

# Package ‘celltrackR’

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**Type** Package

**Title** Motion Trajectory Analysis

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**Description** Methods for analyzing (cell) motion in two or three dimensions.

Available measures include displacement, confinement ratio, autocorrelation, straightness, turning angle, and fractal dimension. Measures can be applied to entire tracks, steps, or subtracks with varying length. While the methodology has been developed for cell trajectory analysis, it is applicable to anything that moves including animals, people, or vehicles.

Some of the methodology implemented in this packages was described by:

Beauchemin, Dixit, and Perelson (2007) <[doi:10.4049/jimmunol.178.9.5505](https://doi.org/10.4049/jimmunol.178.9.5505)>,

Beltman, Maree, and de Boer (2009) <[doi:10.1038/nri2638](https://doi.org/10.1038/nri2638)>,

Gneiting and Schlather (2004) <[doi:10.1137/S0036144501394387](https://doi.org/10.1137/S0036144501394387)>,

Mokhtari, Mech, Zitzmann, Hasenberg, Gunzer, and Figge (2013) <[doi:10.1371/journal.pone.0080808](https://doi.org/10.1371/journal.pone.0080808)>,

Moreau, Lemaitre, Terriac, Azar, Piel, Lennon-

Dumenil, and Bousso (2012) <[doi:10.1016/j.immuni.2012.05.014](https://doi.org/10.1016/j.immuni.2012.05.014)>,

Textor, Peixoto, Henrickson, Sinn, von Andrian, and Westermann (2011) <[doi:10.1073/pnas.1102288108](https://doi.org/10.1073/pnas.1102288108)>,

Textor, Sinn, and de Boer (2013) <[doi:10.1186/1471-2105-14-S6-S10](https://doi.org/10.1186/1471-2105-14-S6-S10)>,

Textor, Henrickson, Mandl, von Andrian, Westermann, de Boer, and Beltman (2014) <[doi:10.1371/journal.pcbi.1003752](https://doi.org/10.1371/journal.pcbi.1003752)>.

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---

 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**

```
## 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,
  count.subtracks = FALSE,
  ...
)
```

**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 <code>wrapTrack</code> (but note that this requires an explicit call <code>aggregate.tracks</code> ).
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: <ul style="list-style-type: none"> <li>• "subtracks" Apply measure to all subtracks according to the parameters <code>subtrack.length</code> and <code>max.overlap</code>.</li> <li>• "prefixes" Apply measure to all prefixes (i.e., subtracks starting from a track's initial position) according to the parameter <code>subtrack.length</code>.</li> </ul>
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: <ul style="list-style-type: none"> <li>• "mean.sd" Outputs the mean and <math>mean - sd</math> as lower and <math>mean + sd</math> as upper bound</li> <li>• "mean.se" Outputs the mean and <math>mean - se</math> as lower and <math>mean + se</math> as upper bound</li> <li>• "mean.ci.95" Outputs the mean and upper and lower bound of a parametric 95 percent confidence interval.</li> <li>• "mean.ci.99" Outputs the mean and upper and lower bound of a parametric 95 percent confidence intervall.</li> <li>• "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</li> </ul> <p>If the string is not equal to any of these, it is passed on to <code>match.fun</code>.</p>
subtrack.length	an integer or a vector of integers defining which subtrack lengths are considered. In particular, <code>subtrack.length=1</code> 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 <code>max(subtrack.length)</code> 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).
count.subtracks	logical. If TRUE, the returned dataframe contains an extra column <code>ntracks</code> showing the number of subtracks of each length. This is useful to keep track of since the returned value estimates for high <code>i</code> are often based on very few subtracks.
...	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

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

## Examples

```
## 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" )
  segments( i, lower, y1=upper )
} )
```

```
## Note that the values at high i are often based on very few subtracks:
msd <- aggregate( TCells, squareDisplacement, count.subtracks = TRUE )
```

```

tail( msd )

## 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 )

```

---

analyzeCellPairs

*Find Distances and Angles for all Pairs of Tracks*


---

### Description

Find all pairs of cells and return the shortest distance between them at any point in time (if they share any time points), as well as the angle between their overall displacement vectors.

### Usage

```
analyzeCellPairs(X, searchRadius = Inf, quietly = FALSE, ...)
```

### Arguments

X	a tracks object
searchRadius	if specified, only return analysis for pairs of cells that are within distance searchRadius from each other at least at one point in time.
quietly	(default FALSE) if TRUE, suppress warnings
...	further arguments passed on to angleCells

### Details

Analyzing track angles at different distances can be useful to detect directional bias or local crowding effects; see (Beltman et al, 2009).

Internally, the function uses [cellPairs](#), [angleCells](#), and [distanceCells](#).

### Value

A dataframe with four columns: two for the indices of cellpairs, one for the distance between them, and one for their angle. Note that the distance will be NA for pairs of tracks that do not share time points, but their angle will still be computed.

## References

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

## See Also

[analyzeStepPairs](#) to do something similar for single steps rather than entire tracks.

## Examples

```
## Plot distance versus angle for all cell pairs. Sample T-cell data here for speed.
pairs <- analyzeCellPairs( sample( TCells, 100 ) )
scatter.smooth( pairs$dist, pairs$angle )
```

---

analyzeStepPairs      *Find Distances and Angles for all Pairs of Steps*

---

## Description

Find cell indices and timepoints where these cells both have a step, then return angles and distances for each pair of steps.

## Usage

```
analyzeStepPairs(  
  X,  
  filter.steps = NULL,  
  searchRadius = Inf,  
  quietly = FALSE,  
  ...  
)
```

## Arguments

X	a tracks object
filter.steps	optional: a function used to filter steps on. See examples.
searchRadius	if specified, only return analysis for pairs of steps that start within distance searchRadius from each other
quietly	(default FALSE) if TRUE, suppress warnings
...	further arguments passed on to angleSteps

## Details

Analyzing step angles at different distances can be useful to detect directional bias or local crowding effects; see (Beltman et al, 2009).

Internally, the function uses [stepPairs](#), [angleSteps](#), and [distanceSteps](#).

**Value**

A dataframe with five columns: two for the indices of cellpairs that share a step, one for the time-point at which they do so, one for the distance between them, and one for their angle.

**References**

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

**See Also**

[analyzeCellPairs](#) to do something similar for entire tracks rather than single steps.

**Examples**

```
## Plot distance versus angle for all step pairs, filtering for those that
## displace at least 2 microns. Sample dataset in this example for speed.
pairs <- analyzeStepPairs( sample( TCells, 100), filter.steps = function(t) displacement(t) > 2 )
scatter.smooth( pairs$dist, pairs$angle )
```

---

AngleAnalysis

*Angle Analysis*

---

**Description**

Analyzing angles to reference directions, points, or planes can be useful to detect artefacts and/or directionality in tracking datasets (Beltman et al, 2009). All these functions take a track and a reference (point/direction/plane) as input and return a distance or angle as output. Angles/distances are by default computed to the first step in the given track.

**Details**

[angleToPoint](#) and [distanceToPoint](#) return the angle/distance of the track to the reference point. The distance returned is between the first coordinate in the track and the reference point. The angle is between the overall displacement vector of the track and the vector from its first coordinate to the reference point. Angles are by default returned in degrees, use `degrees=FALSE` to obtain radians. These functions are useful to detect directional bias towards a point of interest, which would result in an average angle of less than 90 degrees with the reference point (especially for tracks at a small distance to the reference point).

[angleToPlane](#) and [distanceToPlane](#) return the angle/distance of the track to a plane of interest. This plane must be specified by three points lying on it. The distance returned is between the first coordinate in the track and the reference point. The angle is between the overall displacement vector of the track and the plane of interest. These functions are useful to detect tracking artefacts near the borders of the imaging volume. Use [boundingBox](#) to guess where those borders are. Angles are by default returned in degrees, use `degrees=FALSE` to obtain radians.

