# <span id="page-0-0"></span>Package: celltrackR (via r-universe)

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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).

**Depends**  $R (= 3.5.0)$ 

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LazyData true

# URL <http://www.motilitylab.net>

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# **Contents**



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<span id="page-2-1"></span>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



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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 ntracks showing the number of subtracks of each length. This is useful to keep track of since the returned value estimates for high i 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 )
```
<span id="page-5-1"></span>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



#### 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](#page-23-1), [angleCells](#page-9-1), and [distanceCells](#page-26-1).

# 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.

# <span id="page-6-0"></span>analyzeStepPairs 7

# 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](#page-6-1) 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 )
```
<span id="page-6-1"></span>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



# 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](#page-52-1), [angleSteps](#page-10-1), and [distanceSteps](#page-27-1).

<span id="page-7-0"></span>A dataframe with five columns: two for the indices of cellpairs that share a step, one for the timepoint 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](#page-5-1) 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 )
```
<span id="page-7-1"></span>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](#page-13-1) and [distanceToPoint](#page-29-1) 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](#page-12-1) and [distanceToPlane](#page-28-1) 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](#page-22-1) to guess where those borders are. Angles are by default returned in degrees, use degrees=FALSE to obtain radians.

[angleToDir](#page-11-1) 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

# <span id="page-8-0"></span>AngleAnalysis 9

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](#page-10-1) and [distanceSteps](#page-27-1) 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](#page-52-1) to extract all pairs of steps that occur at the same timepoint, and use [analyzeStepPairs](#page-6-1) to do this and then also obtain the angles and distances for each of these pairs.

[angleCells](#page-9-1) and [distanceCells](#page-26-1) 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](#page-23-1) to extract all pairs of cells in the data, and use [analyzeCellPairs](#page-5-1) 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](#page-59-1) 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 \leq sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz))
distances \le- 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" )
```
<span id="page-9-1"></span>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](#page-26-1), this angle is computed even when the two tracks do not share any time points.

#### Usage

angleCells(X, cellids, degrees = TRUE)

#### Arguments



# Value

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

# <span id="page-10-0"></span>angleSteps 11

# See Also

[distanceCells](#page-26-1) to compute the minimum distance between the tracks, and [AngleAnalysis](#page-7-1) 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 )
```
<span id="page-10-1"></span>angleSteps *Angle between Two Steps*

# 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**



# 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](#page-27-1) to compute the distance between the step starting points, [timePoints](#page-56-1) to list all timepoints in a dataset, and [AngleAnalysis](#page-7-1) 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 )
```
<span id="page-11-1"></span>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



# 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.

<span id="page-11-0"></span>

# <span id="page-12-0"></span>angleToPlane 13

# 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](#page-7-1) 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) ) )
```
<span id="page-12-1"></span>angleToPlane *Angle with a Reference Plane*

#### 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



#### <span id="page-13-0"></span>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](#page-28-1) to compute the distance to the reference plane, and [AngleAnalysis](#page-7-1) 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 \leq sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz))
distances \leq 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")
```
<span id="page-13-1"></span>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)
```
#### <span id="page-14-0"></span>angleToPoint 15

#### Arguments



#### 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](#page-29-1) to compute the distance to the reference point, and [AngleAnalysis](#page-7-1) for other methods to compute angles and distances.

```
## 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")
```
<span id="page-15-1"></span><span id="page-15-0"></span>

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



#### 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  $j$   $\langle$  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 retruned.

#### 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)

<span id="page-16-0"></span>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



#### 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'.

```
## Display overall average position of the T cell data
colMeans( as.data.frame( TCells )[-c(1,2)] )
```
<span id="page-17-0"></span>

Coerces a tracks object to a list.

#### Usage

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

#### **Arguments**



# 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 by "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,
```
# <span id="page-18-0"></span>BCells 2008 and 2008 and

```
pos.colums = 3:ncol(x),
  scale.t = 1,
  scale.pop = 1,
  ...
)
```
# Arguments



# 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(\emptyset, \emptyset, \emptyset),
  taxis.mode = 1,
```
<span id="page-19-0"></span>

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```
t.free = 2,
v. free = 18.8,
t.pause = 0.5
```
#### Arguments

