Sensorimotor Coordination and Metastability in a Situated HKB Model

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\textit{RESEARCH ARTICLE}

Oscillatory phenomena are ubiquitous in nature and have become particularly relevant for
the study of brain and behaviour. One of the simplest, yet explanatorily powerful, models of
oscillatory coordination dynamics is the the HKB (Haken-Kelso-Bunz) model. The metastable
regime described by the HKB equation has been hypothesized to be the signature of brain os-
cillatory dynamics underlying sensorimotor coordination. Despite evidence supporting such a
hypothesis, to our knowledge there are still very few models (if any) where the HKB equation
generates spatially situated behaviour and, at the same time, has its dynamics modulated
by the behaviour it generates (by means of the sensory feedback resulting from body move-
ment). This work presents a computational model where the HKB equation controls an agent
performing a simple gradient climbing task and shows i) how different metastable dynamical
patterns in the HKB equation are generated and sustained by the continuous interaction
between the agent and its environment; and ii) how the emergence of functional metastable
patterns in the HKB equation – i.e. patterns that generate gradient climbing behaviour –
deeps not only on the structure of the agent’s sensory input but also on the coordinated
coupling of the agent’s motor-sensory dynamics. This work contributes to Kelso’s theoretical
framework and also to the understanding of neural oscillations and sensorimotor coordination.

\textbf{Keywords:} Sensorimotor coordination; Oscillatory dynamics; Metastability; Coordination
Dynamics.

1. Introduction

Oscillatory phenomena are ubiquitous in nature, of particular importance to us
is the study of oscillatory dynamics as the generating mechanism of sensorimo-
tor behaviour, a phenomenon that expands from lower organisms (Dano et al.
1999, Gardner et al. 2006) to large-scale neurodynamics of the mammalian brains
(Buzsaki 2006, Traub and Whittington 2010). A prominent work in this area is the
empirically grounded theoretical framework of Coordination Dynamics which seeks
to identify general laws of coordination among rhythmic components operating at
different spatial and temporal scales (Kelso 1995). This framework has motivated
many empirical studies of neural oscillatory dynamics underlying sensory and mo-
Lagarde and Kelso 2006) and has opened up discussion in different areas such as

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philosophy of cognitive science (Chemero 2009, Bechtel and Abrahamsen 2010, Stepp et al. 2011, Kaplan and Bechtel 2011) and theoretical neuroscience (Kelso and Tognoli 2009).

The main illustrative model for the Coordination Dynamics framework is that described by the extended HKB equation which captures the temporal relation between the activity of coupled oscillatory elements (Kelso 1995, Kelso et al. 1990). This equation has been carefully studied by manipulating a control parameter that modifies the oscillators’ natural frequencies or their coupling factor. One of its main dynamical properties is the metastable regime in which the phase relation variable engages when the control parameter crosses a certain threshold. Metastable dynamics have been hypothesized to be the dynamical signature of the nervous system underlying sensorimotor coordination (Kelso and Tognoli 2009, Tognoli and Kelso 2009, Bressler and Kelso 2001). Empirical evidence favouring this hypothesis comes, for instance, from studies showing correlation between sensory stimulation and transiently synchronized networks in the brain of animals performing perceptual and motor coordination tasks (Buzsaki 2006, Rodriguez et al. 1999, Varela et al. 2001, Pockett et al. 2009, Singer 2011, Hipp et al. 2011). Despite such evidence supporting the existence of metastable regimes in the brain of behaving animals, to our knowledge there are still very few models (if any) where the HKB equation generates the motor behaviour of an agent interacting in a spatial environment and, at the same time, has its control parameter modulated, through sensory feedback, by the motor behaviour it generates. Thus, in this work we investigate the dynamics of the extended HKB equation within a closed sensorimotor loop by implementing it as the controller of an agent performing a functional behaviour (gradient climbing) in a simulated two-dimensional environment. The “output” of the extended HKB equation (the phase relation variable) generates the agent’s motor behaviour and, at the same time, its control parameter (in our particular case, the variable representing the oscillators’ frequency difference) is modulated by the agent’s behaviour through its sensory activity. The extended HKB equation within the agent’s sensorimotor loop will be referred to as the situated HKB model.

The HKB equation has been used to model cases of sensorimotor coupling such as Kelso et al. (2009), where a human subject receives sensory feedback from a computer screen and the human’s behaviour in turn affects the computer. The novelty of the situated HKB model is that the coupling is spatial and the HKB is not meant to capture the global feedback dynamics but is used directly as a robotic controller. The resulting dynamics will be shown to have special properties (e.g. multiple metastable regimes).

In the next section we briefly present the Coordination Dynamics framework. Next we describe the model and then analyse it; particularly we start by identifying patterns in the agent’s sensorimotor behaviour and studying their underlying metastable regimes; we analyse the mutual coordination between the situated HKB model and its control parameter; and carry out an experiment to compare the dynamical and informational properties of the situated HKB model under open and closed sensorimotor loops. Briefly, we will show i) how different metastable dynamical patterns in the HKB equation are generated and sustained by the continuous interaction between the agent and its environment; and ii) how the emergence of functional metastable patterns in the HKB equation – i.e. patterns that generate gradient climbing behaviour – depends not only on the structure of the agent’s sensory input but also on the coordinated coupling of the agent’s motor-sensory dynamics. The analysis of the extended HKB equation within a sensorimotor loop is a contribution to the Coordination Dynamics framework and, as such, it provides theoretical insights to understanding the interplay between neural oscillations and
sensorimotor behaviour.

2. Coordination Dynamics

*Coordination Dynamics* is a consistent framework which can be used to investigate brain dynamics and behaviour, it was proposed and developed by Kelso (1995) based on Haken’s work on synergetics (Haken 1978). It extends von Holst’s work (von Holst 1937, 1939) by combining empirical experiments and theoretical models formulated mathematically to study how the components of a system interact and produce coherent coordination patterns.