[angleToDir](#) returns the angle of a track's overall displacement vector to a direction of interest. This function is useful to detect directionality in cases where the direction of the bias is known in



advance (e.g. when cells are known to move up a chemotactic gradient): in that case, the average angle to the reference direction should be less than 90 degrees. Angles are by default returned in degrees, use `degrees=FALSE` to obtain radians.

`angleSteps` and `distanceSteps` return the angle/distance between a pair of steps in the data that occur at the same timepoint. Angles are in degrees by default, use `degrees=FALSE` to obtain radians. Use `stepPairs` to extract all pairs of steps that occur at the same timepoint, and use `analyzeStepPairs` to do this and then also obtain the angles and distances for each of these pairs.

`angleCells` and `distanceCells` return the angle/distance between a pair of tracks in the data. The computed angles are between the overall displacement vectors of the tracks, the distance is the shortest distance between them at any timepoint they share. Angles are in degrees by default, use `degrees=FALSE` to obtain radians. Use `cellPairs` to extract all pairs of cells in the data, and use `analyzeCellPairs` to do this and then also obtain the angles and distances for each of these pairs.

## Value

This page is for documentation only and provides an overview of angle analysis functions and their use cases. The return values of each of these functions are documented separately; please follow the link to the documentation page of that specific function.

## References

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

## See Also

[TrackMeasures](#) for other measures that can be used to quantify tracks.

See the vignettes on [Quality Control and Track Analysis](#) for more detailed examples of angle analyses. `browseVignettes( package = "celltrackR" )`

## Examples

```
## Plotting the angle versus the distance to a reference point can be informative to
## detect biased movement towards that point. We should be suspicious especially
## when small angles are more frequent at lower distances.
steps <- subtracks( sample( Neutrophils, 50 ), 1 )
bb <- boundingBox( Neutrophils )
angles <- sapply( steps, angleToPoint, p = bb["max",-1] )
distances <- sapply( steps, distanceToPoint, p = bb["max",-1] )
scatter.smooth( distances, angles )
abline( h = 90, col = "red" )

## Get a distribution of Neutrophil step angles with the reference direction
## in positive y direction. The histogram is enriched for low angles, suggesting
## directed movement:
hist( sapply( steps, angleToDir, dvec=c(1,-1) ) )

## Plotting the angle versus the distance to a reference plane can be informative to
## detect tracking artefacts near the border of the imaging volume.
## We should be suspicious especially when small angles are more frequent at low distances
```

```

## to the border planes; as is the case in the z-dimension for the raw data:
load( system.file("extdata", "TCellsRaw.rda", package="celltrackR" ) )
steps <- subtracks( sample( TCellsRaw, 50 ), 1 )
minz <- boundingBox( TCellsRaw )["min","z"]
## Compute angles and distances to the lower plane in z-dimension
angles <- sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
distances <- sapply( steps, distanceToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
scatter.smooth( distances, angles )
abline( h = 32.7, col = "red" )

## Plot distance versus angle for all cell pairs (here in only a sample to speed things up)
pairs <- analyzeCellPairs( sample( TCells, 50 ) )
scatter.smooth( pairs$dist, pairs$angle )
abline( h = 90, col = "red" )

## Plot distance versus angle for all step pairs, filtering for those that
## displace at least 2 microns
pairs <- analyzeStepPairs( sample( TCells, 50 ), filter.steps = function(t) displacement(t) > 2 )
scatter.smooth( pairs$dist, pairs$angle )
abline( h = 90, col = "red" )

```

---

angleCells

*Angle between Two Tracks*


---

### Description

Compute the angle between the displacement vectors of two tracks in the dataset, or of several such pairs at once. Note that in contrast to [distanceCells](#), this angle is computed even when the two tracks do not share any time points.

### Usage

```
angleCells(X, cellids, degrees = TRUE)
```

### Arguments

X	a tracks object
cellids	a vector of two indices specifying the tracks to get steps from, or a dataframe/matrix of two columns (where every row contains a pair of cellids to compute an angle for)
degrees	logical; should angle be returned in degrees instead of radians? (defaults to TRUE)

### Value

A single angle (if two cellids given), or a vector of angles (if multiple pairs of cellids are supplied).

**See Also**

[distanceCells](#) to compute the minimum distance between the tracks, and [AngleAnalysis](#) for other methods to compute angles and distances.

**Examples**

```
## Find the angle between the tracks with ids 1 and 3
angleCells( TCells, c("1","3") )

## Find the angles of several cell pairs at once
pairs <- data.frame( cell1 = c("1","1"), cell2 = c( "3","4" ) )
angleCells( TCells, pairs )
```

---

angleSteps	<i>Angle between Two Steps</i>
------------	--------------------------------

---

**Description**

Compute the angle between two steps in the dataset that occur at the same timepoint.

**Usage**

```
angleSteps(X, trackids, t, degrees = TRUE, quietly = FALSE)
```

**Arguments**

X	a tracks object
trackids	a vector of two indices specifying the tracks to get steps from, or a dataframe/matrix of two columns (where every row contains a pair of trackids to compute a step angle for)
t	the timepoint at which the steps should start, or a vector of timepoints if trackids is a matrix with multiple step pairs to compute angles for.
degrees	logical; should angle be returned in degrees instead of radians? (defaults to TRUE)
quietly	logical; should a warning be returned if one or both of the steps are missing in the data and the function returns NA?

**Value**

A single angle, or NA if the desired step is missing for one or both of the tracks. If trackids is a matrix with multiple step pairs to compute angles for, the output is a numeric vector of angles (or NA values).

**See Also**

[distanceSteps](#) to compute the distance between the step starting points, [timePoints](#) to list all timepoints in a dataset, and [AngleAnalysis](#) for other methods to compute angles and distances.

**Examples**

```
## Find the angle between the steps of the tracks with ids 1 and 2, at the 3rd
## timepoint in the dataset.
t <- timePoints( TCells )[3]
angleSteps( TCells, c("1","3"), t )

## Do this for multiple pairs and times at once: between cells 1 and 3 at the
## 3rd timepoint, and between 1 and 4 at the fourth timepoint.
pairs <- data.frame( cell1 = c("1","1"), cell2 = c("3","4"))
times <- timePoints(TCells)[3:4]
angleSteps( TCells, pairs, times )
```

---

angleToDir

*Angle with a Reference Direction*


---

**Description**

Compute the angle between a track's overall displacement and a reference direction. Useful to detect biased movement when the directional bias is known (see examples).

**Usage**

```
angleToDir(x, dvec = c(1, 1, 1), from = 1, degrees = TRUE)
```

**Arguments**

x	a single input track; a matrix whose first column is time and whose remaining columns are a spatial coordinate.
dvec	numeric vector specifying a reference direction to compute angles to.
from	index, or vector of indices, of the first row of the track. If from is a vector, angles are returned for all steps starting at the indices in from.
degrees	logical; should angles be returned in degrees rather than radians? (default = TRUE).

**Details**

The average angle of steps to a reference direction should be 90 degrees if there is no bias towards movement in the direction of the reference point. If there is such a bias, there should be an enrichment of smaller angles. The expected distribution without bias is a uniform distribution in 2D or a sine distribution in 3D (Beltman et al, 2009).

**Value**

A single angle.

## References

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

## See Also

[AngleAnalysis](#) for other methods to compute angles and distances.

## Examples

```
## Get a distribution of Neutrophil step angles with the reference direction in positive
## y direction. The histogram is enriched for low angles, suggesting directed movement:
steps <- subtracks( Neutrophils, 1 )
hist( sapply( steps, angleToDir, dvec=c(1,-1) ) )
```

---

angleToPlane	<i>Angle with a Reference Plane</i>
--------------	-------------------------------------

---

## Description

Compute the angle between a track's overall displacement and a reference plane. Useful to detect directed movement and/or tracking artefacts.

