Statistical Methods for Quantitative MS-based Proteomics: Peptide-level Models for Summarization and Inference

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This is part of the online course Proteomics Data Analysis 2021 (PDA21)			
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1 Subset of CPTAC study: A vs B comparison in lab 3

1.1 LFQ

Click to see background and code

1. Import data

```
proteinsFile <- "https://raw.githubusercontent.com/statOmics/PDA21/data/quantification/cptacAvsB_lab3/p
ecols <- grep("LFQ\\.intensity\\.", names(read.delim(proteinsFile)))

peLFQ <- readQFeatures(
   table = proteinsFile, fnames = 1, ecol = ecols,
   name = "proteinRaw", sep = "\t"
)

cond <- which(
   strsplit(colnames(peLFQ)[[1]][1], split = "")[[1]] == "A") # find where condition is stored

colData(peLFQ)$condition <- substr(colnames(peLFQ), cond, cond) %>%
   unlist %>%
   as.factor
```

2. Preprocessing

3. Modeling and Inference

```
peLFQ <- msqrob(object = peLFQ, i = "protein", formula = ~condition)

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## converge in 1 steps
L <- makeContrast("conditionB=0", parameterNames = c("conditionB"))
peLFQ <- hypothesisTest(object = peLFQ, i = "protein", contrast = L)</pre>
```

1.2 Median & robust summarization

Click to see background and code

1. Import Data

```
peptidesFile <- "https://raw.githubusercontent.com/stat0mics/SGA2020/data/quantification/cptacAvsB_lab3

ecols <- grep(
   "Intensity\\.",
   names(read.delim(peptidesFile))
   )

pe <- readQFeatures(
   table = peptidesFile,
   fnames = 1,
   ecol = ecols,
   name = "peptideRaw", sep="\t")

cond <- which(
   strsplit(colnames(pe)[[1]][1], split = "")[[1]] == "A") # find where condition is stored

colData(pe)$condition <- substr(colnames(pe), cond, cond) %>%
   unlist %>%
   as.factor
```

2. Preprocessing

```
rowData(pe[["peptideRaw"]])$nNonZero <- rowSums(assay(pe[["peptideRaw"]]) > 0)

pe <- zeroIsNA(pe, "peptideRaw") # convert 0 to NA

pe <- logTransform(pe, base = 2, i = "peptideRaw", name = "peptideLog")

pe <- filterFeatures(pe, ~ Proteins %in% smallestUniqueGroups(rowData(pe[["peptideLog"]])$Proteins))

pe <- filterFeatures(pe, ~ Reverse != "+")

pe <- filterFeatures(pe, ~ Potential.contaminant != "+")

pe <- filterFeatures(pe, ~ nNonZero >=2)

nrow(pe[["peptideLog"]])
```

[1] 7011

```
pe <- normalize(pe,</pre>
                i = "peptideLog",
                name = "peptideNorm",
                method = "center.median")
pe <- aggregateFeatures(pe,</pre>
 i = "peptideNorm",
 fcol = "Proteins",
 na.rm = TRUE,
 name = "proteinMedian",
fun = matrixStats::colMedians)
## Your quantitative and row data contain missing values. Please read the
## relevant section(s) in the aggregateFeatures manual page regarding the
## effects of missing values on data aggregation.
pe <- aggregateFeatures(pe,</pre>
 i = "peptideNorm",
 fcol = "Proteins",
 na.rm = TRUE,
name = "proteinRobust")
## Your quantitative and row data contain missing values. Please read the
## relevant section(s) in the aggregateFeatures manual page regarding the
## effects of missing values on data aggregation.
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  3. Modeling and inference
pe <- msqrob(object = pe, i = "proteinMedian", formula = ~condition)</pre>
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L <- makeContrast("conditionB=0", parameterNames = c("conditionB"))</pre>
pe <- hypothesisTest(object = pe, i = "proteinMedian", contrast = L)</pre>
pe <- msqrob(object = pe, i = "proteinRobust", formula = ~condition)</pre>
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pe <- hypothesisTest(object = pe, i = "proteinRobust", contrast = L)</pre>
volcanoMedian <- ggplot(rowData(pe[["proteinMedian"]])$conditionB,</pre>
                  aes(x = logFC, y = -log10(pval), color = adjPval < 0.05)) +
  geom_point(cex = 2.5) +
  scale_color_manual(values = alpha(c("black", "red"), 0.5)) +
  theme_minimal() +
  ggtitle(paste0("Median: TP = ",sum(rowData(pe[["proteinMedian"]])$conditionB$adjPval<0.05&grepl(rowna
volcanoRobust<- ggplot(rowData(pe[["proteinRobust"]])$conditionB,</pre>
                  aes(x = logFC, y = -log10(pval), color = adjPval < 0.05)) +
  geom_point(cex = 2.5) +
  scale_color_manual(values = alpha(c("black", "red"), 0.5)) +
```

