

**EMERGENCE OF ADAPTIVE SEARCHING RULES FROM  
THE DYNAMICS OF A SIMPLE NONLINEAR SYSTEM**

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**Abstract**

Various organisms share certain basic rules for a searching behavior. We hypothesize that these rules may emerge from basic properties of nonlinear systems as a whole, rather than being evolved from a scratch gradually. In order to support this hypothesis, we have developed a virtual agent that consists of three simple nonlinear oscillators. These oscillators are driven by an internal noise, which results in phase transitions in their activity. External stimuli modify the activity via sensors and food consumption. The interaction among the activity of oscillators and external influences give rise to an emergence of searching rules that are similar to those shared by various organisms, thus favoring the above hypothesis. The hypothesis can be verified further by investigating various types of nonlinear systems in different environments.

*Keywords:* adaptive rules, dynamic systems, artificial agents

*Running head:* Emergence of searching rules

## 1. Introduction

An adaptive behavior in living beings could be described as a set of rules for adaptive responses to stimulation. This leads naturally to designing of artificial agents provided with explicitly defined rules that control, for example, searching behavior. This approach allows for a study of holistic behavior emerging in individuals from interactions among rules. The subsumption architecture of autonomous robots (Brooks, 1986) and virtual ecosystems (Terzopoulos, Tu, & Grzeszczuk, 1994) are representative examples of such an approach.

However, the research in the field of artificial agents provides also an opportunity to raise a fundamental problem: what is the origin of searching rules in real organisms? One answer to the problem is that the rules are developing gradually, starting from scratch, in a course of natural selection. This answer is intuitively appealing, but, in fact, it provides little insight regarding the origin of adaptive rules. An alternative answer to the problem is that a variety of basic searching rules can emerge as a whole from basic properties of nonlinear dynamics that underlie the animal behavior. The same nonlinear phenomena may reveal themselves in very different systems; therefore, one might expect the resulting searching rules, at least basic ones, to be principally similar in different organisms.

A first step to verify the last answer is to provide a simple nonlinear dynamic system with input from sensors that can perturb its internal activity and, therefore, change its output. Such a system can be investigated as a simulated agent whose movements in a changing environment depend on the output. No purposeful modification of the system should be made in order to produce pre-defined rules. If such a primitive no-purpose agent will be able to reveal, at least, several adaptive searching rules similar to those observed in organisms, this could be seen as an argument in favor of our suggestion. Furthermore, methods based on an artificial evolution of dynamic systems are well developed in the fields of Artificial Life and

robotics (Harvey, Thompson, Husbands, Jakobi, & Cliff, 1997; Beer, 1997; Kodjabachian & Meyer, 1998). These methods possibly could be applied to the primitive agent in order to incrementally make it more complex and capable of producing more wide range of adaptive rules. A success of such an artificial evolution could additionally support the idea that the biological evolution had started with a “ready-made” set of behavioral primitives based on the properties of nonlinear dynamic systems, rather than created the primitives anew.

Herein, we present a simple “dynamic agent” which produces biologically plausible rules for searching behavior of simpler types: unguided wandering, olfactory orientation using one sensor, and response to single food items as well as food patches.

The paper is organized as follows. In the next section, we consider what is required of the dynamic system to study the origin of biologically plausible behavioral rules. Specific searching tasks and searching rules used by organisms to accomplish these tasks are described in Section 3. The architecture of the agent is described in Section 4, and Section 5 shows how the agent accomplish the above tasks and which rules it produces. In the Section 6, we discuss to what extent the agent’s behavior conforms principles of animal behavior (6.2), how the agent produces searching rules (6.3), as well as implications for the use of artificial agents to study the origin of adaptive behavior in living beings (6.4).

## **2. General considerations and approach**

The dynamic approach is well established in the field of “New Artificial Intelligence” based on biological insights (Steels, 1994; Beer, 1997). However, several basic properties of organism’s behavior should be taken into consideration when designing an agent capable of producing a variety of biologically plausible behavioral rules.

### 2.1. Spontaneous activity in organisms

All organisms from unicellular ones to higher animals are capable of displaying spontaneous behavioral activity. In bacteria *Escherichia coli*, for example, this activity stems from an interaction of metabolic cycles within a bacterial cell. This activity manifests itself at a behavioral level as an apparently spontaneous wandering: a sequence of tumbles alternating with straight runs which are randomly directed and have varying duration (Berg & Brown, 1972; Müller, di Primio, & Lengeler, 2001). In higher animals, a nervous system, as well as its components like ganglia, reveals self-organizing dynamics (Erdi, 2000), which may give rise to a complex spontaneous activity. The One example is short-term oscillations of activity in mice, which could be explained by a dynamic chaos in nervous activity (Guillot & Meyer, 2000). Another example is complex fractal activity pattern in *Drosophila* under constant condition (Cole, 1995; Martin, Ernst, & Heisenberg, 1999). In the last case, evidences were found that some neuronal circuits in the neural system of *Drosophila* were responsible for the pattern (Martin, Raabe, & Heisenberg, 1999). Thus, central pattern generators (CPG) drive the spontaneous activity in organisms.

This spontaneity can be interpreted in terms of autopoietic theory. According to the theory, a living being is an operationally closed system, that is, a self-referring system which operates on its own states. The process, which takes place within this system, produces components that interact in such a way that they maintain the same process that produces these components (Maturana, 1980; Varela, 1992). Thus, the process is autopoietic (self-creating) and is aimed solely at its own maintenance, while the observable spontaneous activity is an external manifestation of this process. This implies that the activity per se is not necessarily aimed at accomplishment of any particular task, rather it provides a basis for

generation of adaptive rules for various tasks (see Section 2.3).

## 2.2. *Variability and structure of the spontaneous activity*

It should be emphasized that spontaneous movements of living beings are notoriously variable, like the length and direction of runs in wandering bacteria. Many authors argued (though using different arguments) that the intrinsic behavioral variability is an essential part of behavioral adaptation (see, e.g., Stewart, 1995; Mobus & Fisher, 1999; Inglis, 2000).

This quantitative variability is typically accompanied by a qualitative structure of spontaneous activity. In bacteria *E. coli* (Berg & Brown, 1972; Müller et al., 2001) and nematode *Caenorhabditis elegans* (Pierce-Shimomura, Morse, & Lockery, 1999; Shingai, 2000) this structure consists of alternation of two distinct behavioral modes. In the absence of changes in external stimulation, they spontaneously switch between relatively straight randomly directed runs and sharp changes in movement direction: tumbles in bacteria and sharp turns in nematodes. Spontaneous fractal behavioral sequences also imply apparent temporal structure: behavioral events are clustered, while clusters are divided by wide gaps. In *Drosophila*, for example, events are stops divided by periods of motion (Cole, 1995). Similarly, the swimming of goldfish in the uniform environment consists of runs divided by series of turns (Nepomnyashchikh & Gremyatchikh, 1996). Both the active periods in *Drosophila* and the runs in goldfish have variable duration.

## 2.3. *Generation of behavioral rules*

The autopoietic theory postulates that external influences do not determine the intrinsic spontaneous process; rather they perturb it according to dynamical laws that control the

process. From the viewpoint of external observer, perturbations of the process are seen as responses to external stimuli according to some behavioral rules (Maturana, 1980; Varela, 1992; Riegler, 2001). This means that any behavioral rule reflects dynamical laws of the above basic process. In other words, any behavioral rule an organism is able to produce is nothing else but a modification of the basic spontaneous process.

The postulate can be illustrated using examples from the previous section. The movement pattern of bacteria (Berg & Brown, 1972) and nematode (Pierce-Shimomura et al., 1999) modifies when they perceived a chemical stimulus. Runs directed roughly away from the source of stimulus are quickly terminated by a change in movement direction, while those directed roughly toward the source last longer. As a result, both species reveal an efficient orientation in gradients of chemicals. When goldfish is presented with a visual landmark, turns become clustered around them, so that fish explores an area around the landmark (Nepomnyashchikh, 2000). Thus, the structure of spontaneous activity does not change fundamentally in all these organisms, rather quantitative changes serve to adjust it to the changed external situation.

#### *2.4. Dynamic systems and artificial agents*

A considerable amount of research has been focused on designing dynamic systems to control walking and swimming in artificial agents. This research is inspired by CPGs that control various patterns of locomotion in animals. These CPGs are able to send coordinated output patterns to motor neurons in the absence of any external commands or sensory feedback (that is, spontaneously), and modify the patterns if perturbed by a peripheral sensory feedback or central commands (see reviews: Delcomyn, 1999; Cohen & Boothe, 1999; Cruse, 2002). Various kinds of artificial neural networks (ANN) are typically used to

develop artificial CPGs. “Cells” that are used in ANNs may be of simple sum-and-fire type or are able to generate oscillations of their own. ANNs can be evolved in the course of artificial evolution or configured manually. Herein, we can mention only few results obtained in this research area.

It has been shown that simple ANNs consisting of several cells may possess patterns of intrinsic oscillations with the same phase relationships as gaits observed in bipeds, quadrupeds and hexapods (Collins & Stewart, 1993). The cells have a periodicity of their own, while weights of cell-to-cell connections account for the phase difference among cells and, therefore, for a particular gait. The same CPG is capable of switching among various gaits observed in animals. The switch results from bifurcations caused by a change in connection weights (Stewart, Golubitsky, Buono, & Collins, 1998; Buono & Golubitsky, 2001; Buono, 2001).

Likewise, other researchers have developed the CPGs to model walking gaits and swimming. Stimuli from environment can evoke the switch not only between gaits generated by the CPG, but also between walking and swimming. This is achieved by changing particular state variables in cells by signals from sensors (Arena, 2000; Fortuna, Arena, Bálya, & Zarándy 2001).

ANN-based CPGs, evolved initially for locomotion, potentially allow also for the control of movement direction, provided they receive an input from the olfactory or other sensors (Kodjabachian & Meyer, 1998; Ijspeert & Arbib, 2000; Ijspeert, 2001). One way to achieve such a control is to construct a CPG of cells that reveal nonlinear dynamics and may switch between a limit cycle and stable point depending on an input from the sensors. A hexapod agent driven by such a CPG can avoid obstacles because of the inhibitory input, for example, from the left sensor to the cell that controls the middle right leg. When an obstacle is perceived, the cell switch to the stable point because of the inhibition, and the leg does not lift

until the agent turns away from the obstacle and the cell switches to a limit cycle (Arena, Fortuna, Frasca, & Patané 2002).

These results (and many others) suggest that, besides patterns of locomotion, nonlinear oscillators may provide a basis for generating various kinds of searching behavior as well. Husbands, Harvey, and Cliff (1995) have evolved ANNs for robots using cells of sum-and-fire type, but added some quantity of noise to the sum of inputs to the cell. The noise allowed for evolving ANNs with oscillator loops which would not initiate themselves without the noise. Different ANNs have been evolved for different tasks, including finding the center of an arena, moving towards smaller or larger targets, avoiding obstacles, and orienting toward light (Harvey et al., 1997). Particularly, ANNs have been developed for moving towards a triangle as opposite to a square. In a number of evolved ANNs, rhythmic pattern generation output occurred. The ability of these ANNs to both produce and modify central pattern generation output in response to sensory input accounted for the solution of the task (Smith, Husbands, Philippides, & O'Shea, 2002).