## Usage

```
angleToPlane(
  x,
  p1 = c(0, 0, 0),
  p2 = c(0, 1, 0),
  p3 = c(1, 0, 0),
  from = 1,
  degrees = TRUE
)
```

## Arguments

x	a single input track; a matrix whose first column is time and whose remaining columns are a spatial coordinate.
p1, p2, p3	numeric vectors of coordinates of three points specifying a reference plane to compute distances to.
from	index, or vector of indices, of the first row of the track. If from is a vector, angles are returned for all steps starting at the indices in from.
degrees	logical; should angles be returned in degrees rather than radians? (default = TRUE).

**Details**

The average angle of steps to a reference plane should be roughly 32.7 degrees. Lower angles to the border planes of an imaging volume can be indicative of tracking artefacts, and systematic deviations from 32.7 can indicate a directional bias (Beltman et al, 2009).

**Value**

A single angle.

**References**

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

**See Also**

[distanceToPlane](#) to compute the distance to the reference plane, and [AngleAnalysis](#) for other methods to compute angles and distances.

**Examples**

```
## Plotting the angle versus the distance to a reference plane can be informative to
## detect tracking artefacts near the border of the imaging volume.
## We should be suspicious especially when small angles are more frequent at low distances
## to the border planes.
load( system.file("extdata", "TCellsRaw.rda", package="celltrackR" ) )
steps <- subtracks( TCellsRaw, 1 )
minz <- boundingBox( TCellsRaw )["min","z"]
## Compute angles and distances to the lower plane in z-dimension
angles <- sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
distances <- sapply( steps, distanceToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
scatter.smooth( distances, angles )
abline( h = 32.7, col = "red" )
```

---

angleToPoint

*Angle with a Reference Point*

---

**Description**

Compute the angle between a track's overall displacement vector and the vector from it's first coordinate to a reference point. Useful to detect directed movement towards a point (see examples).

**Usage**

```
angleToPoint(x, p = c(1, 1, 1), from = 1, degrees = TRUE)
```

**Arguments**

x	a single input track; a matrix whose first column is time and whose remaining columns are a spatial coordinate.
p	numeric vector of coordinates of the reference point p to compute angles/distances to.
from	index, or vector of indices, of the first row of the track. If from is a vector, angles are returned for all steps starting at the indices in from.
degrees	logical; should angles be returned in degrees rather than radians? (default = TRUE).

**Details**

The average angle of steps to a reference point should be 90 degrees if there is no bias towards movement in the direction of the reference point. If there is such a bias, there should be an enrichment of smaller angles. The expected distribution without bias is a uniform distribution in 2D or a sine distribution in 3D (Beltman et al, 2009).

**Value**

A single angle.

**References**

Joost B. Beltman, Athanasius F.M. Maree and Rob. J. de Boer (2009), Analysing immune cell migration. *Nature Reviews Immunology* **9**, 789–798. doi:10.1038/nri2638

**See Also**

[distanceToPoint](#) to compute the distance to the reference point, and [AngleAnalysis](#) for other methods to compute angles and distances.

**Examples**

```
## Get a distribution of step angles with a reference point
## Use bb to get the corner with highest x,y (,z) value
## The histogram is enriched for low angles, suggesting directed movement:
steps <- subtracks( Neutrophils, 1 )
bb <- boundingBox( Neutrophils )
hist( sapply( steps, angleToPoint, p = bb["max",-1] ) )

## The same does not hold for movement of T cells towards the point (0,0)
steps <- subtracks( TCells, 1 )
hist( sapply( steps, angleToPoint, p = c(0,0) ) )

## Plotting the angle versus the distance to the reference point can also be informative,
## especially when small angles are more frequent at lower distances.
angles <- sapply( steps, angleToPoint, p = bb["max",-1] )
distances <- sapply( steps, distanceToPoint, p = bb["max",-1] )
scatter.smooth( distances, angles )
abline( h = 90, col = "red" )
```

---

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

```
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 <a href="#">overallAngle</a> .

### Details

The measure is computed for each of the input track's subtracks of length at least `min.segments`, and the resulting values are either returned in a matrix (if `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 `min.segments=1` this is exactly the main diagonal) are set to NA.

### Value

If `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 'matrix' is not set, the mean over the values of the measure for all subtracks of at least 'min.segments' segments is returned.

### Examples

```
## 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

```
## S3 method for class 'tracks'
as.data.frame(
  x,
  row.names = NULL,
  optional = FALSE,
  include.timepoint.column = FALSE,
  idsAsFactors = TRUE,
  ...
)
```

### 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.
idsAsFactors	logical. If TRUE, then the id column of the resulting dataframe will be a factor column, otherwise a character column.
...	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

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

---

as.list.tracks      *Convert from Tracks to List*

---

### Description

Coerces a tracks object to a list.

### Usage

```
## 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.

### Value

A generic list of single tracks, where each track is a matrix with  $t/\delta.t$  rows and 4 columns. This looks a lot like a tracks object, except that its class is not "tracks" anymore.

---

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

---

### Description

Get cell tracks from a data.frame. 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. Further columns contain the spatial coordinates. If there are three or less spatial coordinates, their names will be "x", "y", and "z" (depending on whether the tracks are 1D, 2D or 3D). If there are four or more spatial coordinates, their names will be "x1", "x2", and so on. The names or indices of these columns in the data.frame 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

```
## S3 method for class 'data.frame'
as.tracks(
  x,
  id.column = 1,
  time.column = 2,
```

```

pos.columns = 3:ncol(x),
scale.t = 1,
scale.pos = 1,
...
)

```

### Arguments

<code>x</code>	the data frame to be coerced to a tracks object.
<code>id.column</code>	index or name of the column that contains the track ID.
<code>time.column</code>	index or name of the column that contains elapsed time.
<code>pos.columns</code>	vector containing indices or names of the columns that contain the spatial coordinates. If this vector has two entries and the second entry is NA, e.g. <code>c('x', NA)</code> or <code>c(5, NA)</code> 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.
<code>scale.t</code>	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.
<code>scale.pos</code>	a value, or a vector of values, by which to multiply each spatial position. Useful for changing units.
<code>...</code>	further arguments to be passed to <code>read.csv</code> , for instance <code>sep="\t"</code> can be useful for tab-separated files.

### Value

A tracks object.

---

BCells

*Two-Photon Data: B Cells in a Lymph Node*

---

### Description

GFP-labelled B cells were injected retro-orbitally in healthy CD11c-YFP mice, and intravitally imaged (using two-photon microscopy) inside a cervical lymph node. These data illustrate the characteristic "random-walk-like" motion pattern of B cells in lymph nodes. For full method details, see references below.

### Usage

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

**Format**

## 'BCells' An S3 object of class "tracks"; a list with 74 elements. Each element name identifies a cell track. Each element is a matrix containing the following three columns.

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

**Source**

Data were generated in 2021 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

**References**

Miller MJ and Wei SH and Parker I and Cahalan MD (2002), Two-photon imaging of lymphocyte motility and antigen response in intact lymph node. *Science*, **296**(5574):1869–1873. doi:10.1126/science.1070051  
Wortel IMN and Liu AY and Dannenberg K and Berry JC and Miller MJ and Textor J (2021), CelltrackR: an R package for fast and flexible analysis of immune cell migration data. *ImmunoInformatics*, **1-2**:100003. doi:10.1016/j.immuno.2021.100003

**Examples**

```
## load the tracks
data(BCells)

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

---

beaucheminTrack

*Simulate a 3D Cell Track Using the Beauchemin Model*

---

**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**

```
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.
taxis.mode	specified mode of movement. 1 := orthotaxis, 2 := topotaxis, 3 := klinotaxis.
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.free` at a fixed speed `v.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.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.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

Johannes Textor, Mathieu Sinn and Rob J. de Boer (2013), Analytical results on the Beauchemin model of lymphocyte migration. *BMC Bioinformatics* **14**(Suppl 6), S10. doi:10.1186/1471-2105-14-S6-S10

**Examples**

```
## 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 )
```

---

bootstrapTrack	<i>Simulate Tracks via Bootstrapping of Speed and Turning Angle from a Real Track Dataset</i>
----------------	---

---

**Description**

Returns a simulated dataset by sampling from the speed and turning angle distributions from an original track dataset (only in 2 or 3 dimensions)

**Usage**

```
bootstrapTrack(nsteps, trackdata)
```

**Arguments**

nsteps	desired number of steps (e.g. 10 steps generates a track with 11 positions).
trackdata	a tracks object to extract speeds and turning angles from.

**Details**

The number of dimensions is kept the same as in the original data (if data is 3D but simulated tracks should be 2D, consider calling [projectDimensions](#) on the input data before supplying it to bootstrapTrack). The time interval between "measurements" of the simulated track equals that in the real data and is found via [timeStep](#). The first step starts at the origin in a random direction, with a speed sampled from the speed distribution to determine its displacement. All subsequent steps also have their turning angles sampled from the turning angle distribution in the data.

**Value**

A data frame containing in cell track with nsteps steps in the same number of dimensions as the original data is returned.

