

Chapter 2

Animal behavior

In this chapter, a brief introduction to the topic of animal behavior will be given, along with a description of its relevance to (autonomous) robots.

2.1 Introduction and motivation

Animal behavior is important as a source of inspiration for all work involving autonomous robots. Animals are able to function perfectly in their environment, and to adapt to changes in it. Models of animal behavior, both low-level models involving individual neurons, and high-level phenomenological models, can serve as an inspiration for the development of the corresponding behavior in robots. Furthermore, animals are generally experts in allocating time in an optimal or near-optimal fashion to the many activities (such as eating, sleeping, drinking, fleeing etc.) that they must carry out in various circumstances, and lessons concerning behavior selection in animals can give important clues to the solution of similar problems in robotics.

It should be noted that, in the behavior-based approach to robotics (introduced in detail in Chapter 3), one uses a more generous definition of intelligent behavior than in classical artificial intelligence, which was strongly centered on high-level behavior (e.g. reasoning about abstract things) in humans. By contrast, in behavior-based robotics, simple behaviors in animals, such as gradient-following (taxis), play a very important role, as will be seen during this course.

2.2 Bottom-up approaches vs. black-box approaches

As is the case with many different topics in science, animal behavior can be studied using either a **bottom-up approach** or a **top-down approach**. The bottom-up approach can, in principle, lead to a more complete and detailed

understanding of the objects or organisms under study. However, in sufficiently complex systems, the bottom-up approach may fail to give important insights. For example, when using a computer, it is not necessary to know exactly how the computer manipulates and stores information down to the level of individual electrons. Even without such detailed knowledge, it is certainly possible to use the computer, if only one has information about some programming language available on the computer.

Similarly, in animal behavior, even very simple, top-down models can lead to a good understanding of seemingly complex behavior, as will be shown below e.g. in the example of the orientation of bacteria.

On the other hand, a bottom-up study (on the level of individual neurons) can reveal many important aspects of simple systems, such as e.g. the much-studied worm *C. Elegans* or the sea-slug *Aplysia*. The neural level is relevant also in the field of autonomous robotics, where simple behaviors are often implemented using neural network architectures. However, in such cases, the networks are most often used as **black-box models** (obtained, for example, by means of artificial evolution).

2.3 Nervous systems of animals

In essence, the brain of vertebrates consists of three structures namely, the **fore-brain**, the **midbrain**, and the **hindbrain**. The **central nervous system** (CNS) consists of the brain and the spinal cord. In addition to the CNS, there is the **peripheral nervous system**, which consists of sensory neurons that carry information to the CNS and motor neurons that carry motor signals from the CNS to muscles and glands (see below). The peripheral nervous system can be sub-divided into the **somatic nervous system**, that deals with the external environment (through sensors and muscles) and the **autonomic nervous system** which provides the control of internal organs such as the heart and lungs. The autonomic nervous system is generally associated with involuntary actions, such heart beat and breathing.

It is interesting to note that the embryological development of different vertebrates is quite similar: During development, a neural tube is differentiated into a brain and a spinal cord.

Note that the presence of a nervous system is not a prerequisite for *all* forms of intelligent behavior: even single-celled organisms (which, clearly, cannot contain a CNS: neurons are cells), are able to exhibit rudimentary intelligent behavior. An example involving bacteria will be given below.

In addition to the nervous system, there is a parallel system for feedback in the body of animals, namely the **endocrine system**. The **glands** of the endocrine system release **hormones** (into the blood stream) that influence body and behavior. For example, elevated levels of the hormone **angiotensin** (whose

source is the kidney) lead to a feeling of thirst, whereas **adrenaline** is involved in **fight-or-flight** reactions (fear, anxiety, aggression). Hormone release by the endocrine system is controlled either directly by the brain or by (the levels of) other hormones. The use of artificial hormones in the modulation of behavior and behavior selection in robots will be studied later in this course.

