Package ‘MotilityLab’

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Title   Quantitative Analysis of Motion
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Description Statistics to quantify tracks of moving things (x-y-z-t data),
such as cells, bacteria or animals. Available measures include mean square
displacement, confinement ratio, autocorrelation, straightness, turning angle,
and fractal dimension.
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Description

Statistics to describe moving things such as cells, bacteria or animals. Available measures include mean square displacement, confinement ratio, autocorrelation, asphericity, turning angle, and fractal dimension.

Details

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The MotilityLab package is designed for analyzing cell tracks acquired by time-lapse microscopy (like those provided in the included datasets TCells, BCells and Neutrophils). But it can of course process any x-y-(z)-t data, and we hope that it may be useful for other purposes as well.

The basic data structure that most functions in this package operate on is a set of tracks. A track is a list of spatial coordinates that are recorded at fixed time intervals; the function timeStep can be used to check for fluctuations of the recording intervals. We expect tracks to be stored in a matrix (or data frame, but this is discouraged for efficiency reasons) whose first column denotes a time interval (e.g. seconds elapsed since the beginning of the experiment), and whose remaining
columns denote a spatial coordinate. A set of tracks is stored as a list with S3 class tracks. MotilityLab provides some S3 methods for this class, which are explained in tracks as well as plot.tracks, sort.tracks and as.list.tracks.

A wide range of common track measures are included in the package. These are all functions that take a single track as an input, and output one or several numbers. For instance, the function speed estimates the average instantaneous speed of the track by linear interpolation, and straightness computes the start-to-end distance divided by the trajectory length (a number between 0 and 1, where 1 indicates a perfectly straight track).

MotilityLab is designed to support various flavors of track analysis that have been suggested in the literature. The simplest kind is a track-based analysis, where we compute a single statistic for each track in a dataset (Beltman et al, 2009). Because track sets are lists, this is achieved simply by using lapply or sapply together with the track measure (see Examples).

In step-based analyses (Beltman et al, 2009), we chop each track up into segments of the same length and then apply our measures to those segments. This can help to avoid biases that arise from variations in track length (which are always present in cell tracking experiments). In MotilityLab, step-based analyses are performed by using the subtracks function. Often we want to perform such step-based analyses for all possible subtrack lengths simultaneously, and plot the result as a function of the subtrack length; a famous example is the mean square displacement plot. This can be achieved by using the aggregate.tracks function, which has options to control which subtrack lengths are considered and whether overlapping subtracks are considered.

In a staggered analysis (Mokhtari et al, 2013), we analyse all subtracks (of any length) of a single track, and typically plot the result as a matrix. This can reveal dynamic patterns along a single track, e.g. turning behaviour or local slowdowns. Staggered analyses can be performed using the applyStaggered function.

Lastly, in addition to data analysis, the package contains some function to generate cell tracks by simulation. This is useful to develop and benchmark track analysis methodology (Textor et al, 2011), and for computational biology studies that try to extrapolate the long-term consequences of observed cell migration behaviour. Alongside a simple uncorrelated random walk (brownianTrack), this package implements a simulation model proposed by Beauchemin et al (2007) in the function beaucheminTrack. That model can also simulate directionally biased motion.

For a complete list of functions, use library( help="MotilityLab" ).

Author(s)

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References


Catherine Beauchemin, Narendra M. Dixit and Alan S. Perelson (2007), Characterizing T cell movement within lymph nodes in the absence of antigen. Journal of Immunology 178(9), 5505-5512. doi:10.4049/jimmunol.178.9.5505
aggregate.tracks

Compute Summary Statistics of Subtracks

Description

Computes a given measure on subtracks of a given track set, applies a summary statistic for each subtrack length, and returns the results in a convenient form. This important workhorse function facilitates many common motility analyses such as mean square displacement, turning angle, and autocorrelation plots.

Usage

```r
## S3 method for class 'tracks'
aggregate(x, measure, by = "subtracks", FUN = mean,
    subtrack.length = seq(1, (maxTrackLength(x) - 1)),
    max.overlap = max(subtrack.length), na.rm = FALSE,
    filter.subtracks = NULL, ...)
```

Arguments

- `x` the tracks object whose subtracks are to be considered. If a single track is given, it will be coerced to a tracks object using `wrapTrack` (but note that this requires an explicit call to `aggregate.tracks`).

Examples

```r
## track-based speed comparison
boxplot(sapply(Neutrophils, straightness), sapply(BCells, straightness))

## step-based turning angle comparison
boxplot(sapply(subtracks(Neutrophils, 2), overallAngle),
    sapply(subtracks(BCells, 2), overallAngle))

## mean square displacement plot; a step-based displacement analysis for all step lengths
plot(aggregate(TCells, squareDisplacement)[, "value"])

## 'staggered' analysis of displacement over whole track. Reveals that this track
## slows down near its beginning and near its end.
filled.contour(applyStaggered(TCells[[4]], displacement, matrix=TRUE))

## a simple hierarchical clustering based on 2D asphericity
names(TCells) <- paste0("T", names(TCells))
names(BCells) <- paste0("B", names(BCells))
names(Neutrophils) <- paste0("N", names(Neutrophils))

## project all tracks down to 2D
cells <- projectDimensions(c(TCells, BCells, Neutrophils), c("x", "y"))

## compute asphericity
asph <- lapply(cells, asphericity)

## plot clustering
plot(hclust(dist(asph)))
```
aggregate.tracks

measure

the measure that is to be computed on the subtracks.

by

a string that indicates how grouping is performed. Currently, two kinds of grouping are supported:

• "subtracks" Apply measure to all subtracks according to the parameters subtrack.length and max.overlap.
• "prefixes" Apply measure to all prefixes (i.e., subtracks starting from a track’s initial position) according to the parameter subtrack.length.

