Theoretical Neuroscience Lecture Notes

26th February 2002

Part I
Mathematics

M 1 Elements of Calculus

M 1.1 Numbers

- $\mathbb{N} = \{1, 2, 3, ...\}$ – positive integers
  allowed operations are addition $3 + 8 = 11 \in \mathbb{N}$ and often, but **not** always subtraction: $3 - 5 \notin \mathbb{N}$
- $\mathbb{Z} = \{\ldots, -3, -2, -1, 0, 1, 2, 3, \ldots\}$
  the use addition and subtraction is unrestricted
- $\mathbb{Q} : \left\{ \frac{p}{q} \,|p, q \in \mathbb{Z}, q \neq 0 \right\}$
- $\mathbb{R} : \left\{ \begin{array}{c} \mathbb{Q} \\ \text{irrational numbers} \\ \text{transcendental numbers } (\pi, e) \end{array} \right\}$ solutions of some algebraic equations
- $\mathbb{C} : \left\{ z = a + ib \,\middle| a, b \in \mathbb{R}; i := \sqrt{-1} \right\}$

M 1.2 Functions

A function is al rule that assigns to each number in set D (domain) one and only one number in a set R (range)

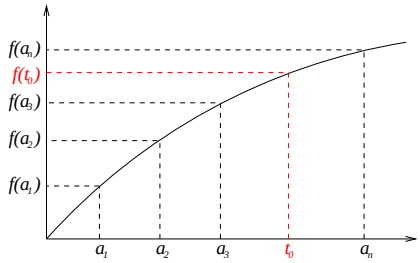
$f : D \mapsto R$
$x \mapsto f(x)$
x: indipendent variable
$f(x)$: dependent variable

The notion of a function can be extended to include more general domains and ranges (mappings).

M 1.3 Continuity

Consider a function with $D, R \in \mathbb{R}$. A function is continuous at some point $x_0 \in D$ if we can draw it without lifting the pencil.

Mathematically, continuity is defined through the limit of an arbitrary sequence of numbers:



sequence $(a_1, a_2, ..., a_n)$
$\lim_{n\mapsto\infty} a_n = x_0$

$$\lim_{n\mapsto\infty} f(a_n) \neq f(x_0) \text{ in this case}$$
$$\lim_{n\mapsto\infty} f(a_n) = f(\lim_{n\mapsto\infty} a_n)$$

Figure M 1.1: Continuity

M 1.4 Differentiation

Differentiation is beside integration the most important concept in calculus.

Differentiation: indination / slope of a function at some position x_0. Independent variable: time t - derivative gives the change of $f(t)$ with time. The slope of the function f at some position x is also called the derivative of f at x, it is written as

$$f'(x) \text{ or } \frac{\partial f(x)}{\partial x} \text{ or } \frac{df(x)}{dx}$$

$f'(x)$ is a function of x if x is considered to be variable. The derivative is defined through a limit process:

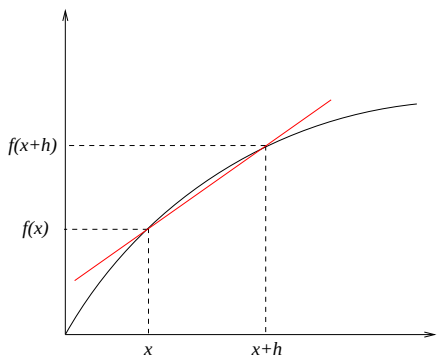


Figure M 1.2: slope of the secant: $\frac{f(x+h)-f(x)}{h}$

M 1.4.1 Rules:

sum rule

$$h(x) = f(x) + g(x)$$

$$h'(x) = f'(x) + g'(x)$$

product rule

$$h(x) = f(x)g(x)$$

$$h'(x) = f'(x)g(x) + f(x)g'(x)$$

quotient rule

$$h(x) = \frac{f(x)}{g(x)}$$

$$h'(x) = \frac{f'(x)g(x) - f(x)g'(x)}{(g(x))^2}$$

chain rule

$$h(x) = g(f(x))$$

$$h'(x) = g'(f(x))f'(x)$$

M 1.4.2 Physical interpretation of the derivative

If time t is the independent variable, $f(t)$ some function of t, e.g. $s(t)$ the distance of an object at time t or $Q(t)$ the charge having entered a neuron since $t = 0$. Then $f'(t)$ is the *temporal change* of $f(t)$. $Q'(t) = I(t)$ would be the current that is running through the membrane at time t.

What can we do with derivation?

1. Curve sketching: what does a function look like

$$f'(x) = 0,\ f''(x) > 0 \Rightarrow f \text{ has a minimum at } x$$

$$f'(x) = 0,\ f''(x) < 0 \Rightarrow f \text{ has a maximum at } x$$

Inflections point at $x \Leftrightarrow f''(x) = 0,\ f'''(x) \neq 0\, etc.$

2. Approximation of functions: the Taylor series computes approximations of (differetiable) functions by polynomials centered around $a \in D$.

$$f(x) = f(a) + \frac{f'(a)}{1!}(x-a) + \frac{f''(a)}{2!}(x-a)^2 + \frac{f'''(a)}{3!}(x-a)^3 ...$$

The approximation usually gets better as higher order terms are included. It is good for x to be close to a, e.g. $f(x) = \sin x,\ a = 0$

$$f(x) \approx 0 + \frac{\cos x}{1!}|_{x=0}^{(x-0)} + \frac{(-\sin x)}{2!}|_{x=0}^{(x-0)^2} + \frac{(-\cos x)}{3!}|_{x=0}^{(x-0)^3} = x - \frac{x^3}{x!}$$

Differentiation is important for nonlinear dynamic systems: consider stationary states (fixed points); from linearizing the equation around the stationary state follows *local stability*.