2.4 Ethology

Historically, different approaches to animal behavior were considered in Europe and the USA. Whereas European scientists, such as the winners of the 1972 Nobel prize for medicine or physiology, Lorenz, Tinbergen, and von Frisch, generally were concerned with the study of the behavior of animals in their natural environment. Indeed, the term **ethology** can be defined as *the study of animals in their natural environment*.

By contrast, American scientists working with animal behavior generally performed experiments in controlled environments (e.g. a laboratory). This field of research is termed **comparative psychology**.

Both approaches have advantages and disadvantages: The controlled experiments carried out within comparative psychology allow more rigour than the observational activities of ethologists, but the behaviors considered in such experiments may, on the other hand, differ strongly from the behaviors exhibited by animals in their natural environment.

However, in both approaches, **phenomenological models** are used, i.e. models which can describe (and make predictions) concerning, e.g. a certain behavior, without modelling the detailed neural activities responsible for the behavior. Indeed, many ethological models (such as the Lorenz model described below) introduce purely artificial concepts (such as **action-specific energy**, which, nevertheless, may offer insight into the workings of a behavior.

Essentially, animal behavior is generally divided into three major classes **reflexes**, **kineses** and **taxes**, and **fixed action patterns**, which will now be described briefly.

2.4.1 Reflexes

Reflexes, the simplest forms of behavior, are involuntary reactions to external stimuli. An example is the withdrawal reflex, which is present even in very simple animals (and, of course, in humans as well). However, even reflexes show a certain degree of modulation. For example, some reflexes exhibit **warm-up**, meaning that they do not reach their maximum intensity instantaneously (an example is the scratch reflex in dogs). Also, reflexes may exhibit **fatigue**, i.e. a reduced, and ultimately disappearing, intensity even if the stimulus remains unchanged. Two obvious reasons for fatigue may be muscular

or sensory exhaustion, i.e. either an inability to move or an inability to sense. However, these explanations are often wrong, since the animal may be perfectly capable of carrying out other actions, involving both muscles and sensors, even though it fails to show the particular reflex response under study. An alternative explanation concerns *neural* exhaustion, i.e. an inability of the nervous system to transmit signals (possibly as a result of neurotransmitter depletion). An example (taken from Slater [38], Chapter 2) is the behavior of *Sarcophagus* (don't ask - you don't want to know) larvae. These animals generally move away from light. However, if placed in a tunnel, illuminated at the entrance, and with a dead end (no pun intended), they move to the end of the tunnel, turn around, and move *towards* the light, out of the tunnel. This is interesting, since these larvae will (if not constrained) always move away from light. However, this is neither a case of muscular exhaustion nor sensory exhaustion. Instead, the larvae have simply exhausted their neural circuits responsible for the turning behavior.

2.4.2 Kineses and taxes

Another form of elementary behavior is orientation of motion, either towards an object, substance, or other stimulus, or away from it. In **taxis**, the animal follows a gradient in a stimulus such as a chemical (**chemotaxis**) or a light source (**klinotaxis**). Typical examples are trail following in ants, an example of chemotaxis, and the motion towards a light source by fly maggots: It is easy to understand how such klinotaxis occurs: the maggots compare the light intensity on each side of their bodies, and can thus estimate the light gradient. Motion towards a higher concentration (of food, for example), is exhibited even by very simple organisms, such as bacteria. One may be tempted to use the same explanation, i.e. comparison of concentrations on different sides of the body, for this case as well. However, the bodies of bacteria are simply too small for the gradient (across their minuscule bodies) to be measurable. In the case of the common *E. Coli* bacterium, concentration differences as small as one part in 10,000 would have to be detectable in order for the organism to follow the gradient in the same way as the fly maggots do. Interestingly, *E. Coli* bacteria are nevertheless able to move towards and accumulate in regions of high food concentration, an ability which is exploited by another predatory bacterium, *M. Xanthus*, which secretes a substance that attracts *E. Coli* in what Shi and Zusman [37] has called "fatal attraction". The fact that the *M. Xanthus* are able to feed on *E. Coli* is made all the more interesting by the fact that the latter move around 200 times faster than the former. Now two questions arise: how do the *E. Coli* find regions of higher food concentration, and how do the *M. Xanthus* catch them?