FUN

a summary statistic to be computed on the measures of subtracks with the same length. Can be a function or a string. If a string is given, it is first matched to the following builtin values:

• "mean.sd" Outputs the mean and \( \text{mean} - \text{sd} \) as lower and \( \text{mean} + \text{sd} \) as upper bound
• "mean.se" Outputs the mean and \( \text{mean} - \text{se} \) as lower and \( \text{mean} + \text{se} \) as upper bound
• "mean.ci.95" Outputs the mean and upper and lower bound of a parametric 95 percent confidence interval.
• "mean.ci.99" Outputs the mean and upper and lower bound of a parametric 95 percent confidence interval.
• "iqr" Outputs the interquartile range, that is, the median, and the 25-percent-quartile as a lower and and the 75-percent-quartile as an upper bound

If the string is not equal to any of these, it is passed on to match.fun.

subtrack.length

an integer or a vector of integers defining which subtrack lengths are considered. In particular, subtrack.length=2 corresponds to a "step-based analysis" (Beltman et al, 2009).

max.overlap

an integer controlling what to do with overlapping subtracks. A maximum overlap of max(subtrack.length) will imply that all subtracks are considered. For a maximum overlap of 0, only non-overlapping subtracks are considered. A negative overlap can be used to ensure that only subtracks a certain distance apart are considered. In general, for non-Brownian motion there will be correlations between subsequent steps, such that a negative overlap may be necessary to get a proper error estimate.

na.rm

logical. If TRUE, then NA’s and NaN’s are removed prior to computing the summary statistic.

filter.subtracks

a function that can be supplied to exclude certain subtracks from an analysis. For instance, one may wish to compute angles only between steps of a certain minimum length (see Examples).

... further arguments passed to or used by methods.

Details

For every number of segments \( i \) in the set defined by subtrack.length, all subtracks of any track in the input tracks object that consist of exactly \( i \) segments are considered. The input measure is applied to the subtracks individually, and the statistic is applied to the resulting values.

Value

A data frame with one row for every \( i \) specified by subtrack.length. The first column contains the values of \( i \) and the remaining columns contain the values of the summary statistic of the measure values of tracks having exactly \( i \) segments.
References


Examples

```r
## A mean square displacement plot with error bars.
dat <- aggregate(TCells, squareDisplacement, FUN="mean.se")
with( dat ,{
  plot( mean ~ i, xlab="time step",
       ylab="mean square displacement", type="l"
     )
})

## Compute a turning angle plot for the B cell data, taking only steps of at least
## 1 micrometer length into account
check <- function(x) all( sapply( list(head(x,2),tail(x,2)), trackLength ) >= 1.0 )
plot( aggregate( BCells, overallAngle, subtrack.length=1:10,
                 filter.subtracks=check )[,2], type='l' )

## Compare 3 different variants of a mean displacement plot
## 1. average over all subtracks
plot( aggregate( TCells, displacement ), type='l' )
## 2. average over all non-overlapping subtracks
lines( aggregate( TCells, displacement, max.overlap=0 ), col=2 )
## 3. average over all subtracks starting at 1st position
lines( aggregate( TCells, displacement, by="prefixes" ), col=3 )
```

---

**applyStaggered**: Compute a Measure on a Track in a Staggered Fashion

**Description**

Computes a measure on all subtracks of a track and return them either as a matrix or return their mean.

**Usage**

```r
applyStaggered(x, measure, matrix = FALSE, min.segments = 1)
```

**Arguments**

- `x`: the track for which the measure is to be computed.
- `measure`: the measure that is to be computed.
- `matrix`: a logical indicating whether the whole matrix of values for the measure for each of the input track’s subtracks is to be returned. Otherwise only the mean is returned.
- `min.segments`: the number of segments that each regarded subtrack should at least consist of. Typically, this value would be set to the minimum number of segments that a (sub)track must have in order for the measure to be decently computed. For example, at least two segments are needed to compute the `overallAngle`.
Details

The measure is computed for each of the input track’s subtracks of length at least \( \text{min\_segments} \), and the resulting values are either returned in a matrix (if \text{matrix} is set), or their mean is returned. The computed matrix is symmetric since the direction along which a track is traversed is assumed not to matter. The values at \([i, i + j]\), where \( j \) is a nonnegative integer with \( j < \text{min\_segments} \), (with the default value \( \text{min\_segments}=1 \) this is exactly the main diagonal) are set to \( \text{NA} \).

Value

If \text{matrix} is set, a matrix with the values of the measure for all the input track’s subtracks is returned. The value of this matrix at position \([i, j]\) corresponds to the subtrack that starts with the input track’s \( j \)th point and ends at its \( i \)th. Thus, with increasing column number, the regarded subtrack’s starting point is advanced on the original track, and the values for increasingly long subtracks starting from this point can be found columnwise below the main diagonal, respectively. If ‘\text{matrix}’ is not set, the mean over the values of the measure for all subtracks of at least ‘\text{min\_segments}’ segments is returned.

Examples

```r
## Compute the staggered matrix for overallAngle applied to all long enough
## subtracks of the first T cell track
applyStaggered(TCells[[1]], overallAngle, matrix=TRUE, min\_segments = 2)
```

---

**as.data.frame.tracks**  
*Convert Tracks to Data Frame*

Description

Converts tracks from the list-of-matrices format, which is good for efficient processing and therefore the default in this package, to a single dataframe which is convenient for plotting or saving the data.

Usage

```r
## S3 method for class 'tracks'
as.data.frame(x, row\_names = NULL, optional = FALSE, 
               include\_timepoint\_column = FALSE, ...)
```

Arguments

- **x**  
  the tracks object to be coerced to a data frame.

- **row\_names**  
  NULL or a character vector giving row names for the data frame. Missing values are not allowed.

- **optional**  
  logical. Required for S3 consistency, but has no effect: column names are always assigned to the resulting data frame regardless of the setting of this option.

- **include\_timepoint\_column**  
  logical. If set to TRUE, then the resulting dataframe will contain a column that consecutively numbers the positions according to their time. Note that this information is anyway implicitly present in the time information.