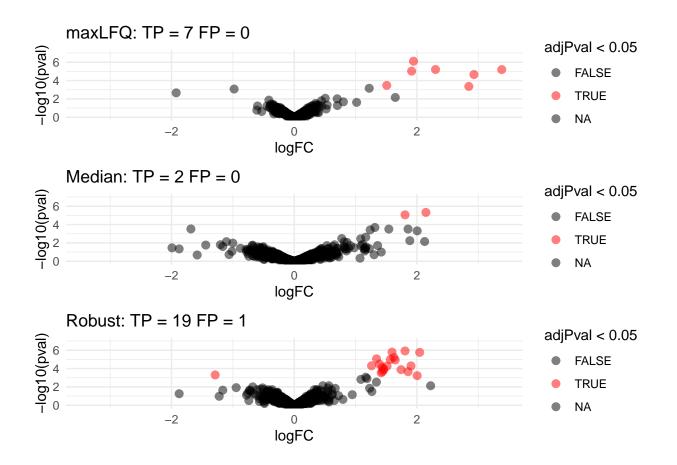
```
ylims \leftarrow c(0,
           ceiling(max(c(-log10(rowData(peLFQ[["protein"]])$conditionB$pval),
               -log10(rowData(pe[["proteinMedian"]])$conditionB$pval),
               -log10(rowData(pe[["proteinRobust"]])$conditionB$pval)),
               na.rm=TRUE))
)
xlims <- max(abs(c(rowData(peLFQ[["protein"]])$conditionB$logFC,</pre>
               rowData(pe[["proteinMedian"]])$conditionB$logFC,
               rowData(pe[["proteinRobust"]])$conditionB$logFC)),
               na.rm=TRUE) * c(-1,1)
compBoxPlot <- rbind(rowData(peLFQ[["protein"]])$conditionB %% mutate(method="maxLFQ") %>% rownames_to
      rowData(pe[["proteinMedian"]])$conditionB %% mutate(method="median")%% rownames_to_column(var="
      rowData(pe[["proteinRobust"]])$conditionB%>% mutate(method="robust")%>% rownames_to_column(var="p
      mutate(ups= grepl(protein,pattern="UPS")) %>%
    ggplot(aes(x = method, y = logFC, fill = ups)) +
    geom boxplot() +
    geom_hline(yintercept = log2(0.74 / .25), color = "#00BFC4") +
```

ggtitle(paste0("Robust: TP = ",sum(rowData(pe[["proteinRobust"]])\$conditionB\$adjPval<0.05&grepl(rowname)</pre>

1.3 Comparison summarization methods

geom_hline(yintercept = 0, color = "#F8766D")

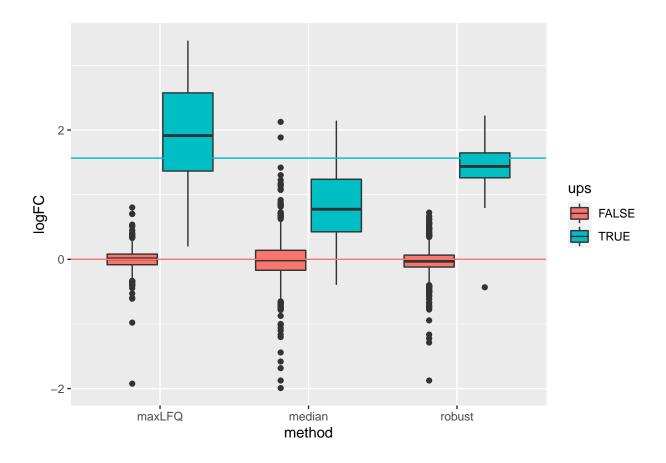
theme_minimal() +



• Robust summarization: highest power and still good FDR control: $FDP = \frac{1}{20} = 0.05$.

compBoxPlot

Warning: Removed 1079 rows containing non-finite values (stat_boxplot).