```
## Generate bootstrapped tracks of the TCell data; compare its speed distribution to the ## original
data (should be the same). T.bootstrap <- bootstrapTrack( 100, TCells )
step.speeds.real <- sapply( subtracks(TCells,1), speed )
step.speeds.bootstrap <- sapply( subtracks( T.bootstrap, 1), speed )
qqplot( step.speeds.real, step.speeds.bootstrap )
```

---

boundingBox	<i>Bounding Box of a Tracks Object</i>
-------------	--

---

**Description**

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

**Usage**

```
boundingBox(x)
```

**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**

```
## 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	<i>Simulate an Uncorrelated Random Walk</i>
---------------	---

---

**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.

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

---

cellPairs

*Find Pairs of Tracks*

---

**Description**

Get all unique combinations of two track ids.

**Usage**

```
cellPairs(X)
```

**Arguments**

X                    a tracks object

**Value**

A dataframe with two columns: one for each of the track ids in the pair. Each row represents a pair.

**Examples**

```
## Find all pairs of cells in the T cell data
pairs <- cellPairs( TCells )
```



---

cheatsheet	<i>Open the package cheat sheet</i>
------------	-------------------------------------

---

**Description**

Running this function will open the package cheat sheet (a pdf) via a call to `system()`.

**Usage**

```
cheatsheet(opencmd = NULL)
```

**Arguments**

`opencmd` The command used to open pdfs from the command line.

**Value**

None

---

clusterTracks	<i>Cluster Tracks</i>
---------------	-----------------------

---

**Description**

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

**Usage**

```
clusterTracks(  
  tracks,  
  measures,  
  scale = TRUE,  
  labels = NULL,  
  method = "hclust",  
  return.clust = FALSE,  
  ...  
)
```

**Arguments**

tracks	the tracks that are to be clustered.
measures	a function, or a vector of functions (see <a href="#">TrackMeasures</a> ). 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 <a href="#">scale</a> before the clustering.
labels	optional: a vector of labels of the same length as the track object. These are used to color points in the visualization.
method	"hclust" for hierarchical clustering, or "kmeans" for k-means clustering.
return.clust	logical: return the clustering object instead of only the plot? (defaults to FALSE).
...	additional parameters to be passed to the corresponding clustering function: <a href="#">hclust</a> or <a href="#">kmeans</a> .

**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 the chosen clustering method. If *scale* is TRUE, the measure values are scaled to mean value 0 and standard deviation 1 (per measure) before the clustering.

Method *hclust* plots a dendrogram of the clustering.

Method *kmeans* plots each computed cluster (x-axis) versus each of the track measures in the measures vector, producing one panel per measure. If labels are given, points are colored according to their "true" label.

**Value**

By default, only returns a plot. If *return.clust*=TRUE, also returns a clustering object as returned by [hclust](#) or [kmeans](#). output object.

**See Also**

[getFeatureMatrix](#) to obtain a feature matrix that can be used for manual clustering and plotting, and [trackFeatureMap](#) to visualize high-dimensional track feature data via dimensionality reduction.

**Examples**

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

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, method = "hclust",
  return.clust = TRUE )

## How many cells are "correctly" clustered?
```

```
sum( real.celltype == c("T","N")[cutree(clust,2)] )
```

---

distanceCells	<i>Minimum Distance between Two Cells</i>
---------------	---

---

### Description

Compute the minimum distance between two cells in the dataset (minimum over all) the timepoints where they were both measured.

### Usage

```
distanceCells(X, cellids, quietly = FALSE)
```

### Arguments

X	a tracks object
cellids	a vector of two indices specifying the tracks to compute distance between, or a dataframe/matrix of two columns (where every row contains a pair of cellids to compute a distance for)
quietly	if TRUE, suppress warnings about returning NA distances.

### Value

A single distance (NA if the the tracks do not have overlapping timepoints), or a vector of such distances if multiple pairs are supplied in cellids.

### See Also

[angleCells](#) to compute the angle between the track displacement vectors, and [AngleAnalysis](#) for other methods to compute angles and distances.

### Examples

```
## Find the minimum distance between the tracks with ids 1 and 3
distanceCells( TCells, c("1","3") )
```

---

distanceSteps                      *Distance between Two Steps*

---

### Description

Compute the distance between two steps in the dataset that occur at the same timepoint. The distance is the distance between the step starting points.

### Usage

```
distanceSteps(X, trackids, t, quietly = FALSE)
```

### Arguments

X	a tracks object
trackids	a vector of two indices specifying the tracks to get steps from, or a dataframe/matrix of two columns (where every row contains a pair of trackids to compute a step angle for)
t	the timepoint at which the steps should start, or a vector of such timepoints if multiple step pairs are supplied in trackids.
quietly	logical; should a warning be returned if one or both of the steps are missing in the data and the function returns NA?

### Value

A single distance (NA if the desired timepoint is missing for one or both of the tracks), or a vector of such distances if multiple step pairs are supplied in trackids.

### See Also

[angleSteps](#) to compute the angle between the steps, [timePoints](#) to list all timepoints in a dataset, and [AngleAnalysis](#) for other methods to compute angles and distances.

### Examples

```
## Find the distance between the steps of the tracks with ids 1 and 3, at the 3rd
## timepoint in the dataset.
t <- timePoints( TCells )[3]
distanceSteps( TCells, c("1","3"), t )

## Do this for multiple pairs and times at once: between cells 1 and 3 at the
## 3rd timepoint, and between 1 and 4 at the fourth timepoint.
pairs <- data.frame( cell1 = c("1","1"), cell2 = c("3","4"))
times <- timePoints(TCells)[3:4]
distanceSteps( TCells, pairs, times )
```

---

distanceToPlane      *Distance to a Reference Plane*

---

### Description

Compute the (shortest) distance between the starting point of a track and a reference plane. Useful to detect directed movement and/or tracking artefacts.

### Usage

```
distanceToPlane(x, p1 = c(0, 0, 0), p2 = c(0, 1, 0), p3 = c(1, 0, 0), from = 1)
```

### Arguments

x	a single input track; a matrix whose first column is time and whose remaining columns are a spatial coordinate.
p1, p2, p3	numeric vectors of coordinates of three points specifying a reference plane to compute distances to.
from	index, or vector of indices, of the first row of the track. If from is a vector, distances are returned for all steps starting at the indices in from.

### Value

A single distance.

### See Also

[angleToPlane](#) to compute the angle to the plane, and [AngleAnalysis](#) for other methods to compute angles and distances.

### Examples