- **...**  
  further arguments to be passed from or to other methods.
Value

A single data frame containing all individual tracks from the input with a prepended column named "id" containing each track's identifier in 'x'.

Examples

```r
## Display overall average position of the T cell data
colMeans( as.data.frame( TCells )[,-c(1,2)] )
```

Description

Coerces a tracks object to a list.

Usage

```r
## S3 method for class 'tracks'
as.list(x, ...)
```

Arguments

- `x` the tracks object to be coerced to a list.
- `...` further arguments to be passed from or to other methods.

BCells

Two-Photon Data: B Cells in a Lymph Node

Description

Labelled B cells were adoptively transfered and intravitally imaged (using two-photon microscopy) inside a peripheral lymph node of the recipient mouse. These data illustrate the characteristic "random-walk-like" motion pattern of B cells in lymph nodes.

Usage

```r
data("BCells")
```

Format

An S3 object of class "tracks"; a list with 24 elements. Each element name identifies a cell track. Each element is a matrix containing the following four columns.

- `t` the time (in seconds)
- `x` The X coordinate (in micrometers)
- `y` The Y coordinate (in micrometers)
- `z` The Z coordinate (in micrometers)
Data were generated in 2012 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

References

Examples
```r
## load the tracks
data(BCells)
## visualize the tracks (calls function plot.tracks)
plot(BCells)
```

### Description
The Beauchemin model is a simple, particle-based description of T cell motion in lymph node in the absence of antigen, which is similar to a random walk (Beauchemin et al, 2007).

### Usage
```r
beaucheminTrack(sim.time = 10, delta.t = 1, p.persist = 0, p.bias = 0.9, bias.dir = c(0, 0, 0), taxis.mode = 1, t.free = 2, v.free = 18.8, t.pause = 0.5)
```

### Arguments
- `sim.time` specifies the duration of the track to be generated
- `delta.t` change in time between each timepoint.
- `p.persist` indicates how probable a change in direction is. With `p.persist = 1`, the direction never changes between steps and with `p.persist = 0`, a new direction is sampled at every step.
- `p.bias` strength of movement in the direction of `bias.dir`.
- `bias.dir` a 3D vector indicating the direction along which there is a preference for movement.
- `t.free` time interval for how long the cell is allowed to move between turns.
- `v.free` speed of the cell during the free motion.
- `t.pause` time that it takes the cell to adjust movement to new direction.
Details
In the Beauchemin model, cells move into a fixed direction for a fixed time $t_{\text{free}}$ at a fixed speed $v_{\text{free}}$. They then switch to a different direction, which is sampled at uniform from a sphere. The change of direction takes a fixed time $t_{\text{pause}}$, during which the cell does not move. Thus, the Beauchemin model is identical to the freely jointed chain model of polymer physics, except for the explicit "pause phase" between subsequent steps.

The default parameters implemented in this function were found to most accurately describe 'default' T cell motion in lymph nodes using least-squares fitting to the mean displacement plot (Beauchemin et al, 2007).

This function implements an extended version of the Beauchemin model, which can also simulate directionally biased motion. For details, see Textor et al (2013).

Value
A track, i.e., a matrix with $t/delta\cdot t$ rows and 4 columns.

References
Catherine Beauchemin, Narendra M. Dixit and Alan S. Perelson (2007), Characterizing T cell movement within lymph nodes in the absence of antigen. Journal of Immunology 178(9), 5505-5512. doi:10.4049/jimmunol.178.9.5505


Examples

```r
## Create track with model parameters and return matrix of positions
out <- beaucheminTrack(sim.time=20, p.persist = 0.3, taxis.mode = 1)
## Plot X-Y projection
plot( wrapTrack(out) )

## Create 20 tracks and plot them all
out <- simulateTracks( 20, beaucheminTrack(sim.time=10,
bias.dir=c(-1,1,0), p.bias=10, taxis.mode = 2,
p.persist = 0.1, delta.t = 1) )
plot( out )
```

boundingBox

Bounding Box of a Tracks Object

Description
Computes the minimum and maximum coordinates per dimension (including time) for all positions in a given list of tracks.

Usage

`boundingBox(x)`
brownianTrack

Arguments

x the input tracks object.

Value

Returns a matrix with two rows and $d + 1$ columns, where $d$ is the number of spatial dimensions of the tracks. The first row contains the minimum and the second row the maximum value of any track in the dimension given by the column.

Examples

```r
## Use bounding box to set up plot window
bb <- boundingBox(c(TCells,BCells,Neutrophils))
plot( Neutrophils, xlim=bb[,"x"], ylim=bb[,"y"], col=1 )
plot( BCells, col=2, add=TRUE )
plot( TCells, col=3, add=TRUE )
```

brownianTrack

Simulate an Uncorrelated Random Walk

Description

Generates a random track with nsteps steps in dim dimensions.

Usage

brownianTrack(nsteps = 100, dim = 3, mean = 0, sd = 1)

Arguments

nsteps desired number of steps (e.g. 10 steps generates a track with 11 positions).
dim desired number of dimensions.
mean stepwise mean drift per dimension; use 0 for an unbiased Brownian motion and other values for Brownian motion with drift.
sd stepwise standard deviation per dimension.

Details

In in every step an for each dimension, a normally distributed value with mean mean and standard deviation sd is added to the previous cell position.

Value

A data frame containing in cell track with nsteps steps in dim dimensions is returned.

```r
## The Hurst exponent of a 1D Brownian track should be near 0.5
hurstExponent( brownianTrack( 100, 1 ) )
```
clusterTracks  

**Cluster Tracks**

**Description**

Perform a hierarchical clustering of a set of tracks according to a given vector of track measures.

**Usage**

```
clusterTracks(tracks, measures, scale = TRUE, ...)
```

**Arguments**

- `tracks`: the tracks that are to be clustered.
- `measures`: a function, or a vector of functions (see `TrackMeasures`). Each function is expected to return a single number given a single track.
- `scale`: logical indicating whether the measures values shall be scaled using the function `scale` before the clustering.
- `...`: additional parameters to be passed to `hclust`.

