The evolution of fidelity in sensory systems

Andrew T. Sornborger\textsuperscript{a,}\textsuperscript{*}, Malcolm R. Adams\textsuperscript{b}

\textsuperscript{a} Department of Mathematics and Faculty of Engineering, University of Georgia, Athens, GA 30602, USA
\textsuperscript{b} Department of Mathematics, University of Georgia, Athens, GA 30602, USA

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A B S T R A C T

We investigate the effect that noise has on the evolution of measurement strategies and competition in populations of organisms with sensory systems of differing fidelities. We address two questions motivated by experimental and theoretical work on sensory systems in noisy environments: (1) How complex must a sensory system be in order to face the need to develop adaptive measurement strategies that change depending on the noise level? (2) Does the principle of competitive exclusion for sensory systems force one population to win out over all others? We find that the answer to the first question is that even very simple sensory systems will need to change measurement strategies depending on the amount of noise in the environment. Interestingly, the answer to the second question is that, in general, at most two populations with different fidelity sensory systems may co-exist within a single environment.

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1. Introduction

Sensory systems are well known to be extremely accurate in detecting environmental signals. The photoreceptors of animals, including our own species, can detect light down to an intensity level (set by thermal noise in rhodopsin molecules) close to that of an individual photon (Hecht et al., 1942; van der Velden, 1944; Barlow, 1956; Yeandle and Spiegler, 1973; Lillywhite and Laughlin, 1979; Baylor et al., 1979; Aho et al., 1988). Bats are known to be able to discriminate between echoes that are received 10–50 ns apart (Simmons et al., 1990). In fact, bats are so good at echolocation that insects use complex avoidance methods including ultrasonic click generation, turning and powered dives and destabilization of their flight trajectory to make their flight path less predictable and to enhance their survival likelihood (Yager et al., 1986; Robert and Rowell, 1992; Dawson et al., 1997; Dudley, 2000). Other sensory systems, such as olfaction, also exhibit optimal detection capabilities (Berg and Purcell, 1977). In the insect visual system, not only do the sensors themselves operate optimally, but information processing also occurs within the optimality limits. For example, the transfer function of the first synapse of the insect visual system has been shown to operate at the information theoretic optimum (Laughlin, 1981; Dubs et al., 1981). Finally, it has been shown (de Ruyter van Steveninck and Bialek, 1988, 1995; de Ruyter van Steveninck et al., 1994, 1996) that the blowfly calculates a running estimate of the motion signal with precision close to that set by photodetector noise and that there is evidence that the structure of the fly’s computation has the same form as the theoretically optimal computation.

In spite of these amazingly accurate sensory systems, organisms are still forced to accept some level of noise. First of all, because of thermal and quantum fluctuations there is always a theoretical limit to how accurate a sensory system can be. But, perhaps more importantly, there can be various levels of noise in the environment that the organism is trying to measure. For example, a visual system will encounter a lower signal-to-noise ratio (SNR) in the dark than in the light of day, or an auditory system’s SNR will decrease as air turbulence increases. The fact that noise amplitudes in the environment might vary widely presents challenges to a sensory system beyond that of optimizing accuracy.

There is evidence that the blowfly visual system switches between different methods of processing visual information depending on the amplitude of noise in the input (Bialek and de Ruyter van Steveninck, 2005). Theoretical calculations show that (see e.g. Bialek, 2002; Bialek and de Ruyter van Steveninck, 2005), for visual motion estimation, at low SNR the optimal estimator results in a correlation based motion computation, whereas at high SNR, it results in a ratio of temporal and spatial derivatives. Further evidence of noise adaptivity may be found in voltaged gated K⁺ channels in Drosophila (Niven et al., 2003a, b). This makes us wonder how pervasive is the need to develop adaptive strategies in the face of varying sensory input noise. How complicated does an organism need to be to find it advantageous to develop two (or more) qualitatively different strategies in the...
presence of varying amounts of noise? Additionally, if it is found that different strategies are optimal at different noise levels, would the increased costs of implementing a noise adaptive sensory strategy be worth paying?

In this paper, we develop two models to investigate the evolutionary pressures on sensory systems in the presence of noise. The first model will focus on the question of determining the optimal (minimal cost) strategy for a given noise level for an organism interacting with a simple, but potentially dangerous, ‘world’. We will show that, even for a very simple organism, the optimal measurement strategy depends on the level of noise. Thus, having a choice among multiple strategies can be advantageous to the organism. The second model will use game theory to describe competition between sensory systems that incur differing costs for different measurement fidelities. This addresses the issue of whether the increased costs of using a (more complicated) adaptive sensory system are evolutionarily worthwhile.

