ISCO 2023
March 3, 2023

Long non-coding RNAs in cellular networks and genome regulation

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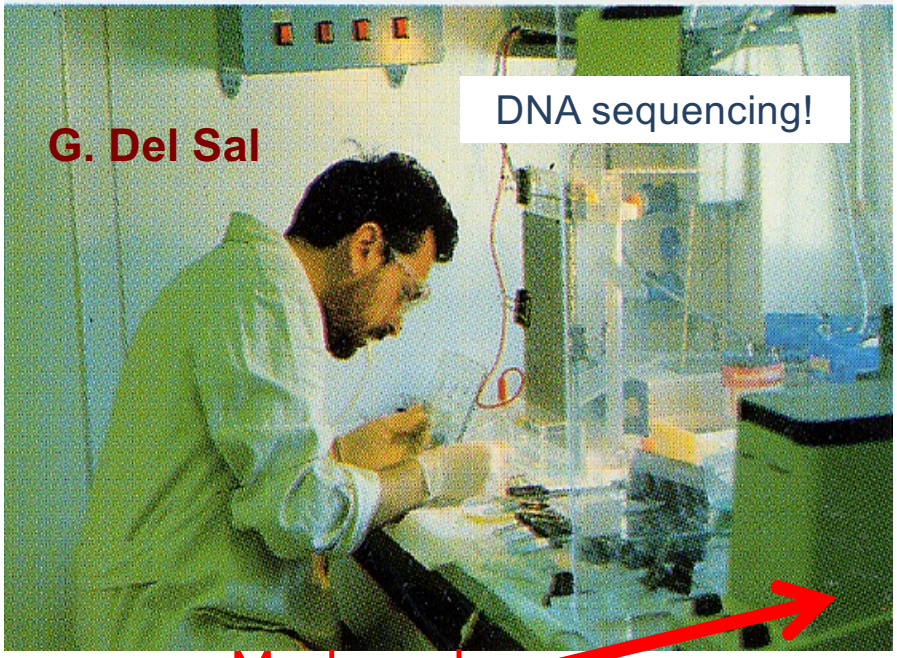
Trieste, Italy
ICGEB (AREA science Park)



Starting with my passion to DNA sequencing in late 80's

Lesson learned:

Technologies make revolutions

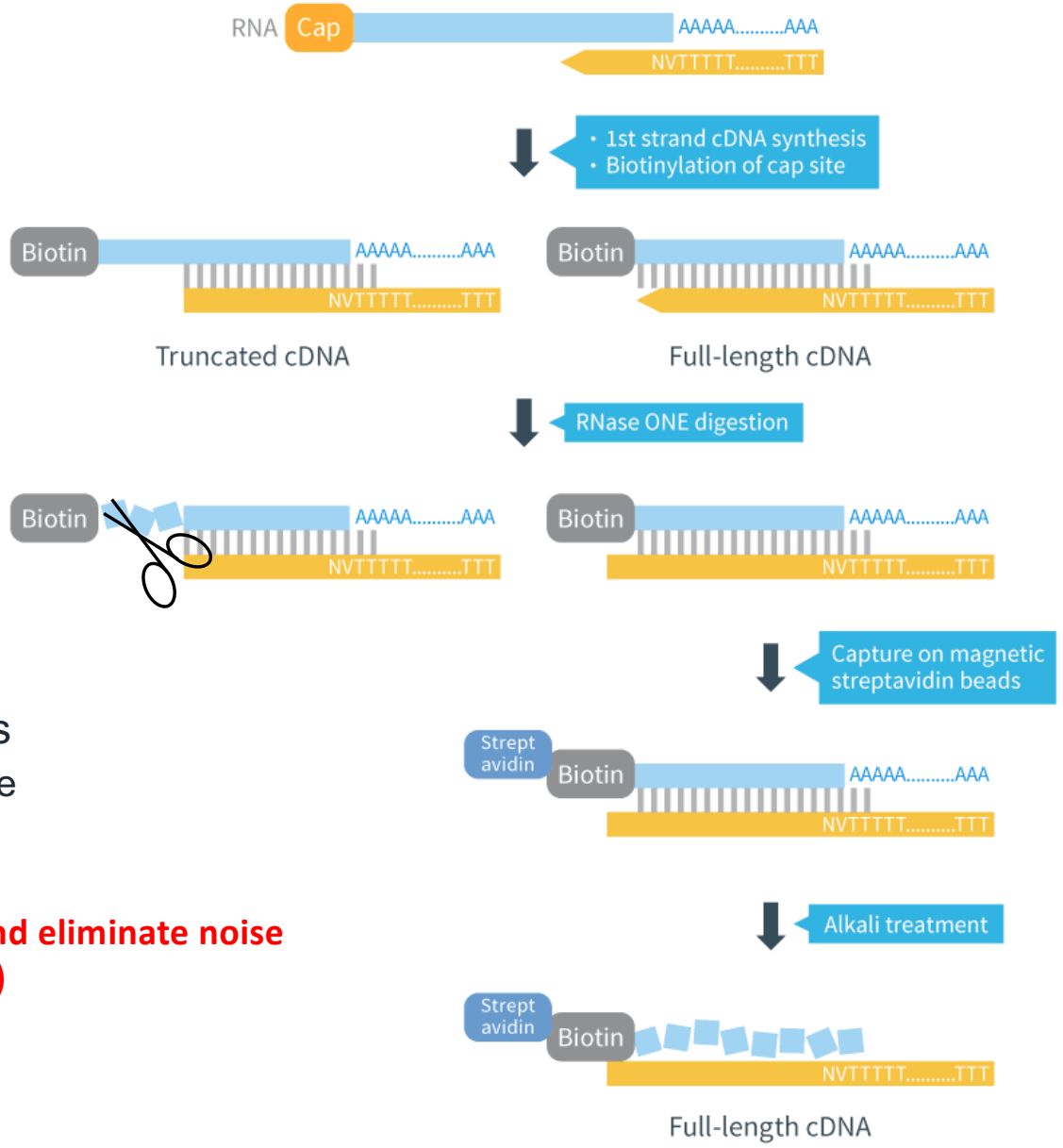
… Often leading far from hypotheses

Technology development - and the establishment of FANTOM

- @ Yoshihide Hayashizaki's lab at RIKEN (1995)
  - RIKEN wanted to develop technology to identify genes in genome-wide scale.
- **How to construct a catalogue of genes;**
  - **How genes are regulated**
    - (1) Full-length cDNA technologies
      - (2) Mapping regulatory elements: Cap Analysis of Gene Expression (CAGE; later in the presentation)

A key technology:
Cap-trapper

1. Cap chemical biotinylation
2. cDNA synthesis
3. Digest incomplete cDNAs
4. Selecting only cDNAs that reach the cap site



KEY: a method to capture complete mRNA molecules and eliminate noise made by fragments of mRNAs (cDNAs)

Where to go, as RIKEN/Japan?

1990-95 **Discussion around the Genome Project**

- All discussions on how to sequence the genome.
- How could possibly RIKEN contribute significantly to a such large project?

1995: started technology development, 1998 started data production for the:

"Mouse genome encyclopedia project"

Development of a series of technologies.

- **Full length cDNA technologies**
- **A large-scale sequencing system**
  384 Capillary sequencer
  40000 clones/ day capacity of plasmid preparator

How to analyze lots of sequences??

- We made the project (the experimental part at least)!
  - Libraries from all mouse tissues/developmental stages,
  - Millions cDNAs *(= expressed genes*) end-sequenced
- >**103,000 cDNAs** fully **sequenced**
- **How to analyze** so much data?
  - Call your friends
    - Make new friends!
  - Bold proposal: invite many new friends to look at the data
- FANTOM Project:
  Functional ANnoTation Of Mammalian Genome


WHAT is FANTOM?
Work hard!
Think hard!
Discuss hard!