**Details**

The measures are applied to each of the tracks in the given `tracks` object. According to the resulting values, the tracks are clustered using a hierarchical clustering (see `hclust`). If `scale` is `TRUE`, the measure values are scaled to mean value 0 and standard deviation 1 (per measure) before the clustering.

**Value**

An object of class *hclust*, see `hclust`.

**Examples**

```r
## Cluster tracks according to the mean of their Hurst exponents along X and Y

cells <- c(TCells,Neutrophils)
real.celltype <- rep(c("T","N"),c(length(TCells),length(Neutrophils)))
## Prefix each track ID with its cell class to evaluate the clustering visually
names(cells) <- paste0(real.celltype,seq_along(cells))
clust <- clusterTracks( cells, hurstExponent )
plot( clust )
## How many cells are "correctly" clustered?
sum( real.celltype == c("T","N")[cutree(clust,2)] )
```
filterTracks

Filter Tracks

Description

Extracts subtracks based on a given function.

Usage

\[ \text{filterTracks}(f, x, \ldots) \]

Arguments

- \( f \): a function that accepts a single track as its first argument and returns a logical value (or a value that can be coerced to a logical).
- \( x \): a tracks object.
- \( \ldots \): further arguments to be passed on to \( f \).

Value

A \texttt{tracks} object containing only those tracks from \( x \) for which \( f \) evaluates to \texttt{TRUE}.

Examples

```r
## Remove short tracks from the T cells data
plot(filterTracks(function(t) nrow(t)>10, TCells ))
```

hotellingsTest

Test Unbiasedness of Motion

Description

Test the null hypothesis that a given set of tracks originates from an uncorrelated and unbiased type of motion (e.g., a random walk without drift). This is done by testing whether the mean step vector is equal to the null vector.

Usage

\[ \text{hotellingsTest}(\text{tracks}, \text{dim} = \text{c("x", "y")}, \text{step.spacing} = 0, \text{plot} = \text{FALSE}, \text{add} = \text{FALSE}, \text{ellipse.col} = \text{"blue"}, \text{ellipse.border} = \text{"black"}, \text{conf.level} = 0.95, \ldots) \]
Arguments

tracks the tracks whose biasedness is to be determined.
dim vector with the names of the track’s dimensions that are to be considered. By default c("x", "y").
step.spacing How many positions are to be left out between the steps that are considered for the test. For persistent motion, subsequent steps will be correlated, which leads to too low p-values because Hotelling’s test assumes that the input data is independent. To avoid this, the resulting p-value should either be corrected for this dependence (e.g. by adjusting the degrees of freedom accordingly), or ‘step.spacing’ should be set to a value high enough to ensure that the considered steps are approximately independent.
plot logical indicating whether the scatter of the step’s directions, origin of ordinates (green circle) and the mean of the data points (green cross) are to be plotted. (In one dimension also the bounds of the confidence interval are given.) Plot works only in one or two dimensions.
add whether to add the plot to the current plot (TRUE) or create a
ellipse.col color with which to draw the confidence ellipse of the mean (for 1D, this corresponds to the confidence interval of the mean). Use NA to omit the confidence ellipse.
ellipse.border color of the confidence ellipse border. Use NA to omit the border.
conf.level the desired confidence level for the confidence ellipse.
... further arguments passed on to plot.

Details

Computes the displacement vectors of all segments in the tracks given in tracks, and performs Hotelling’s T-square Test on that vector.

Value

A list with class htest.

References


Examples

```r
## Test H_0: T-cells migrate by uncorrelated random walk on x and y coordinates, 
## and report the p-value.
hotellingsTest(TCells)$p.value
```
interpolateTrack

**Interpolate Track Positions**

**Description**

Approximates the track positions at given time points using linear interpolation (via the `approx` function).

**Usage**

```r
interpolateTrack(x, t, how = "linear")
```

**Arguments**

- `x`: the input track (a matrix or data frame).
- `t`: the times at which to approximate track positions. These must lie within the interval spanned by the track timepoints.
- `how`: specifies how to perform the interpolation. Possible values are "linear" (which uses `approx` with default values) and "spline" (which uses `spline` with default values).

**Examples**

```r
## Compare interpolated and non-interpolated versions of a track
bb <- boundingBox( TCells[2] )
plot( TCells[2] )
t2i <- interpolateTrack(TCells[[2]], seq(bb[1,"t"],bb[2,"t"],length.out=100),"spline")
plot( tracks( t2i ), add=TRUE, col=2 )
```

maxTrackLength

**Length of Longest Track**

**Description**

Determines the maximum number of positions over the tracks in `x`.

**Usage**

```r
maxTrackLength(x)
```

**Arguments**

- `x`: the tracks object the tracks in which are to be considered.

**Value**

The maximum number of rows of a track in `x`
Description

Labelled neutrophils were adoptively transferred and intravitaly imaged (using two-photon microscopy) inside the lung of the recipient mouse. These cells display a fairly directed kind of motion, as they move towards infection foci.

Usage

data("Neutrophils")

Format

An S3 object of class "tracks"; a list with 10 elements. Each element name identifies a cell track. Each element is a matrix containing the following four columns.

- t the time (in seconds)
- x The X coordinate (in micrometers)
- y The Y coordinate (in micrometers)
- z The Z coordinate (in micrometers)

Source

Data were generated in 2012 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

References


Examples

```r
## load the tracks
data(Neutrophils)
## visualize the tracks (calls function plot.tracks)
plot(Neutrophils)
```
**normalizeToDuration**  
*Normalize a Measure to Track Duration*

**Description**

Returns a measure that divides the input measure by the duration of its input track.

**Usage**

```
normalizeToDuration(x)
```

**Arguments**

- `x`  
a track measure (see TrackMeasures).

**Value**

A function that computes the input measure for a given track and returns the result divided by the track’s duration.