2. The evolution of adaptive strategies in noisy sensory systems

Below, we develop a model of a living organism that is sufficiently abstract to provide a framework to explore the questions that we asked in the Introduction. Because of this abstraction, our model is not meant to faithfully represent any particular organism. However, since we are attempting to determine if adaptive strategies can be advantageous even for simple organisms (simpler than a blowfly, for instance), the reader might find it useful to envision, as an example, a bacterium with one or more chemosensors that is capable of moving from one local chemical environment to another. The organism would be able to make decisions in response to (noisy) input from its chemical sensors. Furthermore, one or more of the local environments that it has access to may be dangerous for its survival. Our model allows us to investigate the success of different strategies for reacting to chemosensory inputs in varying levels of noise (e.g. a strategy might be: stay where you are, or move to another local environment if a certain chemical is detected). We envision noise as possibly arising from two sources: (1) measurement noise, i.e. possible mistakes in the identification of a chemical by a chemosensor, and (2) environmental noise, i.e. random fluctuations in the chemical concentrations in the organism’s environment. It should be remarked that, although in this example we mention possible differences in motor behavior of the bacterium, we could just as well be modeling different methods for processing sensory information, as in the blowfly.

Our general model of a living system consists of an environment acted on by two entities: the organism and the world. The organism is able to occupy different states (local environments) within the environment. Usually the different states of the environment represent different degrees of advantage or disadvantage to the organism. The organism can move from one state of the environment to other states by its own volition, although some states may not be directly attainable from any given state. The world can also change the environmental state that the organism occupies, but the organism is unaware of the mechanism used by the world to change the state. Thus the organism must perform a measurement on the environment to attempt to determine the state it occupies. It is the fidelity of this measurement, along with the randomness with which the world acts, which determines the best strategy for the organism to employ. Before reducing this problem to a very simple case, we will try to outline a discrete version of a relatively general framework in which this type of question may be studied. We attempt to be fairly broad with this framework, but it should be recognized that the framework itself can be extended in many ways to accommodate more complex systems.

In a discrete version of this model, the environment is represented by a directed graph with nodes $E = \{e_1, e_2, \ldots, e_n\}$. Each node represents a possible state of the environment. Two nodes, $e_i$ and $e_k$, are connected by a directed edge (arrow) if the environment is allowed to change from state $e_i$ to state $e_k$. (There should also be an arrow from a state $e_i$ to itself if that state can be left unchanged when either the organism or the world acts.) Actions on the environment (and therefore transitions between nodes on the graph) are defined by a set of admissible operators $\mathcal{F}$ acting on the elements $E$. An operator $t : E \rightarrow E$ is admissible if for each $e_i \in E$, $t(e_i)$ is some $e_j$ for which there is an arrow from $e_i$ to $e_j$. The dynamics on the environment defined by the world is given by a stochastic operator, $W$, from $E$ to itself. Thus $W$ is a $\mathcal{F}$ valued random variable. For $t \in \mathcal{F}$ we let $P_{W}(t)$ denote the probability of application of the operator $t$ on the environment (the expectation that $W$ has value $t$). These probabilities are, of course, subject to the constraint $\sum_{t \in \mathcal{F}} P_W(t) = 1$.

The organism’s action on the environment is determined by a strategy $S$ given by a set of operators, $\{t_1, t_2, \ldots, t_n\}$, acting on the environment. In general, not every operator in $\mathcal{F}$ will be available to the organism for use in its strategy. Usually those available will reflect certain properties of the organism’s environment. The strategy is a Markov process on $E$ in which the probability of transition from state $e_j$ to state $e_k$ is given by

$$S_{jk} = \sum_{l \in \mathcal{R}_j} P_{t_l}(e_k),$$

where $\mathcal{R}_{j} = \{l | t_l(e_j) = e_k\}$. This matrix can be computed more simply by setting $T_{jk}$ to be the transition matrix corresponding to the operator $t_j$ and letting $P(e_i)$ denote the $n \times n$ diagonal matrix whose $k,k$ entry is $P_k(e_k)$. Then

$$S = \sum_{t \in \mathcal{F}} T_{jk}(e_k).$$

For the discrete case that we consider here, evolution proceeds on a turn by turn basis. First, the organism acts, then the world acts, etc. By iterating this process, one can compare strategies under various noise levels to see which is more likely to bring the organism to a desirable state of the environment (or less likely to bring the organism to an undesirable state).

We now turn to a very simple version of the above model in which there are only three states, $E = \{e_1, e_2, e_3\}$. Transitions are allowed between $e_1$ and $e_2$ in either direction, and transitions are allowed from either $e_1$ or $e_2$ to $e_3$ but not in the other direction. It is also allowed that the organism may remain in any of the three

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1 An anonymous reviewer pointed out that this nomenclature could be confused with experimental ‘measurement noise’, so we wish to emphasize that we are not considering experimental measurements of the organism in a laboratory setting in any sense.