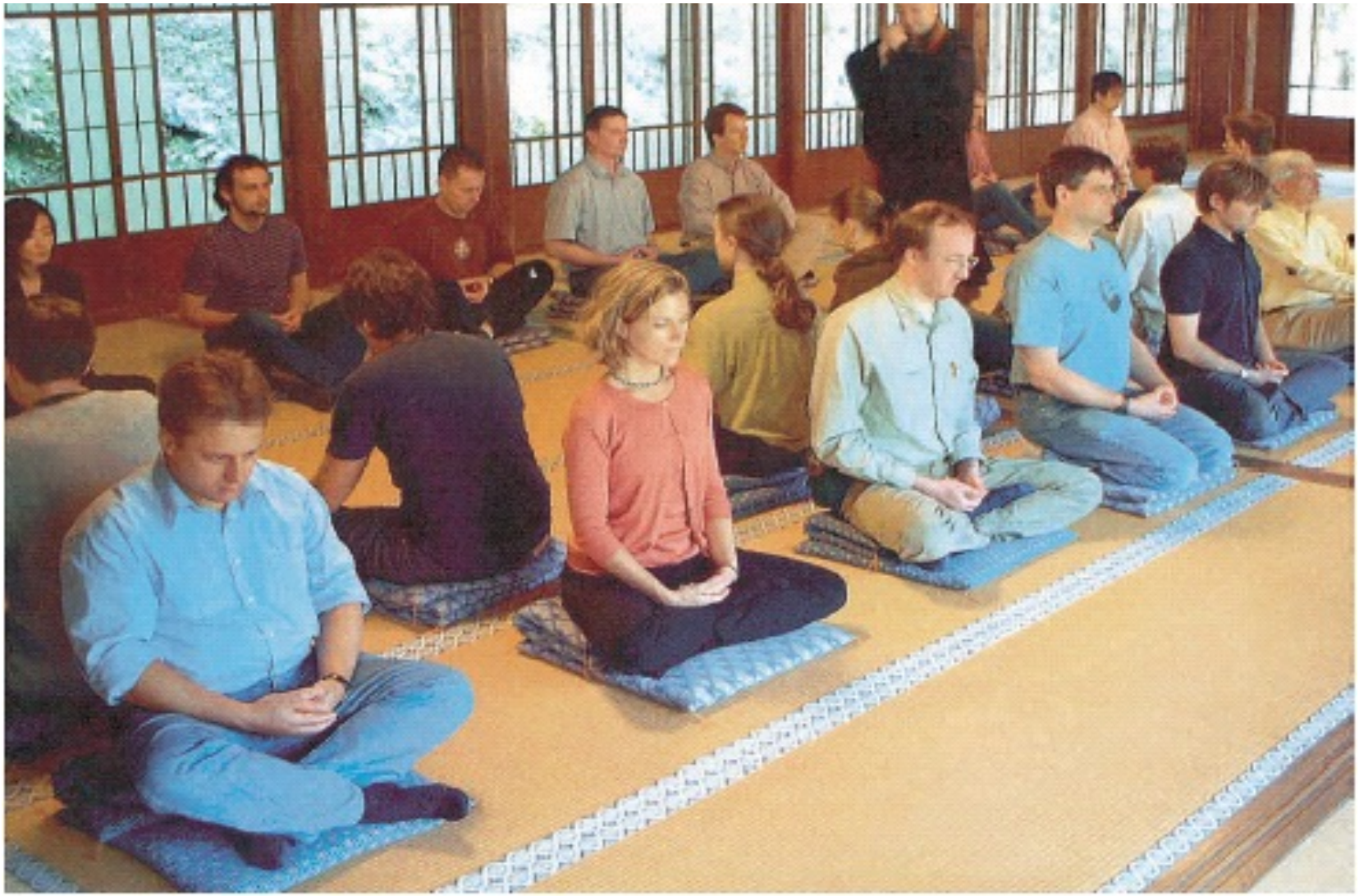


Figure 1 A shot from the Zen meditation ceremony held as an excursion during the FANTOM2 Cherry Blossom Meeting. The Zen meditation was a good break and provided the participants with novel inspiration.

