The adjustment-deployment dilemma in organism's behaviour: theoretical characterization and minimal model

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Abstract—Intermittent behaviour (movement interspersed with pauses) is a broad biological phenomenon which is observed in organisms ranging from protozoans to mammals. We depict a coordination problem that is part of the general structure of intermittent behaviour: the adjustment-deployment dilemma. This dilemma captures the difficult compromise between the time spent in adjusting a response and the time used to deploy it: the adjustment process improves fitness with time but we also assume that such fitness decays with time (e.g. environmental conditions change), if you spend very little time adjusting the fitness of the action is poor, but if you spent too much time before deployment the result is no longer valid. We provide a mathematical model of the dilemma, general enough to be applicable to different instances of it. An optimal solution is then simulated and analysed, the result shows that the optimal strategy is the one that maximizes the number of interactions with the environment. We explore the biological significance of such results and provide a minimal mechanism capable to instantiate an optimal solution. We conclude with a summary of the contributions of the present work and suggest potentially fruitful areas of future work.

I. INTRODUCTION: INTERMITTENT BEHAVIOUR AND THE ADJUSTMENT-DEPLOYMENT DILEMMA

Most models of biological behaviour are based on steady state assumptions, considering that actions occur at constant speeds. However, many organisms' behaviour (ranging from protozoans to mammals) is intermittent: they move, pause briefly, and move again. These pauses last from milliseconds to minutes, being part of a dynamical system by which organisms adjust their behaviour to changing environments [1].

Intermittent behaviour is a widespread biological pattern. And, despite the energetic costs of acceleration and deceleration, a variety of benefits arise when pauses are alternated with action. Intermittent bounding and undulating flight modes in birds (which alternate periods of flapping with pauses where wings are either extended to permit gliding or held close to the body) save mechanical power compared to continuous flight over a broad range of speeds [2]. A similar effect takes place in fishes 'burst-coast' swimming [3]. Many species, when chasing a prey, alternate pauses and moves to stabilize their sensory field. Thus, while moves tend to be straight, both pursuits of a prey and changes of direction are initiated after pauses [4–8]. 'Saltatory search' in foraging animals (from insects and lizards to mammals) minimize the search time by alternating phases of fast motion and phases of intensive search [9; 10].

All these examples, all along the biological spectrum, follow a common underlying pattern that combines two mutually-exclusive stages:

- *Adjustment* would be a behaviour that improves the position of an organism or increases its possibilities of making the most of its situation (by increasing potential energy during flapping, augmenting perception in a pursuit to localize the prey or moving to non-explored areas in searches).
- *Deployment* would be a behaviour that takes advantage of the possibilities generated in the previous phase (by keep flying without further energetic costs, moving towards the chased prey or scanning the new area).

Interestingly, the intermittency between adjustment and deployment is not a mere sequencing of complete or autonomous behavioural patterns, but poses a problem of functional coordination dynamics: how long do I have to spend gliding before I flap again? how much time do I need to spend focusing and pointing before I shoot? what is the best ratio between stopping for orientation and walking in a changing environment? A correct dynamic equilibrium between adjustment and deployment is crucial in most cases and might change under different circumstances. We have coined the term *adjustment-deployment dilemma* to name this generic characterization of this problem. To our knowledge, no explicit theoretical, mathematical or simulation approach has yet explicitly addressed it.

Despite the ubiquity of this intermittency between adjustment and deployment, most computational and theoretical models typically operate on two broad categories of modelling frameworks: a) continuous and situated steady behaviour (e.g. the agent approaches a light source but does not stop to rest, orient or propel itself) or b) some kind of action selection or decision making procedure that operates over a perceived situation and then triggers a behavioural response (without much consideration of the temporal dimensions of the interaction). In both frameworks the temporal structure of the adjustment-deployment dilemma is either absent (due to abstraction and simplification assumptions or due to the constrained scope

Concept	Notation	Behaviour	Description
Suitability	$f(t)$	Adjustment: $f(t) = (1 - e^{-t/\tau})$ Deployment: $f(t) = (e^{-t/\varepsilon})$	Mean ability of an organism of maximizing the achievement of its goals.
Choice	$\gamma(t)$	Adjustment: $\gamma(t) = \gamma_0$ Deployment: $\gamma(t) = \gamma_1$	Binary exclusive choice of an organism between adjustment and deployment.
Performance	$\overline{p}(t)$	$\overline{p}(T) = \frac{1}{T} \int_0^T \gamma(t) \cdot f(t) dt$	Mean results obtained during deployment.
Optimal solution	$f_{opt}(t)$	$f_{opt}(t) = \underset{f(t)}{\arg\max}\ \overline{p}(t)$	Behaviour that maximizes performance.