2 In general there will be two different sets of arrows, one corresponding to the transitions available to the world, and the other to the transitions available to the organism. In this simple model we will take these to be the same.
states. Thus the directed graph is as depicted in Fig. 1. Notice that the state $e_3$ is inescapable. This state will represent death of the organism. Of course, a finite subset of the strategies is available, not including the globally optimal strategy for a given noise level. Of course, a finite subset of the strategies is available, not including the globally optimal strategy for a given noise level. Of course, a finite subset of the strategies is available, not including the globally optimal strategy for a given noise level.

Fig. 1. The graph of allowed paths in the simple cost model. Note that there is no escape from node $e_3$.

21. A cost analysis for all possible strategies

In general, if an organism can measure $B$ elements of the environment and can operate on the environment with $A$ operators, there are $N = A^B$ possible strategies available to the organism. In the simple system that we are considering, there are three operators available to the organism and two states from which the organism can use these operators, thus we have $3^2$ possible strategies. When all three operators are available to the organism, it is never in the interest of the organism to use the + operator in its strategy, since it will either kill the organism or bring it to a state where the environment can do so. However, we include it in our analysis so that we can look at scenarios in which not all three operators are available to the organism. Indeed, in general, constraints might exist for some organism such that only a finite subset of the strategies is available, not including the globally optimal strategy for a given noise level. Of course, a complete analysis would study all 81 strategies given by allowing the organism to choose any of the nine possible elements of $T$ when it is in either of the states $e_1$ or $e_2$. We have chosen to limit our analysis to these nine since this gives a rich enough system to demonstrate the points we wish to make.

For the environment of three possible nodes, $e_1$, $e_2$, and $e_3$ with directed graph given in Fig. 1 and operators $\{+,-,I\}$, as in Fig. 2, available to the organism for strategies, we first write down all possible strategies, $\{S\}$:

$$
\begin{array}{cccccccc}
E & S_1 & S_2 & S_3 & S_4 & S_5 & S_6 & S_7 & S_8 & S_9 \\
M(e_1) & + & + & l & l & l & - & - & - & - \\
M(e_2) & + & l & + & l & - & + & l & - & - \\
\end{array}
$$

Here, $M(e_i)$ denotes a determination via a measurement by the organism that it is in state $e_i$. The measurements $M$ of the environmental state $E$ are implicit functions of the conditional probabilities of the organism's measuring that it is at a given node.

The transition matrices for the operators $+, -, \text{and } I$ are

$$
T_+ = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix}, \quad T_- = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 0 \\ 1 & 0 & 1 \end{pmatrix}, \quad T_I = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}. 
$$

Referring to Eq. (1), the transition matrices for the Markov processes determined by the strategies are then computed to be

$$
S_1 = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix}, \quad S_2 = \begin{pmatrix} P_1(e_2) & 0 & 0 \\ P_1(e_1) & P_2(e_2) & 0 \\ 0 & P_1(e_1) & 1 \end{pmatrix}, \\
S_3 = \begin{pmatrix} 0 & P_2(e_2) & 0 \\ P_1(e_1) & 0 & 0 \\ P_1(e_2) & P_2(e_1) & 0 \end{pmatrix}, \quad S_4 = \begin{pmatrix} 0 & P_2(e_2) & 0 \\ P_1(e_1) & 0 & 0 \\ 0 & P_2(e_1) & 1 \end{pmatrix}, \\
S_5 = \begin{pmatrix} P_1(e_1) & 0 & 0 \\ P_1(e_2) & P_2(e_1) & 0 \\ 0 & P_2(e_2) & 1 \end{pmatrix}, \quad S_6 = \begin{pmatrix} 0 & P_2(e_1) & 0 \\ P_1(e_1) & 0 & 0 \\ 0 & P_2(e_2) & 0 \end{pmatrix}, \\
S_7 = \begin{pmatrix} 0 & P_2(e_1) & 0 \\ P_1(e_1) & 0 & 0 \\ 0 & P_2(e_2) & 0 \end{pmatrix}, \quad S_8 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & P_1(e_1) & 0 \\ 0 & 0 & 0 \end{pmatrix}, \\
S_9 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 1 & 0 & 1 \end{pmatrix}. 
$$

And $W$, the transition matrix for the action of the world, is

$$
W = \begin{pmatrix} P_W(l) & 0 & 0 \\ P_W(+) & P_W(l) & 0 \\ 0 & P_W(+) & 1 \end{pmatrix}. 
$$

One discrete step of evolution is then $W^j a(0)$, where $a$ is a column vector with $\sum a_k = 1$ representing the initial environmental state occupation probabilities of the organismal population. The evolution of state $a(n)$, at the discrete times $n = 0, \ldots, T$ is therefore governed by a homogeneous Markov chain,

$$
a(n) = (W^j)^n a(0) \tag{4}
$$

with $j$ indicating the survival strategy used by the organism. Models involving memory might also be constructed, but our Markov chain model has sufficient complexity to provide insight
into the need for adaptation of sensory strategies in the face of noise.