M 1.4.3 Partial derivatives

Function $f : D \mapsto R$, where D and $R \in \mathbb{R}$
i.e. the function has $n = 3$ variables.

$$f : D \mapsto \mathbb{R},\ D \in \mathbb{R}^3$$

$$(x, y, z) \mapsto f(x, y)$$

$$f(x, y, z) = xy + z \sin x$$

Partial derivatives describe the slope of the function with respect to **one** of the variables; the other variables are kept **fixed**:

$$\begin{aligned}
\frac{\partial f(x,y,z)}{\partial x} &= y + z\cos x \\
\frac{\partial f(x,y,z)}{\partial y} &= x \\
\frac{\partial f(x,y,z)}{\partial y} &= \sin x
\end{aligned}$$

M 1.4.4 Gradient

Consider a function $f : D \mapsto \mathbb{R}$, where $D \in \mathbb{R}^n$. The Gradient of f at some point $(x_1, \ldots, x_n) \in D$ is defined to be

$$grad\, f(x_1, x_2, \ldots, x_n) = \vec{\nabla} f(x_1, x_2, \ldots, x_n) \equiv \left(\frac{\varphi f(x_1, \ldots, x_n)}{\varphi x_1}, \frac{\varphi f(x_1, \ldots, x_n)}{\varphi x_2}, \ldots, \frac{\varphi f(x_1, \ldots, x_n)}{\varphi x_n} \right)$$

where $grad\, f(x_1, \ldots, x_n)$ is an n-dimensional vector.
E.g. $f : \mathbb{R}^2 \mapsto \mathbb{R}$
$(x, y) \mapsto f(x, y)$ Figure M 1.3 shows the gradient, which is perpendicular

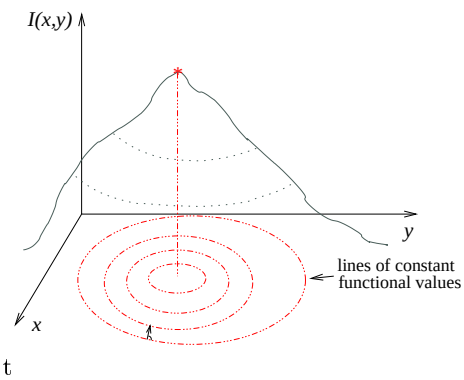
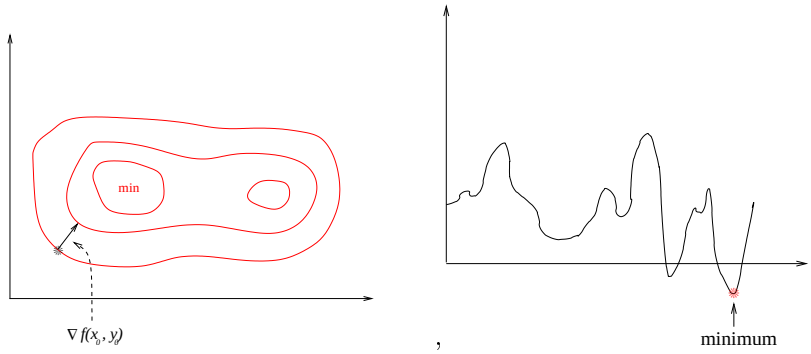


Figure M 1.3: 3-dimensional view of a gradient ascent

to the the lines where f is constant. It points in the direction of the steepest ascent.



(a) the spacing between the contour lines is the steepness at that point

(b) the gradient descent finds the minimum

Figure M 1.4: Gradient descent

M 1.5 Integration

The Integral of a function computes the area of its base-function.

The integral is defined through a limit process. Divide [a,b] in n bins, e.g.

Then

$$\int_a^b f(x)dx \approx (x_1 - a)F_1 + (x_2 - x_1)F_2 + (b - x_2)F_3$$

The more bins one divides of the range, the better gets the approximation → let the number of bins go to ∞:

$$\int_a^b f(x)dx = \lim_{n\to\infty} \sum_{i=1}^{n} b_i F_i$$

M 1.5.1 Indefinite integrals, differentiation and integration

Instead of considering a and b as fixed limits in $\int_a^b f(x)dx$, consider a variable limit x :

$$\int_a^x f(\tilde{x})d\tilde{x} = F(x)$$

Differentiation and integration are inverse operations! $F(x)$ is called an antiderivative of $f(x)$.

M 1.5.2 Fundamental theorem of calculus - how to compute definite integrals

For a given $f(x)$, find an antiderivative $F(x)$. Then:

$$\int_a^b f(x)dx = F(b) - F(a)$$

Finding an antiderivative can be a hard, even impossible, task!

Example:

$$\int_2^3 x^2 dx \rightarrow f(x) = x^2,\ F(x) = \frac{1}{3}x^3$$

$$\int_2^3 x^2 dx = \frac{1}{3}x^3 \mid_2^3 = \frac{1}{3}3^3 - \frac{1}{3}2^3 = \frac{19}{3}$$

M 1.5.3 Integration rules

These rules can be obtained from the rules of differentiation.

1.

$$\int_a^b f(x)dx = -\int_b^a f(x)dx$$

2.

$$\int_a^c f(x)dx = \int_a^b f(x)dx + \int_b^c f(x)dx$$

3. constant factor:

$$\int_a^b cf(x)dx = c\int_a^b f(x)dx$$

4. sum rule:

$$\int_a^b (f(x) + g(x))dx = \int_a^b f(x)dx + \int_a^b g(x)dx$$

5. integration by parts

$$\begin{aligned}\int_a^b f(x)g(x)dx &= f(x)G(x) \mid_a^b - \int_a^b f'(x)G(x)dx \\ &= f(b)G(b) - f(x)G(a) - \int_a^b f'(x)G(x)dx\end{aligned}$$

Sometimes limits are omitted, i.e. search the antiderivative $F(x)\ (+c) = \int f(x)dx$
E.g. $\int xe^x dx$

$\int xe^x dx$	two possibilities	solving this integral
$= xe^x - \int 1e^x dx$	$f(x) = e^x$	$f(x) = x$
$= xe^x - \int e^x dx$	$g(x) = x$	$g(x) = e^x$
$= xe^x - e^x$	$f'(x) = e^x$	$f'(x) = 1$
$\hookrightarrow$Test!	$G(x) = \frac{1}{2}x^2$	$G(x) = e^x$

This $\nearrow$ is more complicated than $\uparrow$ (xe^x)

Now let us test our computed antiderivative by deriving it:

$$F(x) = xe^x - e^x \Rightarrow F'(x) = e^x + xe^x - e^x = xe^x = f(x) \ \surd$$

Our solution is correct, $F'(x) \equiv f(x)$, where $f(x)$ is our funcion from the beginning.