TABLE I

MINIMAL INTERMITTENT BEHAVIOUR MODEL: CONCEPTS

of the modelled behaviour) or is hidden to explicit analysis (since the focus typically remains on global task performance or specific mechanisms and procedures). And yet, despite its lack of modelling attention, the adjustment-deployment dilemma seems perfectly suited to become a widely applicable modelling subject in theoretical biology and Artificial Life (in analogy with other classical modelling subject like the prisoners dilemma [11], the exploration-exploitation dilemma [12], action-selection paradigms [13] or the salesman problem [14]—to mention but a few).

In this paper we abstract and formalize the minimal structure of the adjustment-deployment dilemma providing a general model that covers different instances of it, defining the problem structure and optimal solution. The model is introduced in section II. Section III compares its results with existing experimental data and section IV presents a minimal structure implementing the model and analyzes it in dynamical terms. Finally, section V suggests some directions for future research

II. FORMALIZATION OF THE ADJUSTMENT-DEPLOYMENT DILEMMA

In order to explore the adjustment-deployment dilemma we have simplified the problem to its minimal form. In general terms we have an organism adjusting its behaviour (or solution) and then executing or deploying it. Let us take for example the case of the copepod *Eucalanus pileatus,* which displays intermittent feeding movements depending on its developmental stage and food concentrations [15]. Feeding rates can be affected by the proportion of time during which a copepod moves its appendages, thus creating a feeding current and/or swimming slowly, letting large amounts of water pass close by or over the copepod's sensors. Also, the amount of water displaced is higher when appendages movements are faster. Video recorded observations allow to determine which strategy is triggered depending on the level of food concentration in the environment: as levels of food concentration decrease, copepods spent increasing percentages of time on appendage motion, while appendage movements frequency decreases.

In terms of our adjustment-deployment dilemma, we see how when the environment conditions are harder (low food concentrations), copepods spend more time in adjustment (i.e.,

moving their appendages) while deployed *solution quality* decreases (lower frequency of appendage movement).

More explicitly, we have expressed the model in a series of mathematical terms, which are seen in Table I. We introduce them in the following subsections.

A. Suitability (fitness)

It represents the mean ability of an organism of maximizing the achievement of its goals. The suitability (or the quality) of a solution in an instant t is denoted by $f(t) \in [0, 1]$. We will assume that:

1) The organism has an adjustment mechanism for improving its behaviour over the environment. It is known the functional relation between the quality of a solution and time during adjustment. Generally, it is a nonlinear function (the effort in obtaining better results grows in relative terms with time), and we assume it to be exponential, $f(t) = K(1 - e^{-t/\tau})$, where τ is the adjustment speed.

2) We assume that the solution degrades throughout time as the environment changes. Also being exponential the functional dependency between quality of a solution and time, i.e., $f(t) = K(e^{-t/\varepsilon})$, where ϵ stands for the degradation rate.

B. Choice

The resolution structure of the dilemma can be captured with a single variable denoted by $\gamma(t) \in \{\gamma_0, \gamma_1\}$, that is, as the binary exclusive choice of the system over time, γ_0 representing adjustment and γ_1 deployment.

Now, the following equations to describe the behaviour of the system result from the previous formalization:

- **Adjustment:** $f(t) = 1 - e^{-t/\tau}$, $\gamma(t) = \gamma_0$
- **Deployment:** $f(t) = e^{-t/\varepsilon}$, $\gamma(t) = \gamma_1$

The structure of the dilemma can thus be reduced to finding the strategy (i.e. the value of $\gamma(t)$) that obtain the better results.