To compare these different strategies we will analyze their respective costs. Usually, these costs are broken down into indirect and direct costs. Indirect costs accrue when detrimental incorrect decisions are made. Direct costs are operational costs, such as metabolic and infrastructure investment by the organism, i.e. neural processing, processing hardware (neurons, axons, etc.), maintenance, as well as motor costs. Both direct and indirect costs are included in our model, however, they are not explicitly identified as such. Instead, in our model, each operator incurs a cost which may depend on the state of the organism. The differing costs of different strategies may bias the organism towards a particular strategy, or set of strategies. In general, the full cost analysis for even the simple model we consider here is quite complicated, but we indicate how it should proceed and then make some simplifying assumptions to make some basic points.

For each of the operators used in a strategy, there will be a cost vector whose jth entry describes the cost to the organism of applying that operator when it is in the state e_i. For instance, in our simple model we have three cost vectors:

\[ \vec{c}_+ = (L_+, L_+ + D, 0), \quad \vec{c}_- = (L_-, L_+, 0), \quad \vec{c}_I = (L_-, L_I, 0). \]  \hspace{1cm} (5)

The numbers L_+ , L_-, and L_I are fixed costs to the organism for applying the operator while in either of the living states e_1 or e_2, and D represents the cost of dying, i.e. moving into state e_2. The cost incurred by the organism for applying the jth strategy is summarized in the vector

\[ \vec{c}_j = \vec{c}_{M(e_j)}P(e_1) + \vec{c}_{M(e_j)}P(e_2), \]  \hspace{1cm} (6)

where \( M(e_j) \) denotes the operator which is used by the jth strategy when the measurement indicates that the organism is in the state e_i. If a population of organisms has density vector \( \vec{d} \), then the cost incurred to that population by applying strategy j is given by

\[ \vec{c}_j \cdot \vec{d}, \]

\[ \vec{c}_W = (0, P_W(+), 0), \]

Thus the total cost to the organism after an organism/world increment is given by

\[ (\vec{c}_W S_t + \vec{c}_j) \cdot \vec{d}. \]

Averaging this cost over all possible distributions of populations between the two living states e_1 and e_2 gives the expected cost \( C_j \) to a population using the jth strategy. This gives

\[ C_j = (\vec{c}_W S_t + \vec{c}_j) \cdot (\vec{d}_1, \vec{d}_2, 0). \]

The expected costs for the nine strategies above are given in Appendix A.1.

The manner in which the cost of a given strategy depends on measurement fidelity is represented in Fig. 3. In the left panel, we plot the cost as a function of \( P_W(e_1) \) for all nine strategies. In this plot, \( P_W(+) \) has been fixed at the value 0.3 and \( P_W(e_2) \) is fixed at 0.7. \( L_+ = 1.0, L_I = 0.0, L_+ = 1.0, \) and \( D = 100.0. \) Here, we take \( D > L_+ , L_I, \) and \( L_- \) to demonstrate that the cost of an incorrect measurement can severely affect the optimality of a strategy in a noisy environment. In the right panel, we plot the cost as a function of \( P_W(+) \). In this plot, \( P_W(e_1) \) was fixed at 0.9 and the other parameters are as in the left panel.

Note that in both panels, the minimum cost strategy depends on the amount of noise in the measurement and changes at particular thresholds in \( P_W(e_1) \) and \( P_W(+) \). This is a general characteristic of strategy costs for other parameters than those depicted as well. Therefore, it will benefit the organism to adapt its strategy if the noise in the environment changes past a threshold where the minimum cost strategy changes.

In Fig. 4, we plot the overall minimum cost strategy regions as a function of \( P_W(+) \) and \( P_W(e_1) \). In the left panel, we have fixed \( P_W(e_2) = 0.7 \) and in the right panel, \( P_W(e_1) = P_W(e_2) \) (i.e. the measurement fidelity is the same at both environmental node e_1 and e_2). Again, we see that depending on the measurement fidelity and variability of the environment, it will benefit the organism to adapt its strategy. In Fig. 5, we provide three-dimensional surface plots of all nine costs, \( C_1, \ldots, C_9 \), as a function of \( P_W(e_1) \) and \( P_W(+) \).