**Examples**

```r
## normalizeToDuration(displacement) can be used as an indicator
## for the motion's efficiency
sapply(TCells, normalizeToDuration(displacement))
```

---

**normalizeTracks**  
*Normalize Tracks*

**Description**

Translates each track in a given set of tracks such that the first position is the origin.

**Usage**

```
normalizeTracks(x)
```

**Arguments**

- `x`  
the input tracks object.

**Examples**

```r
## normalization of Neutrophil data reveals upward motion
plot( normalizeTracks( Neutrophils ) )
```
### plot.tracks

#### Plot Tracks in 2D

**Description**

Plots tracks contained in a "tracks" object into a twodimensional space parallell to the data’s axes.

**Usage**

```r
## S3 method for class 'tracks'
plot(x, dims = c("x", "y"), add = FALSE,
     col = order(names(x)), pch.start = 1, pch.end = NULL, cex = 0.5, ...)
```

**Arguments**

- `x` the tracks to be plotted.
- `dims` a vector giving the dimensions of the track data that shall be plotted, e.g. `c("x","y")` for the `x` and `y` dimension.
- `add` boolean value indicating whether the tracks are to be added to the current plot.
- `col` a specification of the color(s) to be used. This can be a vector of size `length(x)`, where each entry specifies the color for the corresponding track.
- `pch.start` point symbol with which to label the first position of the track (see `points`).
- `pch.end` point symbol with which to label the last position of the track.
- `cex` point size for positions on the tracks.
- `...` additional parameters (e.g. `xlab`, `ylab`), to be passed to `plot` (for `add=FALSE`) or `points` (for `add=TRUE`), respectively.

**Details**

One dimension of the data (by default `y`) is plotted against another (by default `x`). The dimensions can be chosen by means of the parameter `dims` and the axes can be labeled accordingly with the aid of `xlab` and `ylab`. The color can be set through `col`. If the tracks should be added to an existing plot, `add` is to be set to `TRUE`.

**See Also**

- `plot3d`
**plot3d**

*Plot Tracks in 3D*

**Description**

Takes an input tracks object and plots them in 3D using the `scatterplot3d` function.

**Usage**

```r
plot3d(x, ...)
```

**Arguments**

- `x` : the tracks which will be plotted in 3d
- `...` : further arguments to be passed on to `scatterplot3d`

**Examples**

```r
if( require("scatterplot3d", quietly=TRUE) ){
  plot3d( TCells )
}
```

---

**plotTrackMeasures**

*Bivariate Scatterplot of Track Measures*

**Description**

Plots the values of two measures applied on the given tracks against each other.

**Usage**

```r
plotTrackMeasures(x, measure.x, measure.y, add = FALSE,
xlab = deparse(substitute(measure.x)),
ylab = deparse(substitute(measure.y)), ellipse.col = "red",
ellipse.border = "black", conf.level = 0.95, ...)
```

**Arguments**

- `x` : the input tracks object.
- `measure.x` : the measure to be shown on the X axis (see `TrackMeasures`).
- `measure.y` : the measure to be shown on the Y axis.
- `add` : a logical indicating whether the tracks are to be added to an existing plot via `points`.
- `xlab` : label of the x-axis. By default the name of the input function `measure.x`.
- `ylab` : label of the y-axis. By default the name of the input function `measure.y`.
- `ellipse.col` : color with which to draw the confidence ellipse of the mean (for 1D, this corresponds to the confidence interval of the mean). Use NA to omit the confidence ellipse.
prefixes

```r
ellipse.border  color of the confidence ellipse border. Use NA to omit the border.
conf.level      the desired confidence level for the confidence ellipse.
...             additional parameters to be passed to plot (in case add=FALSE) or points (add=TRUE).
```

**Details**

Plots the value of measurey applied to x against the value of measurey applied to y. This is useful for "FACS-like" motility analysis, where clusters of cell tracks are identified based on their motility parameters (Moreau et al, 2012; Textor et al, 2014).

**References**


**Examples**

```r
## Compare speed and straightness of 3 example population tracks.
## To make the comparison fair, analyze subtracks of fixed length.
plotTrackMeasures( subtracks(TCells,4,0), speed, straightness, ellipse.col="black" )
plotTrackMeasures( subtracks(BCells,4,0), speed, straightness,
                   col=2, ellipse.col=2, pch=2, add=TRUE )
plotTrackMeasures( subtracks(Neutrophils,4,0), speed, straightness,
                   col=3, ellipse.col=3, pch=3, add=TRUE )
```

### prefixes

**Get Track Prefixes**

**Description**

Creates a `tracks` object consisting of all prefixes (i.e., subtracks starting with the first position of a track) of `x` with `i` segments (i.e., `i`+1 positions).

**Usage**

```r
prefixes(x, i)
```

**Arguments**

- `x`: a single track or a `tracks` object.
- `i`: subtrack length. A single integer, lists are not supported.

**Details**

This function behaves exactly like `subtracks` except that only subtracks starting from the first position are considered.
**projectDimensions**  

*Extract Spatial Dimensions*

**Description**

Projects tracks onto the given spatial dimensions.

**Usage**

```r
projectDimensions(x, dims = c("x", "y"))
```

**Arguments**

- `x`  
  the input tracks object.
- `dims`  
  a character vector (for column names) or an integer vector (for column indices) giving the dimensions to extract from each track. The time dimension (i.e., the first column of all tracks) is always included.

**Value**

A tracks object is returned that contains only those dimensions of the input tracks that are given in `dims`.

**Examples**

```r
## Compare 2D and 3D speeds
speed.2D <- mean( sapply( subtracks( projectDimensions( TCells, c("x","z"), 2 ), speed ) )
speed.3D <- mean( sapply( TCells, speed ) )
```

**read.tracks.csv**  

*Read Tracks from Text File*

**Description**

Reads cell tracks from a CSV or other text file. Data are expected to be organized as follows. One column contains a track identifier, which can be numeric or a string, and determines which points belong to the same track. Another column is expected to contain a time index or a time period (e.g. number of seconds elapsed since the beginning of the track, or since the beginning of the experiment). Input of dates is not (yet) supported, as absolute time information is frequently not available. One to three further columns contain the spatial coordinates (depending on whether the tracks are 1D, 2D or 3D). The names or indices of these columns in the CSV files are given using the corresponding parameters (see below). Names and indices can be mixed, e.g. you can specify `id.column="Parent"` and `pos.columns=1:3`.