C. Performance

In order to compute the quality of the obtained results by a specific $\gamma(t)$ we will define the evolution of the fitness over time:

$$\dot{f}(t) = \begin{cases} \frac{1}{\tau}(1 - f(t)), & \gamma(t) = \gamma_0 \\ -\frac{1}{\varepsilon}f(t), & \gamma(t) = \gamma_1 \end{cases} \quad (1)$$
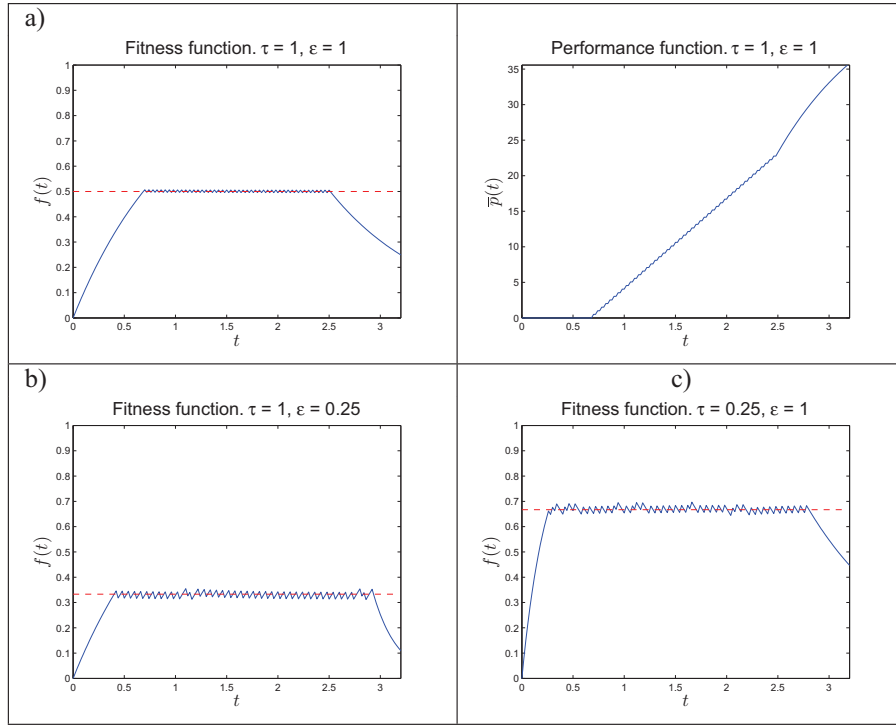
Fig. 1. Representation of the optimal strategy for different situations: a) fitness and performance functions for $\tau = 1, \epsilon = 1$, b) fitness function for $\tau = 1, \epsilon = 0.25$, c) fitness function for for $\tau = 0.25, \epsilon = 1$. The dashed line represents the value of $f_{opt}(t)$.

The agent performance will be obtained just integrating the fitness of the system during the deployment periods (the ones in which the agent is obtaining a benefit from the world, so we will take $\gamma_0 = 0$, and $\gamma_1 = 1$). Both previous functions can be combined, obtaining the global behaviour equation:

$$\dot{f}(t) = -\gamma(t) \cdot \frac{1}{\varepsilon} f(t) + (1 - \gamma(t)) \cdot \frac{1}{\tau}(1 - f(t)) \quad (2)$$

And the quality of the obtained results will be defined by the performance of the agent, $\overline{p}(T)$, evaluated in an interval $(0, T)$:

$$\overline{p}(T) = \frac{1}{T} \int_0^T \gamma(t) \cdot f(t) dt \quad (3)$$

D. Optimal behaviour

The optimal solution of the system, $f_{opt}(t)$, is the one that maximizes $\overline{p}(T)$. Due to the difficulty of obtaining the optimal solution of the model by analytic techniques, we used dynamic programming techniques to solve the problem. Specifically we have chosen to use the Bellman criteria [16]. The obtained strategy tends (as seen in Figure 1):

- not to maximize the fitness but to reach a intermediate value ($f_{opt}(t)$) which is kept until the process is about to end.
- to maximize the number of behavioural changes (i.e the alternation between adjustment and deployment).

The value of the optimal behaviour $f_{opt}(t)$ depends on the relation between τ and ϵ (Figure 2).
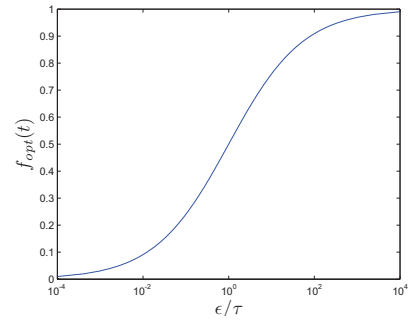

Fig. 2. Quality of the solution for the optimal strategy $f_{opt}(t)$.