Interestingly, a very simple model can account for the ability of *E. Coli* to

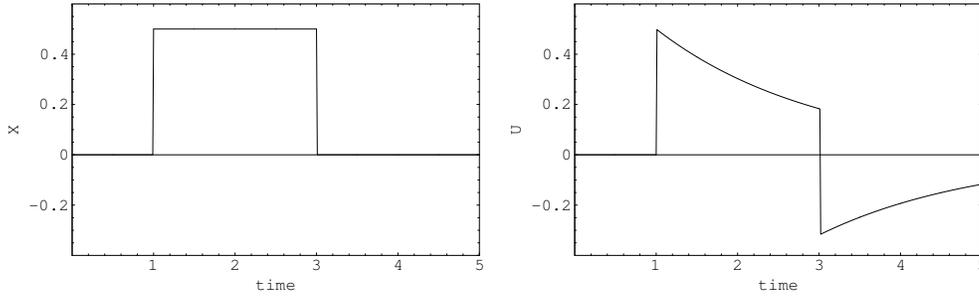


Figure 2.1: An illustration of the switch between straight-line swimming and tumbling in *E. Coli* bacteria, based on a model with a single leaky integrator given in Eq. (2.1). The left panel shows the variation of the attractant concentration $X(t)$, and the right panel shows $U(t)$. The straight-line swimming behavior (B_1) is active between $t = 1$ and $t = 3$.

move towards regions of higher concentration. Essentially, the *E. Coli* bacteria have two behaviors, *straight-line movement*, and *random-walk tumbling*. It can be shown experimentally that, at any given absolute concentration of an attractant substance, the bacteria generally exhibit the tumbling behavior, at least after some time. However, if the bacteria are momentarily placed in a region of higher concentration, they begin moving in straight lines. Now, this cannot be due to gradient following, since there is no (spatial) gradient. However, there is a *temporal* gradient, i.e. a difference in concentration over time, and this provides the explanation: While unable to detect a spatial gradient, the *E. Coli* bacteria are equipped with a rudimentary **short-term memory**, allowing them to detect a temporal gradient. The behavior of the *E. Coli* is an example of **kinesis**. It is *because* of its slow motion that the *M. Xanthus* bacterium is able to catch the *E. Coli*: By releasing an attractant and staying in the same area, the *M. Xanthus* is able to lure the *E. Coli* to the region, and to keep them tumbling there, ending up as food for the *M. Xanthus* - indeed a fatal attraction.

A simple mathematical model of kinesis can now be formulated. Consider a bacterium faced with the choice of activating its straight-line movement behavior (hereafter: B_1) or its tumbling behavior (hereafter: B_2), and introduce a variable U such that B_1 is activated if $U > T$ (where T is the threshold), and B_2 otherwise. Let X be the value of the stimulus (i.e. the concentration of the attractant). Consider now a **leaky integrator**, given by the equation

$$\frac{dV(t)}{dt} + aV(t) = bX(t). \quad (2.1)$$

Now, consider the difference $U(t) = X(t) - V(t)$, and set $T = 0$. In case the bacterium experiences an increase $X(t)$ in the concentration of the attractant, $U(t)$ becomes positive, thus activating B_1 . If X remains constant, $U(t)$ slowly falls towards zero (and eventually becomes negative, if $b > a$). However, if there is a decrease in X , i.e. if the bacterium begins to leave the region of high