The dynamics of these ANNs with oscillator loops was not the same in different environments. There was even a different number of attractors in different environments: in some environments there was one attractor, while there were two in the other, both attractors corresponded to adaptive solutions of the above tasks. Thus, an artificial agent as a whole may be seen as a system with internal dynamics of its own. This system is coupled to the outer world via sensors and motors. Sensory inputs, including those that result from the actions of the agent, perturb the internal dynamics and this coupled interaction generates the agent behavior (Husband et al., 1995).

Generally, however, the considerations listed in Sections 2.1-2.3 are not taken into account in the field of designing adaptive agents. First of all, the demand for spontaneous, independent of external signals activity is frequently neglected. For example, simulations of

metabolism in unicellular organisms were used to design artificial agents capable of avoiding obstacles (Ojala, 1998) and seeking for light (Ziegler, Dittrich, & Banzhaf, 1998). However, an external sensory input is needed to maintain activity of these agents. When deprived of such an input, agents run through a transient phase and reach an equilibrium state.

Even if oscillators capable of intrinsic activity are being developed for artificial agents, they usually lack the spontaneous variability and/or qualitative structure. For example, Clark, Anderson and Skinner (2000) developed the oscillator-based agent that generated varying movements in response to a repeating stimulation, but moved along a straight line if there were no external stimuli. More recently, Di Paolo (2002) developed an agent capable of internally generated zigzag movements that serve as a part of efficient taxis. However, these movements resulted in a fairly predictable wavy path in the absence of orienting stimuli.

To the best of our knowledge, only few oscillators have been developed to produce an animal-like spontaneously variable movement path. Mobus and Fisher (1999) have developed a robot driven by a quasi-chaotic oscillator. The robot moves along a wavy path that resembles the correlated Brownian walk. This type of walk is observed in living creatures and increases the efficiency of a search because it helps to avoid revisiting previously searched areas (see Section 3.1 below). Barton (1995) has developed the ANN, which dynamics can be stable, quasi-periodic or chaotic, depending on some global parameter. He attached sensors and motors to some nodes in the virtual agent. In the absence of an external input, the agent moved along an unstructured trajectory at high (chaotic) values of global parameter. The chaotic motion may be useful in searching the environment in the absence of sensory input indicating the direction to a goal. When the parameter was low (non-chaotic), the agent moved along quasi-periodic trajectory. In the presence of a gradient of stimulation from some target, the agent revealed attraction or repulsion depending on the sign of the input (at non-chaotic values of the parameter). When reaching the target, the

agent did not stop, but "hovered" around the target. Again, the "hovering" is potentially adaptive in that it may help to find more targets, and indeed is observed in a variety of organisms.

Furthermore, agents are typically developed using genetic algorithms or other tools to accomplish some pre-specified particular tasks in a pre-defined environment, e.g. the taxis. As a result, an agent reveals rules needed for known tasks and situations, but remains incapable of solving even the simplest problem that has not been foreseen by the designer. For example, a simple agent consisting of few neurons has been developed purposively for orientation within a continuous odor field (Beer & Gallagher, 1992), but it remains unclear what the agent should do if the field is interrupted by gaps, or the stimulation vanishes completely, or an obstacle is encountered. The same is true for all agents described in this section: they are able to accomplish one or two tasks. If tasks or environment are changed, a structure and/or parameters of oscillators also should be changed.

On the other hand, the efficiency of rule-based agents developed for the orientation in complex and variable environments is based on the use of a number of behavioral rules. Some rules prescribe to an agent which way to move in order to keep itself within an odor plume. If the agent loses the plume, the other rules prescribe how to cross the gap and find the plume again. However efficient these agents are (see, e.g., Belanger & Willis, 1996; Belanger & Arbas, 1998; Lytridis, Virk, Rebour, & Kadar, 2002; Li, Farrell, & Cardé, 2002), they lack for a spontaneous activity, which could drive them under unforeseen conditions. To our knowledge, no attempt has been made to start a development of an agent with a variable and structured "purposeless" spontaneous activity, and then to investigate the role this activity possibly plays in the generation of rules for different tasks and situations.

Additionally, the most widespread method for creating agents is based on ANNs that are capable of revealing complex dynamics (see references in this section). If a number of

neurons are not too large, networks' dynamics can be analyzed (Beer, 1997) and command "neurons" can be identified (Beker, Aharonov, & Ruppin, 2001). However, ANNs developed to control the agents' behavior are typically complex and it is hard to analyze them and see which type of dynamics accounts for the behavioral rules revealed by the agent.

### *2.5. General approach*

We intend to investigate if a searching behavior can emerge from the dynamics of a nonlinear system. The results obtained by various research groups, as outlined in the previous section, show that a nonlinear oscillator is an appropriate building block to construct the agent for this purpose. As we have argued above, the oscillator should possess a variable activity even in the absence of an external input. Thus, we adopt the approach similar to that of Barton (1995) and Mobus and Fisher (1999). Apart from the spontaneous variable activity, all other behaviors should emerge as a result of interaction between the system and environment via sensors and effectors (Husband et al., 1995; Beer, 1997; Stewart et al., 1998).

However, our approach differs from all those described in the Section 2.4 in another respect. Typically, dynamical agents have been evolved purposively for a pre-defined task and their parameters have been tuned to optimize their performance. On the contrary, we want to see if the same agent is able to generate a number of searching rules without any incremental improvement, optimization or complication. A sensory input can be varied, but no attempt should be made to change a structure of the dynamical system itself in order to evolve a particular behavioral rule.

Futhermore, a dynamic process, which controls the agent's behavior, should be clearly specified, if we want to see how the observed behavioral rules are generated. To this end, the

oscillator should be simple and well studied, and the whole system should consist of few oscillators only. On the other hand, we do not intend to find the simplest possible system capable of generating searching rules, or investigate to what extent the rules depend on the type of oscillator, as well as parameters and complexity of the whole system. At this initial stage of the research, our intention is to construct an abstract system and investigate experimentally which rules it can generate at those values of parameters that allows for non-periodic oscillations. At later stages, it should be investigated to what extent results obtained can be generalized to other systems that possess the similar dynamics.

Taking in mind the above considerations, we have chosen the one-dimensional logistic map  $X_{i+1} = \lambda X_i (1 - X_i)$  as a building block. The behavior of the map at various values of its parameter is well studied (May, 1976). The addition of a Gaussian noise to the parameter results in the noise-induced phase transitions at certain values of the parameter (Nepomnyashchikh & Gremyatchikh, 1996). The phenomenon is also well studied (Horsthemke & Lefever, 1984), which makes the observed agent's behavior tractable. The dynamics of the map reveals non-periodic oscillations as a result of the phase transitions.

The searching behavior in majority of unicellular and multicellular animals includes turns in opposite directions and may depend on a sort of general activation. As the searching rules generated by the agent should be compared with those observed in animals, it seems reasonable to reproduce similar turns and activation in the agent by constructing it of three identical oscillators: two of them control rightward and leftward turns in the two-dimensional space, while the third one controls the level of their activation. According to our approach, neither of these oscillators should be responsible for a separate behavioral rule. Instead, each rule should emerge from the activity of the whole system.

### 3. Tasks for the agent

If adaptive behavioral rules really may emerge from basic properties of nonlinear systems, then the same system is expected to produce rules, at least, for those tasks which are equally essential for survival of various organisms, both unicellular and multi-cellular ones. We, therefore, adjusted parameters of agent to ensure phase transitions and provided it with different types of external stimulation, but in no case we changed parameters to improve a performance of agent when it faced different tasks. We suggest that at least some of the essential tasks and expected adaptive rules to accomplish them are as described below.

#### 3.1. *Wandering*

One could suggest an ordinary Brownian walk as a simple rule for the wandering in the absence of guiding cues, but a correlated random walk is a more realistic idealization for animals' searching movements (for the sake of brevity, we refer to a walk as correlated if directions of animal's sequential movements *positively* correlate). The correlated walk has been observed under uniform experimental conditions in as different beings as spermatozoa (Mortimer, Swan, & Mortimer, 1996), mites (Dicke & Burrough, 1988) and fish (Coughlin, Strickler, & Sanderson, 1992). The fact suggests that 1) the correlated walk reflects some basic properties of organism's behavior rather than a specific organization of any particular organism, and 2) some internal mechanism can control the correlated walk even in the absence of ambient cues that could account for the correlation.

Some field and experimental data suggest also the Lévy walk as another idealization for animal wandering (Viswanathan, Buldyrev, Havlin, da Luz, Raposo, & Stanley, 1999;

Levandowsky, White, & Schuster, 1997). Like the Brownian walk, the Lévy one consists of randomly oriented uncorrelated runs, but the distribution of run lengths is different: most runs are very short and keep a walker within a restricted area; series of short runs are interrupted by rare very long runs which lead a Lévy walker far away from searched areas.

Whichever of these two idealizations one chooses for animal walk, in both cases a path of a walker intersects itself less frequently than it can be expected of an Brownian walker. As a result, animals avoid revisiting previously searched sites and find more new sites per time unit (Zollner & Lima, 1999; Viswanathan, Afanasyev, Buldyrev, Havlin, da Luz, Raposo, & Stanley, 2000), which makes the searching behavior more efficient.

Possibly, the simplest way to describe a walk quantitatively is to consider a group of non-interacting animals that spread from the same point. The spread of Brownian walkers may be described as the Gaussian diffusion. In case of non-Brownian walk, the mean squared displacement (MSD) of swarm from the point of release increases with time more rapidly as compared with Brownian walk, resulting in the “anomalous” diffusion. Real organisms indeed reveal the anomalous diffusion (Root & Kareiva, 1984; Johnson, Milne, & Wiens, 1992; Nams, 1996; Levandowsky et al., 1997; Upadhyaya, Rieub, Glaziera, & Sawadac, 2001). Therefore, one can require of wandering agents to reveal the same property in order to be both efficient and biologically plausible.

On the other hand, the anomalous diffusion is not observed over all time scales in most organisms: it becomes progressively more similar to Gaussian diffusion as the time scale increases (Johnson et al., 1992; Turchin, 1996; see also Levandowsky et al., 1997, for brief review of data on leukocytes and fibroblasts). Therefore, the increase of MSD is expected to decelerate at larger scales in a realistic agent.

### *3.2. Orientation*

When an animal finds some cue to guide it, then the wandering should be replaced with another rules. One of the most primitive types of guided movements is orientation within an odor gradient using a single sensor. This orientation is based on the interaction between spontaneous turning behavior on the one hand, and increment of stimulation the organism perceives at sequential movements, on the other. If an agent moves toward a source of stimulation, then the increment is positive and suppresses turns, thus forcing the agent to keep the current heading (Mason, 1975).

### *3.3. Escaping gaps in odor gradients*

An odor gradient is unlikely to be smooth in natural environments. It may be disrupted because of the air turbulence, or because the odor is emitted by pulses, rather than continuously. Under these circumstances, animals may persist moving in the previously chosen direction for a while, even if no odor is perceived. This would help to move through a narrow gap and encounter the next odor pulse. On the other hand, the animal should switch to some kind of searching movement if the odor is not perceived for a long time, because this may mean that the direction is wrong (Vickers, 2000).