In a nutshell, the optimal solution to the adjustment-deployment dilemma can be captured under the following dictum: 'when the environment changes, the best behaviour is the one that maximizes the number of interactions with the world, being the optimal fitness level determined by the dynamics of the environment'.

III. BIOLOGICAL SIGNIFICANCE

Another interesting result of the presented model is that $f_{opt}(t)$ is going to determine the amount of time that the agent spend in adjustment and deployment. Specifically, when execution time tends to infinity, the relative time spent in

deployment is going to be equal to the mean of the optimal fitness value:

$$r_{dep} = \frac{1}{T} \int_0^T \gamma(t) \approx \frac{1}{T} \int_0^T f_{opt}(t) \qquad (4)$$

This result represents that, for example, when adaptation is slower than environment changes, an organism will spend more amount of time in adjustment and will develop strategies with poorer solution quality. That is coherent with empirical data:

- In adult viviparous lizards r_{dep} is around 0.7 and 0.8 for general locomotion, while it is reduced to nearly 0.25 when the lizards are actively searching for prey [17]. That is, when an agent has enough time to exploit its adjustment, it can afford high fitness strategies (Figure 1.c), while low fitness strategies will be developed by an agent when available deployment time is smaller (Figure 1.b).
- Several studies pointed out behavioural changes of animals looking for preys as the searching environment changes. When preys are more difficult to detect or when environments are visually more complex, the value of r_{dep} decrease [18–20].

The percent of the time spent in deployment varies greatly among different organisms. As seen in [1], r_{dep} ranges from 0.04 to 0.94 for different tasks and species. Also, according to experimental data [10], r_{dep} follows a binomial distribution in foraging animals. Meaning that most foragers either spend more time searching than moving or spend more time moving than searching. Being very little the number of foragers that spend similar amounts of time searching and moving. These results can be seen in Figure 2, where, if ϵ/τ is assumed log-uniformly distributed, in most of the cases r_{dep} would be either small or big, and only a little percent of the cases r_{dep} would have medium values.

IV. A MINIMAL MODEL-MECHANISM THAT SOLVES THE ADJUSTMENT-DEPLOYMENT DILEMMA

Assuming the model presented before, is it possible for an agent to implement this optimal strategy in a changing environment? And if so, what structure is necessary to implement such behaviour coupled with the dynamics of the environment? We sued continuous-time recurrent neural networks (CTRNNs) in order to implement a dynamical system capable of developing the optimal strategy.

It was found that just one neuron is able to adapt to certain particular dynamics of the world. Moreover, the same neuron was also able to couple to any other new dynamics without any further training.

A. Continuous-time recurrent neural networks

CTRNNs are a good choice for proposed task because (1) they are the simplest nonlinear, continuous dynamical neural network model; (2) despite their simplicity, they are universal dynamics approximators in the sense that, for any finite interval of time, CTRNNs can approximate the trajectories of any smooth dynamical system [21].

The general form of a CTRNN with N neurons is:

$$\dot{y}_i = \frac{1}{\tau_i}\left(y_i + \sum_{j=1}^N w_{ij}\sigma(g_j(y_j + \theta_j)) + I_i\right) \qquad (5)$$

where $i = 1, 2, ..., N$, y is the state of each neuron, τ is its time constant ($\tau > 0$), w_{ij} is the strength of the connection from the jth to the ith neuron, θ is a bias term, g is a gain term, $\sigma(x) = 1/(1 + e^{-x})$ is the standard activation function, and I represents a constant external input. In this case, the only knowledge the network has about the world was the current quality of the solution being implemented, i.e. $I = K_f \cdot f(t)$, where K_f is a gain term.

One of the neurons (e.g. $i = N$) was considered as the output of the system. This output will determine the values of $\gamma(t)$, and therefore the following $f(t)$.

$$\gamma(t) = \begin{cases} 0, & y_N(t) \leq 0 \\ 1, & y_N(t) > 0 \end{cases} \qquad (6)$$

Once the neural networks were defined, by the use of a genetic algorithm it was found the network that develops an optimal behaviour. The genetic algorithm tended to select with more probability the networks that achieve a higher value of $\bar{p}(T)$ in a simulation.

B. Adaptation

Before the adaptation, they were defined the $\tau(t)$ and $\epsilon(t)$ functions, which defined the dynamics of the world at each moment. These functions will determine the value of $f_{opt}(t)$.