3. Effects of measurement costs on the evolution of fidelity in sensory systems

In the previous section, we demonstrated that depending on the amplitude of either measurement noise or environmental noise, different strategies may be optimal for an individual organism’s survival. From this result, we infer that an adaptive strategy, where the organism could switch between optimal strategies depending on the noise level, would be beneficial to the organism. However, an adaptive strategy would be expected to cost more to the organism, since additional noise monitoring would be necessary to make the decision to switch strategies. In this section, we switch to the framework of evolutionary game theory in order to understand how competition between populations of organisms that are in all ways identical, except for the fidelity of their sensory system and the cost they pay for it, affects their evolution. For instance, what happens when a population
with a more expensive (possibly adaptive) sensory strategy meets a population with a less expensive, but lower fidelity sensory strategy. In fact, our model only considers sensory system fidelity and cost, making no assumptions about the particular strategies being used, whether adaptive or not.

Adopting the standard evolutionary game theoretical approach (Maynard Smith, 1974; Hofbauer and Sigmund, 1998; Weibull, 1996), we consider only pairwise interactions between all organisms. Higher-order effects are neglected. We also assume that, except for the measurement fidelity of an organism, and the cost incurred by each measurement, all organisms are equal. We take the payoff to any strategy to be symmetric, that is, the payoff is independent of which player position it is applied to.

We will assume that the organismal population is divided into $n$ populations with frequencies $\mathbf{x} = (x_1, \ldots, x_n)$. Changes in viability of a given population depend on the difference between the fitness $f_i$ of population $i$ from the average fitness $\bar{f}$. We take the fitness to be $(Ax)_i$, where $A$ is a payoff matrix. Entries $A_{ij}$ in the payoff matrix give the gain to population $i$ when it competes with population $j$. The average fitness is then $\bar{f} = \mathbf{x} \cdot \mathbf{Ax}$, giving the so-called replicator dynamics

$$
\dot{x}_i = x_i ((Ax)_i - \mathbf{x} \cdot \mathbf{Ax}).
$$

(7)

3.1. The measurement game

To determine a game matrix for our question, we cast the problem in the following terms: suppose there are $n$ populations competing against each other. Each population makes observations with fixed SNR. The gain made by an organism depends on the accuracy of the measurement it makes. Each measurement is made for a fixed cost. The payoff is determined in the following

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way: if two interacting organisms make correct measurements, they split the fixed gain; if neither makes a correct measurement, neither gains; if only one of the two makes a correct measurement, then the organism that makes the correct measurement takes the fixed gain. Apportioning the pay-off equally when both measurements are correct is a probabilistic statement that, because we have assumed that the organisms are in all ways the same except for the fidelity of their sensory systems, any competition for the advantage gained of the measurement averaged over time will be equally likely to benefit both. Any costs experienced due to, for instance, operation and maintenance of the sensory system we would consider to be averaged over time and reflected in the epsilon term. An alternative game to consider would be that the gain is forfeited by both players if both make correct measurements. This game turns out always to have an equilibrium with only one population (Adams and Sornborger, 2007); so, in this case, coexistence is ruled out.

If organism j is a member of a population that uses a strategy that makes a correct measurement with probability Pj, and organism k’s population strategy gives probability Pk, then, on average, the gain to organism j will be PjPkJG/2, for encounters where the gain, G, is split because both j and k make correct measurements. For encounters in which only organism j makes the correct measurement, the gain will be Pj(1 − Pk)G. Organism j also pays ej for its measurement, therefore the expected value of organism j’s total payoff when competing with organism k is $P_j(1 - P_k/2)G - e_j$. Arranging such payoffs for n populations we find a game matrix of the form $A_n = P_1(1 - P_2/2)G - e_1$.

3.2. Competing populations

The game matrix, A in the case of two populations is

$$A = \begin{pmatrix} P_1(1 - P_1/2)G - e_1 & P_1(1 - P_2/2)G - e_1 \\ P_2(1 - P_1/2)G - e_2 & P_2(1 - P_2/2)G - e_2 \end{pmatrix}.$$  

(8)

Due to the invariance of the replicator equations under the addition of a constant to a column of the game matrix, we may consider an equivalent game matrix

$$A = \begin{pmatrix} c_1 & 0 \\ 0 & c_2 \end{pmatrix},$$  

(9)

where $c_1 = (P_1 - P_2)(1 - P_1/2)G - (e_1 - e_2)$ and $c_2 = (P_2 - P_1)(1 - P_2/2)G - (e_2 - e_1)$. 2 × 2 games may be grouped in three classes (see e.g. Weibull, 1996). When $c_1 > 0$ and $c_2 < 0$ or $c_1 < 0$ and $c_2 > 0$, we have a Prisoner’s Dilemma-like game with one Nash equilibrium that is also an evolutionarily stable strategy (ESS). In the Prisoner’s Dilemma case, strategy S1 dominates when $c_1 > 0$ and $S_2$ dominates when $c_2 > 0$. When $c_1 < 0$ and $c_2 < 0$, we have a Hawk–Dove-like game with three Nash equilibria. Two of the equilibria are the pure strategies $S_1$ and $S_2$, but the only evolutionarily stable state is at $x = xS_1 + (1 - x)S_2$, where $\lambda = c_2/(c_1 + c_2)$. When $c_1 > 0$ and $c_2 > 0$, we have a Coordination-like game, where there are the same three Nash equilibria as in the Hawk–Dove-like game, but for this case, the roles are reversed. The two pure strategies are evolutionarily stable, and x is unstable. In this game, the final state depends on the initial