The driving example of Coordination Dynamics is the HKB (Haken-Kelso-Bunz) model which describes the relative phase dynamic between two non-linearly coupled oscillators (Haken et al. 1985). This model was originally designed to replicate the type of phase relation dynamics observed in an empirical experiment involving rhythmic behaviour of human fingers. In this experiment a subject rhythmically moves his right and left index fingers in a horizontal plane at the same frequency of a pacing metronome. The HKB model replicates how the angle between the left and right fingers changes over time (the phase relation dynamics) given different initial conditions – fingers in-phase or anti-phase – and at an increasing metronome frequency (Kelso 1995, p.46). This model was mainly used to explore the in-phase and anti-phase stable synchronizations, the transition between them, and their basins of attraction.

Later on Kelso et al. (1990) extended the HKB model by adding a symmetry-breaking parameter in order to replicate a type of phase relation dynamics between non-identical oscillatory components, *i.e.* components with different natural frequencies, which is a more realistic phenomenon in nature (Kelso and Engstrom 2006). One of the main properties of the extended HKB model is the existence of metastable dynamics where the variable representing the temporal relation (*i.e.* phase relation) constantly moves in a transient dynamic through regions of the phase space with low potential energy (representing moments of transient synchronization) followed by regions with high potential energy (representing moments of desynchronization) and without settling down in point attractors (representing moments of stable synchronization). The graphic in Fig. 1 depicts the attractor landscape of the extended HKB model considering different values for the parameter of symmetry breaking. A low value for the parameter of symmetry breaking generates multistable phase relation dynamics, as schematically represented by the lower curve with two stable (filled circles) and unstable (open circles) points depicted on the x axis. As the symmetry breaking parameter increases, the derivative of phase relation also increases (see middle curve) and consequently the attractor landscape becomes monostable – notice that the middle curve has only a single stable point. For higher values of the symmetry breaking parameter a saddle-node bifurcation takes place and both fixed points disappear\(^1\). The dynamics of the phase relation near the region where the fixed points used to be are termed “metastable dynamics”, as Kelso and Tognoli (2009, p.108) put it:

“In coordination dynamics, metastability corresponds to a regime near a saddle-node or tangent bifurcation in which stable coordination states no longer exist (*e.g.*, in-phase synchronization where the relative phase between oscillating components

\(^1\)The saddle-node bifurcation is the basic mechanism by which fixed points are created and destroyed. As a parameter is varied, two fixed points move toward each other, collide, and mutually annihilate” (Strogatz 2000).
lingers at zero), but attraction remains to where those fixed points used to be (remnants of attractor repellors).”

![Phase relation and its derivative](image)

Figure 1. Schematic representation of the extended HKB equation attractor landscape. Each curve depicts the derivative of phase relation (y axis) throughout its state space (x axis) given 3 different values for the symmetry breaking parameter (lower, middle, and upper curves). Stable points are represented by filled circle and unstable ones by open circles. The phase relation dynamics changes from multistable (lower curve) to monostable (middle curve) and eventually metastable (upper curve).

A numerical analysis of the extended HKB equation for a specific set of parameters will be presented in the results section.

Bressler and Kelso (2001) describe the presence of metastable dynamical regimes of phase relations in oscillatory brain signals by recording the local field potential (LFP) from up to 15 sites in one cortical hemisphere of a macaque monkey performing a visual discrimination task. They analysed the density distribution function of phase relations between pairs of LFP signals and detected that two cortical sites transiently synchronized with phase relation near $-54^\circ$ degrees during the interval $[105, 155]$ ms after the stimulus onset. Apart from that time window, during the whole task ($[-70, 400]$ ms) the same cortical sites were found to be desynchronized (they did not present any other significant peaks on the distribution phase relations), which according to them indicates the functional involvement of these sites at a specific stage of the visual discrimination task. Other cortical sites presented different temporal patterns of coordination presumably reflecting different functional involvement during the task.

Despite the detailed mathematical and experimental understanding of oscillatory dynamics of the extended HKB equation, to our knowledge there is no study of how this dynamics might be affected when it is situated within a sensorimotor loop. In parallel with this work, we have elsewhere studied what we have called “the situated HKB model” (Aguilera et al. 2012), formalizing the dynamics of spatial sensorimotor coupling and analytically solving and comparing the situated HKB model with its equivalent decoupled canonical HKB model for a monostable parametric configuration. In this paper, our goal is to study the situated HKB model operating in the metastable dynamics. We analyse relationship between behavioural, sensorimotor and internal oscillatory dynamic patterns; we compare how metastable regimes of phase relations differ between the situated HKB model and the decoupled-HKB model and study the transitions between characteristic regimes in the situated HKB model; we carry out an experiment and show that the dynamical and informational properties of the situated HKB model change in the absence of a coordinated coupling between the agent’s motor and its sensory dynamics, and also that the emergence of functional metastable regimes in the situated HKB model depends on the agent’s motor-sensory coupling.
3. Model description

3.1. The agent and its controller

The model consists of a two dimensional simulated environment and a circular agent whose task is to climb a linear gradient towards the centre of the environment where the peak is located. The agent has a body of of 5 units diameter with two diametrically opposed motors and a sensor randomly positioned at $90^\circ \pm 5^\circ$ relative to the motor axis$^1$. The agent’s sensor is connected to a controller and the latter connected to both motors, as shown in Fig. 2. The controller’s dynamics are governed by the extended HKB equation where the difference in natural frequencies ($\omega$) is modulated by the agent’s sensory input ($s$), as defined in (1).

$$\dot{\phi} = s\omega - a \sin \phi - 2b \sin(2\phi), \quad (1)$$

where $\phi$ is the phase relation between two oscillators at an undetermined level of abstraction$^2$, $s$ is the sensor activation given by $s = c_1 \dot{d}$, where $c_1$ is a constant and $\dot{d}$ is the derivative of the distance from the agent to the centre of the environment; $\omega$ is a constant representing the difference in natural frequencies between two oscillators; $a$ and $b$ are constants representing the coupling factor. By sensing the derivative of the distance $\dot{d}$, the agent is able to perceive a linear radial gradient with its peak at the centre of the environment. We have chosen this type of derivative sensing because many organism’s behaviour is based on interactions with different types of gradients$^3$. Also, for a minimal model, sensing the derivative has the advantage that

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$^1$Although the variation of 5 degrees in the sensor’s position increases the likelihood of the optimization algorithm (explained below) to obtain a more robust solution for the gradient climbing behaviour, it is not necessary for evolving the parameters of the model.