```
## Plotting the angle versus the distance to a reference plane can be informative to
## detect tracking artefacts near the border of the imaging volume.
## We should be suspicious especially when small angles are more frequent at low distances
## to the border planes.
load( system.file("extdata", "TCellsRaw.rda", package="celltrackR" ) )
steps <- subtracks( TCellsRaw, 1 )
minz <- boundingBox( TCellsRaw )["min","z"]
## Compute angles and distances to the lower plane in z-dimension
angles <- sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
distances <- sapply( steps, distanceToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz) )
scatter.smooth( distances, angles )
abline( h = 32.7, col = "red" )
```

---

distanceToPoint      *Distance to a Reference Point*

---

### Description

Compute the distance between the starting point of a track and a reference point. Useful to detect directed movement towards a point (see examples).

### Usage

```
distanceToPoint(x, p = c(0, 0, 0), from = 1)
```

### Arguments

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

**p**                    numeric vector of coordinates of the reference point *p* to compute distances to.

**from**                index, or vector of indices, of the first row of the track. If *from* is a vector, distances are returned for all steps starting at the indices in *from*.

### Value

A single distance.

### See Also

[angleToPoint](#) to compute the angle to the reference point, and [AngleAnalysis](#) for other methods to compute angles and distances.

### Examples

```
## Plotting the angle versus the distance to a reference point can be informative to
## detect biased movement towards that point. We should be suspicious especially
## when small angles are more frequent at lower distances.
steps <- subtracks( Neutrophils, 1 )
bb <- boundingBox( Neutrophils )
angles <- sapply( steps, angleToPoint, p = bb["max",-1] )
distances <- sapply( steps, distanceToPoint, p = bb["max",-1] )
scatter.smooth( distances, angles )
abline( h = 90, col = "red" )
```

---

filterTracks	<i>Filter Tracks</i>
--------------	----------------------

---

**Description**

Extracts subtracks based on a given function.

**Usage**

```
filterTracks(f, x, ...)
```

**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.
...	further arguments to be passed on to f.

**Value**

A tracks object containing only those tracks from x for which f evaluates to TRUE.

**Examples**

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

---

get.immap.metadata	<i>Get Track Metadata from ImmuneMap</i>
--------------------	--

---

**Description**

Get metadata from tracks obtained from <https://immunemap.org> and import into celltrackR.

**Usage**

```
get.immap.metadata(  
  input,  
  warn.exclude = TRUE,  
  exclude.names = c("points", "cellTypeObject", "date")  
)
```

**Arguments**

input	a parsed json file obtained with <a href="#">parse.immap.json</a>
warn.exclude	logical: if TRUE (default), warn when key-value pairs in the json (other than those in exclude.names) are being ignored while parsing immunemap json.
exclude.names	if the json contains keys with these names, they are ignored when reading the metadata.

**Value**

a dataframe with metadata. This function currently only handles metadata with a single value for each track and ignores others (with a warning when warn.exclude=TRUE). column names in the dataframe correspond to the keys in the original json, and values to the values for each track.

**Examples**

```
## Not run:
## Read tracks from immunemap online
input <- parse.immap.json( url = "https://api.immunemap.org/video/14/tracks" )
meta.df <- get.immap.metadata( input )

## Repeat but ignore also the 'color' column:
exclude <- c("points", "cellTypeObject", "date", "color")
meta.df <- get.immap.metadata( input, exclude.names = exclude )

## End(Not run)
```

---

getFeatureMatrix      *Obtaining A Feature Matrix*

---

**Description**

Applies a given vector of track measures directly on a set of tracks, returning output in a matrix with a column for each measure and a row for each track. Can also return a distance matrix, which some clustering methods require.

**Usage**

```
getFeatureMatrix(tracks, measures, dist = FALSE, ...)
```

**Arguments**

tracks	the tracks that are to be analyzed.
measures	a function, or a vector of functions (see <a href="#">TrackMeasures</a> ). Each function is expected to return a single number given a single track.
dist	should a distance matrix rather than a feature matrix be returned?
...	further arguments passed on to "dist"



**Value**

A matrix with a row for each track and a column for each measure.

**See Also**

[clusterTracks](#) for a quick method to compute the feature matrix and a clustering, and [trackFeatureMap](#) to perform dimensionality reduction methods on a set of track features.

**Examples**

```
## Get speed, meanTurningAngle, and straightness for T cell tracks
fm <- getFeatureMatrix( TCells, c(speed,meanTurningAngle,straightness))
str(fm)
```

---

hotellingsTest	<i>Test Unbiasedness of Motion</i>
----------------	------------------------------------

---

**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**

```
hotellingsTest(
  tracks,
  dim = c("x", "y"),
  step.spacing = 0,
  plot = FALSE,
  add = FALSE,
  ellipse.col = "blue",
  ellipse.border = "black",
  conf.level = 0.95,
  ...
)
```

**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

Johannes Textor, Antonio Peixoto, Sarah E. Henrickson, Mathieu Sinn, Ulrich H. von Andrian and Juergen Westermann (2011), Defining the Quantitative Limits of Intravital Two-Photon Lymphocyte Tracking. *PNAS* **108**(30):12401–12406. doi:10.1073/pnas.1102288108

### Examples

```
## 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**

```
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).

**Value**

The interpolated track (a matrix or data frame).

**Examples**

```
## 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	<i>Length of Longest Track</i>
----------------	--------------------------------

---

**Description**

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

**Usage**

```
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

---

Neutrophils

*Two-Photon Data: Neutrophils responding to an infection in the ear*

---

## Description

LysM-GFP mice were infected with *S. aureus* on their ear, and intravitaly imaged using two-photon microscopy proximal to the infection. These cells display a fairly directed kind of motion, as they move towards infection foci. For method details, see the references below.

## Usage

```
data("Neutrophils")
```

## Format

## 'Neutrophils' An S3 object of class "tracks"; a list with 411 elements. Each element name identifies a cell track. Each element is a matrix containing the following three columns.

t the time (in seconds)

x The X coordinate (in micrometers)

y The Y coordinate (in micrometers)

## Source

Data were generated in 2021 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

## References

Lin A and Loughman JA and Zinselmeyer BH and Miller MJ and Caparon MG (2009), Streptolysin S inhibits neutrophil recruitment during the early stages of streptococcus pyogenes infection. *Infect Immun*, **77**(11):5190–5201. doi:10.1128/IAI.00420-09

Wang B and Zinselmeyer BH and McDole JR and Gieselman PA and Miller MJ (2010), Non-invasive imaging of leukocyte homing and migration in vivo. *J Vis Exp*, **46**:e2062. doi:10.3791/2062

Graham DB and Zinselmeyer BH and Mascarenhas F and Delgado R and Miller MJ and Swat W (2009), Itam signaling by Vav family Rho Guanine nucleotide exchange factors regulates interstitial transit rates of neutrophils in vivo. *PLOS ONE*, **2**(2):1–5. doi:10.1371/journal.pone.0004652

Wortel IMN and Liu AY and Dannenberg K and Berry JC and Miller MJ and Textor J (2021), CelltrackR: an R package for fast and flexible analysis of immune cell migration data. *ImmunoInformatics*, **1-2**:100003. doi:10.1016/j.immuno.2021.100003

**Examples**

```
## 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**

```
## 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.

**Value**

an output tracks object with all tracks shifted such that their starting position lies at the origin of the coordinate system.

**Examples**

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

---

<code>pairsByTime</code>	<i>Distance between pairs of tracks at every timepoint</i>
--------------------------	--

---

**Description**

For every timepoint in the dataset, compute pairwise distances between coordinates.

**Usage**

```
pairsByTime(X, searchRadius = Inf, times = timePoints(X), quietly = FALSE)
```

**Arguments**

`X` a tracks object

`searchRadius` if specified, return only pairs that are within this distance of each other. Defaults to `Inf`, so if left unspecified, all pairs are returned.

`times` (optional) a vector of timePoints to check pairs at; by default this is just everything.

`quietly` (default `FALSE`) if `TRUE`, suppress warnings when there are no tracks with overlapping timepoints and an empty dataframe is returned.

**Value**

a dataframe with the following columns:

**cell1** the id of the track to which the first coordinate belongs

**cell2** the id of the track to which the second coordinate belongs

**t** the time point at which their distance is assessed

**dist** the distance between the coordinates at this time

**Examples**

```
## compute find timepoints where two t cells are within 1 micron of each other.
pairsByTime( TCells, searchRadius = 1 )

## indeed, the following two cells nearly touch:
plot( TCells[ c("24","9258") ] )
```

plot.tracks

*Plot Tracks in 2D***Description**

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

**Usage**

```
## S3 method for class 'tracks'
plot(
  x,
  dims = c("x", "y"),
  add = F,
  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 <i>x</i> and <i>y</i> 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 <a href="#">points</a> ).
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 <a href="#">plot</a> (for add=FALSE) or <a href="#">points</a> (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`.