Firstly, it was tried a static situation: $\tau(t) = 1$, $\epsilon(t) = 1$, $f_{opt}(t) = 0.5$. Given these dynamics, the genetic algorithm was executed for various sizes of neural networks. The result was that even for CTRNNs with $N = 1$ (one single neuron), the network was able to obtain the optimal results for the given dynamics (Figure 3).
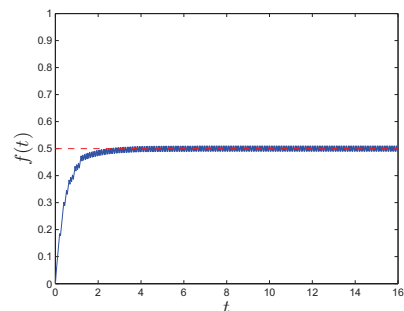

Fig. 3. Fitness function $f(t)$ for $f_{opt}(t) = 0.5$ (dotted line). Response of a single-neuron network.

C. Adaptation without learning

From now on, it was taken the single-neuron network adapted to $f_{opt}(t) = 0.5$ without any change. The objective was to observe the response of this neuron to environments with dynamics that have never seen by the network. The
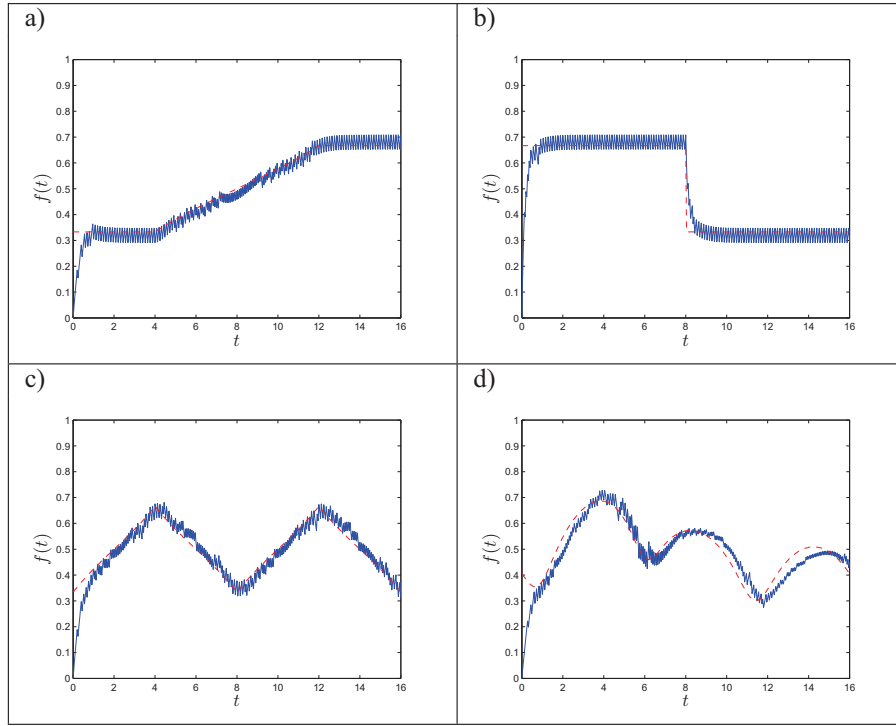
Fig. 4. Fitness $f(t)$ of the resulting neuron, without any further learning, tried for different world dynamics: a) $f_{opt}(t)$ as a ramp function, b) $f_{opt}(t)$ as a step function, c) $f_{opt}(t)$ as a triangle waveform and d) $f_{opt}(t)$ as results of defining $\tau(t)$ and $\epsilon(t)$ as sinusoidal functions.

dynamics tried consisted in defining $f_{opt}(t)$ as a) a ramp function, b) a step function, c) a triangle wave and d) $f_{opt}(t)$ as result of defining $\tau(t)$ and $\epsilon(t)$ as sinusoidal functions.

The result was that the neuron was able to adapt to any of these changing dynamics obtaining an optimal performance (i.e., with $f(t) \approx f_{opt}(t)$) as seen in Figure 4. Therefore, the mechanism implemented for a single neuron for adapting to a particular world dynamic ($f_{opt}(t) = 0.5$) was also able to adapt to any other smoothing changing dynamic without any further training.