$^2$In the experiment carried out by Kelso, the phase relation $\phi$ models the angle between the right and left fingers, as described in section 2. This variable has also been interpreted as the phase relation between neural oscillatory components underlying the fingers’ coordination (Kelso and Tognoli 2009). In the context of this work, $\phi$ describes the phase relation of oscillatory components at an undetermined level of abstraction (it can be interpreted, for instance, as the phase relation between individual neurons, or neuronal groups). Our goal here is not to develop a model with empirical accuracy, but to raise theoretical issues about oscillatory dynamics underlying sensorimotor coordination.

$^3$Most of small scale adaptive behaviour occurs along chemical gradients. The microscopic world is a world of gradients (like thermal gradients or light gradients but mostly chemical gradients). The adaptive behaviour of small animals (e.g. C. elegans) and individual motile cells (e.g. bacteria but also animal cells migrating during development) is mostly a gradient-related adaptive behaviour. Navigating smell or heat gradients is also a stereotypical adaptive task for higher animals.
the agent does not perceive a continuously increasing input, making the dynamics more regular throughout the behaviour of the agent.

The equation is integrated with time step 0.001 seconds using the Euler method. The right and left motors of the agent are governed by Eq. (2) and (3), where \( c_2, c_3 \) and \( c_4 \) are constants.

\[
m_r = c_2(\cos(\phi + c_3) + 1) \tag{2}
\]

\[
m_l = c_2(\cos(\phi + c_4) + 1) \tag{3}
\]

3.2. Optimization with a genetic algorithm

In order to obtain an agent performing gradient climbing, a total of 7 parameters \((c_1, c_2, c_3, c_4, \omega, a, b)\) were optimized with the microbial genetic algorithm (Harvey 2001). These parameters were encoded in a genotype as a vector of real numbers in the range \([0,1]\) linearly scaled, at each trial, to their corresponding range \((a = [0.1, 10], b = [0.1, 10], \omega = [17, 22], c_1 = [0, 3], c_2 = [0, 0.4], c_3 = [0, 2\pi], \text{ and } c_4 = [0, 2\pi])\). The genetic algorithm (GA) setup was: population size (50); mutation rate (0.05); recombination (0.60); reflexive mutation; normal distribution for mutation \((\mu = 0, \sigma^2 = 0.1)\); trial length (150 seconds); and trials for each agent (20). At the end of the 20th trial the worst fitness (out of 20) was used as the selective fitness of the agent. The fitness function was defined by (4):

\[
F = \begin{cases} 
1 - \frac{d_f}{d_i} & \text{if } d_f < d_i; \\
0 & \text{otherwise};
\end{cases} \tag{4}
\]

Where \( F \) is the fitness; \( d_i \) and \( d_f \) are the initial and final distances from the agent to the centre of the environment where the peak of the gradient is located. This fitness function selects the agents that perform gradient climbing in an environment with a peak at its centre. The optimized parameters found by the GA were the following: \( c_1 = 2.72, c_2 = 0.36, c_3 = 3.44, c_4 = 3.21, \omega = 19.67, a = 0.99 \) and \( b = 7.94 \). The GA ran for 150 tournaments (equivalent to 6 generations) and the best agent got a fitness of 0.98. Most solutions found by the GA were monostable controllers. In order to obtain metastable dynamics we had to run different instances of GAs, each one with different ranges of \( \omega \).

There is no specific reason why the microbial genetic algorithm was used, any other optimization method would probably work as the problem is relatively simple. Neither is there a specific reason why \( c_1 \) and \( \omega \) are two different parameters, they could have been optimized as a single variable since their product is what is actually relevant. We have used two parameters to keep the model coherent in the sense that \( c_1 \) represents the sensor strength and the \( \omega \) the frequency difference.

Notice that the purpose of the model developed here is not to solve the problem of gradient climbing (which could be solved by a simple Bratenberg vehicle), but to raise and discuss theoretical issues about interplay between oscillatory and sensorimotor dynamics based on the analysis of the HKB equation controlling an agent’s behaviour under a metastable regime. In this sense, we are not looking for optimum nor general solutions for the gradient climbing behaviour but for a solution where the controller is metastable while the agent is performing the desired
4. Results

In section 4.1 we briefly present two distinct sensorimotor behaviours that the agent engages in during its interaction with the environment and their underlying metastable regimes in the situated HKB model. In section 4.2 we analyse how the metastable regimes are generated and how the transition between them takes place. In section 4.3 we perform an experiment to compare the effects of motor-sensory coupling on the dynamical and informational properties of the situated HKB model.

4.1. Metastable regimes underlying sensorimotor behaviours

Fig. 3 presents the behaviour of an agent during a single trial of gradient climbing. Fig. 3 shows how the distance from the agent to the region of highest gradient (the centre of the environment) changes for 20 trials of the experiment; the agent’s position, orientation and the controller’s phase relation ($\phi$) have a random value at the beginning of each trial. The agents take from 80 up to 105 seconds to move towards the centre of the environment and then they start moving around it. The patterns of sensorimotor behaviour that the agents engage in while they are approaching the centre and then moving around it are shown in Fig. 4. These patterns are defined by different (repeatedly observed) closed orbits in the state space of sensory and motor activities and will be referred to as $SM_1$ and $SM_2$, respectively ($SM_n$ standing for SensoriMotor pattern $n$).

