \cos(\Delta \phi) - \left( r_1^2 + r_2^2 \right) \beta_{22} R \sin(\Delta \phi) \)

\( + \left( r_1 - r_2 \right) \beta_{00} \cos(\Delta \phi) - \left( r_1 + r_2 \right) \beta_{00} R \sin(\Delta \phi) \)

\( \Delta \phi \) 

\( \Delta \phi \) 

\( g(s, \Delta \phi) = f_x \left( \frac{s + d}{2}, \frac{s - d}{2}, \Delta \phi \right) + f_x \left( \frac{s + d}{2}, \frac{s - d}{2}, -\Delta \phi \right) = \)

\( = s \cos(\Delta \phi) \beta_{31} R + \alpha_{00} \right) + d \sin(\Delta \phi) \beta_{00} - \frac{d}{4} \left( s^2 + 3d^2 \right) \left( \beta_{22} \cos(\Delta \phi) + \alpha_{11} \right) \)

\( + \frac{d}{4} \left( s^2 - d^2 \right) \left[ \beta_{31} \sin(2\Delta \phi) - \beta_{31} \sin(2\Delta \phi) \right] + \frac{d}{4} \left( s^2 + d^2 \right) \beta_{22} \sin(\Delta \phi), \)

\( g_\Delta (s, \Delta \phi) = f_x \left( \frac{s + d}{2}, \frac{s - d}{2}, \Delta \phi \right) - f_x \left( \frac{s + d}{2}, \frac{s - d}{2}, -\Delta \phi \right) = \)

\( = -d \left( \cos(\Delta \phi) \beta_{31} R - \alpha_{00} \right) - s \sin(\Delta \phi) \beta_{00} - \frac{d}{4} \left( d^2 + 3s^2 \right) \left( \beta_{22} \cos(\Delta \phi) - \alpha_{11} \right) \)

\( + \frac{d}{4} \left( s^2 - d^2 \right) \left[ \beta_{31} \sin(2\Delta \phi) - \beta_{31} \sin(2\Delta \phi) \right] - \frac{s}{4} \left( 3d^2 + s^2 \right) \beta_{22} \sin(\Delta \phi), \)

\( g_\Delta (s, \Delta \phi) = f_\Delta \left( \frac{s + d}{2}, \frac{s - d}{2}, \Delta \phi \right) = \)

\( = \beta_{00} \cos(\Delta \phi) \left( \frac{4sd}{s^2 - d^2} - 2\beta_{00} \sin(\Delta \phi) \left( \frac{s^2 + d^2}{s^2 - d^2} \right) \right) - \beta_{22} \sin(\Delta \phi) \left( \frac{s^2 + d^2}{s^2 - d^2} \right) \left( \frac{s^2 + d^2}{s^2 - d^2} \right) + \beta_{22} \cos(\Delta \phi) \left( \frac{2sd(s^2 + d^2)}{(s^2 - d^2)} \right) \)

\( - \beta_{31} \sin(2\Delta \phi) \left( \frac{s^2 + d^2}{2} \right) - \beta_{31} \sin(2\Delta \phi) \left( \frac{s^2 - d^2}{2} \right) + (\alpha_{11} + \beta_{31} \cos(2\Delta \phi) - \alpha_{11}) \right]. \)
The terms for the Jacobian matrix in (32) are given by
\[
\begin{align*}
c_1^e &= \lambda + \epsilon (\alpha_{00R} \pm \beta_{0R}) + \frac{3s^2}{4} (\alpha_{01R} + \epsilon (\alpha_{11R} \pm (\beta_{12R} \pm \beta_{11R} + \alpha_{2R} \pm \alpha_{13R} R)) + (\beta_{2R} + \beta_{13R}) \), \\
c_2^e &= \lambda + \epsilon (\alpha_{00R} \pm \beta_{0R}) + \frac{s^2}{4} (3\alpha_{01R} + \epsilon (3(\alpha_{11R} \pm \beta_{2R}) \pm ((\beta_{11R} + \alpha_{2R} \pm \alpha_{13R} R)) \pm (\beta_{2R} + \beta_{13R})), \\
\beta_{0} &= \epsilon \left( -\frac{3}{4} (2\beta_{11R} \pm \beta_{12R} + \beta_{0R}) \right), \\
\beta_{01} &= \epsilon \left( s(0_{2R} - \alpha_{11R} \pm \beta_{0R} \pm 2\beta_{2R}; \pm 4\beta_{01R} \right), \)
\end{align*}
\] (59)

where \(s = s_{\text{osc}}^+\) and consistently with the notation used throughout the article, the \(\pm\) sign corresponds to \(\Delta \varphi = 0, \pi\) respectively.