- Median: biased logFC estimates for spike-in proteins
- maxLFQ: more variable logFC estiamtes for spike-in proteins

2 Full CPTAC study

2.1 Read data

Click to see background and code

1. We use a peptides.txt file from MS-data quantified with maxquant that contains MS1 intensities summarized at the peptide level.

peptidesFile <- "https://raw.githubusercontent.com/statOmics/PDA21/data/quantification/fullCptacDatasSe</pre>

2. Maxquant stores the intensity data for the different samples in columns that start with Intensity. We can retreive the column names with the intensity data with the code below:

```
ecols <- grep("Intensity\\.", names(read.delim(peptidesFile)))</pre>
```

3. Read the data and store it in QFeatures object

```
pe <- readQFeatures(
  table = peptidesFile,
  fnames = 1,
  ecol = ecols,
  name = "peptideRaw", sep="\t")</pre>
```

2.2 Design

Click to see background and code

```
pe %>% colnames

## CharacterList of length 1
## [["peptideRaw"]] Intensity.6A_1 Intensity.6A_2 ... Intensity.6E_9
```

- Note, that the sample names include the spike-in condition.
- They also end on a number.
 - 1-3 is from lab 1,
 4-6 from lab 2 and
 7-9 from lab 3.
- We update the colData with information on the design

• We explore the colData

```
colData(pe)
```

```
## DataFrame with 45 rows and 3 columns
##
                        lab condition spikeConcentration
##
                   <factor> <factor>
                                                <numeric>
                      lab1
                                                     0.25
## Intensity.6A_1
## Intensity.6A_2
                      lab1
                                    Α
                                                     0.25
## Intensity.6A_3
                      lab1
                                    Α
                                                     0.25
## Intensity.6A_4
                      lab2
                                    Α
                                                     0.25
## Intensity.6A_5
                       lab2
                                    Α
                                                     0.25
## ...
                                                       . . .
## Intensity.6E_5
                      lab2
                                    Ε
                                                       20
                                    Ε
                                                       20
## Intensity.6E_6
                      lab2
## Intensity.6E_7
                      lab3
                                    Ε
                                                       20
                                    Ε
                                                       20
## Intensity.6E_8
                      lab3
## Intensity.6E_9
                       lab3
                                    Ε
                                                       20
```

2.3 Preprocessing

2.3.1 Log-transform

Click to see code to log-transfrom the data

• We calculate how many non zero intensities we have for each peptide and this can be useful for filtering.

```
rowData(pe[["peptideRaw"]])$nNonZero <- rowSums(assay(pe[["peptideRaw"]]) > 0)
```

Peptides with zero intensities are missing peptides and should be represent with a NA value rather than
 0.

```
pe <- zeroIsNA(pe, "peptideRaw") # convert 0 to NA
```

• Logtransform data with base 2

```
pe <- logTransform(pe, base = 2, i = "peptideRaw", name = "peptideLog")</pre>
```

2.3.2 Filtering

Click to see code to filter the data

1. Handling overlapping protein groups

In our approach a peptide can map to multiple proteins, as long as there is none of these proteins present in a smaller subgroup.

```
pe <- filterFeatures(pe, ~ Proteins %in% smallestUniqueGroups(rowData(pe[["peptideLog"]])$Proteins))</pre>
```

2. Remove reverse sequences (decoys) and contaminants

We now remove the contaminants, peptides that map to decoy sequences, and proteins which were only identified by peptides with modifications.

```
pe <- filterFeatures(pe,~Reverse != "+")
pe <- filterFeatures(pe,~ Potential.contaminant != "+")</pre>
```

3. Drop peptides that were only identified in one sample

We keep peptides that were observed at last twice.

```
pe <- filterFeatures(pe,~ nNonZero >=2)
nrow(pe[["peptideLog"]])
```

```
## [1] 10478
```

We keep 10478 peptides upon filtering.