Underlying the sensorimotor behavioural patterns $SM_1$ and $SM_2$ there are two distinct metastable regimes of the phase relation ($\phi$). The regimes are defined as the distinct regions of the agent’s dynamics that correspond directly to the empirically observed behaviours $SM_1$ and $SM_2$. As the following analysis shows, the dynamics in these regions have clear differences. Fig. 5-A shows such regimes for 20 successful trials – those presented in Fig. 3-B. Notice that these regimes are depicted by showing the state space of the agent’s controller ($\phi \in [0, 2\pi]$ in the x-axis) and the derivative of $\phi$ throughout the state space (in the y-axis). The derivative $\dot{\phi}$ is calculated by Eq. 1 at each time step of the simulation. For any initial conditions all controllers converge to the metastable regimes $R_1$ and $R_2$ of $\phi$ for the sensorimotor
patterns $SM_1$ and $SM_2$, respectively. In both regimes the derivative of the phase relation is always greater than zero showing that the state of the controller never reaches a fixed point. Fig. 5-B shows the density distributions of $\phi$ for $R_1$ and $R_2$. These distributions were generated by dividing the state space $[0, 2\pi]$ into 48 equally spaced bins and using the values of $\phi$ from the time windows $[10, 50]$ s and $[110, 150]$ s (a total of 40000 data points of each time window) considering a single trial of gradient climbing. The regimes $R_1$ and $R_2$ have two regions where $\phi$ slows down, which can be seen by two peaks in the density distribution of each regime ($\phi$ spends more time in the regions with low derivative, that is why there are peaks in the density distributions). The difference between distributions (represented by the line without marks in the graphic) maintains a level slightly below zero and has a peak in between $[\pi, 3\pi/2]$.

Basically, the purpose of the next section is to understand the coordination between the agent’s metastable oscillatory regimes – $R_1$ and $R_2$ – and its sensorimotor behaviours – $SM_1$ and $SM_2$. We will study how these oscillatory regimes are generated and maintained during the agent’s interactions with its environment and also how the transition between them takes place.

4.2. Generation and transition between metastable regimes

We shall start by analysing the extended HKB equation without the sensorimotor loop. This analysis does not present any new result that has not been previously presented by Kelso et al. (1990) and Kelso (1995). However, it is important in the context of this paper to set the ground to study the situated HKB model. The purpose here is to understand how the control parameter $s$ affects the derivative of $\phi$ throughout its state space $[0, 2\pi]$. The controller is studied within the parameter range $s = [-3.92, 3.92]$, which is the interval of sensory activation when the agent is behaving in the environment.

Fig. 6-A shows $\phi$ throughout the state space of $\phi$ given three constant values of
Figure 5. Metastable regimes of phase relation ($\phi$) that the agent engages in while it is moving towards the centre of the environment and while it is moving around it. **Graphic A** shows the metastable regimes in terms of $\phi$ (x axis) and $\dot{\phi}$ (y axis) underlying SM$_1$ (black line) and SM$_2$ (grey line). These regimes will be referred to as $R_1$ and $R_2$, respectively (see legend). **Graphic B** shows the density distributions of $R_1$ (line with circles), $R_2$ (line with crosses) and the difference between the distributions (line without markers).

$s$. When $s = -3.92$ the state space contains an attractor (black-filled circle) and a repeller (white circle). When $s = 0$ and $s = 3.92$ there are no fixed points and the dynamics of $\phi$ are metastable. By keeping $s$ constant the derivative $\dot{\phi}$ always presents a global minimum at $\phi = 0.796$ and a local minimum at $\phi = 3.916$ radians. From now on these two points will be referred to as $\phi_G$ and $\phi_L$, respectively. Fig. 6-B shows how $s$ changes the derivative at minima $\phi_G$ and $\phi_L$; note the linear relationship between these variables. For $s < -3.09$ (see vertical dashed line) the derivative is negative at global minimum $\phi_G$ and positive at the local minimum $\phi_L$, showing that the state space has at least two fixed points. Above $s > -3.09$ the derivative is positive at $\phi_G$, showing that the state space does not have fixed points. Fig. 6-C shows the bifurcation diagram of $\phi$ for the independent variable $s$. As $s$ increases within the range [-3.92, -3.09) both fixed points (attractor and repeller) approach each other; when $s \approx -3.09$ both points merge into a single half-stable point; and when $s > -3.09$ this single point disappears and $\phi$'s dynamics become metastable. Summing up, $s$ affects the dynamics of the agent’s controller by linearly changing the derivative of $\phi$ throughout the entire state space $[0, 2\pi]$; additionally, a) within a certain range of $s$ the attractor landscape presents two fixed points (an attractor and a repeller) that approach each other as $s$ increases; and b) above this range the fixed points disappear and the phase relation dynamics fall into a metastable regime.

We now move to the analysis of the situated HKB model which has its control parameter $s$ and phase relation $\phi$ co-modulating each other through the sensorimotor loop. We selected a small time window of 1.5 seconds during a single trial of gradient climbing in order to start presenting the dynamics of $s$ and $\phi$ (see Fig. 7). **Graphic 7-A** shows how the derivative $\dot{\phi}$ at the points of minima $\phi_G$ and $\phi_L$ are changing over time. The sensor dynamics $s$ (in graphic 7-B) and the derivative at $\phi_G$ and $\phi_L$ (in graphic 7-A) move up and down together due to their linear relationship. Although the fixed points appear in the state space around the minimum $\phi_G$ during $t_1 = [10.53, 10.60]$ and $t_2 = [11.18, 11.25]$ seconds, the phase relation does not reach the attractor. The reason for that is that during $t_1$ and $t_2$ the phase relation $\phi$ is away from the minimum $\phi_G$ moving in the region near the local min-
Figure 6. **Graphic A.** Phase relation $\phi$ (x axis) and its derivative $\dot{\phi}$ (y axis) for 3 different values of constant inputs $s = -3.92$ (lower curve), $s = 0$ (middle curve) and $s = 3.92$ (upper curve). When $s = -3.92$ the state space contains an attractor (black-filled circle) and a repeller (white circle). When $s = 0$ and $s = 3.92$ there are two points of minima at $\phi = 0.796$ and $\phi = 3.916$, respectively. **Graphic B.** Relation between $s$ and the derivative at the points of minima $\phi = 0.796$ (black line) and $\phi = 3.916$ (grey dashed line). For $s < -3.09$ (see vertical dashed line) the derivative at $\phi = 0.796$ is negative, and for $s > -3.09$ both points of minima are positive. **Graphic C.** Bifurcation diagram of $\phi$ (see y axis) for the independent variable $s$ (x axis). Vertical dashed line is at $s = -3.09$. The black-filled circles represent point attractors and the white circles represent the repellers. When $s > -3.09$ the phase relation dynamics are metastable.