6. Integration by substitution

$$\int_a^b f(g(x))g'(x)dx = \int_{g(a)}^{g(b)} f(z)dz$$

$$\left[\int_a^b f(g(x))dx = \int_{g(a)}^{g(b)} f(z)g^{-1}(z)dz\right]$$

M 2 Differential equation

M 2.1 What is a differential equation and why do we care?

Systems that evolve in time are called *dynamical systems*. The description of dynamical systems splits up into two categories:

- time-continuous systems are usually described by *differential* equations. E.g. the concentration of vitamin C:

$$\frac{dc}{dt} = -kc(t) \Rightarrow c(t) = ?$$

- time-discrete systems are described by *difference* equations., E.g.the population density of insects after successive years:

$$x_{t+1} = \alpha x_t e^{\beta x_t^3} \Rightarrow x_t = ?$$

The Goal is to compute the system behaviour as a function of time

- analytically: only possible in special cases
- numerically; at least find special properties of the solution:
  - fixed points $\equiv$ steady states (e.g. point where concentration does not change any more)
  - stability of fixed points
  - chaotic behaviour

M 2.1.1 Terminology

The highest derivative is called the *order* of the differential equation, e.g. $x''(t)+x=0 \Rightarrow 2^{\text{nd}}$order. So far we haveconsidered differential equations with one variable (time), e.g. $\frac{dV(t)}{dt}+\frac{V(t)}{\tau}=\frac{I(t)}{C}$ for the membrane potential $V(t)$. Such differential equations are called *Ordinary Differential Equations (ODEs)*. Differential equations can be formulated for more than one variable.

Example: Cable equation for $V(x,t)$ in the dendrite

$$r_m c_m \frac{\partial V(x,t)}{\partial t} = \frac{r_m}{r_c}\frac{\partial^2 V(x,t)}{\partial x^2} - V(x,t) + r_m I_{ext}(t)$$

c_m = membrane capacity	r_m = membrane resistance
I_{ext} = applied current density	r = internal resistance

A differential equation gives a relationship between a function and its derivative(s).
A simple example is exponential decay:

Exponential decay can be found in many Systems (i.e. radioactive decay; mortality in a population; decay of vitamin C dissolved in water).

Consider a small time intervall $\triangle t$ at time t. Let $N(t) = const$ during this time. $N_0 \approx 10^{23}$, decay rate 20 atoms/sec $\mapsto 10^{23} - 20$ does not really matter. During this time intervall a number $N(t) - N(t+\triangle t) > 0$ of atoms decay. Let $\triangle N(t) = N(t+\triangle t) = N(t) < 0$. Now comes the observation, the natural law:

$$\triangle N \alpha N(t) \triangle t \tag{M 2.1a}$$

$$\triangle N(t) = -kN(t)\triangle t\,,\ k>0\,,\ \textit{decay constant} \tag{M 2.1b}$$

$$\Leftrightarrow \frac{\triangle N(t)}{\triangle t} = -kN(t)$$

Now let $\triangle t \to 0$ to obtain an exact relationship:

$$\underbrace{\lim_{\triangle t\to\infty}\frac{\triangle N(t)}{\triangle t}} = -kN(t)$$

$$\frac{\partial N(t)}{\partial t} \equiv N'(t) \Leftrightarrow \frac{\partial N(t)}{\partial t} = -kN(t)$$

$$N'(t) = -kN(t) \tag{M 2.2}$$

Pay attention: sometimes $N'(t)$ is written as $\frac{\partial N}{\partial t}$ or $\dot{N}(t)$!

Another example:

$$c\frac{\partial V}{\partial t} = \underbrace{-I(t)}_{\text{depends on } V}$$

Solving a differential equation means finding a function that satisfies the equation. E.g. M 2.2: which function $N(t)$ satisfies $N'(t) = -kN(t)$? Solving a differential equation is a hard task. Simple integration is not possible:

E.g. M 2.2

$$\begin{aligned} N'(t) &= -kN(t) \\ \int_0^t N(\tilde{t})d\tilde{t} &= -k\int_0^t N(\tilde{t})d\tilde{t} \end{aligned} \quad \Bigg| \quad \text{integrate both sides } \int_0^t \dots d\tilde{t}$$

M 2.1.2 Fundamental theorem of calculus (2)

$$\begin{aligned} N(t) - N(0) &= -k\int_0^t N(\tilde{t})d\tilde{t} \\ N(t) &= N(0) - k\int_0^t N(\tilde{t})d\tilde{t} \end{aligned}$$

However, it is easy to check, if a givensolution os correct:

E.g. $N' = -kN$ M 2.2

Is $N(t) = 42e^{-kt}$ a solution?

$$N'(t) = 42(-k)e^{-kt} = -k * \underbrace{42e^{-kt}}_{N(t)} = -kN(t) \ \surd$$

The factor 42 is arbitrary: the solution is not unique!

Often additional conditions are provided, e.g. an initial value:

$$N'(t) = -kN(t) \qquad \text{(M 2.2)}$$
$$N(0) = 42 \qquad \text{(M 2.3)}$$

$\rightarrow$ initial value problem

The function $N(t) = 42e^{-kt}$ solves the initial value problem:

$$N(0) = 42e^0 = 42 \ \surd$$

and the solution is unique!

M 2.2 Numerical integration of ordinary differential Equations (ODE's): Euler routine

Consider the initial value problem

$$\begin{aligned} \frac{dx(t)}{dt} &= f(x,t) \\ x(t_0) &= x_0 \end{aligned} \qquad \text{(M 2.4)}$$

E.g.:

$$\begin{array}{rcl} \frac{dx(t)}{dt} & = & t^3 \sin t + e^{-\frac{x(t)}{t}} \\ x(2) & = & 0.7 \end{array} \tag{M 2.5}$$

Goal: Numerical approximation of the solution of (M 2.4).