### *3.4. Area-restricted search*

The next rule is a thorough search within a restricted area which the animals performs upon finding a single prey (Bell, 1991; Grünbaum, 1998). This rule is obviously adaptive: the

food and other resources are typically clustered in natural environments. This area-restricted search (ARS) is accompanied by a significant increase in tortuosity of animals' paths, which helps to keep it within the area. Even if the path significantly differs from random before a prey capture, it may become Brownian after the capture (Winkelman & Vinyard, 1991).

### *3.5. Sampling food patches*

The consequence of ARS is that animals show a general preference for more rich food patches. However, animals may leave even a rich patch to “sample” other patches. This sampling obviously results in a sub-optimal patch use in a short run, but might be adaptive in a long run, because it allows for tracking temporal changes in the environment and, potentially, discover most profitable food sources (Stephens and Krebs, 1986). The sampling can be observed even under simplified and stable experimental conditions, where only few food patches are available, and their distribution and quality are known to animals (Wildhaber & Crowder, 1991). This means that the sampling is not necessarily a response to the patch quality or other external influences, but may be one more manifestation of the intrinsic spontaneous activity.

## **4. Simulations**

### *4.1. Agent*

The agent consists of three oscillators and has a single odor sensor (figure 1). All oscillators are always active, while external stimuli perturb their activity via the sensor and

[ FIGURE 1 ABOUT HERE]

the food consumption. The first oscillator influences the activity of the other two, right and left oscillators that control rightward and leftward turns. Outputs of these oscillators are activating ( $F$ ), and right ( $R$ ) and left ( $L$ ) turn tendencies respectively. The outputs change by discrete steps ( $i$ ) and are kept within a restricted range by means of feedback:

$$F_{i+1} = \lambda^F_i F_i (1 - F_i)$$

$$L_{i+1} = \lambda^L_i L_i (1 - L_i) \tag{1}$$

$$R_{i+1} = \lambda^R_i R_i (1 - R_i), \quad 0 < F, L, R < 1, \quad 0 < \lambda < 4$$

We assume that there is an internal noise in oscillators that is added to parameters  $\lambda$ . For the sake of simplicity, we assume the noise in each oscillator to be white Gaussian and independent of the noise in the other oscillators. We assume further that the activating oscillator sends to both turn oscillators the excitatory output. Finally, turn oscillators inhibit one another and receive a sensory input  $I$ . Like the noise, all these excitatory and inhibitory inputs are added to parameters  $\lambda$ . Basing on these assumptions, the parameters are defined as follows:

$$\lambda^F_i = \mu + \sigma \xi^F_i$$

$$\lambda^L_i = \mu + \sigma \xi^L_i + F_i - R_i - I_i \tag{2}$$

$$\lambda^R_i = \mu + \sigma \xi^R_i + F_i - L_i - I_i ,$$

where  $\mu$  is the average parameter,  $\xi$  is the Gaussian noise varying between  $-1.0$  and  $+1.0$ , and  $\sigma$  is the peak magnitude of internal noise.

The sensor does not respond to the absolute intensity of ambient stimulation  $\mathcal{S}$ . Instead, the sensory input into oscillators represents the increment of stimulation, that is, the relative difference between the stimulation intensities perceived at steps  $i$  and  $i-1$ :  $I_i = (\mathcal{S}_i - \mathcal{S}_{i-1}) / \mathcal{S}_{i-1}$ . Thus, a positive increment causes a decrease in parameters  $\lambda$  (equations 2), and vice versa. Note that sensory inputs into the right and left turn oscillators are equal.

The output of oscillators may sink down to zero in case if a high sensory input suppresses it and/or the noise achieves the peak negative magnitude ( $-1.1$ ). We set the lower threshold for the output ( $10^{-6}$ ) in order to avoid the sinking.

To simulate a two-dimensional walk, we assume that at any step the agent turns by angle  $T_i$  (in radians) that is simply the difference between right and left turn tendencies at the step  $i$ :

$$T_i = R_i - L_i. \quad (3)$$

Upon turning, the agent moves ahead for 1 distance unit.

#### 4.2. Dynamics of oscillators

The behavior of the logistic map depends on the average parameter  $\mu$  in the absence of noise and external stimulation. The output of oscillator tends to zero at  $\mu < 1$ , asymptotically approaches a non-zero constant value at  $1 < \mu < 3$ , becomes periodic at  $\mu > 3$ , and then chaotic at a certain range of higher values of  $\mu$  (May, 1976). The results reported in the rest of the paper were obtained at  $\mu = \sigma = 1.1$  unless otherwise indicated.

[ FIGURE 2 ABOUT HERE]

Figure 2 shows how the output changes when the noise is added to  $\mu$ . The output is symmetrically distributed around the stable point if the peak noise magnitude  $\sigma$  does not exceed 0.4, but the distribution is skewed and small output values are most probable at  $\sigma = 1.1$  (intermediate noise magnitudes result in an intermediate skewness). This change of the distribution under the influence of noise can be described as the noise-induced phase transition (Horsthemke & Lefever, 1984).

[ FIGURE 3 ABOUT HERE]

Figure 3 shows the activity of oscillators in the absence of an external stimulation. The noise-induced transition results in series of high and low activity of the activating oscillator (figure 3a). The similar activity pattern is observed in symmetrical right and left turn oscillators that receive the input from the activating oscillator and inhibit one another (figures 3b and 3c). The correlation between consecutive output values of the activating oscillator is clearly seen in figure 4. Spearman correlation coefficient  $r_s$  equals 0.98 (1000 steps of iterations,  $p < 0.001$ ). The similar strong correlation is observed in the other two oscillators.

[ FIGURE 4 ABOUT HERE]

The correlation is explained as follows. An accidental temporary burst of the noise boosts the activity of oscillator. The activity remains high for a while after the burst ceases, because the behavior of the oscillator depends on its previous states. Likewise, a decrease in the noise results in a long decrease of the activity. Besides this state-dependent dynamics, the alteration

of series of high and low values depends also on random variations of the noise and therefore is not periodic.

[ FIGURE 5 ABOUT HERE]

The right and left turn oscillators are negatively correlated because of inhibitory connections between them ( $r_s = -0.21$ ,  $p < 0.001$ ). As a result, alternating series of right and left turns of the agent are observed (figure 5;  $r_s$  between consecutive turns equals 0.97,  $p < 0.001$ ). The same competition has the additional effect. An increase of excitatory output from the activating oscillator generally leads to a greater difference between turn tendencies and, therefore, to greater absolute values of turns ( $r_s$  between the activity of activating oscillator and absolute turn values equals 0.36,  $p < 0.001$ ). In other words, the activating oscillator modulates the tortuosity of agent's movements.

The effect of external stimulation on the activating oscillator is shown in figure 6. The high level of oscillator's output caused by a excitatory stimulus does not drop immediately after the stimulation ceases, but needs a time to decay. Similarly, the output needs a time to recover after being suppressed by an inhibitory stimulus. Note that the effect of stimulation depends on the state of oscillator: the excitatory stimulus produces the noticeable peak of output if the output is already high, but the response is hard to perceive if the output has not yet recover after the inhibitory stimulation. The turn oscillators respond to a stimulation in the similar way.

[ FIGURE 6 ABOUT HERE]

We will show in Section 5 that the properties of oscillators described above account for behavioral rules observed in the agent. Quantitatively similar rules are observed if the parameters  $\mu$  and  $\sigma$  are varied 1.05 to 1.20. Noise-induced phase transitions do not occur if  $\mu$  falls below 1.05, so that the outputs of all oscillators became constant and equal, and the agent moves along a straight line and is not able to respond to stimuli. If  $\mu$  exceeds 1.20, and  $\sigma$  is varied in proportion to  $\mu$  in order to ensure the phase transitions, non-periodic oscillations and responses to stimuli still are observed, but the agent reveals qualitatively different rules, especially when the parameter reaches chaotic regions. The agent still is able to perform the tasks described below, but the new rules either impair or improve the performance depending on the particular task and values of the parameters (the more detailed description to be reported elsewhere).

#### *4.3. Tasks and simulation details*

Simulations were started with all variables set to 0.1, and initial headings of agents distributed uniformly and randomly within  $360^\circ$ . Each individual run consisted of 1,000 to 100,000 steps for different tasks and was preceded by 1,000 idle steps to avoid the influence of possible transient process on agent's movements. At least 100 individual runs were performed for each task presented to the agent.

**Wandering.** In order to simulate a wandering, 100 individuals were positioned at the same point in space, and then their movements were tracked for 10,000 steps. Thus, all individual paths taken together can be viewed upon as a dispersal of the group comprised of non-interacting individuals. We assumed an ambient stimulation to be constant in the case of wandering, so that the sensor sent no input into the oscillators.

**Orientation.** Each individual path within an odor gradient started with placing the agent at 500, 1,000, 5,000 or 10,000 distance units from the center of continuous Gaussian-shaped field of “odor”, and finished after the agent had either reached the source of odor (the circle with a radius of 5 unit in the center of the field), or traveled for the total distance of 100,000 units. The absolute intensity of stimulation at the center was 100 arbitrary units.

We also inserted no-stimulation gaps across the odor field. The gaps stretched over the distance 1000 to 800 units from the source (200 units wide) or from 1000 to 500 units (500 units wide), while the initial distance from the odor source was 5000 units.

We calculated the performance rate of the agent as the initial bee-line distance to the source divided by the distance actually traveled in a successful run. In case if the agent failed to reach the source, an additional run was performed in order to replace the unsuccessful one.

**Response to a prey.** Simulations of ARS were based on the following assumptions. When an animal actually finds a prey, a time is needed to consume it. We assume that this time is relatively short in comparison with the whole process of search. Accordingly, the feeding lasted for 5 steps only in our simulations. A real animal may either eat or reject a prey it finds, depending on the prey profitability and the level of hunger. We, however, simplified our simulations and assume that all prey items are identical and the level of hunger does not changes after feeding.

As we have mentioned in the Section 4.1, all oscillators remains active anytime. That is, the activating oscillator sent its excitatory output into other two oscillators at any step of simulation, regardless of whether the agent found a prey. We assume that a food intake increases the agent’s activation. Therefore, the arbitrary chosen constant (1.0) was added to the average parameter  $\mu$  in the activating oscillator at each of 5 steps of feeding in order to simulate the excitatory effect of food intake.

Finally, we assume that the turn oscillators are still active during feeding and receive an

input from the activating oscillator, but the agent does not actually move when it consumes a food item. We used absolute values of turn angles to characterize an after-effect of feeding on tortuosity of subsequent path. The reason is that the after-effect was not long enough to calculate MSD. Simulation runs lasted for 100 steps.

For the sake of comparison, we also investigated (in separate simulations) the effect of dampening of activating oscillator on agent's movement. To this end, we added a negative constant ( $-1.0$ ) to the parameter instead of the positive one.