In $\phi_L = 3.916$ (see horizontal line in graphic 7-C) and when $\phi$ reaches the region near $\phi_G$ the sensor value has increased and the fixed points have disappeared. The main point to understand from this analysis is that the control parameter $s$ linearly changes the derivative throughout the entire state space of $\phi$, as a result, although for some values of $s$ the state space shows one or two attractors, the continuous sensorimotor modulation of $s$ in coordination with $\phi$ never allows the system to settle down on such attractors.

By looking at the values of $s$ shown in Fig. 8 we can see how the derivative throughout the state space of $\phi$ is changing during $R_1$ and $R_2$. The greatest difference in the derivative takes place when $\phi$ is around the local minima $\phi_L$; exactly at $\phi_L$, for instance, the values of $s$ are $\approx -1.94$ and $\approx 1.55$ during $R_1$ and $R_2$, respectively; showing that when $\phi$ is at the point of local minima, the derivative throughout the entire state space is lower during $R_1$ than during $R_2$. This difference explains why there is a peak in between $\pi$ and $3\pi/2$ in the graphic of density distribution shown in Fig. 5-B. The state space has its lowest derivative and also fixed points around the global minimum $\phi_G$ in two situations: a) when $\phi$ is within
Figure 7. **Graphic A** shows how the derivative $\dot{\phi}$ at points of minima $\phi_G$ (black line) and $\phi_L$ (grey line) are changing over time. The horizontal line highlights $\dot{\phi} = 0$. **Graphic B** shows how $s$ (y axis) is changing over time. The horizontal line highlights $s = -3.09$, the threshold at above which the fixed points disappear. **Graphic C** shows how $\phi$ is changing over time. The horizontal lines highlight the points $\phi_G$ and $\phi_L$. Vertical dashed lines highlight the time intervals $t_1 = [10.53, 10.60]$ and $t_2 = [11.18, 11.25]$ seconds where the fixed points appear in the state space.

[3.69, 3.82] during $R_1$, and b) when $\phi$ is within [2.65, 3.12] during $R_2$; both shown in the graphic by the values of $s$ below the horizontal dashed line. Despite the presence of fixed points, $\phi$ dynamics never reaches a stable or unstable state as the state space changes when $\phi$ is around the global minimum $\phi_G$ (see that the values of $s$ are above the horizontal dashed line when $\phi$ is around the global minimum $\phi_G = 0.796$). The main point to understand from this analysis is how $s$ changes the derivative of the state space of $\phi$ in different ways during the regimes $R_1$ and $R_2$.

We have been describing how $s$ modulates $\phi$ by changing the derivative of the latter; however, $\phi$ also modulates the dynamics of $s$ by moving the agent in the environment – i.e. the dynamics of $s$ and $\phi$ are generated by a process of co-modulation between these variables. Thus, the regimes $R_1$ and $R_2$ are generated and sustained by continuously modifying the derivative throughout the state space of $\phi$ in a structured way through $s$ and, at the same time, by continuously modulating $s$ through $m_r$ and $m_l$. Notice that as $\phi$ maps onto $m_r$ and $m_l$ according to Eq. (2) and (3), respectively, it is possible to analyse the system by considering only $s$ and $\phi$; that is, the dynamics of the loop $s \rightarrow \phi \rightarrow (m_r, m_l) \rightarrow s$ can be reduced to the co-modulation dynamics $s \leftrightarrow \phi$. Briefly, the main message of the analysis we have presented so far is that the regimes $R_1$ and $R_2$ are generated and sustained by different dynamics of co-modulation $s \leftrightarrow \phi$. Having seen how $R_1$ and $R_2$ are generated, in the rest of this section we analyse the transition between these regimes in terms of the stability of the co-modulation $s \leftrightarrow \phi$.

The stability of $s \leftrightarrow \phi$ during a single trial of gradient climbing is presented in Fig. 9 by using the Poincare map. At $t = 0.2$ and $t = 0.7$ seconds the co-modulation is unstable but moving towards the region of stability represented by the diagonal line; at $t = 1.2$ seconds it is near the stable region with $s = -2.3$; at $t = 7.7$ seconds it stabilizes with $s = -1.98$, corresponding to $R_1$ (some values are not
shown in the graphic). The co-modulation dynamics maintains stability while the agent is moving towards the centre of the environment engaged in the sensorimotor behaviour $SM_1$. As soon as the agent approaches the centre, at $t = 80$ seconds, the co-modulation starts losing its stability, as shown by the sequence of grey points near the region pointed at by the arrow $R_1$. At $t = 101$ seconds the co-modulation is totally unstable and transiting to another stable region; after $t = 104$ seconds it is near the stable region, and at $t = 107$ seconds it stabilizes with $s = 1.2$. The stabilization completes the transition from $R_1$ to $R_2$. In sum, the dynamics of $s \leftrightarrow \phi$ starts unstable, converges to the stable pattern corresponding to $R_1$, becomes unstable again, and then converges to another stable pattern corresponding to $R_2$.

The Poincare map can also be interpreted in an alternative way. This map was generated for the phase relation $\phi = \pi/2$ which corresponds to the motor activity $m_r = 1.16$ and $m_l = 0.96$ – according to Eq. (2) and (3), respectively. We can read the Poincare map as being the representation of the agent’s sensory input when its motor states are $m_r = 1.16$ and $m_l = 0.96$. In this case, when the agent is moving towards the centre of the environment these motor states map onto a sensory input $s \sim -1.98$ (point of stabilization in the Poincare map corresponding to the regime $R_1$); and when it approaches the centre the motor-sensory dynamics become unstable and eventually settle down in a different stable pattern with $s \sim 1.2$ (point of stabilization in the Poincare map corresponding to the regime $R_2$). For both values of $s$ ($s \sim -1.98$ and $s \sim 1.2$) there is a micro variation in the order of $10^{-2}$ as the agent’s movement and consequently the derivative of the distance to the centre of the environment, which is measured by the agent’s sensor, do not vary smoothly (shown by the small oscillations in the distance depicted in graphic 3-B).