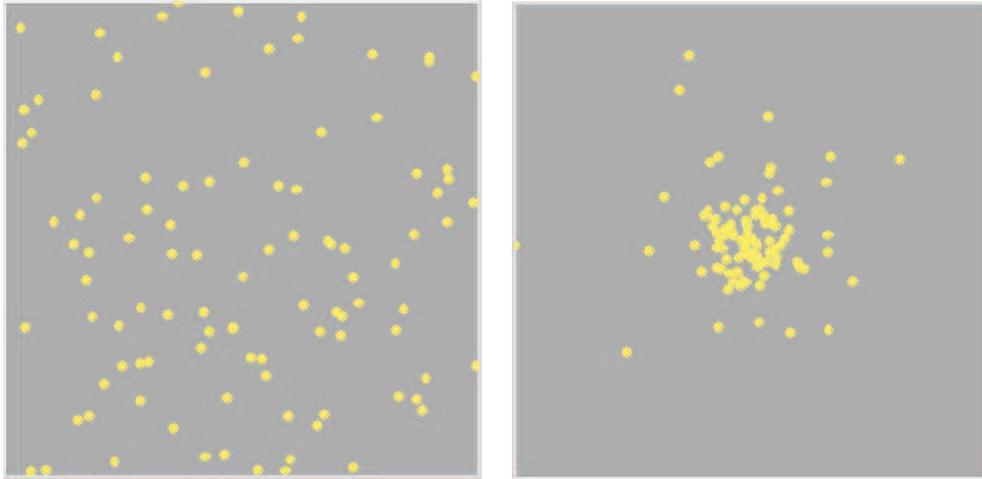


Figure 2.2: The motion of simulated *E. Coli* bacteria based on the behavior switch defined above. 100 bacteria were simulated, and the parameters a and b were both equal to 1. The attractant had a gaussian distribution, with its peak at the center of the image. The threshold was set to 0. The left panel shows the initial distribution of bacteria, and the right panel shows the distribution after 10 simulated seconds, using a time step of 0.01.

attractant concentration, $U(t)$ becomes negative, and B_2 is activated, keeping the bacterium approximately stationary. Thus, the kinesis of *E. Coli* can be modelled with a single leaky integrator.

Finally, note the importance of taxes in simple behaviors for autonomous robots. For example, it is easy (using e.g. two infrared (IR) sensors) to equip a robot with the ability to follow a light gradient. Thus, for example, if a light source is placed next to, say, a battery charging station, the robot may achieve long-term autonomy, by activating a klinotactic behavior whenever the battery level drops below a certain threshold. The problems of such behavior selection in autonomous robots (and animals, for that matter) will be studied further in Chapters 5 and 6 where the concept of **utility** will be discussed in detail. The simple kinesis of the *E. Coli* can be considered as a case of utility-based behavior selection, in which one behavior, B_2 , has a fixed utility T , and the utility of the other, B_1 , is given by $U(t)$.

2.4.3 Fixed action patterns

The third class of animal behaviors are the so called *fixed action patterns* (FAPs). The concept of FAPs was introduced to describe more complex behaviors that are extended over time (beyond the temporal extension of the stimulus) and may involve a sequence of several actions. It should be noted, however, that the term FAP is used less frequently today, since it has been observed that

several aspects of such behaviors are not at all fixed. Some behaviors, such as courtship behaviors are, however, quite stereotyped, since they are required to be strongly indicative of the species in question.

An example of an FAP is the egg-retrieving behavior of geese, which is carried out to completion (i.e. the goose moves its beak all the way towards its chest) even if the egg is removed.

However, many other animal behaviors are highly adaptive, such as prey tracking by various mammals. On the other hand, in e.g. insects such as the praying mantis, the attack behavior is completely stereotyped and, once started, always carried out to completion regardless of the feedback from the environment (in the case of the praying mantis, the attack occurs with terrifying swiftness, making it essentially impossible for the animal to modulate its actions as a result of sensory feedback).

FAPs may also be **motivated**, i.e. dependent not only on external (sensory) stimuli, but also on the **internal state** of the animal. A simple model for motivation will be studied briefly below.