**Sampling.** Environment was simulated as an infinite number of parallel strips of infinite length and 100 units wide. The strips were designated as rich, poor and empty patches and allocated in the non-random sequence: rich – empty – poor – rich – empty – poor... (see also figure 12). As it was said above, the agent does not move when eating a food and so cannot find a new item during 5 steps of feeding. When moving, it encountered a food item after a different number of steps depending of the food density in a patch. The food densities varied among four independent simulation (Table). The regular rather than stochastic encounters with food items were simulated in order to avoid runs of bad luck that could provoke the agent to leave the patch. Each simulated run started with the agent placed at a random position within the environment and lasts for 10,000 steps. Each simulation included 100 independent runs.

The response of the agent to rich patches was evaluated using the performance index: the number of steps spent moving within rich patches divided by the overall number of steps spent moving in the course of a single run. The index does not include the time spent feeding, for the obvious reason that the agent should stop when feeding and this would result in a false preference of patches with higher food density.

[ FIGURE 7 ABOUT HERE]

## 5. Results

### 5.1. *Wandering*

The representative fragment of wandering path is shown in figure 7. Typically, the paths have a noticeable structure: it consists of relatively straight runs and more or less tight loops between them. Representative log-log plot of MSD vs. time spent spreading is shown in figure 8. The plot is typical in that MSD increases with time more rapidly than it is expected of a group of Brownian walkers. Thus, the agent really reveals anomalous diffusion and, therefore, non-Brownian walk without any external guidance.

[ FIGURE 8 ABOUT HERE]

On the other hand, the MSD should rise at the same rate over all time scales in case of ideal Lévy walkers, i.e. the log-log plot of MSD vs. time should fit a straight line. This is by no means a case for MSD in our simulations: agents reveal deceleration of MSD, which is consistent with the dispersal of real organisms.

The behavior of agent is explained as follows. As it was described in Section 4.2, noise-induced phase transitions result in alternating series of high and low output values in each oscillator. The analysis of individual paths has shown that loops correspond to series where the difference between turn tendencies is large. Spontaneous bursts of high output values in the activating oscillator (also caused by the transitions) enhances the activity of turn oscillators, which results in a higher difference between their outputs. As opposite, straight

runs correspond to series of similar and low values of turn tendencies, and low values of the activating oscillator's output.

## 5.2. *Orientation*

Movements of the agent within the odor gradient path consist predominantly of straight runs that are rarely directed exactly toward the source (figure 9a,b). This behavior is explained as follows.

Both the positive increment in ambient stimulation and the occasional decrease of noise magnitude suppress turn tendencies (equations 1 and 2). If these two events occur simultaneously, this may result in a series of low output of both turn oscillators and, consequently, in a straight path, even if the agent deviates from the right direction to the source.

A course correction is evoked by two events that act either separately, or in combination. First, the increment of stimulation lessens or even becomes progressively negative when the agent deviates from the source. Second, an occasional burst of internal noise may result in a spontaneous series of high output in one of oscillators.

Once the increment increases as a result of turning toward the right direction and/or the spontaneous series of high output in oscillators break off, the agent stop turning and follows a new course persistently, even if it also deviates from the source.

As a result of all these events, the agent generally turns more frequently if it moves away from the source and vice versa, which is consistent with orientation rules of bacteria and nematodes described in Section 2.3.

[ FIGURE 9 a and b ABOUT HERE ]

The agent does not stop at the odor source upon reaching it. Instead, it repeatedly leaves the source in various directions and returns to it again (not shown in figures). The agent may move up to 300 units away the source during these excursions, which could be interpreted as a sort of sampling behavior. An excursion starts when series of low output occur simultaneously in both turn oscillators under the influence of internal noise.

The agent practically always reaches the odor source from any of the four initial distances tested in the absence of no-stimulation gaps. Performance rates of the agent are shown in figure 10a. The performance for the longest distance is much lower than for any other distance (Mann-Whitney test,  $p < 0.001$ ). However, there are no significant differences among shorter distances ( $p > 0.05$ ). It may look surprising that the performance for shortest distance is not better than that for two greater distances. We did not yet analyzed this effect in details, but note that the agent frequently turns in the vicinity of the target and may repeatedly miss the target before reaching it (figure 9a,b). This “hovering” takes relatively greater part of the path if the distance is short, thus accounting for (at least, partially) the low rate of performance.

### 5.3. Gaps in gradients

The agent always reaches the source in the presence of gaps, with the exception of 6 unsuccessful runs with the initial distance of 5000 steps and the gap 500 steps wide. When entering a gap, the agent does not respond to it immediately, but follows a previously chosen course for a while. As a result, it may cross the narrow gap (200 units wide) as if it does not exist at all (figure 9a). The performance rate does not much differ from that for the conditions with no gaps and the same initial distance of 5000 units (Mann-Whitney test,  $p > 0.05$ ; compare figures 10a and 10b). This is explained by the fact that the agent is driven by the

dynamic process which depends on a “memory” of its own previous states. Namely, if the both turn tendencies have been suppressed by a high stimulation increment during a movement up the gradient, then the tendencies cannot recover rapidly, even if the stimulation have ceased (Section 4.2 and figure 6).

[ FIGURE 10 ABOUT HERE]

However, the memory span is limited, and the output eventually increases in the wider gap. As a result, the agent switches to the wandering. As the wandering path includes long straight runs, the agent has good chances to escape a gap and resume its movement toward the source (figure 9b). However, as figure 10b shows, the wandering leads to significantly lower performance in comparison with the narrow gap conditions ( $p < 0.001$ ).

#### 5.4. *Area-restricted search*

Figure 11 shows absolute values of turn angles before and after eating a single prey. It is seen that even the short feeding exerts a pronounced after-effect on turn angles, and therefore, path tortuosity. Turn angles still proceed to increase for a while after the feeding ceases, thus keeping the agent within a restricted area, and then gradually decrease. The duration of after-effect varies from 10 to 100 steps among individuals. The ARS during the feeding results from the increase of the activating oscillator’s output caused by the addition of the positive constant to the oscillator. In turn, this increase enhances the activity of turn oscillators and, therefore, evokes the intensive turning, because of competition between the two oscillators (Section 4.2). The after-effect of feeding is explained in the same way as the bee-line

movement through narrow gaps in odor gradients (Section 5.3): the tortuosity of agent's path depends on its previous states (see also figure 6).

Figure 11 also shows the response to addition of negative constant to the activating oscillator. Turn angles proceed to decrease for relatively long time after the addition, while the subsequent increase is very slow. The resulting paths are straighter than before the addition and take the agent away from the spot where the stimulation was received. Thus, the agent is able to perform not only the ARS, but also a sort of the opposite behavior that can be viewed upon as an avoidance of the area where an "unfavorable" stimulation was received.

[ FIGURE 11 ABOUT HERE ]

### *5.5. Sampling*

The fragment of individual path is shown in figure 12. After spending some time within the poor patch, the agent crosses the empty patch and finds a rich one. In general, agent's paths are more tortuous in rich patches, because more frequent encounters with food results in more frequent ARSs. However, transitions from rich patches to poor ones are also possible. Even in the simulation with the highest difference of encounter rates between rich and poor patches, agents left a rich patch in 52 of 100 runs. Like excursions to a vicinity of odor source (Section 5.2), these departures from patches are explained by spontaneous series of low oscillators' outputs. Besides, the agent's responses on stimulation depend on its state: if the turn tendencies are close to zero, the stimulation produces no effect (see figure 6). In such a case, the food consumption may not result in ARS, and the agent may stay for more shot time even in a reach patch.

The mean performance index for ratios of food densities 5:1 to 3:2 equal  $0.83\pm 0.07$ ,  $0.72\pm 0.09$ ,  $0.64\pm 0.11$  and  $0.51\pm 0.08$  respectively. Thus, rich patches were preferred to poor and empty patches at three higher ratios.

[ FIGURE 12 ABOUT HERE]

The agent Figure 13 shows Box-whisker plots of agent's performance. The indices for ratios 5:1, 3:1 and 2:1 are significantly greater than the index for ratio 3:2 (Mann-Whitney test,  $p < 0.01$ ). However, differences between these three greater ratios are not significant ( $p < 0.05$ ).

Thus, the agent reveals a behavior that is similar to sampling observed in animals. This sampling results in the preference of rich patches. On the other hand, the ability of our agent to choose more "profitable" food patches is inferior to abilities of many animals: if animals have a choice, they may spend almost 100% in a most reach patch independently of absolute food density in other patches, which is the optimal solution for similar patch choice problems (see, e.g. Stephens & Krebs, 1986). A possible (and partial) explanation is that the agent does not slow down its movements during ARS as many animals do: a slower speed of movement should increase the time spent in a rich patch. The behavior of animals is "tuned" to environments they live in, and one cannot expect of an oscillator placed in an arbitrarily constructed environment to find the optimal solution.

[ FIGURE 13 ABOUT HERE]

## 6. Discussion

### 6.1. Searching rules produced by the agent

The agent reveals searching rules, which have not been pre-programmed explicitly or evolved gradually. The rules, however, have their counterparts in real organisms, and these counterparts have obvious adaptive value:

- If deprived of guiding ambient stimuli, the agent performs a non-Brownian walk, which consists of spontaneous switches from relatively straight long runs to tight loops and vice versa. This walk results in an anomalous diffusion observed in population of agents.
- The agent switches to the oriented movement when odor gradient is found. When moving to the source of odor, it does not follow changes in stimulation continuously, but leaps roughly toward the source and corrects the chosen direction only rarely.
- If there is a gap in the gradient, the agent persists with the chosen direction for a while, which helps to get through narrow gaps and not to lose the way to source. If a gap is wide, the agent eventually resumes non-Brownian walk, which helps to find a way out of the gap more efficiently as compared to the ordinary Brownian walk.
- Upon finding a food item in some area, the agent initiates a thorough search within a restricted area and keeps doing so for a while, even if there are no more prey to stimulate the search. On the other hand, the agent leaves an area if experiences an “unfavorable” stimulus.
- The agent prefers patches with higher food density, but also reveals a sampling behavior known in foraging animals. When within a food patch, the agent may leave it

and sample elsewhere, which provides an opportunity to find richer patches. Similarly, upon reaching an odor source, it makes excursions in various directions, taking a chance to find other possible sources.

## *6.2. Are the rules biologically relevant?*

Obviously, the agent behaves in adaptive way within its simplified environment. The searching rules, which could be derived from its behavior, are strikingly similar to what is observed in many real organisms (compare Sections 3, 5 and 6.1). However, are these rules relevant to biological reality in more essential ways, besides the apparent similarity to behavior of real organisms? Many authors pointed to those principles of animal behavior, which account for their ability to solve real world problems efficiently. In this section, we compare some of these principles with those seen in the agent's behavior. To do so, we will describe the behavior of the agent as seen by an external observer, with no reference to underlying mechanisms. Also, in spite of the fact that principles defined in different ways by different authors are closely interrelated, we will consider these principles separately for the sake of clarity.

First, the adaptive behavior is autonomous. The notion of autonomy is rather broad one. As a minimum, an autonomous being selects an appropriate rule all by itself, with no instructions from outside. Our agent reveals such a minimal autonomy. However, it was argued that a real autonomy requires also an ability to create rules anew for new tasks, rather than to select them from a list prepared by the designer (Smithers, 1997). Obviously, rules described here are produced anew.