**Usage**

```r
read.tracks.csv(file, id.column = 1, time.column = 2, pos.columns = c(3, 4, 5), scale.t = 1, scale.pos = 1, header = TRUE, sep = "", track.sep.blankline = FALSE, ...)
```
Arguments

file the name of the file which the data are to be read from, a readable text-mode connection or a complete URL (see \texttt{read.table}).

id.column index or name of the column that contains the track ID.

time.column index or name of the column that contains elapsed time.

pos.columns vector containing indices or names of the columns that contain the spatial coordinates. If this vector has two entries and the second entry is \texttt{NA}, e.g. \texttt{c('x',NA)} or \texttt{c(5,NA)} then all columns from the indicated column to the last column are used. This is useful when reading files where the exact number of spatial dimensions is not known beforehand.

scale.t a value by which to multiply each time point. Useful for changing units, or for specifying the time between positions if this is not contained in the file itself.

scale.pos a value, or a vector of values, by which to multiply each spatial position. Useful for changing units.

header a logical value indicating whether the file contains the names of the variables as its first line. See \texttt{read.table}.

sep a character specifying how the columns of the data are separated. The default value \"\t\" means columns are separated by tabs or other spaces. See \texttt{read.table}.

track.sep.blankline logical. If set to \texttt{TRUE}, then tracks are expected to be separated by one or more blank lines in the input file instead of being designated by a track ID column. In this case, numerical track IDs are automatically generated.

... further arguments to be passed to \texttt{read.csv}, for instance \texttt{sep="\t"} can be useful for tab-separated files.

Details

The input file’s first four fields are interpreted as id, pos, t and x, respectively, and, if available, the fifth as y and the sixth as z. The returned object has the class \texttt{tracks}, which is a list of data frames representing the single tracks and having columns \texttt{t} and \texttt{x}, plus \texttt{y} and \texttt{z}, if necessary. The tracks’ ids are retained in their position in the list, while the field pos will be unmaintained.

Value

An object of class \texttt{tracks} is returned, which is a list of matrices, each containing the positions of one track. The matrices have a column \texttt{t}, followed by one column for each of the input track’s coordinates.

repairGaps \hspace{1cm} \textbf{Process Tracks Containing Gaps}

Description

Many common motility analyses, such as mean square displacement plots, assume that object positions are recorded at constant time intervals. For some application domains, such as intravital imaging, this may not always be the case. This function can be used to pre-process data imaged at nonconstant intervals, provided the deviations are not too extreme.
selectTracks

Usage

repairGaps(x, how = "split", tol = 0.05, split.min.length = 2)

Arguments

x the input tracks object.
how string specifying what do with tracks that contain gaps. Possible values are:
  • "drop": the simplest option – discard all tracks that contain gaps.
  • "split": split tracks around the gaps, e.g. a track for which the step between
    the 3rd and 4th positions is too long or too short is split into one track cor-
    responding to positions 1 to 3 and another track corresponding to position
    3 onwards.
  • "interpolate": approximate the track positions using linear interpolation
    (see interpolateTrack). The result is a tracks object with constant step
    durations.

tol nonnegative number specifying by which fraction each step may deviate from
  the average step duration without being considered a gap. For instance, if the
  average step duration (see timeStep) is 100 seconds and tol is 0.05 (the de-
  fault), then step durations between 95 and 105 seconds (both inclusive) are not
  considered gaps. This option is ignored for how="interpolate".

split.min.length nonnegative integer. For how="split", this discards all resulting tracks shorter
  than this many positions.

Examples

```r
## The Neutrophil data are imaged at rather nonconstant intervals
print( length( Neutrophils ) )
print( length( repairGaps( Neutrophils, tol=0.01 ) ) )
```

selectTracks Select Tracks by Measure Values

Description

Given a tracks object, extract a subset based on upper and lower bounds of a certain measure. For
instance, extract all tracks with a certain minimum length.

Usage

selectTracks(x, measure, lower, upper)

Arguments

x the input tracks.
measure measure on which the selection is based (see TrackMeasures).
lower specifies the lower bound (inclusive) of the allowable measure.
upper specifies the upper bound (inclusive) of the allowable measure.
Examples

### Slower half of T cells
slow.tcells <- selectTracks( TCells, speed, -Inf, median( sapply(TCells, speed) ) )

#### simulateTracks

**Generate Tracks by Simulation**

**Description**

Generic function that executes `expr`, which is expected to return a track, `n` times and stores the output in a `tracks` object. Basically, this works like `replicate` but for tracks.

**Usage**

```r
simulateTracks(n, expr)
```

**Arguments**

- `n` number of tracks to be generated.
- `expr` the expression, usually a call, that generates a single track.

**Value**

A `tracks` object containing `n` tracks.

**Examples**

```r
## Generate 10 tracks, 100 steps each, from a random walk with standard normally
distributed increments and plot them
plot( simulateTracks(10, brownianTrack(100, 3)) )
```

#### sort.tracks

**Sort Track Positions by Time**

**Description**

Sorts the positions in each track in a `tracks` object by time.

**Usage**

```r
## S3 method for class 'tracks'
sort(x, decreasing = FALSE, ...)
```

**Arguments**

- `x` the `tracks` object whose tracks are to be sorted by time.
- `decreasing` logical. Should the sort be increasing or decreasing? Provided only for consistency with the generic sort method. The positions in each track should be sorted in increasing time order.
- `...` further arguments to be passed on to `order`.
splitTrack

Details
Sorts the positions of each track (represented as a data frame) in the tracks object by time (given in the column t).