Trick: Remember

$$\frac{dx(t)}{dt} = \lim_{h \to 0} \frac{x(t+h) - x(t)}{h}$$

The tangent gives an approximation, which is very near to the value, which is to be computed. Now choose a small stepsize h and omit the limit. M 2.4:

$$\rightarrow \underbrace{\frac{dx(t)}{dt}} = f(x,t)$$

$$\approx \frac{x(t+h) - x(t)}{h} \Rightarrow \frac{x(t+h) - x(t)}{h} \approx f(x,t)$$

$$\Rightarrow x(t+h) \approx h - f(x,t) + x(t) \tag{M 2.6}$$

E.g. M 2.5

$$x(t+h) = x(t) + h\left\{t^3 \sin t + e^{-\frac{x(t)}{t}}\right\} \quad - \text{error is } O(h^2)$$

Matlab-routine: implement a routine with stepsize, initial values. To proof the quality of the solution compute the function backwards. The nearer you get to the initial position the better is the solution.

M 2.3 Separation of variables

If an ODE has the form that

$$\frac{\partial x}{\partial t} : f(x)g(t) \tag{M 2.7a}$$

with initial condition

$$x(t_0) = x_0 \tag{M 2.7b}$$

it can be solved in the following way:

<u>Separate</u> the variables x and t

$$\frac{1}{f(x)} dx = g(t) dt$$

and integrate $\downarrow$ variables $\downarrow$

$$\int_{x_0}^{x(t)} \frac{1}{f(\tilde{x})} d\tilde{x} = \int_{t_0}^{t} g(\tilde{t}) d\tilde{t}$$

$\uparrow$ initial values $\uparrow$

Finally, solve the equation for $x(t)$.

Example: exponential decay (*initial value problem*) separation:

$$\frac{dN(t)}{dt} = -kN(t) \tag{M 2.3}$$

$$N(0) = N_0 \tag{M 2.8}$$

<u>separation:</u> (mind that $\frac{dN(t)}{dt} = \frac{dN}{dt}$ and $-kN(t) = -kN$)

$$\frac{1}{N}dN = -kdt$$

integration:

$$\begin{aligned}
\int_{N_0}^{N(t)} \frac{1}{\tilde{N}} d\tilde{N} = \int_0^t -kd\tilde{t} \quad &\Rightarrow \quad \ln \tilde{N} \mid_{N_0}^{N(\tilde{t})} = -k\tilde{t} \mid_0^t \\
&\Rightarrow \quad \ln N(z) - \ln N_0 = -kt + 0 \\
&\Rightarrow \quad \ln \frac{N(z)}{N_0} = -kt \quad \mid exp \\
&\Rightarrow \quad \frac{N(t)}{N_0} = e^{-kt} \\
&\Rightarrow \quad N(t) = N_0 e^{-kt}
\end{aligned}$$

This solution solves the initial value problem M 2.2 & M 2.8.

M 3 Linear ordinary differential equations

A linear ODE has the form

$$\frac{\partial x(t)}{\partial t} = a(t)x + b(t) \tag{M 3.1}$$

i.e., it is linear in the dependent variable x, whereas $a(t)$ and $b(t)$ can be arbitrary functions of the independent variable t. Example: IaF neuron (N 1.9)

$$V(t) + \frac{V(t)}{\tau} = \frac{I(t)}{C} \Leftrightarrow V'(t) = \underbrace{-\frac{V(t)}{\tau}}_{a(t) = -\frac{1}{\tau}} + \underbrace{\frac{I(t)}{C}}_{b(t)}$$

here: $a(t)$ does not depend on t

M 3.1 The homogenous differential equation

For $b(t) \equiv 0$, equation (M 3.1) results in the homogenous linear equation

$$\frac{\partial x(t)}{\partial t} = a(t)x(t) \tag{M 3.2a}$$

Let

$$x(t_0) = x_0 \tag{M 3.2b}$$

The initial value problem M 3.2a & M 3.2b can be solved using the separation of variables technique (see M2):

$$
\begin{aligned}
\frac{dx}{dt} = a(t)x \quad &\Rightarrow \quad \frac{1}{x}dx = a(t)dt \\
&\Rightarrow \quad \int_{x_0}^{x(t)} \frac{1}{\tilde{x}} d\tilde{x} = \int_{t_0}^{t} a(\tilde{t}) d\tilde{t} \\
&\Rightarrow \quad \ln \tilde{x} \,|_{x_0}^{x(t)} = \int_{t_0}^{t} a(\tilde{t}) d\tilde{t} \\
&\Rightarrow \quad \ln x(t) - \ln x_0 = \int_{t_0}^{t} a(\tilde{t}) d\tilde{t} \\
&\Rightarrow \quad \ln \frac{x(t)}{x_0} = \int_{t_0}^{t} a(\tilde{t}) d\tilde{t} \quad | \, exp \\
&\Rightarrow \quad \frac{x(t)}{x} = e^{\int_{t_0}^{t} a(\bar{t}) d\bar{t}} \\
&\Rightarrow \quad x(t) = x_0 e^{\int_{t_0}^{t} a(\bar{t}) d\bar{t}} \qquad \text{(M 3.3)}
\end{aligned}
$$

M 3.2 The inhomogenous linear equation

The complete equation M 3.1 is called the inhomogenous linear ODE where $b(t)$ is called the inhomogenity. Due to the linearity, the solution of M 3.1 & M 3.2b can be written down:

$$x(t) = \varphi(t) \left(x_0 + \int_{t_0}^{t} \frac{1}{\varphi(\tilde{t})} b(\tilde{t}) d\tilde{t} \right) \qquad \text{(M 3.3)}$$

$$\text{where } \varphi(t) = e^{\int_{t_0}^{t} a(\bar{t}) d\bar{t}}$$

(variation of constants)

How can we see that?

$$
\begin{aligned}
\frac{\partial x}{\partial t} &= \varphi'(t) \{\ldots\} + \varphi(t) \underbrace{\{\ldots\}'}_{\frac{1}{\varphi(t)} b(t)} \\
&= \varphi'(t) \{\ldots\} + b(t) \\
&= \underbrace{e^{\int_{t_0}^{r} a(\bar{t}) d\bar{t}}}_{\varphi(t)} a(t) \{\ldots\} + b(t) \\
&= a(t)\varphi(t) \{\ldots\} + b(t) \\
&= a(t)x(t) + b(t)
\end{aligned}
$$

Example

$$\begin{aligned} x(t_0) &= x_0 \\ \varphi(t_0) &= e^0 = 1 \\ x(t_0) &= 1\,\{x_0 + 0\} = x_0 \;\rightarrow\; \text{the solution is correct} \end{aligned}$$

M 3.2.1 The principle of superposition

Consider again the linear system M 3.1. The inhomogeneity $b(t)$ can be regarded as an <u>input</u> to the system, $x(t)$ is the <u>response</u>.