Second, it is now only a commonplace to say that an adaptive behavior is a result of interaction between intrinsic dynamics of the agent and dynamics of its environment (see e.g.,

Beer, 1997). This is the case with the agent. For example, its movements in the odor field results from the interaction between dynamics of oscillators, on the one hand, and changes of external stimulation, on the other.

Third, animals typically do not respond to a short-term stimulation by an equally short-term action. Instead, the action lasts longer than the stimulation. For example, caddis fly worms hide inside their cases when disturbed and stay there for a while even if the disturbance is not repeated. Moreover, animals may produce a prolonged sequence of actions in response to a transient stimulus. A typical example is the avoidance behavior in some juvenile organisms that performs a prolonged series of maneuvers in response to a short touch, thus avoiding more attacks. This behavior is proactive in that it does not follow a sequence of stimuli, but completely changes the external situation. It was also shown experimentally that robots avoid obstacles and get out of corners more efficiently, if they are able to produce a rather long behavioral sequence in response to a momentary stimulation (Clark et al., 2000). Our agent reveals a proactive behavior when, for example, it leaves an area where it experienced the “unfavorable” stimulation.

Forth, the agent produces rules which can be said anticipatory: the agent acts as if it expects a certain result in future even if a current stimulation does not confirm expectations. For example, the agent persists moving in a chosen direction after it has entered a gap despite the stimulation does not increase anymore. The anticipatory behavior of this primitive type is typical of real organisms, and it has been argued (Riegler, 2001), that anticipatory rules are crucial for really adaptive behavior. Furthermore, it was argued that organisms do not track continuously the stimulation from the environment. Instead, they check for external changes and correct their behavior at some moments of time only, while relying on internal anticipations at any other time. Thus, organisms avoid the unaffordable task of tracking every minute change in the incessant flow of external stimulation (Riegler, 2001). In line with the

argument, the agent corrects its movement in gradients from time to time only, and neglects external changes during lengthy time intervals.

Fifth, because an operationally closed system operates on its own states only, it has been argued also, that it does not discriminate between internal and external perturbations (Peschl and Riegler, 1999). As a result, a behavior could be generated in response to internal perturbations, with no reference to external events. This is exactly what takes place when the agent leaves the source of odor and “inspects” surrounding areas, or when it leaves a food patch and crosses an empty area when sampling patches. These inspections are potentially adaptive, because the agent has a chance to find a new odor source or a richer patch. Again, this consideration returns us to the importance of spontaneity and variability for behavioral adaptation. Agents’ movements never repeat themselves, and this accounts for variability in duration of ARS or unpredictable sampling of patches. This variability is typical of animals, and could be viewed upon as a primitive form of exploratory behavior observed in a simple agent.

Thus, behavioral rules revealed by the agent do conform, at least, some of those principles that have been proposed to account for the adaptability of animal behavior.

### *6.3. Where do the rules emerge from?*

The process that controls behavior of our agent is driven by the internal noise, which results in phase transitions and the non-periodic dynamics in each of oscillators. In turn, oscillators interact to produce movements of the agent. The observed spontaneous wandering behavior is an external manifestation of this process. All other rules produced by the agent are externally caused modifications of the wandering. There would be no emerging rules if not for this basic spontaneous behavior. These results favor a hypothesis that searching

rules shared by a variety of organisms may be rooted in basic properties of nonlinear systems. Primitive types of adaptive behavior may emerge as a whole, even from as simple system as we described here.

#### *6.4. Conclusions and implications*

The current dynamical approach to adaptive behavior is based on an assumption that desirable behavioral traits can be evolved in the course of evolution gradually, by mutation and selection of dynamic systems and their components (see e.g., Husband et al., 1995; Beer, 1997). This approach does not presume that a primitive adaptive behavior may, in a sense, be inherited to these systems. Our results lead to quite a different suggestion. An adaptive behavior in living being need not be evolved from scratch in the course of evolution. Instead, the evolution needs only develop further behavioral primitives that already had existed. This suggestion can be verified by simulating evolution of the same oscillatory system in different environments.

The behavioral rules revealed by the agent are a small part of what can be observed even in simple organisms. However, a modification of these systems may give rise to more rules. The study may start with a variation of system's parameters: for example, the logistic map used in our simulations reveals chaotic dynamics within a certain range of parameters (May, 1976), which may result in an emergence of new rules. Besides, our preliminary results suggest that new adaptive rules may emerge even without any changes of previously set parameters if the agent is provided with additional sensors. For example, we added a sensor that was activated by contact with an obstacle and sent inhibitory output into both turn oscillators in the same way as the odor sensor does. Rather unexpectedly, this made the agent capable of avoiding obstacles when moving in the odor gradient. The same sensor also made

the agent capable of wall following. The agent could “voluntarily” change the direction of wall following, or leave a wall and resume the unguided walk.

Furthermore, the searching rules described here are primitive in both meanings of the word: they are simple, and they are similar to those rules that might have evolved at the earlier stages of evolution. The problem is whether the basic simple system can be developed so that more advanced rules could emerge “ready-made”, similar to the emergence of primitive rules, without the necessity to develop them gradually. For example, is it possible to achieve this goal by adding more oscillators to an agent? Can a complex action sequence (like, e.g., foraging trips in bees) emerge in this way? Will primitive rules still be preserved, as an agent grows more complex?

Additionally, the artificial evolution of dynamic agents similar to the agent described here may provide an opportunity to raise and investigate the following problems. How simple can an underlying dynamic system be to ensure viability of populations of agents in a given environment? Why rules observed in real organisms are as they are? Why do very different organisms use essentially similar behavioral rules for similar purposes, while other rules can be imagined, at least in principle? In other words, to what extent adaptive abilities of living being, as well as evolution of these abilities, are constrained and steered by laws of the nonlinear dynamics?

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## FIGURE CAPTIONS

Figure 1. Architecture of the agent. Arrowheads and circles represent excitatory and inhibitory connections respectively.

Figure 2. Frequency distribution of output magnitudes in the oscillator at  $\sigma = 0.4$  (dotted line) and  $\sigma = 0.1.1$  (solid line). Data are obtained from the single run (1000 steps). The magnitude at  $\sigma = 0.0$  is marked with arrow.

Figure 3. Simultaneous outputs of activating (a), right turn (b) and left turn (c) oscillators.

Figure 4. First return map for consecutive output magnitudes. The map corresponds to figure 3a.

Figure 5. Sequence of turns corresponding to oscillators' outputs represented in figure 3.

Figure 6. Effect of stimulation on the output of activating oscillator. Data are averaged over 100 independent runs of simulation. Head-up and head-down arrows mark excitatory and inhibitory stimuli respectively. The length of each stimulus equals 5 steps. Note the difference between responses to the first and last excitatory stimuli.

Figure 7. Fragment of simulated path, 1000 steps long.

Figure 8. Plot of MSD vs. time spent spreading by the “swarm” of 100 individuals (circles). The line below represents MSD expected of Gaussian diffusion (slope equals 1). The upper line represents the linear regression approximation of the “swarm” MSD at first 100 steps (slope equals 1.73,  $R^2 = 0.99$ ) Note that the MSD progressively deviates from the straight line at later steps because of deceleration.

Figure 9. Fragments of agent’s path in odor gradients. Sources of odor are marked with black circles. No-stimulation gaps 200 (a) and 500 (b) units wide are represented by gray stripes.

Figure 10. Box-whisker plot of performance rates in the odor gradients. The whiskers indicate the minimum and maximum observed rates, the box is defined by the lower and upper quartiles, and the line within the box is the median ( $n = 100$ ). (a) Rates for different initial distances from the source in the continuous gradient. (b) Rates for the initial distance 5000 steps and no-stimulation gaps of different lengths.

Figure 11. The influence of “feeding” and “unfavorable stimulation” on the degree of subsequent turns (in radians). Data are averaged over 100 individuals. Vertical bar indicates duration of feeding. Black line: positive constant (1.0) is added to activating oscillator. Grey line: negative constant (-1.0) is added.

Figure 12. The fragment of agent’s path in patchily environment. Lines denote borders between patches of different quality. The start point is marked with arrow. The agent started in poor patch, crossed empty patch and finished in rich one.

Figure 13. Box-whisker plots of performance indices at different ratios of food densities in rich and poor patches. X-axis labels denote the ratio of the food density in rich patches to the density in poor patches.

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Table. Food densities and their ratios in rich and poor patches.

Simulation	1		2		3		4	
Patch type	Rich	Poor	Rich	Poor	Rich	Poor	Rich	Poor
Food density (number of food items / number of steps of movement needed to find a food item)	1/20	1/100	1/30	1/90	1/40	1/80	1/48	1/72
Ratio of encounter rates in rich patches to the density in poor patches	5:1		3:1		2:1		3:2	