Another concept, which has also fallen out of fashion, is the **innate releasing mechanism** (IRM). An IRM was considered a built-in mechanism, characteristic of the species in question, inside the animal which caused it to perform some action based on a few salient features of a stimulus. An example of such a **sign stimulus** is the red belly of male stickleback fish in breeding condition. When competing for a female, the male stickleback must identify and chase away other males. It has been shown in experiments involving the presentation of various crude models of fish to a male stickleback, that the detection of the red color of the belly of other males causes the fish to assume an aggressive posture (rather than, say, the detailed shape of the model, which seems to be more or less irrelevant). Note that several aspects of IRMs, e.g. the question of whether they really are inborn mechanisms, have been called into question.

2.4.4 Animal motivation

Animals generally do not simply react to the immediate stimuli available from the environment, but maintain also an **internal state**, which *together* with the external (sensory) stimuli determine which action to take. Behaviors which depend on an internal state are said to be **motivated**, and the study of animal motivation is an important part of ethology. In early models of motivation, the concept of **drive** was central. A simple model of motivation, based on drives, is the so called **Lorenz' psychohydraulic model**.

Lorenz introduced the (artificial) concept of an **action-specific energy**, accumulating in a tank with a valve. In this model, the level of action-specific energy is raised as a result of the passage of time (if the behavior is not being executed), leading to the eventual opening of the valve, and the flow of action-

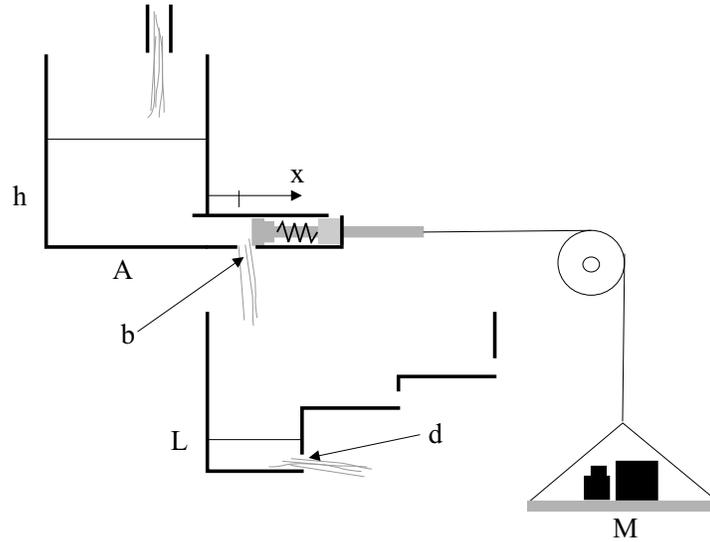


Figure 2.3: Lorenz' psychohydraulic model of motivation in animals.

specific energy into a bucket with several holes on different levels, representing different aspects of the behavior in question. The flow of action-specific behavior into the bucket can also be increased by external factors, represented by weights on a scale, connected to the valve by means of a string. As the energy flows into the bucket, the low-threshold parts of the behavior are immediately expressed, and higher-threshold aspects are expressed if the level of energy reaches sufficiently high. Before proceeding with a simple set of equations for this model, one should note that the modern view of motivation is more complex than the simple feedback model just described. For example, in Lorenz' model, action-specific energy, for a given behavior, increases gradually with the passage of time. Such a simple model may work for certain behaviors, e.g. eating or drinking, but not for others, e.g. aggression. Also, the model cannot properly take into account the *consequences* (feedback) resulting from the execution of the behavior. Furthermore, certain behaviors, e.g. the intake of food, can modify the internal state of an animal in different ways depending, for example, on the exact composition of the food.