**Value**

None

**See Also**

[plot3d](#)

---

plot3d

*Plot Tracks in 3D*

---

**Description**

Takes an input tracks object and plots them in 3D using the [scatterplot3d](#) function.

**Usage**

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

**Arguments**

`x` the tracks which will be plotted in 3d  
`...` further arguments to be passed on to [scatterplot3d](#)

**Value**

None.

**Examples**

```
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**

```
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 <a href="#">TrackMeasures</a> ).
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 <a href="#">points</a> .
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.
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 <a href="#">plot</a> (in case add=FALSE) or <a href="#">points</a> (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).

**Value**

None

**References**

Moreau HD, Lemaitre F, Terriac E, Azar G, Piel M, Lennon-Dumenil AM, Bousso P (2012), Dynamic In Situ Cytometry Uncovers T Cell Receptor Signaling during Immunological Synapses and Kinapses In Vivo. *Immunity* **37**(2), 351–363. doi:10.1016/j.immuni.2012.05.014

Johannes Textor, Sarah E. Henrickson, Judith N. Mandl, Ulrich H. von Andrian, Jürgen Westermann, Rob J. de Boer and Joost B. Beltman (2014), Random Migration and Signal Integration Promote Rapid and Robust T Cell Recruitment. *PLoS Computational Biology* **10**(8), e1003752. doi:10.1371/journal.pcbi.1003752

**Examples**

```
## 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**

```
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.

**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 start at the first registered coordinate of the given track.

**See Also**

[subtracks](#) to extract all subtracks of a given length, [subtracksByTime](#) to extract all subtracks of a given length starting at some fixed timepoint, and [selectSteps](#) to extract single steps starting at a fixed timepoint from a subset of trackids.

---

projectDimensions      *Extract Spatial Dimensions*

---

**Description**

Projects tracks onto the given spatial dimensions.

**Usage**

```
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**

```
## Compare 2D and 3D speeds
load( system.file("extdata", "TCellsRaw.rda", package="celltrackR" ) )
speed.2D <- mean( sapply( subtracks( projectDimensions( TCellsRaw, c("x", "z") ), 2 ), speed ) )
speed.3D <- mean( sapply( TCellsRaw, 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. Further columns contain the spatial coordinates. If there are three or less spatial coordinates, their names will be "x", "y", and "z" (depending on whether the tracks are 1D, 2D or 3D). If there are four or more spatial coordinates, their names will be "x1", "x2", and so on. 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

```
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

<code>file</code>	the name of the file which the data are to be read from, a readable text-mode connection or a complete URL (see <a href="#">read.table</a> ).
<code>id.column</code>	index or name of the column that contains the track ID.
<code>time.column</code>	index or name of the column that contains elapsed time.
<code>pos.columns</code>	vector containing indices or names of the columns that contain the spatial coordinates. If this vector has two entries and the second entry is NA, e.g. <code>c('x', NA)</code> or <code>c(5, NA)</code> 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.
<code>scale.t</code>	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.

<code>scale.pos</code>	a value, or a vector of values, by which to multiply each spatial position. Useful for changing units.
<code>header</code>	a logical value indicating whether the file contains the names of the variables as its first line. See <a href="#">read.table</a> .
<code>sep</code>	a character specifying how the columns of the data are separated. The default value "" means columns are separated by tabs or other spaces. See <a href="#">read.table</a> .
<code>track.sep.blankline</code>	logical. If set to 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.
<code>...</code>	further arguments to be passed to <code>read.csv</code> , for instance <code>sep="\t"</code> 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 *tracks*, which is a list of data frames representing the single tracks and having columns *t* and *x*, plus *y* and *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 *tracks* is returned, which is a list of matrices, each containing the positions of one track. The matrices have a column *t*, followed by one column for each of the input track's coordinates.

---

ReadImmuneMap	<i>Read tracks from ImmuneMap</i>
---------------	-----------------------------------

---

### Description

Reads tracks from <https://immunemap.org> for import into celltrackR. This produces both tracks object(s) and a dataframe with metadata.

### Usage

```
read.immap.json(
  url,
  tracks.url = NULL,
  keep.id = TRUE,
  scale.auto = TRUE,
  scale.t = NULL,
  scale.pos = NULL,
  warn.scaling = TRUE,
  simplify.2D = TRUE,
  warn.celltypes = TRUE,
```

```

    split.celltypes = FALSE,
    ...
)

parse.immap.json(url)

get.immap.tracks(
  input,
  keep.id = TRUE,
  scale.t = NULL,
  scale.pos = NULL,
  warn.scaling = TRUE,
  simplify.2D = TRUE
)

```

### Arguments

<code>url</code>	of the json file to download from immunemap; this should be the url to the video metadata without the "/tracks" suffix. With this method, the metadata will be used to automatically scale time to seconds and coordinates to microns if <code>scale.auto=TRUE</code> .
<code>tracks.url</code>	optional: alternatively, provide directly the url of the tracks (ending with "/tracks"), or an url of a local json file with tracks. With this method, scales must be set manually. If not specified, it is assumed that adding the suffix "/tracks" to the supplied <code>url</code> will provide the track data.
<code>keep.id</code>	logical: keep track ids from immunemap? If false, new unique ids are generated. Defaults to TRUE. If there are no ids in the input json, a warning will be returned; this can be suppressed by setting <code>keep.id = FALSE</code> .
<code>scale.auto</code>	logical: if TRUE (the default), scales will be set automatically using the metadata found in <code>url</code> . This works only if the <code>url</code> is given, not if only <code>tracks.url</code> is supplied.
<code>scale.t</code>	optional: multiply timepoints with constant factor to rescale time. By default, immunemap returns time in # frames.
<code>scale.pos</code>	optional: multiply coordinates with constant factor to rescale lengths. By default, immunemap measures coordinates in pixels.
<code>warn.scaling</code>	logical: if <code>scale.t</code> and <code>scale.pos</code> are not set, warn the user that units are pixels and #frames instead of microns and min/sec. Defaults to TRUE.
<code>simplify.2D</code>	logical: if TRUE (default), automatically project to 2D when the z-coordinate has only one value.
<code>warn.celltypes</code>	logical: if TRUE (default), warn when the user is either trying to return a single tracks object while the metadata indicates there are multiple celltypes in the data, or when the user is trying to set <code>split.celltypes = TRUE</code> when there is only one celltype present.
<code>split.celltypes</code>	logical: if TRUE (default = FALSE), return not one tracks object but a list of tracks objects for each celltype in the data (as determined from the metadata in the immunemap json).

... additional parameters to be passed to [get.immap.metadata](#).  
input the output of `parse.immap.json` serves as input for `get.immap.tracks`

### Details

`read.immap.json` internally uses `parse.immap.json` to parse the json file, `get.immap.tracks` to extract the tracks, and [get.immap.metadata](#) to read the metadata.

### Value

`read.immap.json` returns a list with:

`tracks` either a single tracks object or a named list of tracks objects per cell type (if `split.celltypes = TRUE`)  
`metadata` a dataframe with metadata for all the track.ids; this is read from the immunemap json file.

`parse.immap.json` simply returns the R list generated from the input json file.

`get.immap.tracks` returns a single tracks object.

### Note

This functionality requires the jsonlite package to be installed.

### See Also

[get.immap.metadata](#).

### Examples