Figure 1

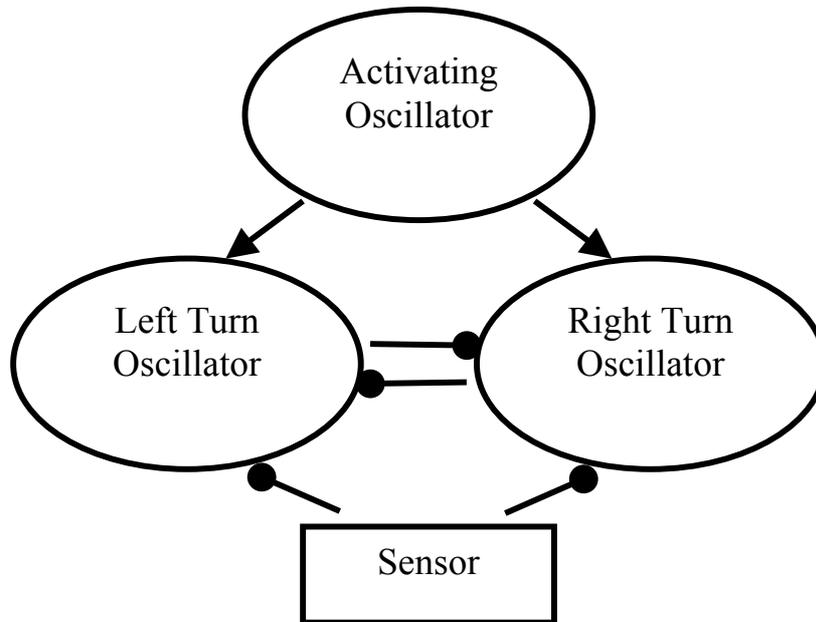


Figure 2

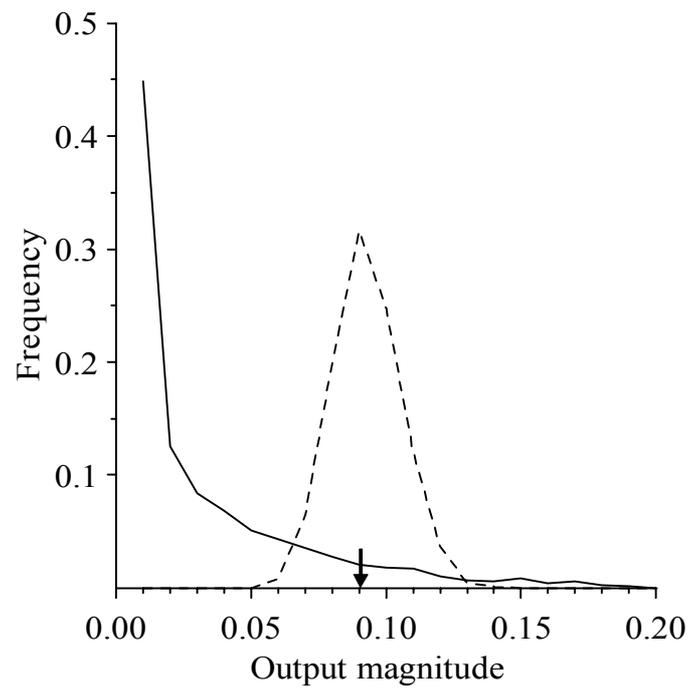


Figure 3

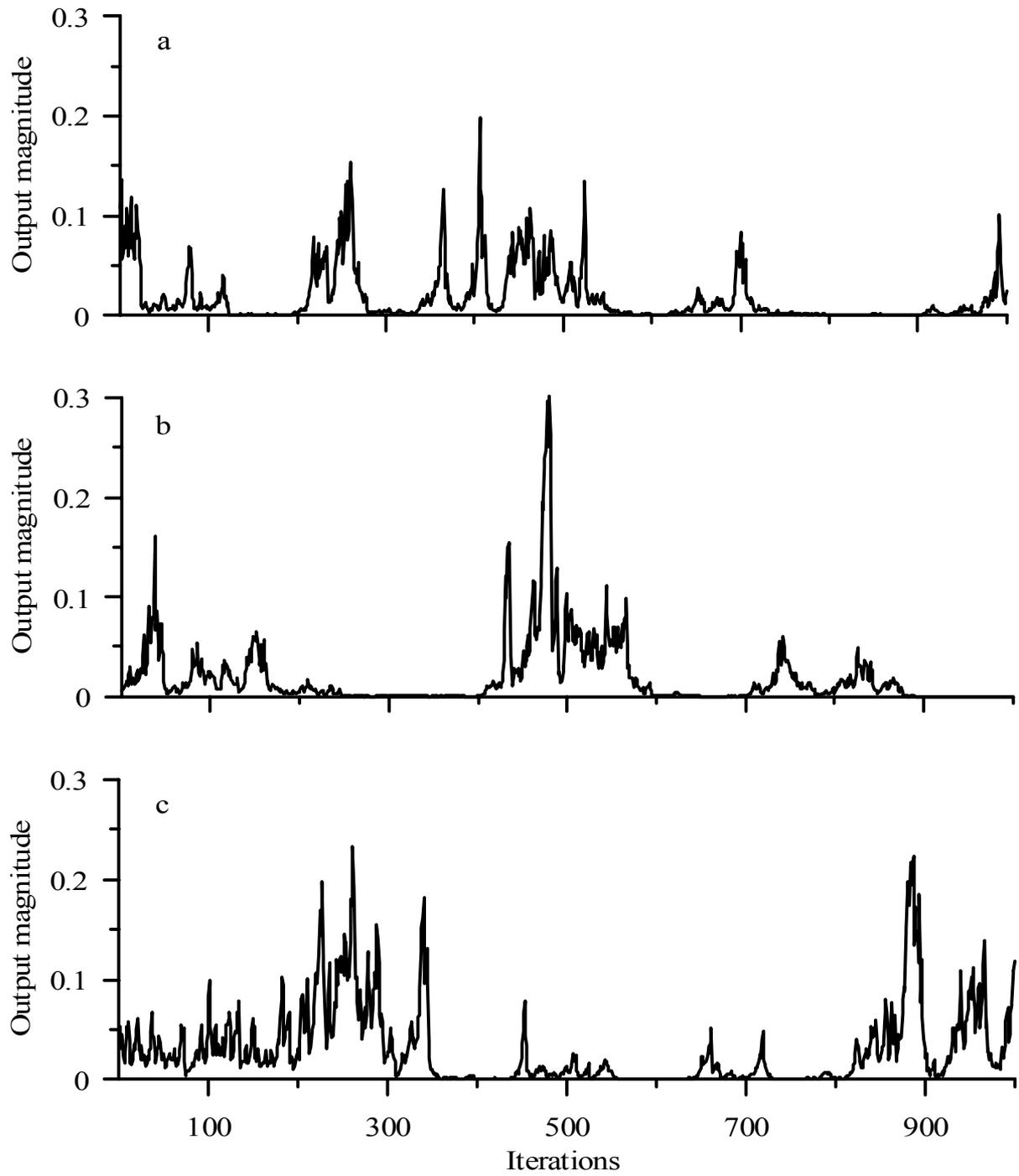


Figure 4

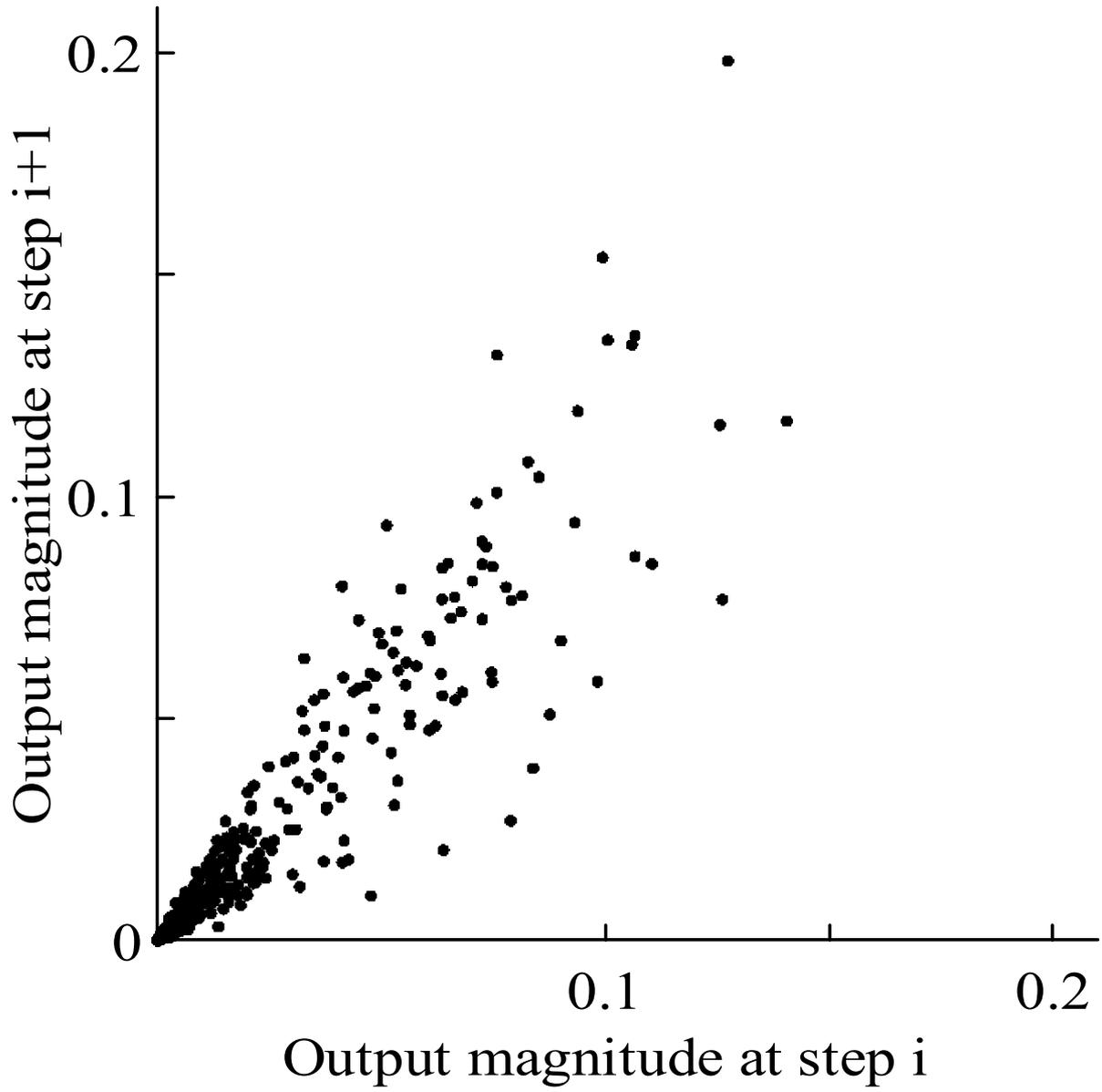


Figure 5