Fig. 5. The nine different cost functions, $C_1$, ..., $C_9$, as a function of $P_1(e_1)$ and $P_2(e_2)$ with $P_1(e_2) = 0.7$. Operator costs for these plots are $L_i = 1, L_o = 1, I_l = 0,$ and $D = 100$. Axes are all as in the lower left panel.
conditions. If the initial state $x_{init} = (1 - \gamma)S_1 + \gamma S_2$ and $\gamma < \lambda$, then the population evolves to the pure state $S_1$. Conversely, if $\gamma > \lambda$ then the population evolves to the pure state $S_2$.

Let us order the strategies $S_{1,2}$ in $A$ such that $P_1 > P_2$. In other words, strategy $S_1$ has a higher measurement fidelity than $S_2$. We also assume that $\epsilon_1 > \epsilon_2$, that is, that it costs more to make a high fidelity measurement.

With the above stipulations, we find for the two population measurement game, $A$.

\[
\begin{align*}
    c_1 &
    \equiv 0 \Rightarrow \frac{\epsilon_1 - \epsilon_2}{c} \equiv \left(1 - \frac{P_1}{P_2}\right) (P_1 - P_2) \\
    c_2 &
    \equiv 0 \Rightarrow \frac{\epsilon_1 - \epsilon_2}{c} \equiv \left(1 - \frac{P_2}{P_1}\right) (P_1 - P_2)
\end{align*}
\]

and

$c_1$ is positive for $\epsilon_1 - \epsilon_2$ small, and becomes negative as $\epsilon_1 - \epsilon_2$ increases. $c_2$ is negative for $\epsilon_1 - \epsilon_2$ small, and becomes positive as $\epsilon_1 - \epsilon_2$ increases. Examining the regions where $c_1$ and $c_2$ cross zero, we find three cases: (1) $c_1 > 0$ and $c_2 < 0$, (2) $c_1 < 0$ and $c_2 < 0$, and (3) $c_1 < 0$ and $c_2 > 0$. Clearly, cases (1) and (3) are Prisoner’s Dilemma-like games with one dominating strategy and case (2) is a Hawk–Dove-like game in which the two strategies coexist.

From the above deliberations, we see that for two competing populations with different measurement fidelities, one dominating population is the rule, but for a range of measurement cost differences, $\epsilon_1 - \epsilon_2$, a mixed evolutionarily stable state where both populations survive is also possible.

Finally, we address the question: What happens when many populations with different sensory fidelities compete? We have investigated the possible dynamics of this type of replicator equation in (Adams and Sornborger, 2007). Our results show that, generically, local equilibria may exist with two coexisting populations, but no more than two populations may coexist. This result is based on the fact that the game matrix for the measurement game is only two-dimensional (rank 2), regardless of the dimension of the space that the populations evolve in.

4. Discussion and conclusions

We set out to investigate the effect of noise on the evolution of sensory systems. With our first model, we showed that the optimal strategy can depend on the amplitude of the noise. This led to the conclusion that adaptive strategies could increase the likelihood of survival of the organism if it lives in an environment with varying levels of noise. However, due to the increased cost of adaptive strategies, competition needed to be considered in order to determine whether higher fidelity, yet more expensive sensory systems would win out over lower fidelity, cheaper sensory systems. With our second model, and reasonable assumptions about competition between sensory systems, we showed that at most two coexisting populations with different sensory systems could survive.

Evidence for noise adaptive sensory systems exists in flies (Niven et al., 2003a, b; Bialek and de Ruyter van Steveninck, 2005). Our results imply that the need for noise adaptive sensory systems is so fundamental that it should also be observable in far simpler organisms. Although our framework is very abstract and the example model that we develop is so simple that it should not be thought of as a model for any actual organism, we see three types of general questions relating to our work that may be of interest to experimentalists: (1) In what simple organisms can we find evidence that different sensory strategies are optimal at different levels of noise? (2) Is there evidence that such organisms can adapt between different strategies depending on the noise level? (3) Can we quantify the costs and benefits of developing an adaptive strategy?