2.4 Normalization

Click to see R-code to normalize the data

3 Peptide-level models

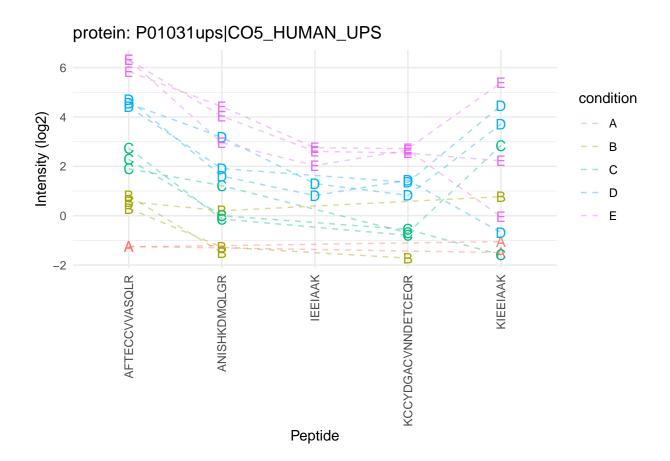
3.1 Summarization

Click to see code to make plot

```
prot <- "P01031ups|C05_HUMAN_UPS"</pre>
data <- pe[["peptideNorm"]][</pre>
 rowData(pe[["peptideNorm"]])$Proteins == prot,
  colData(pe)$lab=="lab3"] %>%
  assay %>%
  as.data.frame %>%
  rownames_to_column(var = "peptide") %>%
  gather(sample, intensity, -peptide) %>%
 mutate(condition = colData(pe)[sample,"condition"]) %>%
 na.exclude
sumPlot <- data %>%
  ggplot(aes(x = peptide, y = intensity, color = condition, group = sample, label = condition), show.le
  geom_text(show.legend = FALSE) +
  theme_minimal() +
 theme(axis.text.x = element_text(angle = 90, vjust = 0.5, hjust = 1)) +
  xlab("Peptide") +
  ylab("Intensity (log2)") +
 ggtitle(paste0("protein: ",prot))
```

Here, we will focus on the summarization of the intensities for protein P01031ups|CO5_HUMAN_UPS.

```
sumPlot +
geom_line(linetype="dashed",alpha=.4)
```



3.1.1 Median summarization

We first evaluate median summarization for protein P01031ups |CO5_HUMAN_UPS. Click to see code to make plot

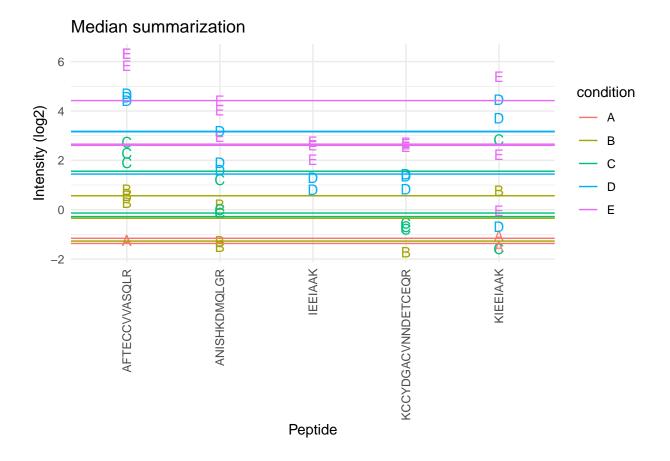
```
dataHlp <- pe[["peptideNorm"]][
    rowData(pe[["peptideNorm"]]) $Proteins == prot,
    colData(pe) $lab=="lab3"] %>% assay

sumMedian <- data.frame(
    intensity= dataHlp
    %>% colMedians(na.rm=TRUE)
,
    condition= colnames(dataHlp) %>% substr(12,12) %>% as.factor )

sumMedianPlot <- sumPlot +
    geom_hline(
    data = sumMedian,
    mapping = aes(yintercept=intensity,color=condition)) +
    ggtitle("Median summarization")</pre>
```

sumMedianPlot

Warning: Removed 1 rows containing missing values (geom_hline).



- The sample medians are not a good estimate for the protein expression value.
- Indeed, they do not account for differences in peptide effects
- Peptides that ionize poorly are also picked up in samples with high spike-in concentration and not in samples with low spike-in concentration
- This introduces a bias.