The same results were observed when the genetic algorithm obtained in the first place a neuron adapted to any other given dynamics different to $f_{opt}(t) = 0.5$. The resulting neuron was always able to adapt to the new changing $f_{opt}(t)$.

D. System behaviour

This result was achieved because of the resulting structure of the neuron and its consequent behaviour. That behaviour is based on the coupling between the externals (the environment) dynamics and the internal (the neuron) dynamics of the system. The system external dynamics were represented by the variations of the fitness function $f(t)$, that is, $\dot{f}(t)$ (representing the effect of the agent behaviour on its own situation in the world). Similarly, we took $\dot{y}(t)$ for representing the system internal dynamics, determined by the variations of the internal state $y(t)$. With the purpose of seeing intuitively the effects of the different dynamics ($\dot{f}(t)$ and $\dot{y}(t)$ are quite spiky functions), the systems dynamics were represented by the variables $\dot{f}_m(t)$ and $\dot{y}_m(t)$, being the filtered moving averages of $\dot{f}(t)$ and $\dot{y}(t)$.

Within these parameters the neuron behaviour could be explained at different levels:

1) When $f(t) \simeq f_{opt}(t)$ (Figure 5), the neuron feedback loop is able to compensate the output deviations. That makes the neuron behave like an nonlinear oscillator around $f_{opt}(t)$.
2) If $f_{opt}(t)$ has a constant value, but fitness is not at this optimal value, i.e., $f(t) \gtrless f_{opt}(t)$ (Figures 6.a and 6.b), then the system tends to converge to $f(t) = f_{opt}(t)$. Internal and external dynamics ($\dot{y}(t)$ and $\dot{f}(t)$) act together in order to adapt fitness to its optimal value.
3) In the last case, when $f_{opt}(t)$ is changing throughout time (Figure 6.c), the following happens. If $f_{opt}(t)$ changes, that means that the world dynamics (i.e. the adaptation and degradation rates) are changing, therefore $\dot{f}_m(t)$ changes and $f(t)$ is no longer around $f_{opt}(t)$. Nevertheless, the system dynamics $\dot{y}(t)$ are going to change in reaction to the changes in $\dot{f}_m(t)$, counteracting them. This will recover the equilibrium of the system in a new point, which will be $f(t) = f_{opt}(t)$.