Returning now to Lorenz' model, let the inflow of action-specific energy be represented by the variable $\dot{V}(t)$. The variation in depth h of the fluid, assuming for the moment that the valve is closed, will then be

$$\dot{h}(t) = \dot{V}(t)/A, \quad (2.2)$$

where A is the area of the tank. For simplicity, assume that the volume flow is constant, so that

$$\dot{h}(t) = v_0, \quad (2.3)$$

for some value of v_0 . The pressure p at depth h is given by

$$p = p_0 + \rho gh, \quad (2.4)$$

where p_0 is the pressure just above the surface (which will be neglected from now on), ρ is the density of the fluid and g is the gravitational constant. Assuming that the area of the valve is equal to a , and neglecting the variation in depth over the extent of the valve, the force exerted on the valve by the fluid equals

$$F_f = pa = \rho gha \equiv ch, \quad (2.5)$$

where c is a constant. The force exerted on the valve by the external weights (mass M) equals

$$F_w = Mg. \quad (2.6)$$

Using the spring equation, the displacement x of the spring and valve (mass m) is given by

$$m\ddot{x} = F_f + F_w + F_s, \quad (2.7)$$

where

$$F_s = -kx - c_d\dot{x}, \quad (2.8)$$

is the spring force (k is the spring constant, and c_d is a damping constant). So far, the closed-valve situation has been considered. The opening of the valve is more difficult to model but, assuming that the valve is either completely closed (if $x \leq x_0$, where x_0 is a constant) or completely open (if $x > x_0$), and using Torricelli's principle

$$v_{\text{out}} = \sqrt{2gh(t)}, \quad (2.9)$$

for the velocity (v_{out}) of the fluid emerging from the container, and assuming that the exit from the tank has area b , the dynamical equations determining the displacement x of the valve and the volume of fluid in the tank become

$$m\ddot{x} = ch(t) + Mg - kx - c_d\dot{x}, \quad (2.10)$$

where

$$\dot{h}(t) = v_0 \text{ if } x \leq 0, \quad (2.11)$$

and

$$A\dot{h}(t) = Av_0 - b\sqrt{2gh(t)} \text{ if } x > 0. \quad (2.12)$$

The outflow from the bucket can be modelled in a similar way. Assuming the area of the lower level of the bucket equals A_2 , the rate equation for the fluid level L in the bucket becomes

$$A_2\dot{L}(t) = b\sqrt{2gh(t)} - d\sqrt{2gL(t)}, \quad (2.13)$$

again using Torricelli's principle (d is the area of the opening in the bucket). A similar, slightly more complex equation, can be written down for the case

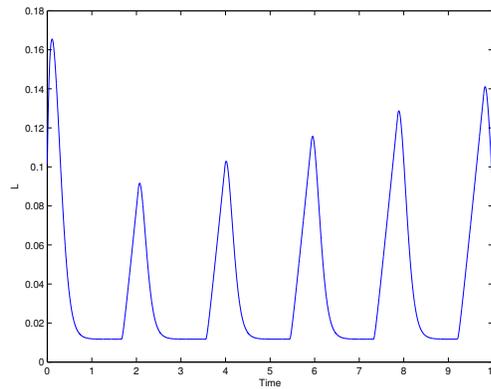


Figure 2.4: The variation of the level L for a particular parameter setting in Lorenz' model. A similar curve can easily be obtained for h .

where the water level exceeds the threshold L_1 to the second level in the bucket. An example of the variation in h and L is given in Fig. 2.4. Lorenz' model is simple, intuitive, and pedagogical but, alas, does not fit observations of animal behavior very well. In the modern view of motivation, a given internal state is maintained through a combination of several regulatory mechanisms, and rather than postulating the concept of drives for behaviors, the tendency to express a given behavior is considered as a combination of several factors, both internal and external. The **physiological state** of the animal (e.g. its temperature, amount of water in the body, amount of different nutrients etc.) can be represented as a point in a multi-dimensional **physiological space**. In this space, lethal boundaries can be introduced, i.e. levels which the particular variable (e.g. body temperature) may not exceed or fall below.

The **motivational state** of the animal is, in this view, generated by the combination of the physiological state and the **perceptual state** (i.e. the signals obtained through the sensory organs of the animal), and can be represented as a point in a **motivational space**.

2.5 Other topics

Animal behavior is a vast topic, and the discussion above is merely a very brief introduction. However, animal behavior will be considered further in this course. For example, two optimization methods based on swarm behavior in animals will be introduced and adaptive behavior (e.g. learning) in animals and robots will be considered as well.