3.1.2 Mean summarization

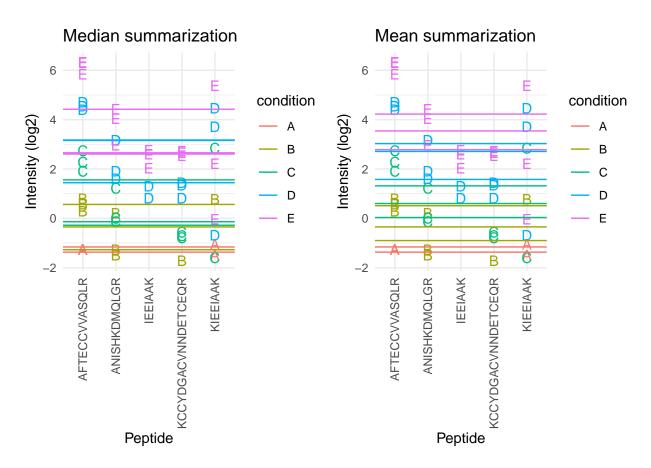
$$y_{ip} = \beta_i^{\text{sample}} + \epsilon_{ip}$$

```
sumMeanMod <- lm(intensity ~ -1 + sample,data)

sumMean <- data.frame(
  intensity=sumMeanMod$coef[grep("sample",names(sumMeanMod$coef))],
  condition= names(sumMeanMod$coef)[grep("sample",names(sumMeanMod$coef))] %>% substr(18,18) %>% as.fac

sumMeanPlot <- sumPlot + geom_hline(
  data = sumMean,
  mapping = aes(yintercept=intensity,color=condition)) +
  ggtitle("Mean summarization")</pre>
```

Warning: Removed 1 rows containing missing values (geom_hline).



3.1.3 Model based summarization

We can use a linear peptide-level model to estimate the protein expression value while correcting for the peptide effect, i.e.

$$y_{ip} = \beta_i^{\text{sample}} + \beta_p^{peptide} + \epsilon_{ip}$$

Click to see code to make plot

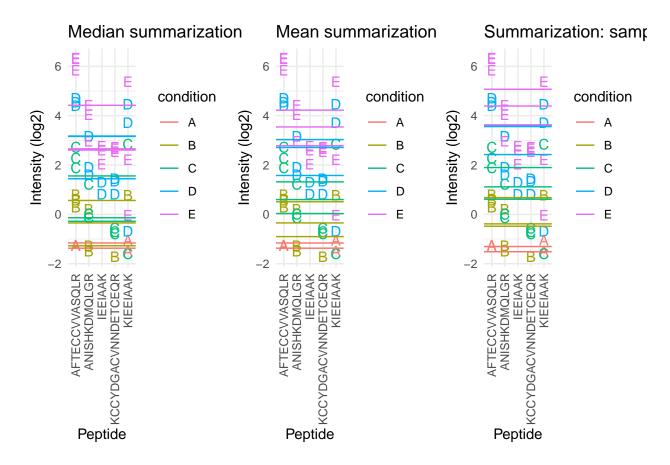
```
sumMeanPepMod <- lm(intensity ~ -1 + sample + peptide,data)
sumMeanPep <- data.frame(
  intensity=sumMeanPepMod$coef[grep("sample",names(sumMeanPepMod$coef))] + mean(data$intensity) - mean(
  condition= names(sumMeanPepMod$coef)[grep("sample",names(sumMeanPepMod$coef))] %>% substr(18,18) %>%
fitLmPlot <- sumPlot + geom_line(
  data = data %>% mutate(fit=sumMeanPepMod$fitted.values),
```

mapping = aes(x=peptide, y=fit,color=condition, group=sample)) +

```
ggtitle("fit: ~ sample + peptide")
sumLmPlot <- sumPlot + geom_hline(
   data = sumMeanPep,
   mapping = aes(yintercept=intensity,color=condition)) +
   ggtitle("Summarization: sample effect")</pre>
```

```
grid.arrange(sumMedianPlot, sumMeanPlot, sumLmPlot, nrow=1)
```

Warning: Removed 1 rows containing missing values (geom_hline).