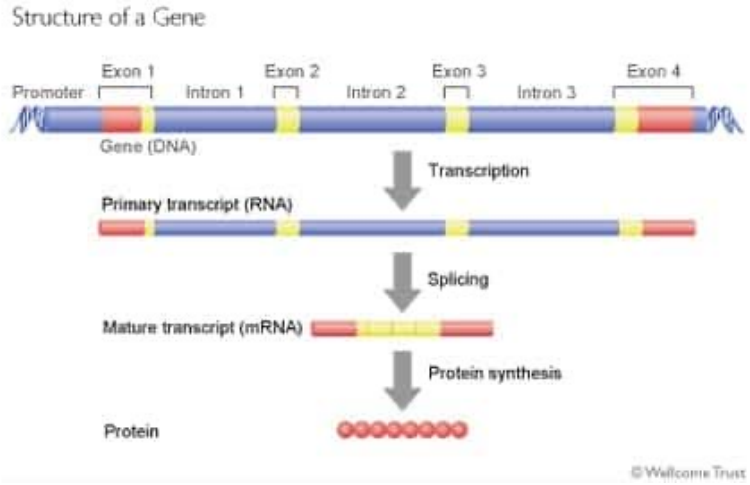
Unexpected discoveries

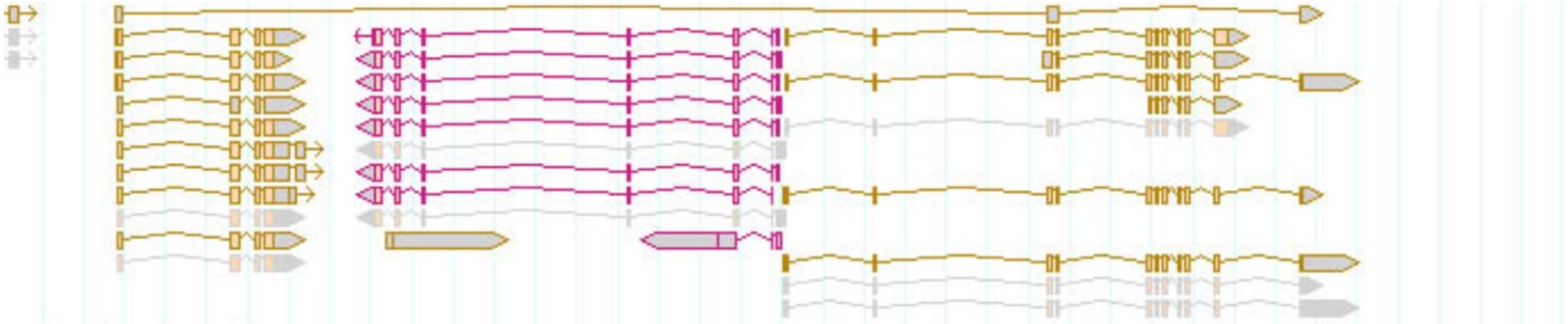
There is much more than what in textbooks

Expectations ←???→ Data

Old Textbook image of a gene

Intended as "**protein coding gene**"