```
## Not run:  
## Read tracks from immunemap online, using the video info for automatic scaling  
tr <- read.immap.json( url = "https://api.immunemap.org/video/14" )  
  
## Read tracks and rescale time (.5min/frame) and coordinates (2microns/pixel)  
tracksUrl <- "https://api.immunemap.org/video/14/tracks"  
tr <- read.immap.json( tracks.url = tracksUrl, scale.auto = FALSE, scale.t = .5, scale.pos = 2 )  
  
## End(Not run)  
  
## Read tracks from a file  
# tr <- read.immap.json( tracks.url = "my-file.json", warn.scaling = FALSE )
```

---

 repairGaps

*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.

### 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: <ul style="list-style-type: none"> <li>• "drop": the simplest option – discard all tracks that contain gaps.</li> <li>• "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 corresponding to positions 1 to 3 and another track corresponding to position 3 onwards.</li> <li>• "interpolate": approximate the track positions using linear interpolation (see <a href="#">interpolateTrack</a>). The result is a tracks object with constant step durations.</li> </ul>
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 <a href="#">timeStep</a> ) is 100 seconds and tol is 0.05 (the default), 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.

### Value

A [tracks](#) object with gaps fixed according to the chosen method.

### Examples

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



---

selectSteps	<i>Get Single Steps Starting at a Specific Time from a Subset of Tracks</i>
-------------	---

---

**Description**

Obtain all single steps starting at a given timepoint *t* from a subset of tracks of interest.

**Usage**

```
selectSteps(X, trackids, t)
```

**Arguments**

<i>X</i>	Tracks object to obtain subtracks from
<i>trackids</i>	Character vector with the ids of tracks of interest
<i>t</i>	Timepoint at which the subtracks should start

**Value**

A *tracks* object is returned which contains all the extracted steps.

**See Also**

[subtracks](#) to extract all subtracks of a given length, [prefixes](#) to extract all subtracks of a given length starting from the first coordinate in each track, [subtracksByTime](#) to extract all subtracks of a given length starting at some fixed timepoint, and [timePoints](#) to return all timepoints occurring in the dataset.

**Examples**

```
## Get and plot all steps starting at the third timepoint in tracks 1 and 3 of
## the T cell dataset
subT <- selectSteps( TCells, c("1","5"), timePoints(TCells)[3] )
plot( subT )
```

---

selectTracks	<i>Select Tracks by Measure Values</i>
--------------	--

---

**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 <a href="#">TrackMeasures</a> ).
lower	specifies the lower bound (inclusive) of the allowable measure.
upper	specifies the upper bound (inclusive) of the allowable measure.

**Value**

A [tracks](#) object with the selected subset of tracks.

**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**

```
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**

```
## 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**

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

**Arguments**

x	the <i>tracks</i> 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.

**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.

**Value**

An object of class *tracks* with the resulting splitted tracks.

---

staggered	<i>Staggered Version of a Function</i>
-----------	--

---

**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 <a href="#">TrackMeasures</a> ).
...	further parameters passed on to <a href="#">applyStaggered</a> .

**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**

Zeinab Mokhtari, Franziska Mech, Carolin Zitzmann, Mike Hasenberg, Matthias Gunzer and Marc Thilo Figge (2013), Automated Characterization and Parameter-Free Classification of Cell Tracks Based on Local Migration Behavior. *PLoS ONE* **8**(12), e80808. doi:10.1371/journal.pone.0080808

**Examples**

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

---

stepPairs

*Find Pairs of Steps Occurring at the Same Time*


---

**Description**

Find cell indices and timepoints where these cells both have a step.

**Usage**

```
stepPairs(X, filter.steps = NULL)
```

**Arguments**

`X` a tracks object  
`filter.steps` optional: a function used to filter steps on. See examples.

**Value**

A dataframe with three columns: two for the indices of cellpairs that share a step, and one for the timepoint at which they do so.

**Examples**

```
## Find all pairs of steps in the T cell data that displace at least 2 microns.
pairs <- stepPairs( TCells, filter.steps = function(t) displacement(t) > 2 )
```

---

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.

**Value**

A [tracks](#) object with the new, more coarse-grained tracks.

**See Also**

[interpolateTrack](#), which can be used for more flexible track coarse-graining.

**Examples**

```
## 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.

**See Also**

[prefixes](#) to extract all subtracks of a given length starting from the first coordinate in each track, [subtracksByTime](#) to extract all subtracks of a given length starting at some fixed timepoint, and [selectSteps](#) to extract single steps starting at a fixed timepoint from a subset of trackids.

---

subtracksByTime      *Extract Subtracks Starting at a Specific Time*

---

### Description

Obtain all subtracks of  $i$  steps ( $i+1$  positions) starting at a given timepoint  $t$ .

### Usage

```
subtracksByTime(X, t, i = 1, epsilon = 1e-04, tlo = t, thi = t)
```

### Arguments

$X$	Tracks object to obtain subtracks from.
$t$	Timepoint at which the subtracks should start. This value is ignored if $tlo$ and $thi$ are specified, see below.
$i$	Subtrack length (in number of steps). Set this to NULL to obtain subtracks of varying length but within a specified interval [ $tlo$ , $thi$ ] (see below).
$epsilon$	Small error allowed when comparing timepoints because of numerical inaccuracies, see details. Timepoints in tracks are returned if they are within [ $tlo-epsilon$ , $thi+epsilon$ ].
$tlo$ , $thi$	Interval specifying the timepoints to be returned. By default, these are not used and tracks starting at timepoint $t$ with exactly $i$ steps are returned; see details.

### Details

If  $i$  is specified, the given  $t$  is retrieved for all tracks in  $X$  that contain that timepoint, and any subtracks starting from that time that have exactly  $i$  steps are returned. For numerical reasons, timepoints in the data are allowed to deviate a small amount  $epsilon$  from  $t$  (because otherwise, equal timepoints can seem unequal because of very small deviations).

If  $i$  is set to NULL, subtracks are returned with all timepoints lying in the interval [ $tlo - epsilon$ ,  $thi + epsilon$ ]. These subtracks do NOT have to be of equal length.

### 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 start at the given timepoint  $t$ , OR a *tracks* object with all the timepoints of any track in the input *tracks* object that are between  $tlo$  and  $thi$ .

### See Also

[subtracks](#) to extract all subtracks of a given length, [prefixes](#) to extract all subtracks of a given length starting from the first coordinate in each track, [selectSteps](#) to extract single steps starting at a fixed timepoint from a subset of trackids, and [timePoints](#) to return all timepoints occurring in the dataset.

**Examples**

```
## Get all the single steps (i=1) starting at the third timepoint in the T cell tracks.
subT <- subtracksByTime( TCells, timePoints(TCells)[3], 1 )

## These all have the same number of steps:
sapply( subT, nrow )

## Or set i to NULL and return all subtracks within the five first timepoints:
subT2 <- subtracksByTime( TCells, NULL, i = NULL,
  tlo = timePoints( TCells )[1], thi = timePoints( TCells )[5] )

## These are not all the same length:
sapply( subT2, nrow )
```

---

TCells

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


---

**Description**

RFP-labelled T cells were injected retro-orbitally in healthy CD11c-YFP mice, and intravitally imaged (using two-photon microscopy) inside a cervical lymph node. These data illustrate the characteristic "random-walk-like" motion pattern of T cells in lymph nodes. For full method details, see references below.

**Usage**

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

**Format**

```
## 'TCells' An S3 object of class "tracks"; a list with 199 elements. Each element name identifies a cell track. Each element is a matrix containing the following three columns.
```

```
t the time (in seconds)
x The X coordinate (in micrometers)
y The Y coordinate (in micrometers)
```

**Source**

Data were generated in 2021 in the Mark J. Miller Lab, Department of Medicine, Washington University in St Louis, USA.