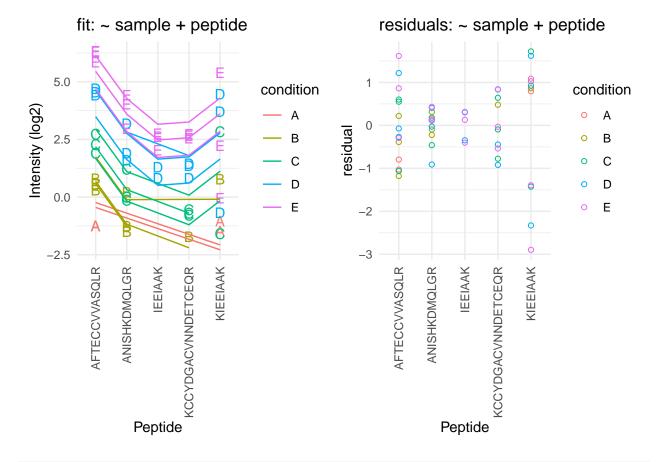


- By correcting for the peptide species the protein expression values are much better separated an better reflect differences in abundance induced by the spike-in condition.
- Indeed, it shows that median and mean summarization that do not account for the peptide effect indeed overestimate the protein expression value in the small spike-in conditions and underestimate that in the large spike-in conditions.
- Still there seem to be some issues with samples that for which the expression values are not well separated according to the spike-in condition.

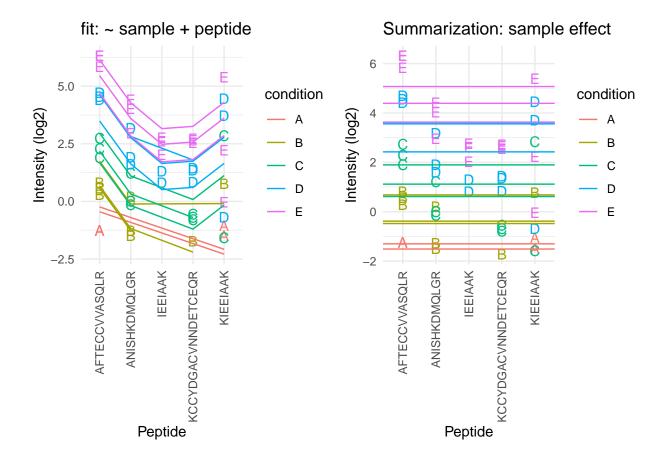
A residual analysis clearly indicates potential issues:

```
resPlot <- data %>%
  mutate(res=sumMeanPepMod$residuals) %>%
  ggplot(aes(x = peptide, y = res, color = condition, label = condition), show.legend = FALSE) +
  geom_point(shape=21) +
  theme_minimal() +
  theme(axis.text.x = element_text(angle = 90, vjust = 0.5, hjust = 1)) +
  xlab("Peptide") +
  ylab("residual") +
  ggtitle("residuals: ~ sample + peptide")
```

grid.arrange(fitLmPlot, resPlot, nrow = 1)



grid.arrange(fitLmPlot, sumLmPlot, nrow = 1)



- The residual plot shows some large outliers for peptide KIEEIAAK.
- Indeed, in the original plot the intensities for this peptide do not seem to line up very well with the concentration.
- This induces a bias in the summarization for some of the samples (e.g. for D and E)

3.1.4 Robust summarization using a peptide-level linear model

$$y_{ip} = \beta_i^{\text{sample}} + \beta_p^{peptide} + \epsilon_{ip}$$

• Ordinary least squares: estimate β that minimizes

$$OLS: \sum_{i,p} \epsilon_{ip}^2 = \sum_{i,p} (y_{ip} - \beta_i^{\text{sample}} - \beta_p^{\text{peptide}})^2$$

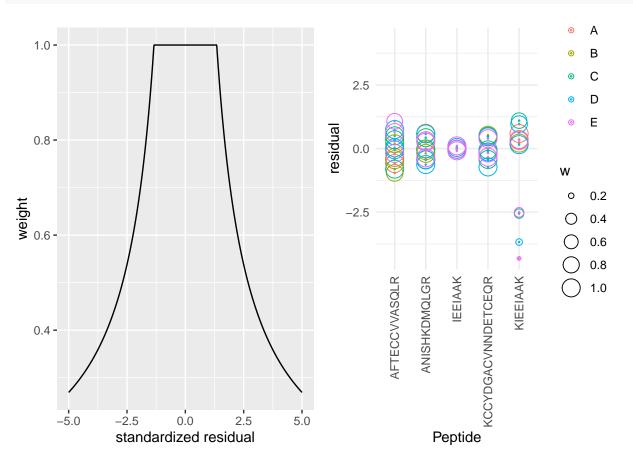
We replace OLS by M-estimation with loss function

$$\sum_{i,p} w_{ip} \epsilon_{ip}^2 = \sum_{i,p} w_{ip} (y_{ip} - \beta_i^{\text{sample}} - \beta_p^{\text{peptide}})^2$$