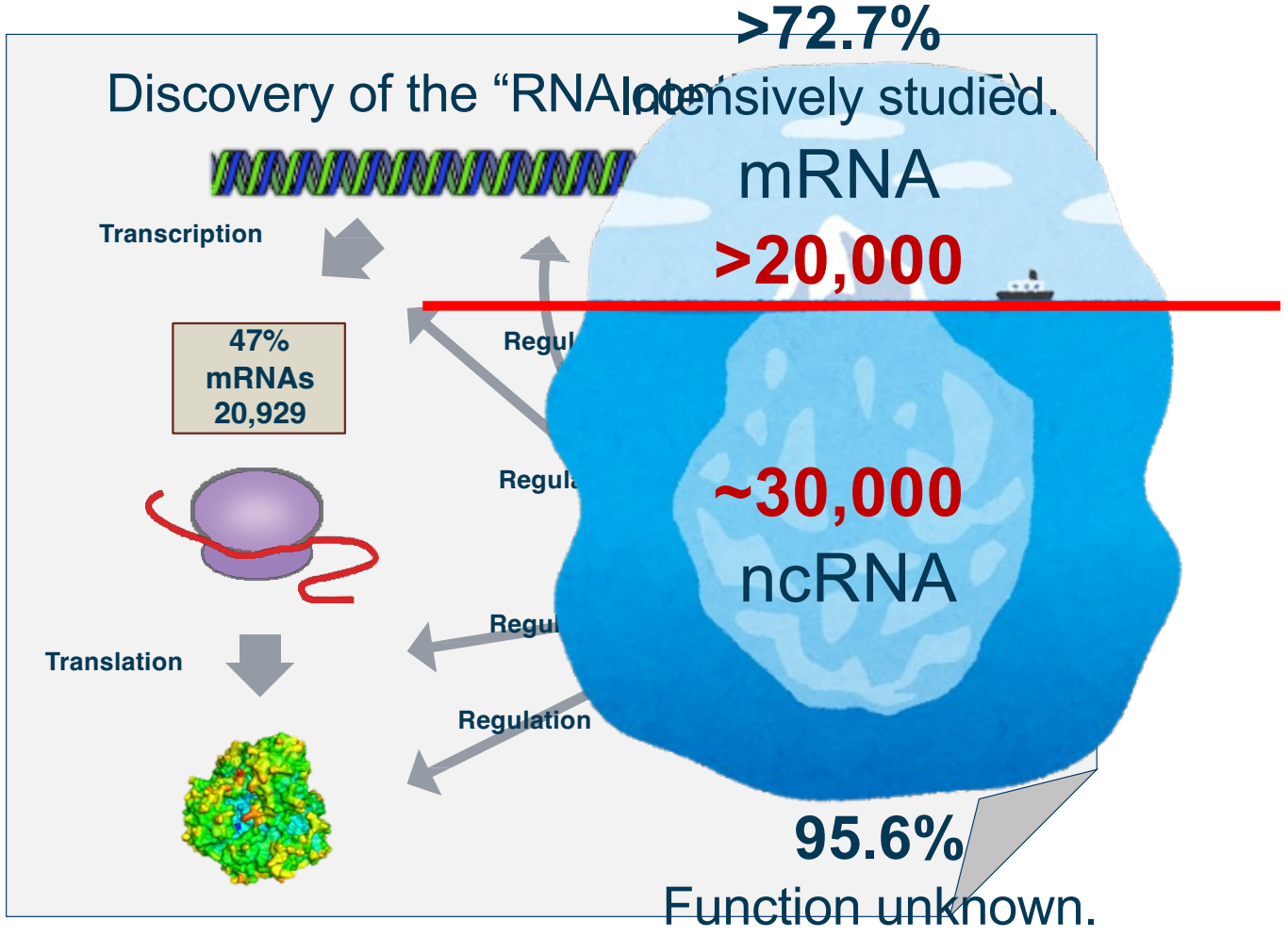




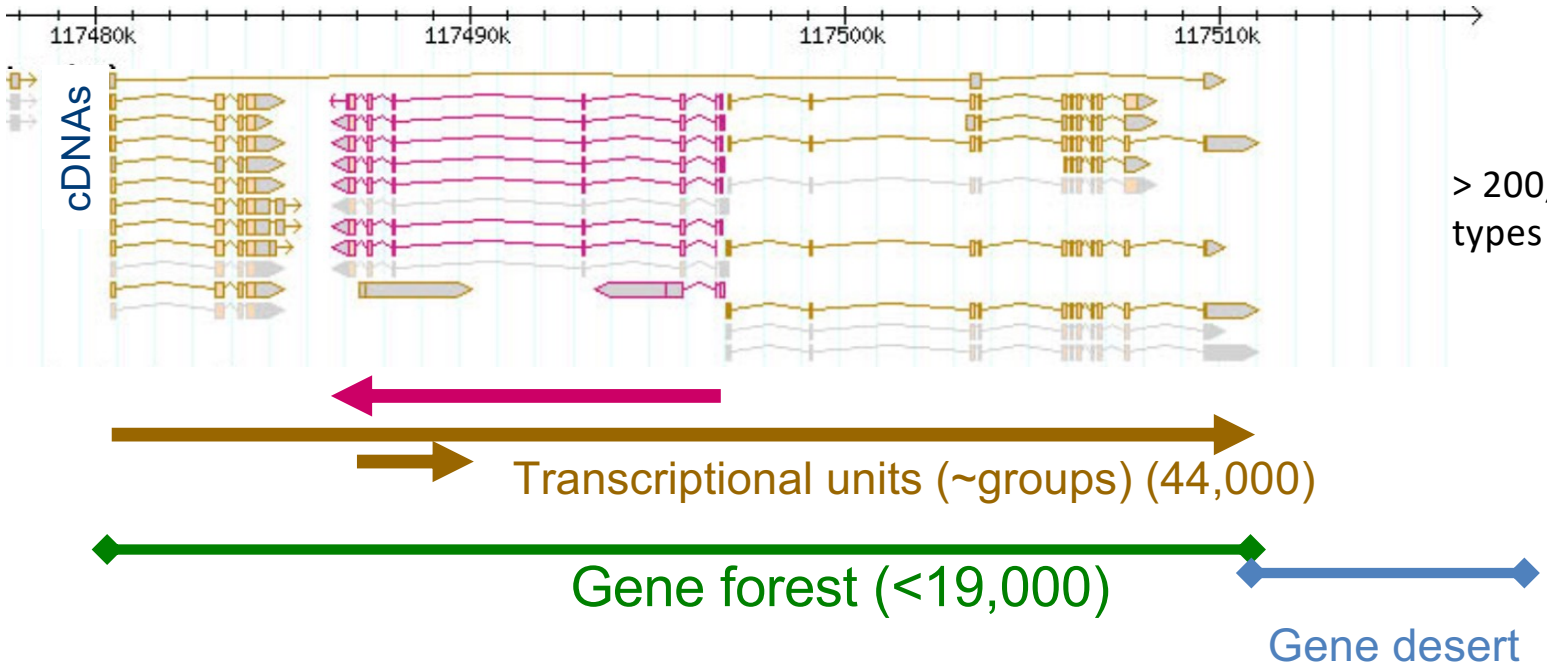
New reality- many more RNAs (mRNA, other "non coding" RNAs)