As seen, the system is able to act in two different time levels. On the first one the agent can respond to transient changes of $f(t)$, keeping the fitness at its optimal value alternating adaptation and deployment. On the second time level (slower than the first one) the agent can adapt its average fitness value to $f_{opt}(t)$, expanding the adaptive opportunities of the agent.
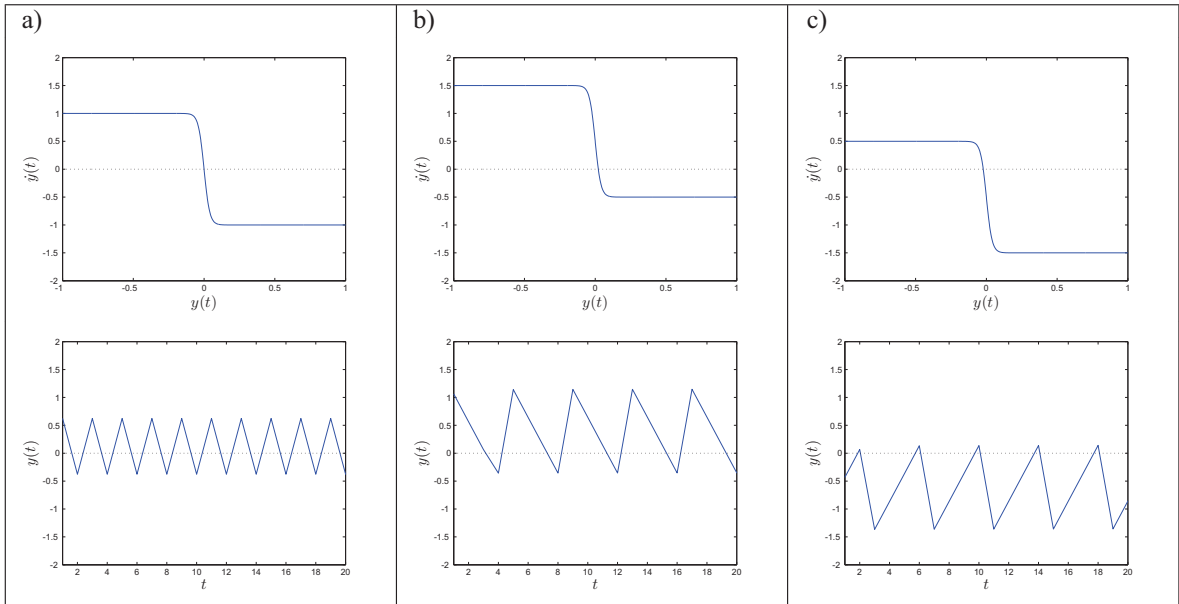
Fig. 5. Values of $\dot{y}(t)$ and $y(t)$ when a) $f(t) = 0.5$, b) $f(t) = 0.25$ and c) $f(t) = 0.75$. $y(t) \gtrless 0$ determines if the neuron generates or executes a solution (notice that in each case $r_{dep} = f(t)$). Therefore the functions describe a case where the neuron a) generates solutions as much times as it executes them, b) generates solutions more times than it executes them and c) generates solutions less times than it executes them.
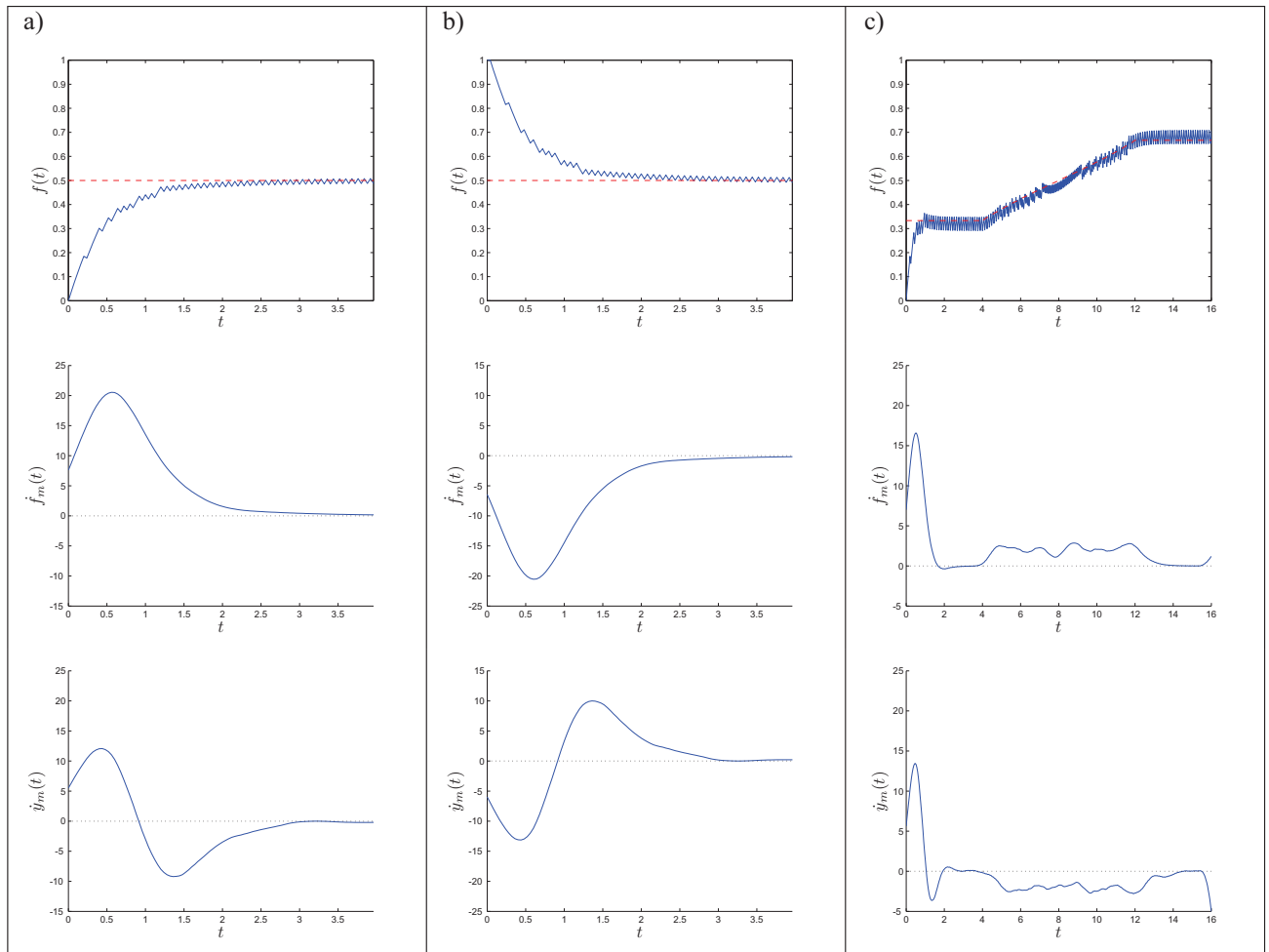