- Iteratively fit model with observation weights w_{ip} until convergence
- The weights are calculated based on standardized residuals

```
sumMeanPepRobMod <- MASS::rlm(intensity ~ -1 + sample + peptide,data)</pre>
resRobPlot <- data %>%
  mutate(res = sumMeanPepRobMod$residuals,
         w = sumMeanPepRobMod$w) %>%
  ggplot(aes(x = peptide, y = res, color = condition, label = condition, size=w), show.legend = FALSE) +
  geom_point(shape=21,size=.2) +
  geom_point(shape=21) +
  theme minimal() +
  theme(axis.text.x = element_text(angle = 90, vjust = 0.5, hjust = 1)) +
  xlab("Peptide") +
  ylab("residual") +
  ylim(c(-1,1)*max(abs(sumMeanPepRobMod$residuals)))
weightPlot <- aplot(</pre>
  seq(-5,5,.01),
  MASS::psi.huber(seq(-5,5,.01)),
  geom="path") +
  xlab("standardized residual") +
  ylab("weight")
```

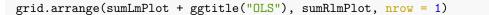
grid.arrange(weightPlot,resRobPlot,nrow=1)

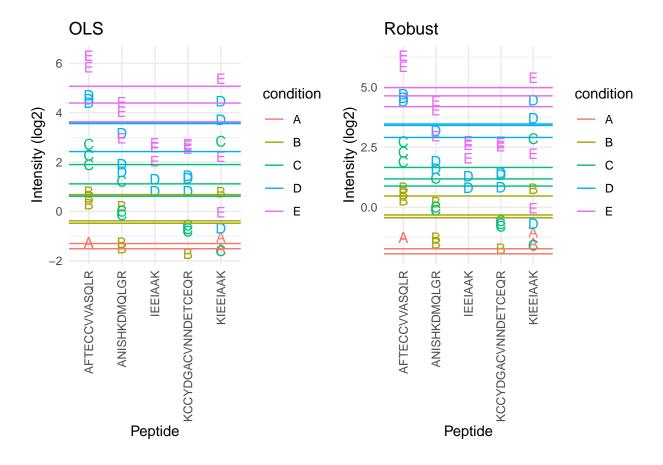


• We clearly see that the weights in the M-estimation procedure will down-weight errors associated with outliers for peptide KIEEIAAK.

```
sumMeanPepRob <- data.frame(
  intensity=sumMeanPepRobMod$coef[grep("sample",names(sumMeanPepRobMod$coef))] + mean(data$intensity) -
  condition= names(sumMeanPepRobMod$coef)[grep("sample",names(sumMeanPepRobMod$coef))] %>% substr(18,18

sumRlmPlot <- sumPlot + geom_hline(
  data=sumMeanPepRob,
  mapping=aes(yintercept=intensity,color=condition)) +
  ggtitle("Robust")</pre>
```





• Robust regresion results in a better separation between the protein expression values for the different samples according to their spike-in concentration.

3.1.5 Comparison summarization methods

• maxLFQ

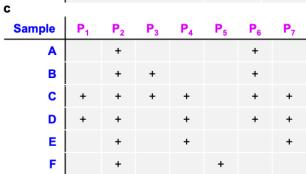
a >P63208

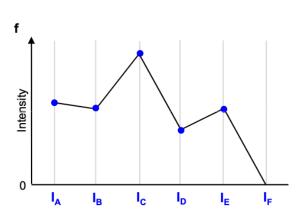
MPSIKLQSSDGEIFEVDVEIAKQSVTIKTMLEDLGMDDEGDD
DPVPLPNVNAAILKKVIQWCTHHKDDPPPPEDDENKEKRTDD
IPVWDQEFLKVDQGTLFELILAANYLDIKGLLDVTCKTVANM
IKGKTPEEIRKTFNIKNDFTEEEEAQVRKENQWCEEK

b **Peptide** Sequence Charge Mod. species 2 LQSSDGEIFEVDVEIAK 3 P_2 LQSSDGEIFEVDVEIAK 2 P_3 RTDDIPVWDQEFLK P_4 TVANMIK 2 2 P_5 TVANMIK Oxid. 3 **TPEEIRK** 2