Discovery of “non-coding” RNA

Still we know very little



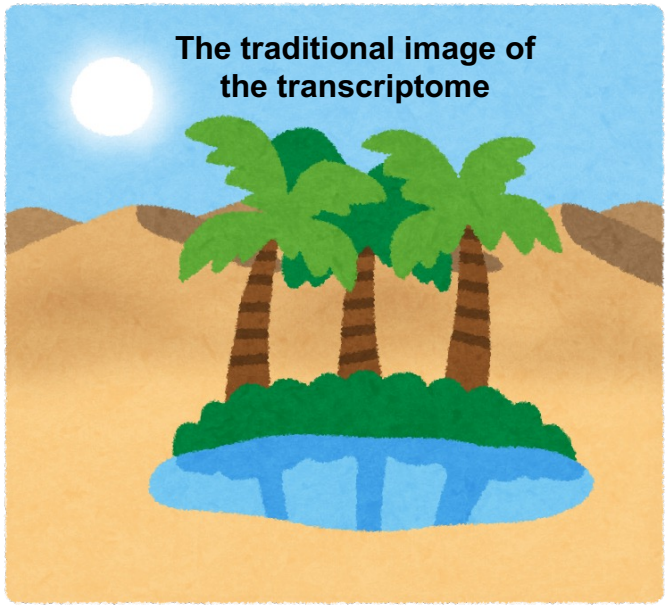
Charting genome output: gene forests, lncRNAs, antisense



> 200,000 different types of transcripts

Regions of the genome are used multiple times, multiple RNAs as output

The new transcriptional landscape



The RNA world is crowdy:
"DARK MATTER"
of the transcriptome?

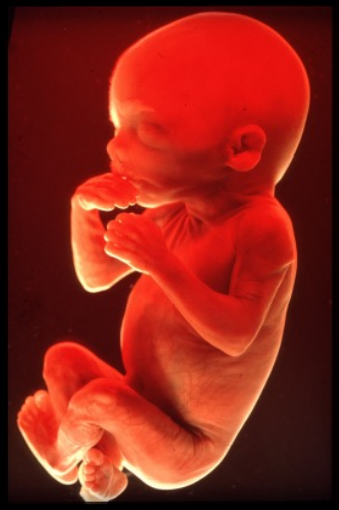
"transcriptome" refers to the collection of all the RNA transcripts

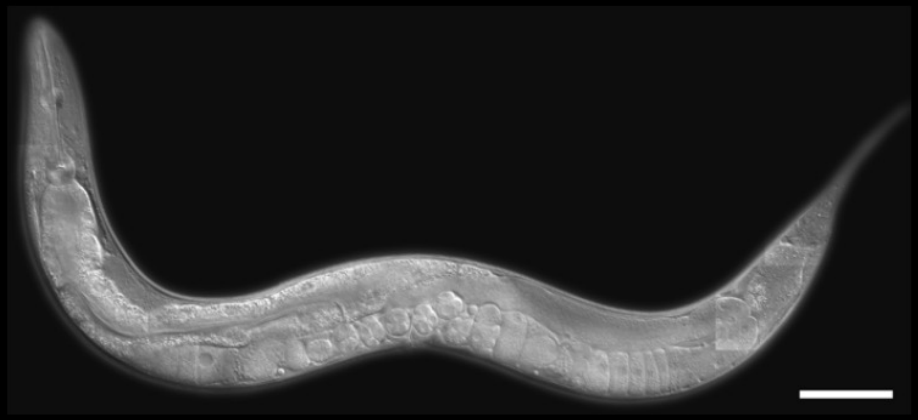
Controversy? from 2002- 2012 and beyond

- ✓ **Some attacks**
  - ✓ The RIKEN cDNA libraries are full of “junk”.
    → Discovery of lncRNAs
  - ✓ The RIKEN library are full of cDNA in the wrong orientation.
    → Discovery of antisense RNAs.
- ✓ **Papers attacking the findings**
- ✓ **Papers supporting the findings**
- ✓ **Subsequent papers confirming the findings**

“Dogma” versus evidence from new data

The genetic basis of developmental complexity





- Humans (and other vertebrates) have approximately the same number of protein-coding genes (~20,000) as *C. elegans*.
- Most of the proteins are orthologous and have similar functions from nematodes to humans, and many are common with yeast.
- Where is the information that programs our complexity?