PoS: Responses to different $b(t)$ can be superimposed. More specifically, let $x_1(t)$ be a solution for the input $b_1(t)$ and $x_2(t)$ a solution for the input $b_2(t)$. Then an input $k_1 b_1(t) + k_2 b_2(t)$ yields a response $x(t) = k_1 x_1(t) + k_2 x_2(t)$. this holds for linear differential equations.

Proof:

- multiplication by k

$$\begin{aligned} \frac{dx_1}{dt} &= ax_1 + b1\,|{*}k \\ k\frac{dx_1}{dt} &= kax_1 + kb_1 \\ \Rightarrow \frac{d}{dt}(kx_1) &= a(kx_1) + kb_1 \end{aligned}$$

- addition of solutions:

$$\begin{aligned} \frac{dx_1}{dt} &= ax_1 + b_1 \\ \frac{dx_2}{dt} &= ax_2 + b_2 \\ &\Rightarrow \\ \frac{dx_1}{dt} + \frac{dx_2}{dt} &= ax_1 + ax_2 + b_1 + b_2 \\ \Leftrightarrow \frac{d}{dt}(x_1 + x_2) &= a(x_1 + x_2) + (b_1 + b_2) \end{aligned}$$

M 4 Discrete Dynamical Systems

M 4.1 Difference equations

Example: Let $x(t) = x_t$ be the density of an insect population in a swamp. The density is measured in fixed time intervals, e.g. of a week. a model for the density as given by the next measurement is

$$x_{t+1} = Rx_t - \frac{R}{2000}x_t^2 \qquad R: \text{ constant } (1 \leq R \leq 4) \tag{M 4.1}$$

e.g.

$$R = 1$$

$$x_0 = 1000 \Rightarrow x_1 = 500 \Rightarrow x_2 = 375 \Rightarrow x_3 ...$$

The equation $f(x) = Rx - \frac{R}{2000}x^2$ is *iterated* with a given start value. It is a *difference equation.*

In general, we consider difference equations of the form

$$\begin{array}{rcl} x_{t+1} & = & f(x_t) \text{ or} \\ x(t+1) & = & f(x(t)) \\ t & = & 0.12 \end{array} \tag{M 4.2}$$

M 4.2 is equipped with an initial condition

$$x(t=0) = x_0 \tag{M 4.3}$$

$\Leftarrow$ initial value problem

Example: consider the linear difference equation

$$x_{t+1} = Rx_t \; R \in \mathbb{R}$$

$$x_0 = X > 0 \tag{M 4.4}$$

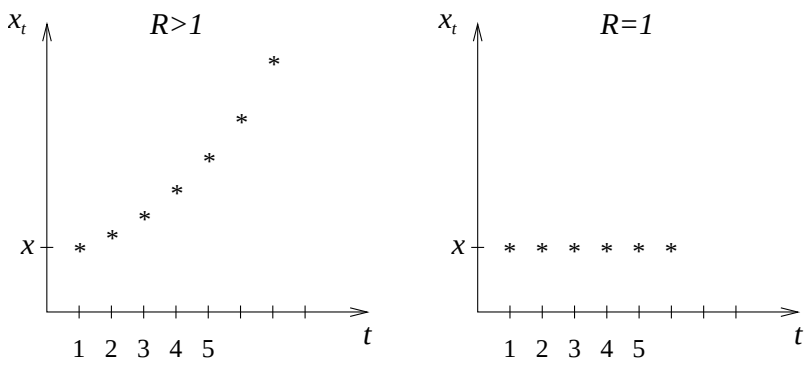
You can say here (only example): "What is x for all the time (no iterations needed here)."

Solution: $x_t = XR^t \;\; (R * R * R * R * ... * R(x))$

Proof:

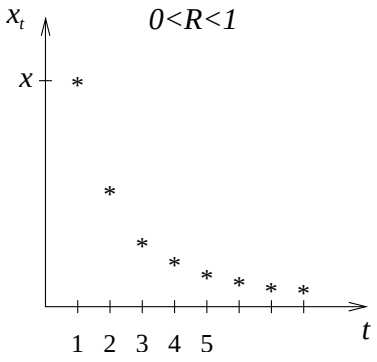
$$\begin{array}{rcl} x_{t+1} & = & XR^{t+1} \\ & = & (XR^t)R \\ & = & Rx_t \end{array}$$

initial value: $x_0 = XR^0 = X \;\surd$
The behaviour of the system depends on R :

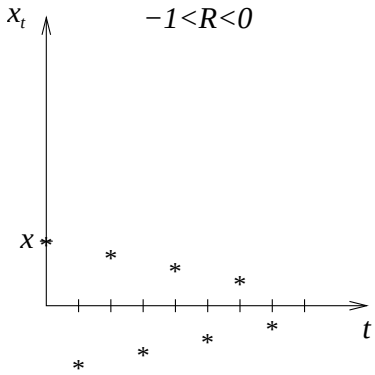


(a) exponential growth

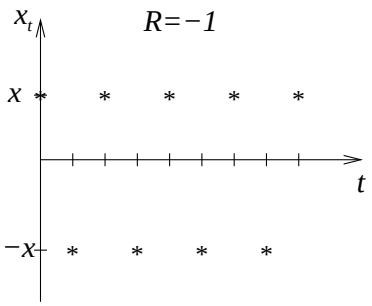
(b) an arbitrary start value is a fixed point of the dynamics



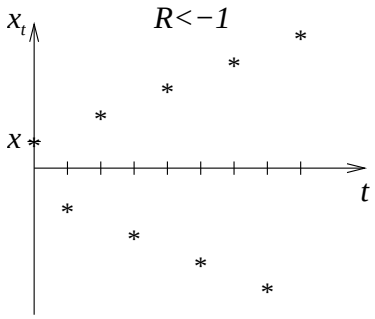
(c) exponential decay



(d) alternating exponential decay



(e) periodic orbit / cycle of period 2(x,-x)