In order to explore the implications of our results, let us return to the example of the chemotactic bacterium of Section 2. We discuss the bacterium for its relative simplicity (vs. the blowfly), although it is still quite complicated in the context of our models. Using the mathematical framework of our first model, the measurements, $M$, consist of the bacterium sensing chemicals in its environment via receptors in its cell membrane, together with the processing of the information from the receptors via signaling pathways (molecular or genetic). This information influences the bacterium’s behavior, which corresponds to the operators, $T$, in our model. Noise in the measurements could be due either to thermal effects that could change the binding efficacy of the receptor (measurement noise) or could be due to stochastic fluctuations in the chemical environment of the receptor (environmental noise), or other unforeseen changes. These sources of noise would affect the probabilities, $P$, both in the strategies, $S$, and in the action of the world, $W$. Operator costs, $c$, could reflect metabolic and infrastructural costs of the receptor and signaling pathways, the cost of the measurement, motor costs for the behavior and the cost of sustaining the organism in a particular environmental state (e.g. $D$).

Of course, it is possible that for the bacterium’s sensory needs, a non-adaptive strategy is optimal. How would we determine the existence of an adaptive strategy for a bacterium? There are two general methods of observing this experimentally, our previous discussion might lead one to look for gross changes in the bacterium’s behavior that depended on noise amplitude. Controlling such an experiment would probably be extremely difficult. Potentially more illuminating and maybe easier, would be to search for multiple genetic (or molecular) pathways associated with the response to chemical stimulation of a particular kind of receptor in different noise environments (see comments on Shaker $K^+$-channels below). If multiple responses occur, the next question is: what pathway or mechanism is responsible for making the decision to switch measurement or behavioral strategies? That is, how does the bacterium measure the SNR?

The answers to these latter questions would address at least part of the question of what extra costs are incurred by the adaptive strategy. In fact, a candidate system may exist in Escherichia coli, where an adaptive clustering mechanism for sensing attractant gradients in a wide range of concentrations has been proposed (Bray et al., 1998). In this system the ligand-bound, low-activity state of the receptor induces receptor clustering, an adaptive mechanism for improving signal in noisy (low concentration) chemical environments. Multiple pathways and noise monitoring mechanisms (in E. coli, the mechanism for expressing the ligand) for such systems must certainly incur metabolic and infrastructure costs. Detailed accounting of the elements of the pathways could help quantify these costs. If an adaptive strategy is found to exist, then from the evolutionary viewpoint, the benefits of using it must outweigh its costs, both direct and indirect. Therefore, one may infer that the bacterium lives in an environment with big enough changes in noise amplitude that the adaptive strategy was effective. Our second model addresses these questions and leads to further potential experimental questions.

Let us look more carefully at the case of two competing (e.g. bacterial) populations. $P_1$ and $P_2$ represent the fidelities of the sensory systems of the two populations. In general, these will depend on the measurement and environmental noise. Now let us assume that the first population uses a non-adaptive strategy, which is optimal at some noise level, let us call it $N_1$. This strategy has fixed cost, $c_1$, per measurement. We also assume that the second population can adapt its strategy between that of the first population and a second strategy which is optimal at a different
noise level, $N_3$. This adaptive strategy would have a higher fixed cost, $c_2$, per measurement. Now, if the noise level stays constant at $N_1$, then the first population has an advantage (because its cost is lower) and will dominate. Furthermore, if the noise level is constant at $N_2$, the second population will dominate as long as $c_2 > 0$. Now, assuming ergodicity if the noise randomly varies between $N_1$ and $N_2$, the fidelity of the first population's measurements goes down (because it is not optimal all of the time), while the fidelity of the second population must be higher (because the organism can always use an optimal strategy). Therefore, to probe the various equilibria of the competing population model, one might perform a number of experiments on a uniform bacterial population. With low fluctuation of noise levels, the population should evolve to one with a non-adaptive strategy. Increasing fluctuation in noise level should favor the evolution of populations with adaptive strategies. Furthermore, according to the inequalities given in Section 3.2, for some amount of fluctuation in noise level, coexistence of populations with both non-adaptive and adaptive strategies should occur.

Whether adaptive strategies might exist in bacteria is, of course, pure conjecture (although we remarked on a candidate mechanism in E. coli above), but our discussion has allowed us to make more concrete the implications of our models. Many of our statements concerning bacteria have analogies in higher organisms. In this case, evolutionary questions become much more difficult to study directly because of increases in the interval between generations. In higher organisms, the genetic and molecular pathways in the bacterium would be replaced by neural circuits. Of particular experimental interest in systems with known adaptive mechanisms is: what is the monitoring mechanism that makes the decision to switch measurement strategies? Many of the costs involved in neural circuits have already been studied, including the metabolic and infrastructural costs (Niven et al., 2003b, 2007, 2008; Laughlin et al., 1998; Cherniak, 1994; Chklovskii et al., 2002). However, identification of the neural circuit responsible for adaptive switching would allow us to more accurately calculate the additional costs involved in noise adaptive sensory systems. In particular, because of the detailed understanding of the mechanisms involved, the Shaker $K^+$-channels studied in (Niven et al., 2003a, b) might be the most straightforward system to investigate in this regard.