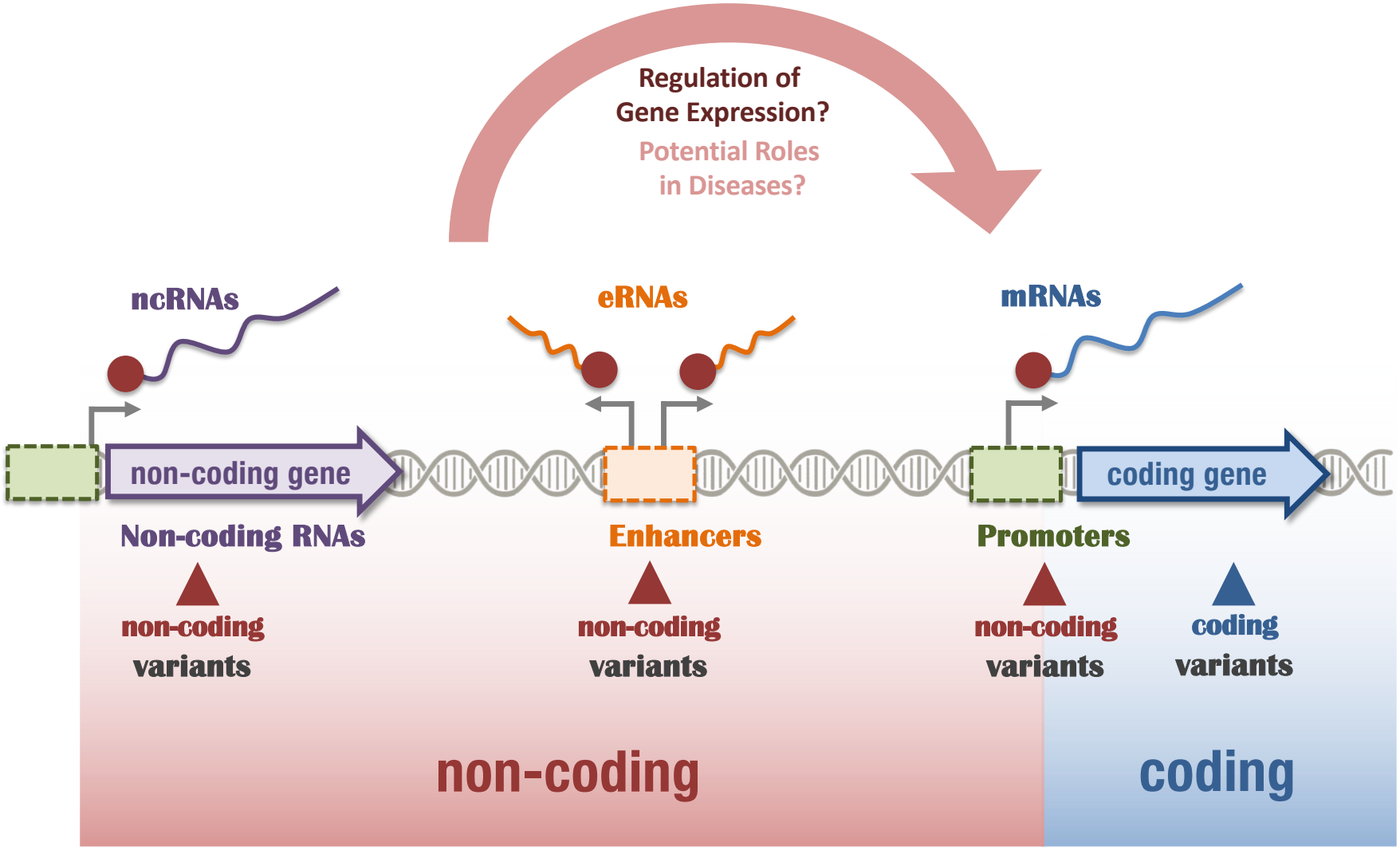
Slide courtesy of John Mattick

Next to the “gene catalogue”: How to broadly study gene regulation?