(f) alternating exponetial growth

Figure M 4.1: different system behaviours

<u>Numerical evaluation of</u> $x_{t+1} = f(x_t)$:

$$x_o \mapsto f(x_0) \mapsto f(f(x_0)) = f^{(2)}(x_0) \mapsto f(f(f(x_0))) = f^{(3)}(x_0) \mapsto \ldots$$

<u>Graphical evaluation of</u> $x_{t+1} = f(x_t)$

Draw $f(x)$ and the diagonal; iterate by

- moving vertically to $f(x)$
- moving horizontally to the diagonal

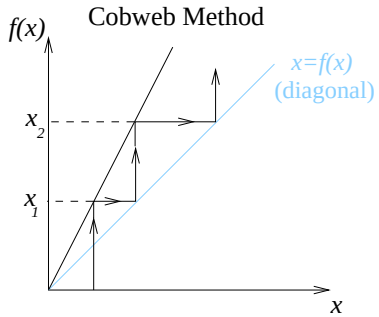


Figure M 4.2: Cobweb Method; $f(x_t) = Rx_t$

M 4.2 Nonlinear discrete dynamical systems

Dynamics is interesting if x_t cannot grow to infinity. E.g., population dynamics:

$$x_{t+1} = Rx_t,\ R > 1 \Rightarrow \text{exponential growth}$$

However, a population cannot grow without bounds. Let x_{t+1} become smaller for large x_t :

$$x_{t+1} = cx_t(1 - x_t),\ x \in [0, 1],\ 0 \leq c \leq 4 \qquad \text{(M 4.5)}$$

E.g., quadratic map; logistic map (Feigenbaum; Großmann & Thomae).

What happens in this system when M 4.5 is iterated?

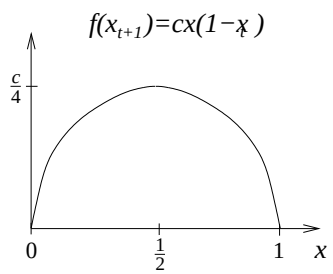


Figure M 4.3: Logistic map

The behaviour strongly depends on c. It turns out: <u>the dynamics is very complex!</u>

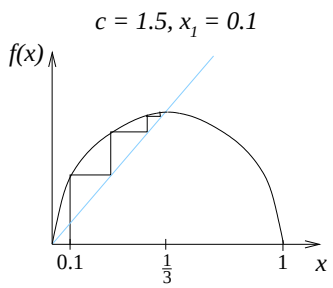


Figure M 4.4: Logistic map iteration

The trajectory (i.e., the sequence of values x_o, x_1, x_2, ...) converges to a fixed point (steady state).

A fixed point is characterized by the equation

$$x_{t+1} = x_t in$$

out case:

$$\begin{aligned} \underbrace{cx_t(1-x_t)}_{x_{t+1}} &= x_t \quad \Leftrightarrow \quad x_t = 0 \quad \vee \quad c(1-x_t) = 1 \\ &\quad\;\; \Leftrightarrow \quad x_t = 0 \quad \vee \quad x_t = 1 - \tfrac{1}{c} \end{aligned}$$

i.e., for $c = \frac{3}{2}$:

$x_t = \frac{1}{3} \vee x_t = 0 \;\; \Rightarrow$ two steady states!

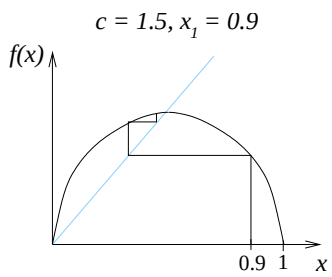


Figure M 4.5: The same behaviour

M 4.2.1 Fixed Points

Fixed points x^* of the dynamical system M 4.2 can be computed from the equation

$$x^* = f(x^*) \tag{M 4.6}$$

A fixed point is called locally asymptotically stable (locally unstable)if, for initial condition in a neighbourhood of x^*, subsequent iterates eventually approach the fixed point (leave the neighbourhood).

Criterion: a fixed point x^* is locally asymptotically stable (or locally unstable) if

$$|f'(x^*)| < 1 \tag{M 4.7}$$

$$(\text{ or } \quad |f'(x^*)| > 1 \quad) \tag{M 4.8}$$

For $|f'(x^*)| = 1$ the behaviour cannot be directly inferred.

Why M 4.7, M 4.8?

We write $f(x)$ in a Taylor series about x^* :

$$f(x) = f(x^*) + f'(x^*)(x - x^*) + \frac{f''(x^*)}{2!}(x - x^*)^2 + ...$$

For simplicity let $x^* = 0 \;\Rightarrow\; f(x^*) = 0$:

$$f(x) = f'(x^*)x + \frac{1}{2}f''(x^*)x^2 + ...$$

For stability considerations it is sufficient to look at the linear term only!

$$f(x) \approx f'(0)x$$

Compare the linear system

$$\begin{aligned} f(x) = Rx \quad &\rightarrow \quad \text{stable for } |R| < 1 \\ &\rightarrow \quad \text{unstable for } |R| > 1 \\ R \triangleq f'(x^*) \end{aligned}$$

For $|R| \triangleq |f'(x^*)| = 1$, higher order terms have to be taken into account.