Value
A tracks object that contains the tracks from the input object sorted by time is returned.

splitTrack  Split Track into Multiple Tracks

Description
Split Track into Multiple Tracks

Usage
splitTrack(x, positions, id = NULL, min.length = 2)

Arguments
x  the input track (a data frame or a matrix).
positions  a vector of positive integers, given in ascending order.
id  a string used to identify the resulting tracks; for instance, if id="X", then the resulting tracks are named X_1, X_2 and so forth. Otherwise, they are simply labelled with integer numbers.
min.length  nonnegative integer. Resulting tracks that have fewer positions than the value of this parameter are dropped.

staggered  Staggered Version of a Function

Description
Returns the "staggered" version of a track measure. That is, instead of computing the measure on the whole track, the measure is averaged over all subtracks (of any length) of the track.

Usage
staggered(measure, ...)

Arguments
measure  a track measure (see TrackMeasures).
...  further parameters passed on to applyStaggered.
Details

This is a wrapper mainly designed to provide a convenient interface for track-based staggered computations with `lapply`, see example.

Value

Returns a function that computes the given measure in a staggered fashion on that track.

References


Examples

```r
hist(sapply(TCells, staggered(displacement)))
```

---

**subsample**  
Subsample Track by Constant Factor

Description

Make tracks more coarse-grained by keeping only every \(k\)th position.

Usage

`subsample(x, k = 2)`

Arguments

- `x`: an input track or tracks object.
- `k`: a positive integer. Every \(k\)th position of each input track is kept.

See Also

`interpolateTrack`, which can be used for more flexible track coarse-graining.

Examples

```r
## Compare original and subsampled versions of the T cell tracks
plot(TCells, col=1)
plot(subsample(TCells, 3), col=2, add=TRUE, pch.start=NULL)
```
subtracks

### Decompose Track(s) into Subtracks

**Description**

Creates a *tracks* object consisting of all subtracks of 'x' with 'i' segments (i.e., 'i'+1 positions).

**Usage**

```
subtracks(x, i, overlap = i - 1)
```

**Arguments**

- `x`: a single track or a *tracks* object.
- `i`: subtrack length. A single integer, lists are not supported.
- `overlap`: the number of segments in which each subtrack shall overlap with the previous and next subtrack. The default `i - 1` returns all subtracks. Can be negative, which means that space will be left between subtracks.

**Details**

The output is always a single *tracks* object, which is convenient for many common analyses. If subtracks are to be considered separately for each track, use the function `staggered` together with `lapply`. Subtrack extraction always starts at the first position of the input track.

**Value**

A *tracks* object is returned which contains all the subtracks of any track in the input *tracks* object that consist of exactly 'i' segments and overlap adjacent subtracks in 'overlap' segments.

---

**TCells**

### Two-Photon Data: T Cells in a Lymph Node

**Description**

Labelled T cells were adoptively transfered and intravitaly imaged (using two-photon microscopy) inside a peripheral lymph node of the recipient mouse. These data represent the characteristic "random-walk-like" motion pattern of T cells in lymph nodes.

**Usage**

```
data("TCells")
```

**Format**

An S3 object of class "tracks"; a list with 22 elements. Each element name identifies a cell track. Each element is a matrix containing the following four columns.

- `t`: the time (in seconds)
- `x`: The X coordinate (in micrometers)
- `y`: The Y coordinate (in micrometers)
- `z`: The Z coordinate (in micrometers)
Source

Data were generated in 2012 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

References


Examples

```r
## load the tracks
data(TCells)

## visualize the tracks (calls function plot.tracks)
plot(TCells)
```

timeStep

*Compute Time Step of Tracks*

Description

Applies a summary statistics on the time intervals between pairs of consecutive positions in a track dataset.

Usage

```r
timeStep(x, FUN = median, na.rm = FALSE)
```

Arguments

- `x`: the input tracks.
- `FUN`: the summary statistic to be applied.
- `na.rm`: logical, indicates whether to remove missing values before applying FUN.

Details

Most track quantification depends on the assumption that track positions are recorded at constant time intervals. If this is not the case, then most of the statistics in this package (except for some very simple ones like `duration`) will not work. In reality, at least small fluctuations of the time steps can be expected. This function provides a means for quality control with respect to the tracking time.

Value

Summary statistic of the time intervals between two consecutive positions in a track dataset.
Examples

```r
## Show tracking time fluctuations for the T cell data
d <- timeStep(TCells)
plot(sapply(subtracks(TCells, 1), duration) - d, ylim=c(-d,d))
```

Description

Statistics that can be used to quantify tracks. All of these functions take a single track as input and give a single number as output.

Usage

```r
trackLength(x)
duration(x)
speed(x)
displacement(x, from = 1, to = nrow(x))
squareDisplacement(x, from = 1, to = nrow(x))
displacementVector(x)
maxDisplacement(x)
displacementRatio(x)
outreachRatio(x)
straightness(x)
overallAngle(x, from = 1, to = nrow(x), xdiff = diff(x))
meanTurningAngle(x)
overallDot(x, from = 1, to = nrow(x), xdiff = diff(x))
asphericity(x)
hurstExponent(x)
fractalDimension(x)
```

Arguments

- `x` a single input track; a matrix whose first column is time and whose remaining columns are a spatial coordinate.
TrackMeasures

from index, or vector of indices, of the first row of the track.
to index, or vector of indices, of last row of the track.
xdiff row differences of x.

Details

Some track measures consider only the first and last position (or steps) of a track, and are most useful in conjunction with \texttt{aggregate.tracks}; for instance, \texttt{squaredisplacement} combined with \texttt{aggregate.tracks} gives a mean square displacement plot, and \texttt{overallAngle} combined with \texttt{aggregate.tracks} gives a turning angle plot (see the examples for \texttt{aggregate.tracks}). To speed up computation of these measures on subtracks of the same track, the arguments \texttt{from}, \texttt{to} and possibly \texttt{xdiff} are exploited by \texttt{aggregate.tracks}.