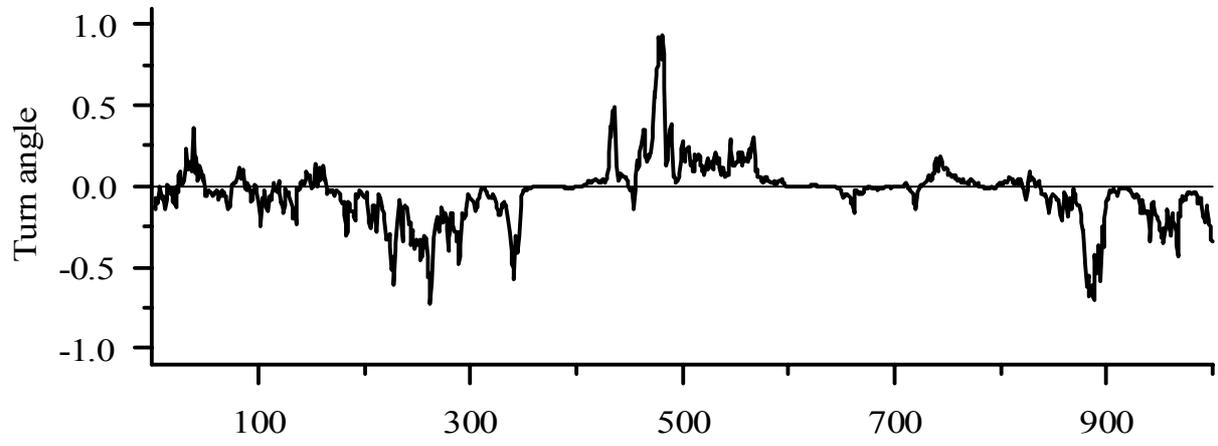


Figure 6

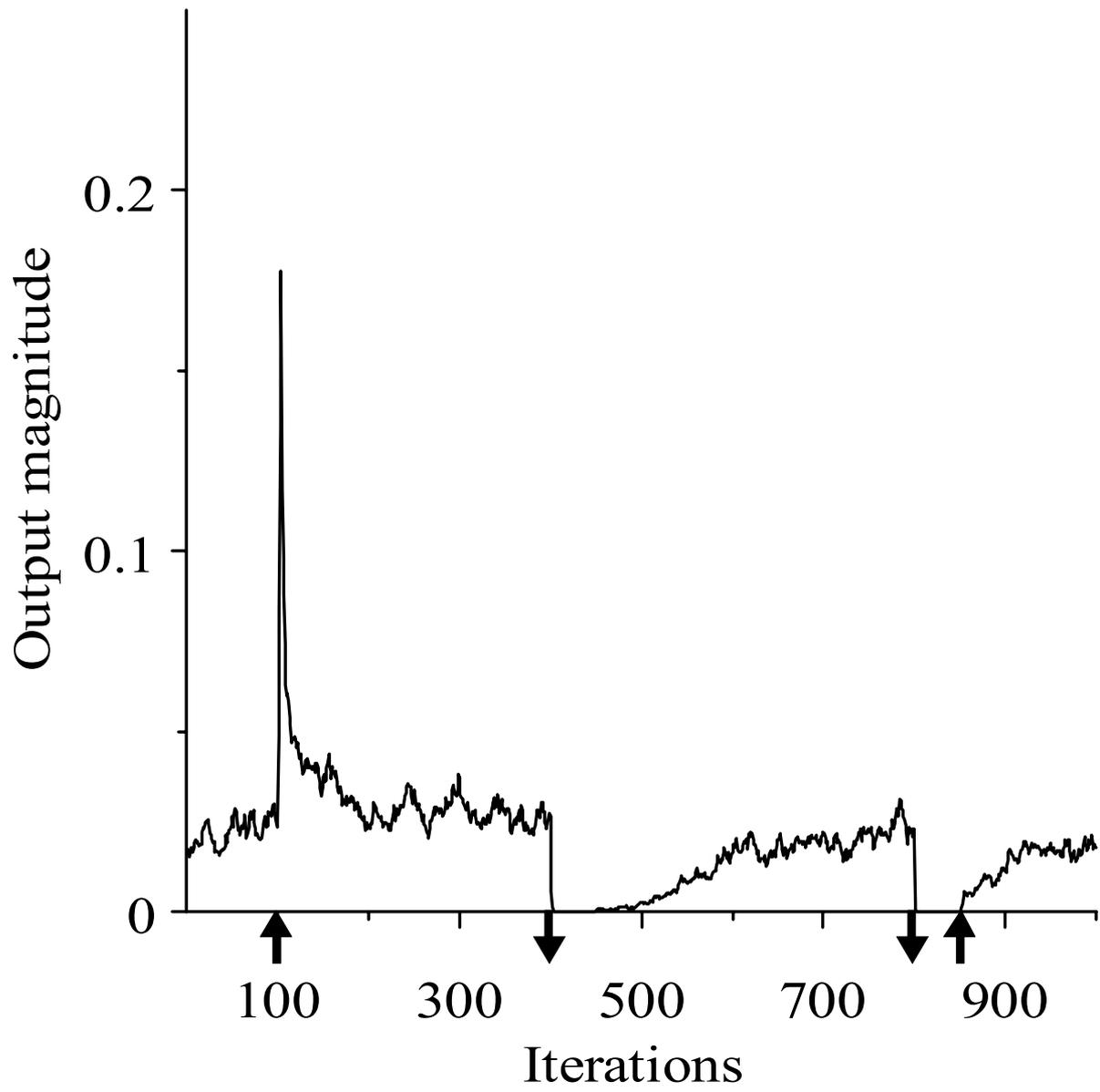


Figure 7

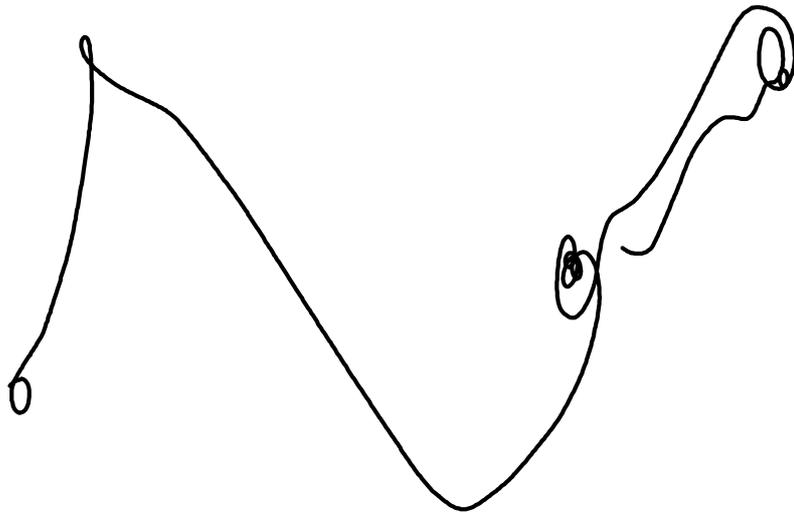


Figure 8

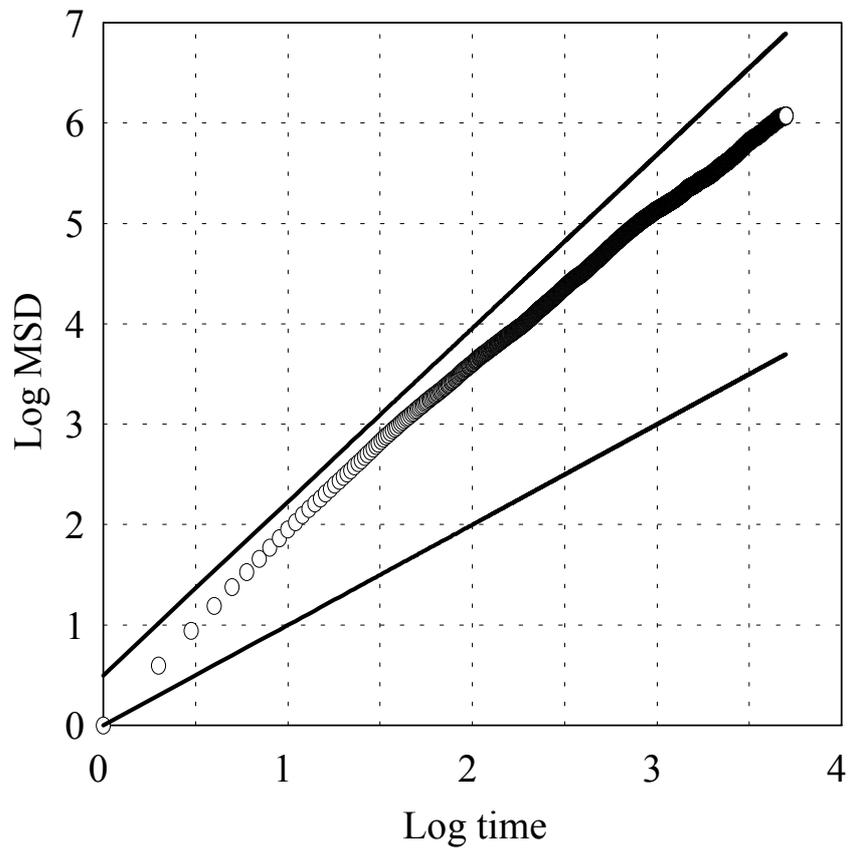


Figure 9a

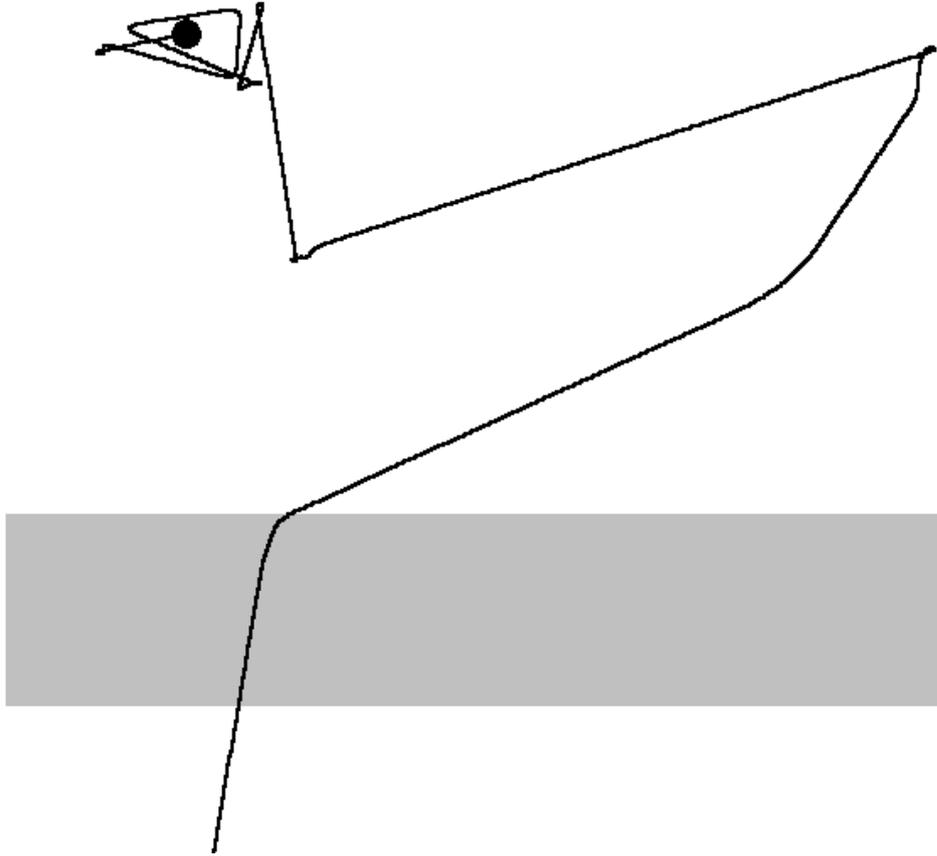