Example: logistic map

$$\begin{aligned} f(x) &= cx(1-x) \\ &= cx - cx^2 \\ f'(x) &= c - 2cx \end{aligned}$$

- <u>fixed point $x^* = 0$:</u> $f'(0) = c$

$$\Rightarrow x^* = 0 \text{ is } \begin{cases} \text{stable} & \text{for } c < 1 \\ \text{unstable} & \text{for } c > 1 \end{cases}$$

- <u>fixed point $x^* = 1 - \frac{1}{c}$:</u>

$$\begin{aligned} f'(1-\tfrac{1}{c}) &= c - 2c(1-\tfrac{1}{c}) \\ &= c - 2c + 2 \quad = \quad 2 - c \end{aligned}$$

$$\Rightarrow x^* = 1 - \frac{1}{c} \text{is } \begin{cases} \text{stable for} & 1 < c < 3 \\ \text{unstable for} & c > 3 \end{cases}$$

M 4.2.2 Bifurcation diagram

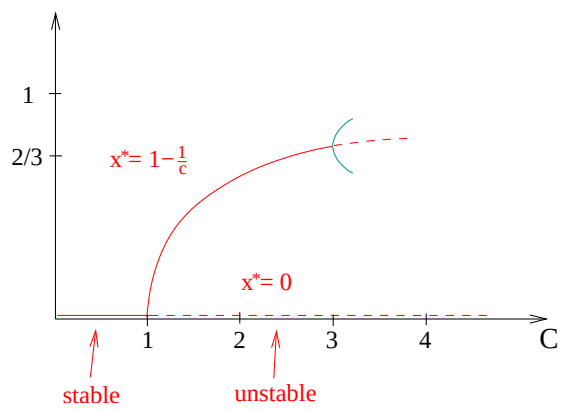


Figure M 4.6: fixed points

What happens at $c = 3$?

A <u>cycle (periodic orbit</u>, <u>periodic cycle</u>) of period 2 appears. Iterates x_1^*, x_2^* where $x_2^* = f(x_1^*)$ and $x_1^* = f(x_2^*)$. In the bifurcation diagram, a <u>bifurcation</u> occurs.

M 4.2.3 Periodic orbits (cycles)

The dynamical system M 4.2 has a periodic orbit (cycle) of length n, - x_1^*, x_2^*, ..., x_n^* - if

1. the values x_i^* ($i = 1, ..., n$) are different from each other
2. $x_{i+1}^* = f(x_i)$ ($i = 1, ..., n-1$) and $x_1^* = f(x_n^*)$,

A cycle of period n is obtained from equation

$$x^* = \underbrace{f(f(\dots f(x^*)\dots))}_{n \text{ times}} = f^{(n)}(x^*)$$

This equation has n roots: $f^{(n)}(x)$ has n fixed points.

Example: logistic map, $f(x) = cx(1-x)$; $c = 3.3$.

$$\begin{aligned} f(f(x)) &= cf(x)(1-f(x) = c\,(cx(1-x))\,(1-(cx(1-x))) \\ &= c^2x(1-x-cx+2cx^2-cx^3) \end{aligned}$$

Criterion: A cycle of period n, - x_1^*, ..., x_n^* - is asymptotically stable (unstable) if, for some x_i^* ($i = 1, ..., n$)

$$\begin{aligned} \left|f'^{(n)}(x_i^*)\right| &< 1 \\ \left(\left|f'^{(n)}(x_i^*)\right| &> 1\right) \end{aligned}$$

Like for fixed points, we cannot determine the stability if $\left|f'^{(n)}(x_i^*)\right| = 1$.

M 4.2.4 Period doubling

At $c = 3$, the fixed point $x^* = 1 - \frac{1}{c} of$ the logistic map becomes unstable. A stable orbit of period 2 emerges. The 2-cycle becomes unstable at $c = 1+\sqrt{6} \approx 3.4495$. A stable orbit of period 4 emerges. In both cases we speak of a period doubling. As c is further increased, a cascade of period-doubling bifurcations occurs (cycles of periods 2, 4, 8, 16, 32, ...) for values of c which are closer and closer together. Finally, at $c_\infty = 3.5699452...$, irregular (chaotic) behaviour emerges (Großmann and Thomae 1977).

A cascade of period-doubling bifurcations is a route to chaos.

For $c > c_\infty$ the chaotic behaviour is interweaved with periodic behaviour.

An attractor is a set which attracts trajectories (asymptotic stable fixed points or periodic orbits; chaotic (stable) attractors). The described route to chaos has a universal character: it occurs also for other dynamical systems than the quadratic map. This is true non quantitatively.

Example: Consider the distances between successive bifurcations at values c_k.

The value

$$\lim_{k\to\infty} \frac{c_{k+1} - c_k}{c_{k+2} - c_{k+1}} =: \delta = 4.66920 \qquad \text{(M 4.9)}$$

is called the Feigenbaum constant (Feigenbaum 1978). δ is a universal constant like π or e.

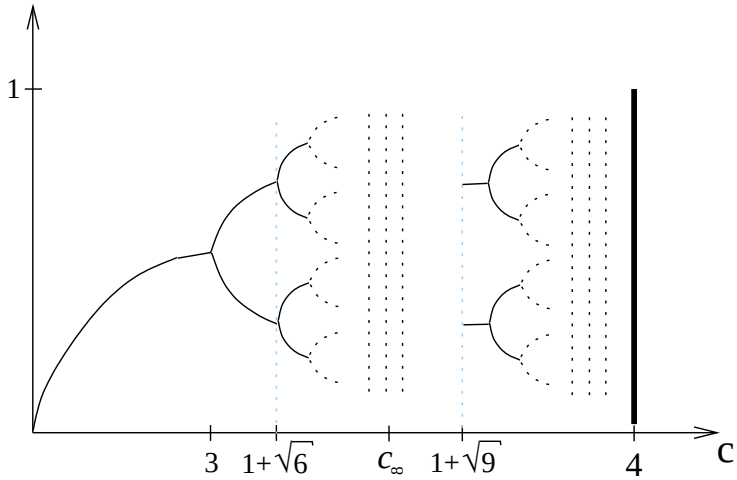
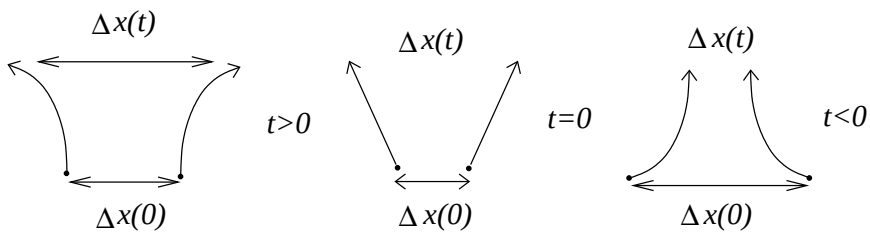