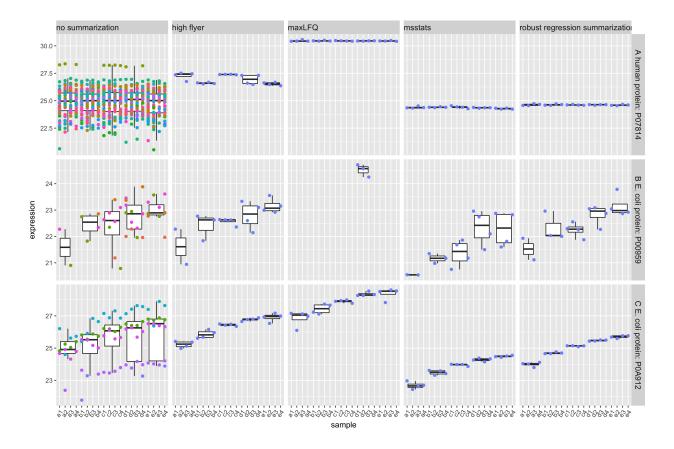
	A	В	C	D	E	F
F	r _{FA}	r _{FB}	r _{FC}	r _{FD}	r _{FE}	
E	r _{EA}	r _{EB}	r _{EC}	r _{ED}		
D	r _{DA}	r _{DB}	r _{DC}			
C	r _{CA}	r _{CB}				
В	r _{BA}					
A						
d						

•		
$r_{BA} = I_B / I_A$	$r_{CA} = I_C / I_A$	$r_{CB} = I_C / I_B$
$r_{DA} = I_D / I_A$	$r_{DB} = I_D / I_B$	$r_{DC} = I_D / I_C$
$r_{EC} = I_E / I_C$	$r_{ED} = I_E / I_D$	<i>I_F</i> = 0
EC - E/C	ED - E / D	1F - 0





- MS-stats also uses a robust peptide level model to perform the summarization, however, they typically first impute missing values
- Proteus high-flyer method: mean of three peptides with highest intensity



- (Sticker et al. 2020)
- doi: https://doi.org/10.1074/mcp.RA119.001624
- pdf

3.2 Estimation of differential abundance using peptide level model

- Instead of summarising the data we can also directly model the data at the peptide-level.
- But, we will have to address the pseudo-replication.

$$y_{iclp} = \beta_0 + \beta_c^{\text{condition}} + \beta_l^{\text{lab}} + \beta_p^{\text{peptide}} + u_s^{\text{sample}} + \epsilon_{iclp}$$

- · protein-level

 - $\begin{array}{l} -\ \beta_c^{\rm condition} \colon {\rm spike\text{-in}}\ {\rm condition}\ c=b,\ldots,e \\ -\ \beta_l^{\rm lab} \colon {\rm lab}\ {\rm effect}\ l=l_2\ldots l_3 \\ -\ u_r^{\rm run} \sim N\left(0,\sigma_{\rm run}^2\right) \rightarrow {\rm random}\ {\rm effect}\ {\rm addresses}\ {\rm pseudo-replication} \end{array}$
- peptide-level
 - $-\beta_p^{\text{peptide}}$: peptide effect
 - $-\epsilon_{rp} \sim N\left(0, \sigma_{\epsilon}^{2}\right)$ within sample (run) error
- DA estimates:

$$\begin{split} \log_2 FC_{B-A} &= \beta_B^{\text{condition}} \\ \log_2 FC_{C-B} &= \beta_C^{\text{condition}} - \beta_B^{\text{condition}} \end{split}$$

- Mixed peptide-level models are implemented in msqrob2
- It has the advantages that
 - 1. it correctly addresses the difference levels of variability in the data
 - 2. it avoids summarization and therefore also accounts for the difference in the number of peptides that are observed in each sample
 - 3. more powerful analysis
- It has the disadvantage that
 - 1. protein summaries are no longer available for plotting
 - 2. it is difficult to correctly specify the degrees of freedom for the test-statistic leading to inference that is too liberal in experiments with small sample size
 - 3. sometimes sample level random effect variance are estimated to be zero, then the pseudo-replication is not addressed leading to inference that is too liberal for these specific proteins
 - 4. they are much more difficult to disseminate to users with limited background in statistics

Hence, for this course we opted to use peptide-level models for summarization, but not for directly inferring on the differential expression at the protein-level.

References

Sticker, A., L. Goeminne, L. Martens, and L. Clement. 2020. "Robust Summarization and Inference in Proteome-wide Label-free Quantification." *Mol Cell Proteomics* 19 (7): 1209–19.