\texttt{trackLength} sums up the distances between subsequent position; in other words, it estimates the length of the underlying track by linear interpolation (usually an underestimation). The estimation could be improved in some circumstances by using \texttt{interpolateTrack}.

duration returns the time elapsed between x’s first and last positions.

speed simply divides \texttt{trackLength} by \texttt{duration}.

displacement returns the Euclidean distance between the track endpoints and \texttt{squaredisplacement} returns the squared Euclidean distance.

displacementVector returns the vector between the track endpoints.

\texttt{maxDisplacement} computes the maximal Euclidean distance of any position on the track from the first position.

\texttt{displacementRatio} divides the \texttt{displacement} by the \texttt{maxDisplacement}; \texttt{outreachRatio} divides the \texttt{maxDisplacement} by the \texttt{trackLength} (Mokhtari et al, 2013). Both measures return values between 0 and 1, where 1 means a perfectly straight track. If the track has \texttt{trackLength} 0, then \texttt{NaN} is returned.

\texttt{straightness} divides the \texttt{displacement} by the \texttt{trackLength}. This gives a number between 0 and 1, with 1 meaning a perfectly straight track. If the track has \texttt{trackLength} 0, then \texttt{NaN} is returned.

\texttt{asphericity} is a different approach to measure straightness (Mokhtari et al, 2013): it computes the asphericity of the set of positions on the track _via_ the length of its principal components. Again this gives a number between 0 and 1, with higher values indicating straighter tracks. Unlike \texttt{straightness}, however, asphericity ignores back-and-forth motion of the object, so something that bounces between two positions will have low \texttt{straightness} but high \texttt{asphericity}. We define the asphericity of every track with two or fewer positions to be 1. For one-dimensional tracks with one or more positions, \texttt{NA} is returned.

\texttt{overallAngle} Computes the angle (in radians) between the first and the last segment of the given track. Angles are measured symmetrically, thus the return values range from 0 to pi; for instance, both a 90 degrees left and right turns yield the value pi/2. This function is useful to generate autocorrelation plots (together with \texttt{aggregate.tracks}).

\texttt{meanTurningAngle} averages the \texttt{overallAngle} over all adjacent segments of a given track; a low \texttt{meanTurningAngle} indicates high persistence of orientation, whereas for an uncorrelated random walk we expect 90 degrees. Note that angle measurements will yield \texttt{NA} values for tracks in which two subsequent positions are identical.

\texttt{overall1Dot} computes the dot product between the first and the last segment of the given track. This function is useful to generate autocovariance plots (together with \texttt{aggregate.tracks}).

\texttt{hurstExponent} computes the corrected empirical Hurst exponent of the track. This uses the function \texttt{hurstexp} from the ‘pracma’ package. If the track has less than two positions, \texttt{NA} is returned.

\texttt{fractalDimension} estimates the fractal dimension of a track using the function \texttt{fd.estim.boxcount}
from the ‘fractaldim’ package. For self-affine processes in \( n \) dimensions, fractal dimension and Hurst exponent are related by the formula \( H = n + 1 - D \). For non-Brownian motion, however, this relationship need not hold. Intuitively, while the Hurst exponent takes a global approach to the track’s properties, fractal dimension is a local approach to the track’s properties (Gneiting and Schlather, 2004).

References


Examples

```r
## show a turning angle plot with error bars for the T cell data.
with( (aggregate(BCells,overall1Dot,FUN="mean",na.rm=TRUE)),{
  plot( mean ~ i, xlab="time step",
       ylab="turning angle (rad)", type="l" )
  segments( i, lower, y=upper )
})
```

---

### tracks

**Tracks Objects**

**Description**

The function `tracks` is used to create tracks objects. `as.tracks` coerces its argument to a tracks object, and `is.tracks` tests for tracks objects. `c` can be used to combine (concatenate) tracks objects.

**Usage**

```r
as.tracks(x, ...)
```

## S3 method for class 'list'

```r
as.tracks(x, ...)
```

```r
is.tracks(x)
```

## S3 method for class 'tracks'

```r
c(...)
```

```r
tracks(...)
```
wrapTrack

Arguments

* x
  - an object to be coerced or tested.
  - for *tracks*, numeric matrices or objects that can be coerced to numeric matrices.
  - Each matrix contains the data of one track. The first column is the time, and the remaining columns define a spatial position. Every given matrix has to contain the same number of columns, and at least two columns are necessary.
  - For *c*, tracks objects to be combined.
  - For *as.tracks*, further arguments passed to methods (currently not used).

Details

Tracks objects are lists of matrices. Each matrix contains at least two columns; the first column is time, and the remaining columns are a spatial coordinate. The following naming conventions are used (and enforced by *tracks*): The time column has the name ‘t’, and spatial coordinate columns have names ‘x’, ‘y’, ‘z’ if there are three or less coordinates, and ‘x1’, ‘x2’, ‘x3’ if there are *k* ≥ 4 coordinates. All tracks in an object must have the same number of dimensions. The positions in a track are expected to be sorted by time (and the constructor *tracks* enforces this).

Examples

```r
## A single 1D track
x <- tracks( matrix(c(0, 8, 10, 9, 20, 7, 30, 7, 40, 6, 50, 5), ncol=2, byrow=TRUE ) )

## Three 3D tracks
x2 <- tracks( rbind( c(0,1,0), c(1,1,3), c(2,1,3), c(3,5,6) ),
                  rbind( c(0,1,1), c(1,1,4), c(2,5,4), c(3,5,1), c(4,-3,1) ),
                  rbind( c(0,7,0), c(1,7,2), c(2,7,4), c(3,7,7) ) )
```

wrapTrack

Create Track Object from Single Track

Description

Makes a *tracks* object containing the given track.

Usage

wrapTrack( x )

Arguments

* x
  - the input track.

Value

A list of class *tracks* containing only the input track *x*, which is assigned the name "1".
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