Figure 9b

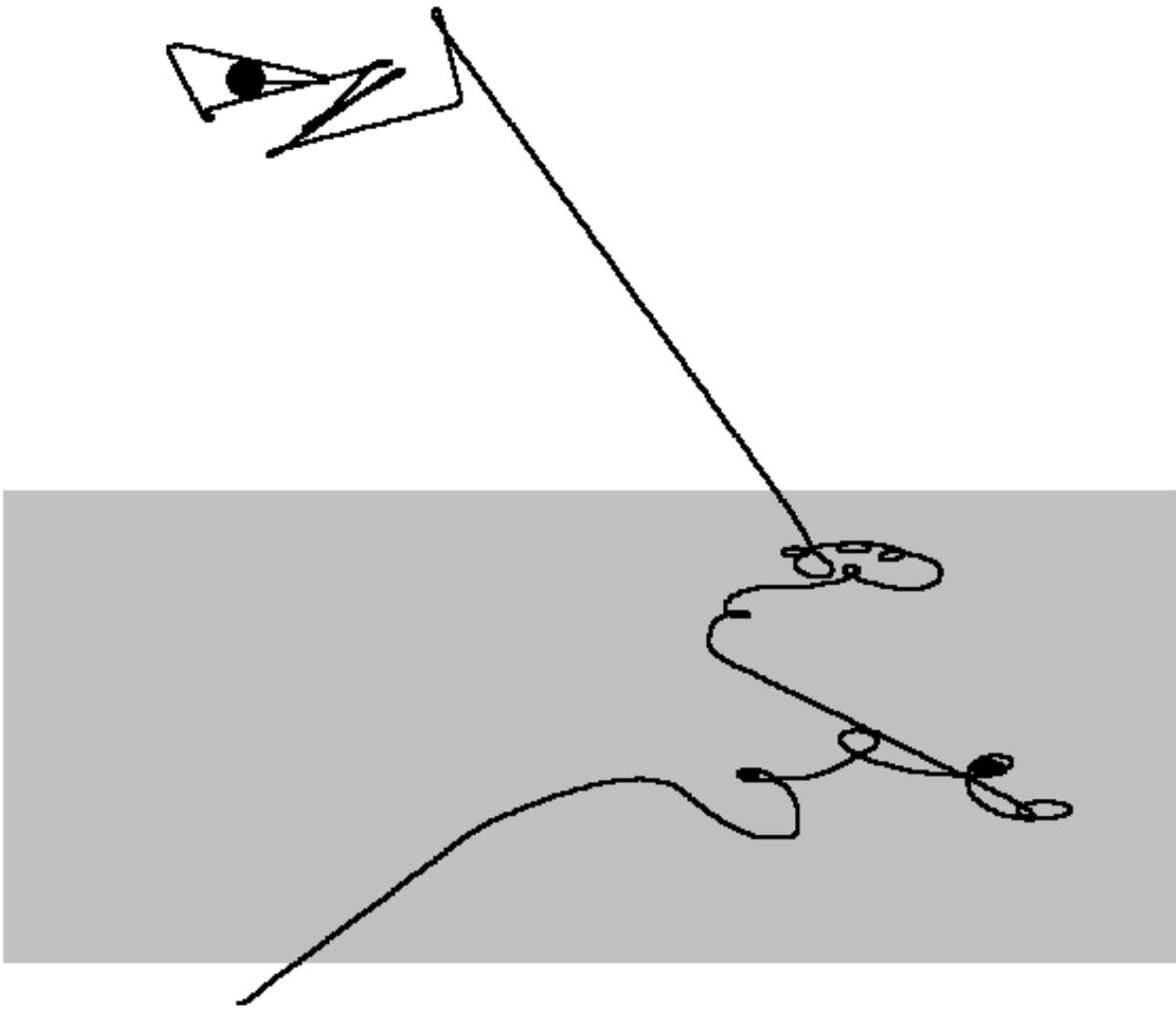


Figure 10

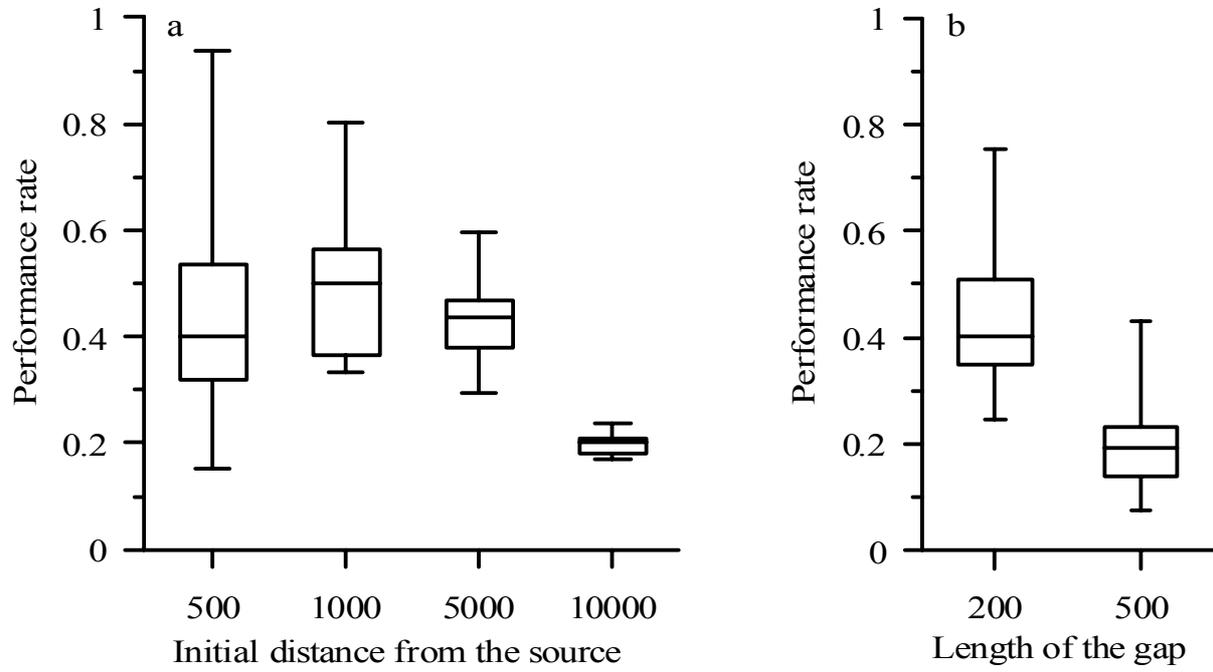


Figure 11

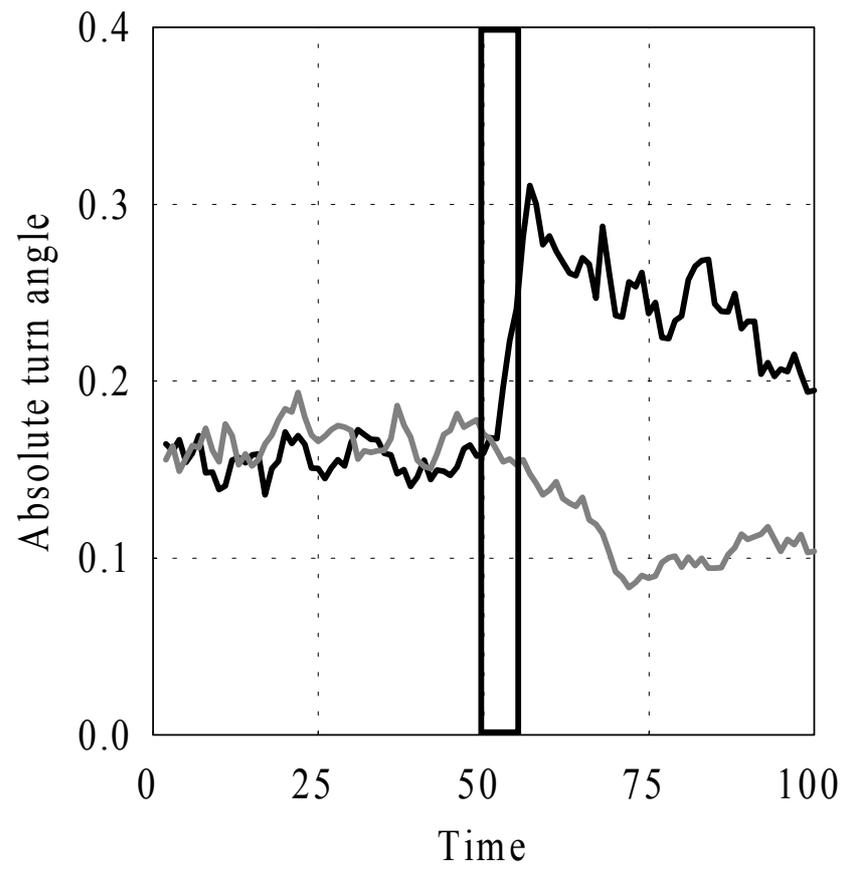


Figure 12

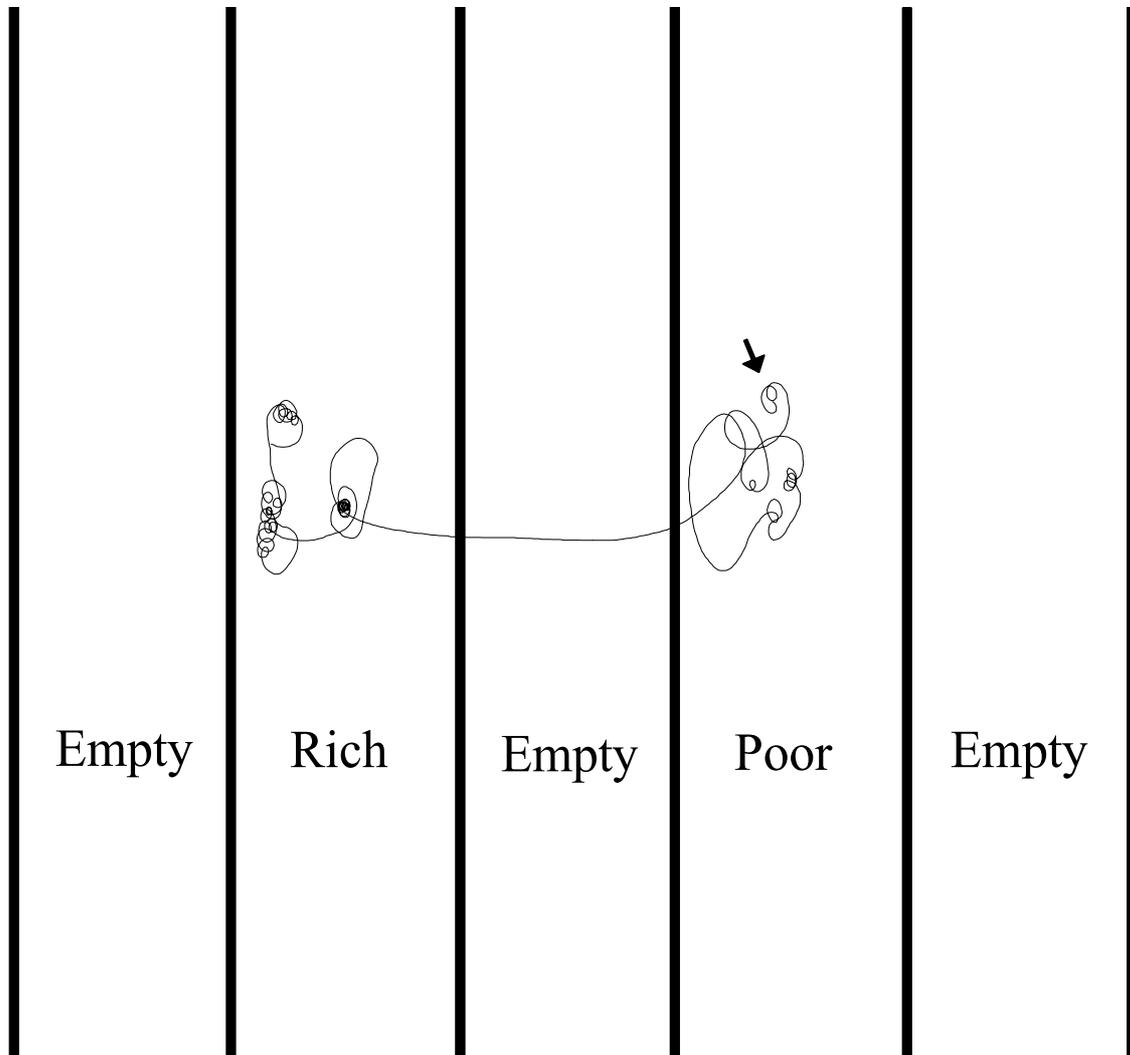


Figure 13