### B Normal Form Computation

In this appendix we provide a brief description of the numerical procedure used to compute the coefficients of the normal form (3). The procedure is related to normal form techniques in which one constructs a change of variables of the form
\[
z = y + Q_2(y, \bar{y}) + Q_3(y, \bar{y}),
\] (60)

where \(Q_2(y, \bar{y})\) and \(Q_3(y, \bar{y})\) are polynomials or order 2 and 3, respectively, such that the system (1) expressed in the variables \(y\) and \(\bar{y}\) has the simplest expression possible. That is,
\[
y_1 = A y + f_2(y, \bar{y}) + f_3(y, \bar{y}) + O_4(y, \bar{y}),
\] (61)

where \(A\) is the linearized system (3) around the origin, \(f_2 = 0\) and \(f_3\) has the same monomials appearing in (3), namely: \(y_1|y_1|^2, y_1|y_2|^2, yy_1y_2^2, y_1^2, y_2^2\) and \(y_1y_2^2\).

To that aim we perform the following steps:

1. Consider the Taylor expansion of system (1) around the origin:
   \[
   \begin{align*}
   \dot{z} &= Az + P_2(z, \bar{z}) + P_3(z, \bar{z}) + O_4(z, \bar{z}), \\
   \dot{\bar{z}} &= \bar{A} \bar{z} + \bar{P}_2(z, \bar{z}) + \bar{P}_3(z, \bar{z}) + O_4(z, \bar{z}),
   \end{align*}
   \] (62)

   where \(z = (z_1, z_2), \bar{z} = (\bar{z}_1, \bar{z}_2) \in \mathbb{C}^2\), \(A = \text{diag}(\mu^+, \mu^-)\) is a diagonal matrix with \(\mu^+, \mu^- \in \mathbb{C}\), \(P_2\) and \(P_3\) in (62) correspond to polynomials of degree 2 and 3, respectively. As \(\bar{z}\) is the complex conjugate of \(z\), we will just consider the first equation in (62).

2. Compute the \(q_{ij}\) coefficients of the polynomial \(Q_2(y, \bar{y})\) given by
   \[
   Q_2(y, \bar{y}) = \prod_{i=1}^{N_y} \prod_{j=1}^{N_{\bar{y}}} q_{ij} y_i \bar{y}_j,
   \] (63)

   where \(y_1 = \bar{y}_1\) and \(y_4 = \bar{y}_2\), by solving the following equation for each monomial
   \[
   AQ_2(y, \bar{y}) - D_q Q_2(y, \bar{y}) Ay - D_{\bar{y}} Q_2(y, \bar{y}) \bar{A} \bar{y} = f_2(y, \bar{y}) - P_2(y, \bar{y}).
   \] (64)

   With this choice, all the monomials in \(f_2\) in (61) are null.

3. Compute \(f_3(y, \bar{y})\) given by the expression
   \[
   f_3(y, \bar{y}) = D_q P_2(y, \bar{y}) Q_2(y, \bar{y}) + D_{\bar{y}} P_2(y, \bar{y}) Q_2(y, \bar{y}) + P_3(y, \bar{y}),
   \] (65)

   thus obtaining the coefficients corresponding to the surviving monomials in (3): \(y_1|y_1|^2, y_1^2 \bar{y}_j, y_1|y_1|^2, \)

\(y_1|y_2|^2, \bar{y}_j, y_1|y_2|^2\) \(i = 1, 2, j \neq i\).
4. Perform the change of coordinates $y = Cx$ in system (61), where

$$C = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & 1 & 0 & 0 \\ 1 & -1 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & -1 \end{pmatrix},$$

(66)

so that the system is written in the form (3).

Notice that to compute the coefficients of $f_3$ in (61) it is enough to compute the change in (60) up to order two. As a final remark, notice that apart from $\omega$ and $\alpha_{01}$ all the coefficients $\alpha_{\epsilon i}, \beta_{\epsilon i}$ ($i = 0, \ldots, 3$) in (3) are multiplied by $\epsilon$. Therefore, to obtain the value of the coefficients we follow the procedure described above for $\epsilon = 0$, thus obtaining $\omega$ and $\alpha_{01}$, and then repeat the same procedure for a small $\epsilon \neq 0$, which, using that $\omega$ and $\alpha_{01}$ are known, provides the coefficients $\alpha_{\epsilon i}, \beta_{\epsilon i}$. 