 $\lambda$ 



#### 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 \leq 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 )
```


#### **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



#### 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](#page-42-1) 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](#page-56-2). 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 )

<span id="page-21-0"></span>

<span id="page-22-1"></span><span id="page-22-0"></span>

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 *Simulate an Uncorrelated Random Walk*

# Description

Generates a random track with nsteps steps in dim dimensions.

#### Usage

```
brownianTrack(nsteps = 100, dim = 3, mean = 0, sd = 1)
```
# <span id="page-23-0"></span>Arguments



# 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(  $100, 1)$ )

<span id="page-23-1"></span>

# 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.

```
## Find all pairs of cells in the T cell data
pairs <- cellPairs( TCells )
```
<span id="page-24-0"></span>

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

<span id="page-24-1"></span>clusterTracks *Cluster Tracks*

# 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,
  ...
\mathcal{L}
```
#### <span id="page-25-0"></span>**Arguments**



# 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](#page-0-0) or [kmeans](#page-0-0). output object.

#### See Also

[getFeatureMatrix](#page-31-1) to obtain a feature matrix that can be used for manual clustering and plotting, and [trackFeatureMap](#page-57-1) to visualize high-dimensional track feature data via dimensionality reduction.

# Examples

## Cluster tracks according to the mean of their Hust 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?

#### <span id="page-26-0"></span>distanceCells 27

```
sum( real.celltype == c("T","N")[cutree(clust,2)])
```
<span id="page-26-1"></span>distanceCells *Minimum Distance between Two Cells*

#### 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



#### 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](#page-9-1) to compute the angle between the track displacement vectors, and [AngleAnalysis](#page-7-1) for other methods to compute angles and distances.

```
## Find the minimum distance between the tracks with ids 1 and 3
distanceCells( TCells, c("1","3") )
```
<span id="page-27-1"></span><span id="page-27-0"></span>

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



#### 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](#page-10-1) to compute the angle between the steps, [timePoints](#page-56-1) to list all timepoints in a dataset, and [AngleAnalysis](#page-7-1) for other methods to compute angles and distances.

```
## 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 )
```
<span id="page-28-1"></span><span id="page-28-0"></span>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



#### Value

A single distance.

#### See Also

[angleToPlane](#page-12-1) to compute the angle to the plane, and [AngleAnalysis](#page-7-1) for other methods to compute angles and distances.

```
## 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 \leq sapply( steps, angleToPlane, p1 = c(0,0,minz), p2 = c(1,0,minz), p3 = c(0,1,minz))
distances \le- 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")
```
<span id="page-29-1"></span><span id="page-29-0"></span>

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



# Value

A single distance.

# See Also

[angleToPoint](#page-13-1) to compute the angle to the reference point, and [AngleAnalysis](#page-7-1) for other methods to compute angles and distances.

```
## 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" )
```
<span id="page-30-0"></span>filterTracks *Filter Tracks*

# Description

Extracts subtracks based on a given function.

# Usage

filterTracks(f, x, ...)

# Arguments



# 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 ) )
```
<span id="page-30-1"></span>get.immap.metadata *Get Track Metadata from ImmuneMap*

# 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")
\mathcal{L}
```
#### <span id="page-31-0"></span>**Arguments**



#### 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)
```
<span id="page-31-1"></span>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



# <span id="page-32-0"></span>hotellingsTest 33

# Value

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

#### See Also

[clusterTracks](#page-24-1) for a quick method to compute the feature matrix and a clustering, and [trackFeatureMap](#page-57-1) 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 *Test Unbiasedness of Motion*

# Description

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

#### Usage