Figure 8. Relations between $s$ and $\phi$ that generate the dynamical regimes $R_1$ (black line) and $R_2$ (grey line), respectively. Horizontal dashed line highlight the value of $s$ below which the fixed points appear in the state space of $\phi$.

Figure 9. Poincare map showing the values of $s$ at every time $\phi = \pi/2$. The diagonal line highlights the region of the map where $s$ remains constant at $\phi = \pi/2$. The numbers near the black points show the approximated time in seconds of the value of $s$ shown on the y axis. The arrows indicate the regions to where the co-modulation dynamics $s \leftrightarrow \phi$ converge during $R_1$ and $R_2$. These regions are highlighted by the black points.
Notice that the topology of the state space underlying $R_1$ is different from the one underlying $R_2$; more specifically, the transition from $R_1$ to $R_2$ is not characterized by a movement of the system to a different region of the state space (e.g. movement to a different basin of attraction), but by a modification on the topology of the state space $[0, 2\pi]$ caused by a different dynamic structure of $s$.

Also notice that whereas the agent’s internal dynamics operates in a metastable regime, the agent as a whole operates in a stable limit cycle dynamics – represented by the trajectories in state space defined by $s$ and $\phi$ depicted in Fig. 8. These regimes are compatible with each other as the fact that the variable $\phi$ is metastable – characterized by the passage near saddle node bifurcation points ($\phi_G$ and $\phi_L$) – does not exclude the existence of stable limit cycles in the whole system consisting of $s$, $\phi$, $m_r$ and $m_l$.

Basically, so far we have shown two patterns of sensorimotor behaviours $SM_1$ and $SM_2$ and their underlying metastable dynamical regimes $R_1$ and $R_2$, we have shown that these dynamical regimes are generated and sustained by the continuous co-modulation between $s$ and $\phi$; and have analysed how the transition between regimes takes place in relation to the stability of the co-modulation $s \leftrightarrow \phi$.

### 4.3. Effects of the motor-sensory coordinated coupling on the HKB model

In this section we perform an experiment to analyse how the dynamical and informational properties of the agent’s internal oscillatory dynamics change when the modulations $s \rightarrow \phi$ and $\phi \rightarrow s$ are not coupled with each other. A single trial of the experiment consists of an agent performing gradient climbing starting from a random position and orientation in the environment and with random initial phase relation. We record the sensory dynamics of this agent and then play it back to the same agent starting from the same position and random initial phase relation. By doing that the controller of both agents (normal and recorded) are modulated by the same control parameter dynamics – i.e. $s \rightarrow \phi$ is the same for both agents – however only the first agent is able to modulate its own control parameter – i.e. only the first agent has $\phi \rightarrow s$ coupled to $s \rightarrow \phi$. The agents will be referred to as “coupled” and “decoupled”.

For all initial conditions tested (10000 trials) the dynamics of the internal oscillatory dynamics of the coupled agent always converges to $R_1$ and then it switches to $R_2$ (such dynamical pattern transition will be written as $R_1 \rightsquigarrow R_2$). This result is exactly what we have shown in the previous section. On the other hand, the internal dynamics of the decoupled agent might converge either to the same pattern $R_1 \rightsquigarrow R_2$ or to a different one $R_3 \rightsquigarrow R_4$, see the density distributions of phase relations for these patterns in Fig. 10. Accordingly, the dynamics between $s$ and $\phi$ in the coupled and decoupled agents may also differ from each other, as shown in Fig. 11.

The probabilities of convergence to either $R_1 \rightsquigarrow R_2$ or $R_3 \rightsquigarrow R_4$ depend on the difference between the initial values of $\phi$ in the coupled and decoupled agents, as shown in Fig. 12. The initial distance from the agent to the centre of the environment and the angle of the agent’s body in relation to the centre do not affect the regimes to which the controller converges. The probability of the decoupled agents to converge to $R_1 \rightsquigarrow R_2$ given an initial phase lag within $(0,0.17]$ is 97.6% (see first bar on the left of the graphic); and for a lag within $(6.11,6.28]$ the probability is 99.3% (see last bar on the right of the graphic). The probability of the decoupled agents to converge to $R_3 \rightsquigarrow R_4$ given an initial phase lag within $(2.62,2.79]$ is 98.2% (see the longest grey bar in the region before $\pi$ radians). When the agent converges to $R_3 \rightsquigarrow R_4$ the agent’s behaviour is totally non-functional as it keeps moving in
Figure 10. Density distributions of the oscillatory regimes that the decoupled agents (those that receive the recorded input of an agent with full sensorimotor coupling—see text for details) might converge to. The oscillatory dynamics converges either to $R_1 \rightarrow R_2$ or to $R_3 \rightarrow R_4$ (see legends). Lines without markers show the difference between $R_1$ and $R_3$ (graphic A) and $R_2$ and $R_4$ (graphic B).

circles around its starting position. Summing up, the dynamical properties of the agent’s controller depends on whether $\phi$ modulates $s$; when there is modulation, the controller always converges to $R_1 \rightarrow R_2$. In the absence of modulation the controller might converge either to the functional $R_1 \rightarrow R_2$ or to the non-functional $R_3 \rightarrow R_4$. This result suggest that the emergence of functional metastable patterns in the situated HKB model – i.e. patterns that generate gradient climbing behaviour – depend not only on the structure of the agent’s sensory input but also on a coordinated coupling of the agent’s motor-sensory dynamics.

Finally, we study how the informational properties of the system change when the modulations $s \rightarrow \phi$ and $\phi \rightarrow s$ are not coupled to each other. The amount of information that the controller of the decoupled agent carries about sensory stimulation is equal or smaller than the amount of information carried by the controller of the coupled agent. The amount of information is equal when the
controller converges to \( R_1 \rightarrow R_2 \) and smaller when it converges to \( R_3 \rightarrow R_4 \).