**References**

Miller MJ and Wei SH and Parker I and Cahalan MD (2002), Two-photon imaging of lymphocyte motility and antigen response in intact lymph node. *Science*, **296**(5574):1869–1873. doi:10.1126/science.1070051

Wortel IMN and Liu AY and Dannenberg K and Berry JC and Miller MJ and Textor J (2021), CelltrackR: an R package for fast and flexible analysis of immune cell migration data. *ImmunoInformatics*, **1-2**:100003. doi:10.1016/j.immuno.2021.100003



**Examples**

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

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

---

**timePoints***Find All Unique Time Points in a Track Dataset*

---

**Description**

Return a vector of all the timepoints *t* found in any of the matrices in the tracks object.

**Usage**

```
timePoints(X)
```

**Arguments**

*X* a tracks object.

**Value**

A numeric vector of unique timepoints.

**Examples**

```
## Get all timepoints in the T cell dataset
tp <- timePoints( 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**

```
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

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

---

trackFeatureMap

*Dimensionality Reduction on Track Features*

---

### Description

Perform a quick dimensionality reduction visualization of a set of tracks according to a given vector of track measures.

### Usage

```
trackFeatureMap(
  tracks,
  measures,
  scale = TRUE,
  labels = NULL,
  method = "PCA",
  return.mapping = FALSE,
  ...
)
```

**Arguments**

tracks	the tracks that are to be clustered.
measures	a function, or a vector of functions (see <a href="#">TrackMeasures</a> ). 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 <a href="#">scale</a> before the mapping is performed.
labels	optional: a vector of labels of the same length as the track object. These are used to color points in the visualization.
method	"PCA" for a scatterplot along principal components, "MDS" for multidimensional scaling, "UMAP" for a UMAP. Note that for "UMAP", the uwot package must be installed.
return.mapping	logical: return the mapping object instead of only the plot? (defaults to FALSE).
...	additional parameters to be passed to the corresponding function: <a href="#">prcomp</a> (for method="PCA"), <a href="#">cmdscale</a> (for method="MDS"), or <a href="#">umap</a> (for method="UMAP").

**Details**

The measures are applied to each of the tracks in the given *tracks* object. According to the resulting values, the tracks are mapped to fewer dimensions using the chosen method. If `scale` is TRUE, the measure values are scaled to mean value 0 and standard deviation 1 (per measure) before the mapping.

The dimensionality reduction methods PCA, MDS, and UMAP each produce a scatterplot of all tracks as points, plotted along the principal component axes generated by the corresponding method.

**Value**

By default, only returns a plot. If `return.clust=TRUE`, also returns a clustering object as returned by [hclust](#), [kmeans](#), [prcomp](#) (returns `$x`), [cmdscale](#), or [umap](#) (returns `$layout`). See the documentation of those functions for details on the output object.

**See Also**

[getFeatureMatrix](#) to obtain a feature matrix that can be used for manual clustering and plotting, and [clusterTracks](#) to perform hierarchical or k-means clustering on a tracks dataset.

**Examples**

```
## Map tracks according to speed, mean turning angle, straightness, and asphericity
## using multidimensional scaling, and store output.

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))
map <- trackFeatureMap( cells, c(speed,meanTurningAngle,straightness, asphericity),
  method = "MDS", return.mapping = TRUE )
```

TrackMeasures

*Track Measures*

---

**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**`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), degrees = FALSE)``meanTurningAngle(x, degrees = FALSE)``overallDot(x, from = 1, to = nrow(x), xdiff = diff(x))``overallNormDot(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.

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.
degrees	logical; should angles be returned in degrees rather than radians?

## Details

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

## Value

`trackLength` sums up the distances between subsequent positions; 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 [interpolateTrack](#). The function returns a single, non-negative number.

`duration` returns the time elapsed between `x`'s first and last positions (a single, non-negative number).

`speed` simply divides [trackLength](#) by [duration](#)

`displacement` returns the Euclidean distance between the track endpoints and `squareDisplacement` returns the squared Euclidean distance.

`displacementVector` returns the vector between the track endpoints. This vector has an element (can be negative) for each (x,y,z) dimension of the coordinates in the track.

`maxDisplacement` computes the maximal Euclidean distance of any position on the track from the first position.

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

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

`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 [straightness](#), however, `asphericity` ignores back-and-forth motion of the object, so something that bounces between two positions will have low `straightness` but high `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, NA is returned.

`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 [aggregate.tracks](#)). Angles can also be returned in degrees, in that case: set `degrees = TRUE`.

`meanTurningAngle` averages the `overallAngle` over all adjacent segments of a given track; a low `meanTurningAngle` indicates high persistence of orientation, whereas for an uncorrelated random walk we expect 90 degrees. Note that angle measurements will yield NA values for tracks in which two subsequent positions are identical. By default returns angles in radians; use `degrees = TRUE` to return angles in degrees instead.

`overallDot` 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 [aggregate.tracks](#)).

`overallNormDot` computes the dot product between the unit vectors along the first and the last segment of the given track. This function is useful to generate autocorrelation plots (together with [aggregate.tracks](#)).

`hurstExponent` computes the corrected empirical Hurst exponent of the track. This uses the function `hurstexp` from the ‘`pracma`’ package. If the track has less than two positions, NA is returned. `fractalDimension` estimates the fractal dimension of a track using the function `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

Zeinab Mokhtari, Franziska Mech, Carolin Zitzmann, Mike Hasenberg, Matthias Gunzer and Marc Thilo Figge (2013), Automated Characterization and Parameter-Free Classification of Cell Tracks Based on Local Migration Behavior. *PLoS ONE* **8**(12), e80808. doi:10.1371/journal.pone.0080808

Tillmann Gneiting and Martin Schlather (2004), Stochastic Models That Separate Fractal Dimension and the Hurst Effect. *SIAM Review* **46**(2), 269–282. doi:10.1137/S0036144501394387

## See Also

[AngleAnalysis](#) for methods to compute angles and distances between pairs of tracks, or of tracks to a reference point, direction, or plane.

## Examples

```
## show a turning angle plot with error bars for the T cell data.
with( (aggregate(BCells,overallDot,FUN="mean.se",na.rm=TRUE)),{
  plot( mean ~ i, xlab="time step",
        ylab="turning angle (rad)", type="l" )
  segments( i, lower, y1=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**

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

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

is.tracks(x)

## S3 method for class 'tracks'
c(...)

tracks(...)
```

**Arguments**

<code>x</code>	an object to be coerced or tested.
<code>...</code>	for <code>tracks</code> , 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 <code>c</code> , tracks objects to be combined. For <code>as.tracks</code> , 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'`, ..., `'xk'` if there are  $k \geq 4$  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).

**Value**

A tracks object.

**Examples**

```
## 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(0,5,0), c(1,5,3), 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) ) )
```

vecAngle

*Angle Between Two Vectors***Description**

Compute the angle between two vectors a and b, which can be numeric vectors or matrices in which each row represents a numeric vector. In the last case, one angle is returned for each row. By default, angles are returned in degrees – set degrees = TRUE to return radians.

**Usage**

```
vecAngle(a, b, degrees = TRUE)
```

**Arguments**

a	the first vector or set of vectors. Must be a numeric vector or a matrix where each row represents a numeric vector.
b	the second vector or set of vectors, for which angles with the vector (set) a must be computed. Must have the same dimensions as a.
degrees	logical: if TRUE (default), return angles in degrees instead of radians.

**Value**

A single angle (if a and b are single vectors) or a numeric vector of angles (if a and b are matrices; in that case, the output vector contains one angle for each row in matrices a and b).

**Examples**

```
## The angle between the vectors [0,1] and [1,0] is 90 degrees:
vecAngle( c(0,1), c(1,0) )
## The same holds for 3D angles:
vecAngle( c(0,1,0), c(1,0,0) )
```



---

`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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