Figure M 4.7: attractors

M 4.2.5 Chaotic behaviour

Chaotic behaviour ("deterministic chaos") is characterized by four features:

- nonperiodic behaviour exists
- the dynamics is restricted, iterates do not converge to $\pm\infty$ but stay in a bound region
- the system is deterministic, i.e., an initial condition ties the behaviour down for all times.
- there is a sensitive dependence on initial conditions: neighbouring points deviate exponentially from each other



(a) deviation at t>0 (b) deviation at t=0 (c) deviation at t<0

Figure M 4.8: exponential deviation

$$\Delta x(t) = k\Delta x(0)e^{\lambda t}$$
$$\lambda > 0$$

M 5 Supplement to M2: nonlinear continuous dynamical systems

Remind time continous systems, which are described by differential equations. In chapter 3 we discuss linear systems. This supplement defines non-linear systems:

M 5.1 Fixed points of differential equations and their stability

Consider an autonomous[1] ODE:

$$\frac{dx}{dt} = f(x) \tag{M 5.10}$$

$$\left[\frac{dx}{dt} = a(t)x + b(t) \text{ in the linear system}\right]$$

$$\begin{aligned} C\tfrac{dV}{dt} &= -\tfrac{V}{R} + I(t) \quad &\text{(linear)} \\ \Rightarrow \quad C\tfrac{dV}{dt} &= -\tfrac{V}{R} \quad &\text{(nonlinear)} \end{aligned}$$

1. A fixed point x^* of M 5.10 is a solution of M 5.10 which is constant in time. $x(t) \equiv x^*$. A fixed point of M 5.10 is given by the condition $\frac{dx(t)}{dt} = 0$ for $x(t) = x^*$.
   So: $f(x^*) = 0$

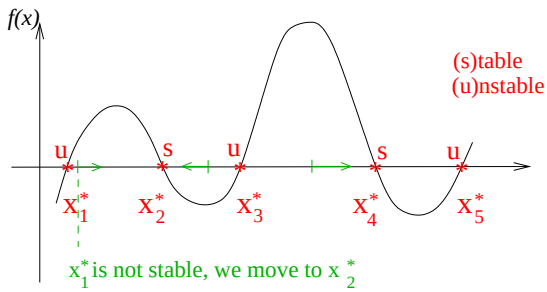


Figure M 5.1: Criterion of stability: x_1^* is not a stable fixed point - between x_1^* and x_2^*we move to x_2^*, which is a stable fixed point

In Figure M 2.1 x_1^*, x_3^* and x_5^* are unstable fixed points, x_2^* and x_4^* are stable.
A fixed point $x^*$of M 5.10 is unstable if $f'(x^*) > 0$. It is asymptotically stable if $f'(x^*) < 0$. For $f'(x^*) = 0$ we cannot determine the stability $\rightarrow$ use the graphical approach.

Example: cows in a field:

Mai (1977) described the dynamics of the vegetation of a field in the presence of a herd of cows.

[1] autonomous: no explicit dependence on t

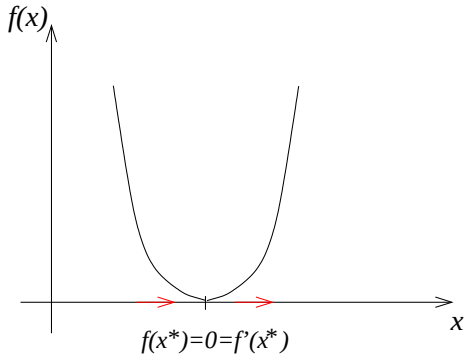


Figure M 5.2: determine the stability graphical

V : amount of vegetation

$$\frac{dV}{dt} = \underbrace{rV(1-\frac{V}{K})} - \underbrace{H\frac{\beta V^2}{V_0^2+V^2}}$$

$$\frac{dV}{dt} = \underbrace{rV(1-\frac{V}{K})}_{\substack{\text{growth of vegetation} \\ \text{Verhulst} - \text{growth}}} - \underbrace{H\frac{\beta V^2}{V_0^2+V^2}}_{\substack{\text{consumption of vegetation per cow} \\ \text{because : } \frac{H:\#\text{ of cows}}{C(V)}}}$$

What happens for different herd sizes?

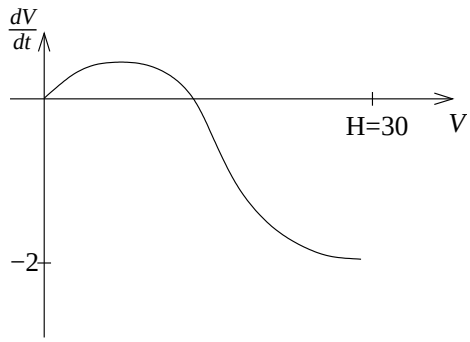


Figure M 5.3: herd size of 30

Mixed points in discrete & continuous systems:

property	discrete systems	continuous systems
basic equation	difference equation $x_{t+1} = f(x_t)$	differential equation (ODE); 1 independent variable (time) $\frac{dx}{dt} = f(x)$
fixed points equation	$x^* = f(x^*)$	$f(x^*) = 0$
stability criterion	$\lvert f'(x^*)\rvert < 1$ stable $\lvert f'(x^*)\rvert > 1$ unstable	$f'(x^*) < 0$ stable $f'(x^*) > 0$ unstable

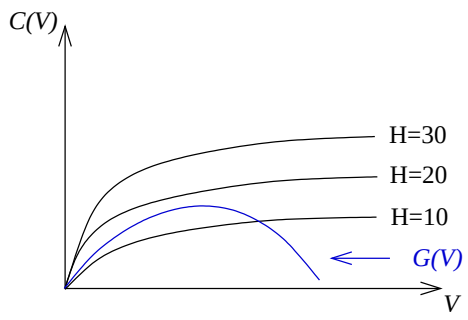


Figure M 5.4: different herd sizes

M 5.2 More complex behaviour?

In difference equations we found more complex behaviour: periodic orbits, chaotic behaviour. This is different for ODE's!

- with one variable, e.g. M 5.10 only fixed points are possible.
- 2 functions: fixed points and/or limit cycles ($\doteq$ periodic behaviour)