This difference is analyzed with information-theoretic measures applied to \( s \) and \( \phi \) dynamics considering 20 trials of the experiment in which the coupled agent converges to \( R_1 \rightarrow R_2 \) and the decoupled one to \( R_3 \rightarrow R_4 \) (methods are described in the Appendix). Particularly, we measured: a) the Shannon entropy of the sensor – referred to as \( H(s) \) – which gives the amount of bits needed to "codify" the sensory dynamics; b) the mutual information between \( s \) and \( \phi \) of the decoupled agent – referred to as \( I(s; \phi_d) \) – which gives the amount of information the controller has about the sensory dynamics; and c) the conditional mutual information between \( s \) and \( \phi \) of the coupled agent given \( \phi \) dynamics of the decoupled agent – referred to as \( I(s; \phi_c | \phi_d) \) – which gives the amount of information carried by the controller of the coupled agent that is not already present in the controller of the decoupled agent. In essence these measures will inform us about how the information present in the controller about sensory activity changes with and without the modulation \( \phi \rightarrow s \) – see Fig. 13.

The agent’s sensory dynamics needs \( \approx 5 \) bits to represent all its possible states, as shown by \( H(s) \). The controller of the decoupled agent carries \( \approx 3.5 \) bits of information about the sensory dynamics, as shown by \( I(s; \phi_d) \); and by adding the modulation \( \phi \rightarrow s \) the amount of information increases by \( \approx 0.5 \) bits (\( \approx 14\% \)), as shown by \( I(s; \phi_c | \phi_d) \). This result suggests that the informational content that the agent’s controller carries about its control parameter \( s \) is greater when \( \phi \) and \( s \) modulates each other than when only \( s \) modulates \( \phi \) or, in other words, the modulation of sensory activity by motor behaviour increases the amount of information present in the agent’s oscillatory network.

5. Discussions and conclusions

The contribution of this paper is twofold, it presents a dynamical analysis of the extended HKB equation within a closed sensorimotor loop and also gives theoretical insights into the interplay of sensorimotor behaviour and neural oscillatory dynamics.

We have shown qualitatively different sensorimotor behaviours – \( SM_1 \) and \( SM_2 \) – and their underlying metastable regimes of phase relations – \( R_1 \) and \( R_2 \), respectively. This result is relevant mainly in the context of the Coordination Dynamics framework as it presents a simple case of the relation between metastability in the HKB model and sensorimotor behaviour. We have also shown that the regimes

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Figure 12. Percentage of agents (y axis) that converge to either \( R_1 \rightarrow R_2 \) (black bars) or \( R_3 \rightarrow R_4 \) (grey bars) according to the difference between the initial \( \phi \) in coupled and decoupled agents. The state space \([0, 2\pi]\) was divided into 36 equally spaced intervals represented by the bars.
Figure 13. Information-theoretic measures for the agent’s controller with and without the modulation \( \phi \rightarrow s \). All measures represent the mean over 20 trials and error bars their standard deviation. On average the agent’s sensor entropy \( H(s) \) remains around 5 bits. Under open loop conditions the mutual information between the decoupled agent’s controller and its sensor \( I(s; \phi_d) \) stays at \( \approx 3.3 \) bits while the agent is approaching the centre of the environment (time in seconds is represented on the x axis) and slightly increases to \( \approx 3.6 \) when the agent is moving around the centre of the environment. The controller of the coupled agent carries 0.5 bits of additional information about the sensor that is not present in the controller of the decoupled agent, shown by \( I(s; \phi_c|\phi_d) \).

\( R_1 \) and \( R_2 \) are generated and sustained by continuously modifying the derivative throughout the state space of \( \phi \) in a structured way through \( s \), and, at the same time, by continuously modulating \( s \) through \( \phi \) via \( m_r \) and \( m_l \). In the context of Coordination Dynamics, this result helps to understand how different metastable regimes can be generated and sustained by the HKB model when it is within a sensorimotor loop. More generally, this result suggests that an agent’s internal oscillations depend on sensorimotor dynamics to engage in functional metastable regimes; that is, the ongoing interaction involving an agent and its environment generates and sustains the agent’s coherent metastable oscillatory regimes.

The density distributions of phase relations for the regimes \( R_1 \) and \( R_2 \) – presented in graphic 5-B – suggest that, for this specific model, the synchronization strength between the oscillators is enough to distinguish between the different sensorimotor patterns the agent can engage in. Particularly, during \( SM_1 \) and \( SM_2 \) the oscillators get synchronized in the same ranges of phase difference \([0, \pi/2]\) and \([\pi, 3\pi/2]\); but the magnitude of synchronization at \([\pi, 3\pi/2]\) is higher during \( SM_1 \) than during \( SM_2 \). This result is in accordance with some empirical works in neuroscience that seek to identify synchronized clusters in the brain correlated to an animal perceptual-motor activity, as cited in the Introduction section. Hipp et al. (2011), for instance, have found that the magnitude of synchronization in the beta and gamma frequencies across distributed brain areas could predict a subject perception – bars crossing one another or bouncing off each other. For a more detailed discussion on the functional roles of synchronous and desynchronous oscillations for the generation of coherent sensorimotor coordinations see Santos et al. (2012). There the authors analyse a theoretical model and suggest that i) the information about an agent’s sensorimotor dynamics is evenly distributed throughout the entire range of phase relations without a privileged status to either synchronous or desynchronous oscillations and ii) both synchronous and desynchronous oscillations carry similar causal contribution for the generation of an agent’s coherent sensorimotor coordination.

Another result we have shown is that the transition from \( R_1 \) to \( R_2 \) takes place when the co-modulation between \( s \) and \( \phi \) becomes unstable. This result suggests that an agent’s internal oscillations switches between functional metastable regimes when the dynamics of interaction involving the agent and its environment becomes unstable. While a pattern of motor activity is mapped onto another pattern on the agent’s sensory activity – i.e. the interaction is stable – then the agent’s internal dynamics settles down into a metastable pattern (e.g. \( R_1 \)); but once the same mo-
tor activity starts generating a different sensory stimulation – i.e. the interaction becomes unstable – the agent’s internal dynamics makes a transition to another metastable pattern (e.g. $R_2$). This result shows how the transition between dynamical regimes in the situated HKB model depends on the stability of the agent’s sensorimotor contingencies.