```
hotellingsTest(
  tracks,
  dim = c("x", "y"),
  step.spacing = 0,
  plot = FALSE,
  add = FALSE,ellipse.col = "blue",
  ellipse.border = "black",
  conf. level = 0.95,...
\mathcal{L}
```
# Arguments



<span id="page-33-0"></span>

#### 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

<span id="page-33-1"></span>interpolateTrack *Interpolate Track Positions*

# Description

Approximates the track positions at given time points using linear interpolation (via the [approx](#page-0-0) function).

# <span id="page-34-0"></span>maxTrackLength 35

# Usage

 $interpolateTrack(x, t, how = "linear")$ 

# Arguments



# 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 *Length of Longest Track*

# 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

<span id="page-35-0"></span>

LysM-GFP mice were infected with S. aureus on their ear, and intravitally 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), Noninvasive 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

# <span id="page-36-0"></span>normalizeToDuration 37

# 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\)](#page-59-1).

#### 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)

#### <span id="page-37-0"></span>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 ) )

pairsByTime *Distance between pairs of tracks at every timepoint*

# Description

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

#### Usage

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



#### 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

# <span id="page-38-0"></span>plot.tracks 39

# 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 pallelel to the data's axes.

# Usage

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



# Details

One dimension of the data (by default  $y$ ) is plotted against another (by default  $x$ ). The dimesions 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](#page-39-1)

# <span id="page-39-1"></span>plot3d *Plot Tracks in 3D*

# Description

Takes an input tracks object and plots them in 3D using the [scatterplot3d](#page-0-0) function.

# Usage

 $plot3d(x, ...)$ 

# Arguments



# Value

None.

```
if( require("scatterplot3d",quietly=TRUE) ){
  plot3d( TCells )
}
```
<span id="page-39-0"></span>

<span id="page-40-0"></span>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



# 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).

# <span id="page-41-0"></span>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, J\"urgen 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 )
```
<span id="page-41-1"></span>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



#### Details

This function behaves exactly like [subtracks](#page-53-1) except that only subtracks starting from the first position are considered.

# <span id="page-42-0"></span>projectDimensions 43

# 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](#page-53-1) to extract all subtracks of a given length, [subtracksByTime](#page-54-1) to extract all subtracks of a given length starting at some fixed timepoint, and [selectSteps](#page-48-1) to extract single steps starting at a fixed timepoint from a subset of trackids.

<span id="page-42-1"></span>projectDimensions *Extract Spatial Dimensions*

# Description

Projects tracks onto the given spatial dimensions.

#### Usage

```
projectDimensions(x, dims = c("x", "y"))
```
# Arguments



# Value

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

```
## 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 ) )
```
<span id="page-43-0"></span>

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 by "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.column = c(3, 4, 5),scale.t = 1,scale.pop = 1,
  header = TRUE,
  sep = "",track.sep.blankline = FALSE,
  ...
)
```
# Arguments



<span id="page-44-0"></span>

#### 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 *Read tracks from ImmuneMap*

#### <span id="page-44-1"></span>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,
  ...
\overline{)}parse.immap.json(url)
get.immap.tracks(
  input,
  keep.id = TRUE,scale.t = NULL,
  scale.pos = NULL,
  warn.scaling = TRUE,
  simplify.2D = TRUE
)
```
# Arguments



# <span id="page-46-0"></span>ReadImmuneMap 47



# 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](#page-30-1) to read the metadata.

# Value

read.immap.json returns a list with:



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](#page-30-1).

```
## 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 )
```
<span id="page-47-0"></span>

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



# Value

A [tracks](#page-62-1) object with gaps fixed according to the chosen method.

```
## The Neutrophil data are imaged at rather nonconstant intervals
print( length( Neutrophils ) )
print( length( repairGaps( Neutrophils, tol=0.01 ) ) )
```
<span id="page-48-1"></span><span id="page-48-0"></span>

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

### Usage

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



#### Value

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

# See Also

[subtracks](#page-53-1) to extract all subtracks of a given length, [prefixes](#page-41-1) to extract all subtracks of a given length starting from the first coordinate in each track, [subtracksByTime](#page-54-1) to extract all subtracks of a given length starting at some fixed timepoint, and [timePoints](#page-56-1) 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 *Select Tracks by Measure Values*

# Description

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

# Usage

selectTracks(x, measure, lower, upper)

#### Arguments



# Value

A [tracks](#page-62-1) 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](#page-0-0) but for tracks.