Fig. 6. Values of the system fitness $f(t)$, the system external dynamics $\dot{f}_m(t)$ and the system internal dynamics $\dot{y}_m(t)$ for different situations. The different situation dynamics are defined by the value of $f_{opt}(t)$, represented by the dashed line.

V. Conclusion

In this paper we have depicted an essential aspect of intermittent behavior, namely the *adjustment-deployment dilemma*, the dynamic interplay between the time spent on adjusting a solution to the environment or bodily circumstances before deploying it, and the execution time taken by the deployment of the solution. Despite its ubiquity in biological behaviour, to our knowledge, this is the first characterization, formalization and modelling approach to the adjustment-deployment problem. We have formalized mathematically the structure of this dilemma and numerically computed its optimal solution for different values of the problem-structuring parameter which turns out to be the ratio between speed of adjustment and speed of the adjusted solution decay while deployment takes place. The optimal solution to the adjustment-deployment dilemma, for fixed ratio between increasing quality of adjustment and decay-rate while deploying, turns out to require a compromise with non-maximal quality and a high rate of alternation between adjustment and deployment.

The distribution of optimal strategies over the range of parametric values takes a sigmoidal shape, meaning that, overall distribution of solution should show many instances of biological behaviour where adjustment is very fast and longer periods of deployment are present or the contrary; i.e. long periods of adjustment followed by quick deployment. The distribution of intermittency in animal behaviour seems to match our model's optimal solution distribution.

But what are the mechanisms capable to achieve the optimal solution under changing conditions? A CTRNN composed of a single node was shown to be capable of achieving this optimal solution, being its input an indicator of the success of its deployment. The results suggests that optimal solutions to the adjustment-deployment dilemma could, in principle, be instantiated on very simple mechanisms, if the appropriate conditions are met, and should therefore be accessible even to unicellular systems.

Needless to say the present model is still in need of further development. Some of the underlying assumptions should be relaxed and the model complexified. For instance, many crucial temporal aspects of the adjustment-deployment dilemma were left aside in this study and many of them might provide avenues for future research. The inclusion of forced perceptual delays, evaluation delays (the organisms need to take some time to taste a food source, or to evaluate the outcome of its interaction), the possibility of overlap between adjustment and deployment, constraints on deployment duration, etc. should be included in further development. The measurement of fitness and quality of solution could also be enriched by including additional cost function to deployment (energy expenditure), adjustment (risk of being detected/hunted) or associated with the switching between the both of them, and a variety of spatial and embodiment constraints.

Future development should also include reference-to and modelling-of specific examples of animal behaviour that face the adjustment-deployment dilemma, compare the model to existing data and include the necessary adjustments on parameters and, most probably, add more dimensions to the problem.

We have shown that, when faced with the adjustment-deployment dilemma, we gain more by assuming a compromise with a suboptimal quality solution and maximizing our interactions with the environment. Is this a principle of minimal cognition? The generality of the model and the robust results indicate that it should be [22]. But further work is needed to extend and appropriately support the results developed along this paper. Interestingly our preliminary results support the adequacy of the situatedness principle that is so characteristic of the artificial-life-route-to-artificial-intelligence: recurrent testing of our solution into the environment renders betters results than indefinitely adjusting our models of the solution. We have also shown how very simple mechanisms can find solutions to relatively complex problems, illustrating how a wide range of living systems could successfully cope with domain invariant adaptive problems like the adjustment-deployment dilemma. Our model also brings forth the necessity to include the temporal dimension of cognitive processes into our theoretical framework. Speed, intermittency, decay-rates, and deployment duration crucially matters when it comes to real-world problem solving. We hope to have contributed with the beginning of yet another dimension, the adjustment-deployment dilemma, of the multidimensional structure of living behaviour.

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