Finally, the result from our game theoretic model, that only two of $n$ populations may survive in the measurement game that we set up is interesting in that it implies that, in some cases, one population of sensory systems may benefit by coexisting with another population. The biological interpretation of this result is that an invading, higher fidelity but higher cost sensory system, may find it easier to compete with lower fidelity sensory systems than its own. Conversely, lower fidelity sensory systems may take advantage of higher fidelity sensory systems by shoudering the costs of providing easier competition for the high-fidelity sensory system, but in the end lower cost per measurement on themselves. This mutual dependence occurs because the game that we analyzed above involves a shared gain when both organisms make a correct measurement. If the gain is forfeited by both organisms, then the game matrix becomes one-dimensional and only one population dominates.

The survival of two out of $n$ populations in our measurement game is a particular example of the principle of biological exclusion. This has been stated in the framework of Lotka–Volterra equations in (Hofbauer and Sigmund, 1998). In the game theoretic framework, the statement is that, generically, equilibria with $m$ coexisting populations can only exist in games with game matrices of rank $m$ or greater. We show this in Appendix A.2. Due to the exclusion principle, we expect that if further contingencies were built into the survival probabilities and costs in our measurement game, thus increasing the rank of the game matrix, then more populations could potentially coexist. Thus, we see that biological niches may arise due to the varying cost of information to organisms competing with sensory systems of differing fidelity.

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Appendix A

A.1. Strategy costs

\[
C_1 = \frac{1}{2}[2L_n + D(1 + PW(+)i)],
\]

\[
C_2 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_1) + P_2(e_1) + P_3(e_1))],
\]

\[
C_3 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_1) + P_2(e_1) + P_3(e_1))],
\]

\[
C_4 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_2) + P_2(e_1) + P_2(e_1))],
\]

\[
C_5 = \frac{1}{2}[2D + DPW(+)i].
\]

\[
C_6 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_1) + P_2(e_1) + P_2(e_1))],
\]

\[
C_7 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_1) + P_2(e_1) + P_2(e_1))],
\]

\[
C_8 = \frac{1}{2}[L_n(Pl_1(e_1) + P_2(e_1)) + L_n(Pl_1(e_2) + P_2(e_2)) + D(Pl_1(e_1) + P_2(e_1) + P_2(e_1))],
\]

\[
C_9 = \frac{1}{2}[2L_n + D].
\]

A.2. Proof of generalized biological principle of exclusion

For the replicator equations (7), if an equilibrium point, $\bar{v}$, is in the interior of the simplex (denoted $\text{Int} \Delta_{n-1}$), then we have

\[
(A\bar{v})_1 = (A\bar{v})_2 = \cdots = (A\bar{v})_n = \bar{v}^T A\bar{v}.
\]

We can rewrite this as

\[
A\bar{v} = (\bar{v}^T A\bar{v}) \bar{u},
\]

where $\bar{u}$ is a column n-vector with every component equal to 1.

In the following, we will denote the ith row of a matrix $M$ by $\bar{M}_i$. Then, if $\bar{v} \in \text{Int} \Delta_{n-1}$ is an equilibrium, we have

\[
(A\bar{v})_i = \bar{A}_i \cdot \bar{v} = \bar{A}_i \cdot \bar{v}, \quad \text{for all } i,
\]

thus $\bar{v}$ will be in the kernel of the matrix $\bar{B}$ with rows defined by $\bar{B}_i = \bar{A}_i - \bar{A}_i$.

A game matrix of rank $m \leq n$ may be written

\[
A = \sum_{i=1}^{n} \bar{b}_i \bar{b}_i^T.
\]

Thus, the $i$th row of $\bar{B}$ has the form

\[
\bar{B}_i = \bar{A}_i - \bar{A}_i = \sum_{j=1}^{m} (a_{ij} - a_{ij}) \bar{b}_j^T.
\]

Now, if $\bar{v} \in \text{ker } B$, then $\bar{B}_i \cdot \bar{v} = 0$ for all $i$. We see that $\bar{v} \in \text{ker } B$ implies

\[
\sum_{j=1}^{m} (a_{ij} - a_{ij}) \bar{b}_j \cdot \bar{v} = 0
\]
for all $i$. This is equivalent to the condition

$$
p\bar{u} = \sum_{j=1}^{m} \bar{a}_j q_j,
$$

where $p \equiv \sum_{j=1}^{m} a_j (\bar{b}_j \cdot \bar{v})$ and $q_j \equiv \bar{b}_j \cdot \bar{v}$. This implies that the vectors $\{\bar{a}_j\}$ and $\bar{u}$ must be linearly dependent for an equilibrium to exist in $\text{Int} \Delta_m$. Since, when $m < n$, the generic situation is that these vectors are linearly independent, we can conclude that, generically, there are no interior equilibria for systems with $\text{rank} A < n$.

References