The experiment with recorded input further investigates the continuous mutual coordination and interdependence between the agent’s sensorimotor behaviour and its internal oscillatory dynamics. It shows that the dynamical properties of the agent’s controller depends on whether $\phi$ modulates $s$; when there is modulation the controller always converges to $R_1 \leadsto R_2$ and in the absence of modulation the controller converge to either $R_1 \leadsto R_2$ or $R_3 \leadsto R_4$. In other words, the modulation of the agent’s sensory dynamics by its motor activity ($\phi \rightarrow s$) assures that the controller converges to the functional metastable regimes $R_1$ and $R_2$ that generate coherent sensorimotor behaviours for the agent to perform gradient climbing. In the absence of this modulation the agent’s internal oscillations and its motor-sensory dynamics might become uncoordinated and consequently generate a non-functional interaction between the agent and its environment. More generally, this experiment suggests that functional metastable oscillatory regimes are tightly dependent on the agent’s sensorimotor contingencies, as when the agent’s sensory activity is not coordinated to what the agent is doing then the internal oscillations might converge to a non-functional regime.

The modulation of the agent’s sensor by its motor behaviour through the environment not only influences the dynamical properties of the agent’s controller, but might as well increase the mutual information between the agent’s controller and its sensory dynamics. Particularly, we have shown that the mutual information between $\phi$ and $s$ is greater when there is co-modulation $s \leftrightarrow \phi$ than when only $s$ modulates $\phi$. This result should be more carefully investigated with more variations of the experiment as it could be only by chance that the regimes $R_3$ and $R_4$ presented a mutual information lower than $R_1$ and $R_2$; however, it still remains interesting for opening the discussion on whether the uncertainty of neural oscillations about sensory stimuli decreases under modulation of motor activity.

These results and the type of mathematical analysis we have carried out throughout this paper can contribute to the ongoing debate about the constitutive role of action for perception, bringing it down to the field of neurodynamics. In short, proponents of the constitutive role of action for perception (O’Regan and Noe 2001a,b, Noe 2004, Myin and O’Regan 2008) claim that perceiving is a form of action:

In the sensorimotor contingency theory, the experienced quality of perceptual feelings is taken to arise from the precise ways in which one perceptually explores one’s environment. Sensorimotor contingencies […] are the ways in which, during such an exploration, perceptual input varies as a function of perceptual exploratory actions. (Myin and O’Regan 2008, p.192)

Opponents of this view (Clark 2006, Prinz 2006), concede that action is causally relevant for perception, but not that it is necessary for perception to occur, i.e. action is not constitutive of perception. Without going into details we want to point out that the abstract philosophical discussion about the role of action for perception can benefit from the mathematical and computational modelling we have presented here. In particular it can illustrate in detail the notion of constitution. In the case of our agent, reaching $R_1 \leadsto R_2$ was not just the result of receiving the appropriate input (caused by direct or indirect motor activity), but the result of a fine grained coordination process that depends on fine grained sensorimotor contingencies. In more complex and realistic sensorimotor conditions (both on the side of the controller, the environment and the sensory and motor functions), it is to be expected
that the available number of metastable regimes \( R_n \) be much higher than the 4 we found on our agent. As a result, if one was to interpret a particular metastable regime as a neural correlate of a perceptual “state”, it would be practically impossible to achieve it without the right sensorimotor contingencies being generated-by and, in turn, modulating the very metastable oscillatory regime. It is in this sense that the constitutive nature of action for perception can be explicitly identified and characterized. In the context of the coordination dynamics theoretical paradigm, the present model becomes an explicit illustration of the interaction between what Kelso and Engstrom (2006) call the organism~environment complementary pair and the perception~action complementary pair.

The metastable regimes that the HKB model can illustrate have been hypothesized to be the signature of brain functioning. Despite evidence of metastability in empirical experiment of animals performing perceptual motor coordination tasks (as described in the introduction), to our knowledge there was no previous model of a situated HKB system that operates in a metastable region, coupling internal metastable oscillations to sensorimotor coordination dynamics through a control parameter. The model we have developed and analyzed in this paper has contributed to fill this gap and has shown the tight dependency that can be established between an agent’s neural oscillatory metastable regimes and the sensorimotor contingencies it makes possible when coupled to the environment.

Appendix A. Information-theoretic measures

Shannon’s entropy (Shannon 1948) is shown in Eq. (A1), where \( p(x_k) \) is probability mass function of the outcome \( x_k \).

\[
H(X) = -\sum_{k=1}^{b} p(x_k) \log(x_k), \quad (A1)
\]

The mutual information (Shannon 1948, Cover and Thomas 2005) is shown in Eq. (A2), where \( H(X) \), \( H(Y) \) are the entropies of the sets \( X \) and \( Y \) respectively, and \( H(X, Y) \) is the joint entropy of both sets.

\[
I(X; Y) = H(X) + H(Y) - H(X, Y), \quad (A2)
\]

The standard measure of conditional mutual information (Cover and Thomas 2005) is shown in Eq. (A3).

\[
I(X; Y|Z) = \sum_{x \in X} \sum_{y \in Y} \sum_{z \in Z} p(x, y, z) \log_2 \frac{p(x, y|z)}{p(x|z)p(y|z)} \quad (A3)
\]

where \( X, Y \) and \( Z \) are sets of discrete random variables; and \( p \) is the probability mass function for the given subscripts \( (x, y \) and \( z) \).

The temporal dynamics of the information-theoretic measures were captured by using a moving window of 10 seconds; i.e. the probability mass functions were calculated considering a moving window containing 10000 data points. The continuous value of \( s \in [-3.92, 3.92], \phi_c \) and \( \phi_d \in [0, 2\pi) \) are discretized into 50 equally spaced bins.
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