# Usage

simulateTracks(n, expr)

# Arguments



# Value

A tracks object containing n tracks.

```
## Generate 10 tracks, 100 steps each, from a random walk with standard normally
## distributed increments and plot them
plot( simulateTracks( 10, brownianTrack(100,3) ) )
```
<span id="page-49-0"></span>

<span id="page-50-0"></span>

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

# Usage

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



# 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)
```
#### <span id="page-51-0"></span>Arguments



# Value

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

<span id="page-51-1"></span>

staggered *Staggered Version of a Function*

# Description

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

#### Usage

staggered(measure, ...)

# Arguments



# 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

#### <span id="page-52-0"></span>stepPairs 53

# Examples

```
hist( sapply( TCells, staggered( displacement ) ) )
```
<span id="page-52-1"></span>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



# 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



# <span id="page-53-0"></span>Value

A [tracks](#page-62-1) 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 )
```
<span id="page-53-1"></span>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



# 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](#page-51-1) 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](#page-41-1) to extract all subtracks of a given length starting from the first coordinate in each track, [subtracksByTime](#page-54-1) to extract all subtracks of a given length starting at some fixed timepoint, and [selectSteps](#page-48-1) to extract single steps starting at a fixed timepoint from a subset of trackids.

<span id="page-54-1"></span><span id="page-54-0"></span>

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



# 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](#page-53-1) to extract all subtracks of a given length, [prefixes](#page-41-1) to extract all subtracks of a given length starting from the first coordinate in each track, [selectSteps](#page-48-1) to extract single steps starting at a fixed timepoint from a subset of trackids, and [timePoints](#page-56-1) 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

<span id="page-55-0"></span>

#### <span id="page-56-0"></span>timePoints 57

# Examples

```
## load the tracks
data(TCells)
## visualize the tracks (calls function plot.tracks)
plot(TCells)
```
<span id="page-56-1"></span>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 )
```
# <span id="page-56-2"></span>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

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

#### <span id="page-57-0"></span>**Arguments**



# 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](#page-59-2)) 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) )
```
<span id="page-57-1"></span>

#### 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,
  ...
)
```
# <span id="page-58-0"></span>trackFeatureMap 59

#### **Arguments**



#### 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](#page-0-0), [kmeans](#page-0-0), [prcomp](#page-0-0) (returns \$x), [cmdscale](#page-0-0), or [umap](#page-0-0) (returns \$layout). See the documentation of those functions for details on the output object.

# See Also

[getFeatureMatrix](#page-31-1) to obtain a feature matrix that can be used for manual clustering and plotting, and [clusterTracks](#page-24-1) 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)
```
<span id="page-59-1"></span><span id="page-59-0"></span>TrackMeasures *Track Measures*

#### <span id="page-59-2"></span>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.

# <span id="page-60-0"></span>TrackMeasures 61



# **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](#page-2-1); for instance, squareDisplacement combined with [aggregate.tracks](#page-2-1) gives a mean square displacement plot, and overallAngle combined with [aggregate.tracks](#page-2-1) 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](#page-2-1).

# Value

trackLength sums up the distances between subsequent positsion; 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](#page-33-1). 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](#page-59-2) by [duration](#page-59-2)

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 appraoch 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](#page-59-2), 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](#page-2-1)). 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](#page-2-1)).

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](#page-2-1)).

hurstExponent computes the corrected empirical Hurst exponent of the track. This uses the function [hurstexp](#page-0-0) 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](#page-0-0) 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](#page-7-1) for methods to compute angles and distances between pairs of tracks, or of tracks to a reference point, direction, or plane.

```
## 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 )
} )
```
<span id="page-61-0"></span>

<span id="page-62-1"></span><span id="page-62-0"></span>

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, \ldots)## S3 method for class 'list'
as.tracks(x, \ldots)is.tracks(x)
## S3 method for class 'tracks'
c(\ldots)tracks(...)
```
#### Arguments



#### 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 \le tracks( matrix(c(0, 8, 1)10, 9,
20, 7,
30, 7,
40, 6,
50, 5), ncol=2, byrow=TRUE ) )
## Three 3D tracks
x2 <- tracks( rbind(
c(\emptyset,5,\emptyset), 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



# 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).

```
## 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) )
```
<span id="page-63-0"></span>

<span id="page-64-1"></span><span id="page-64-0"></span>

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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