- Long journey to map regulatory elements and identify, characterize and use novel RNAs

- Technologies ←→ biology and medicine

Understanding regulatory elements in genome

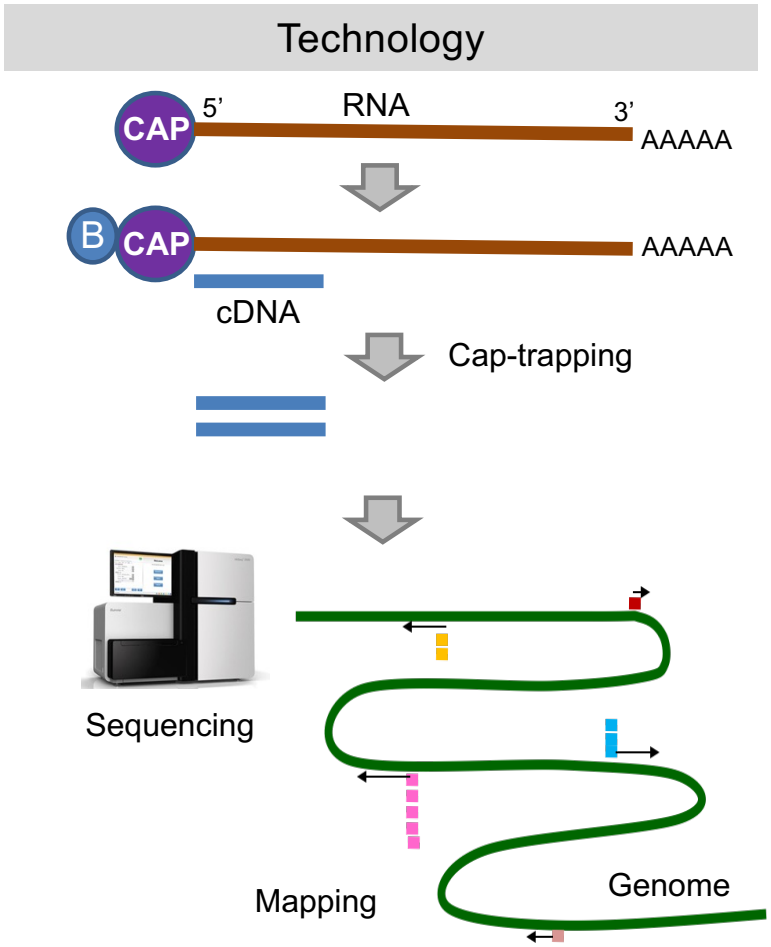


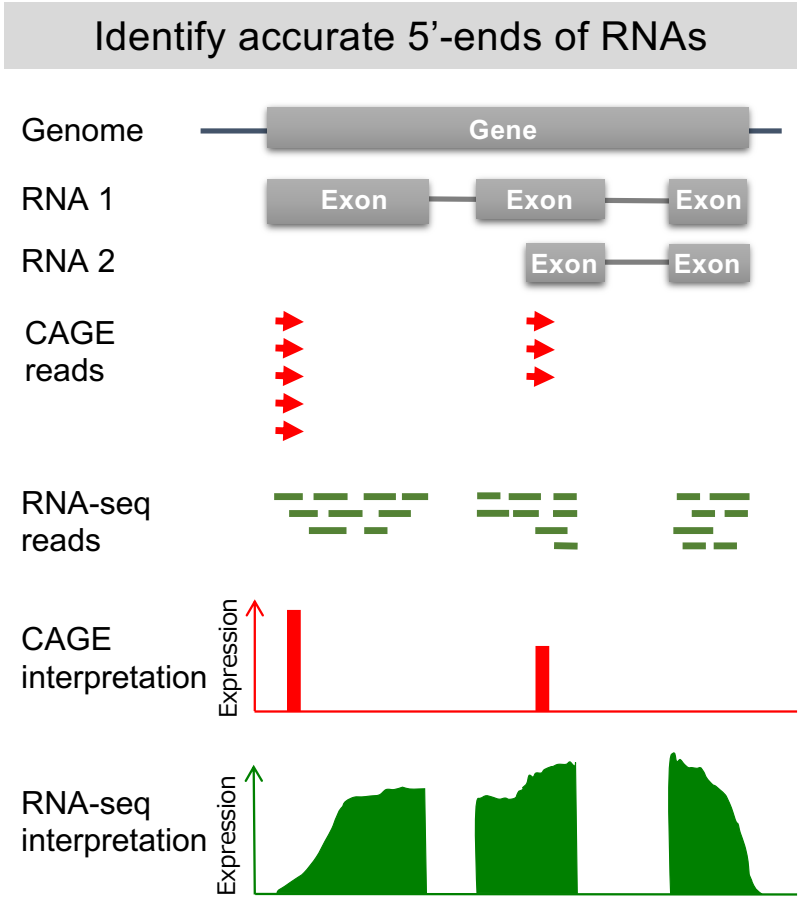
CAGE to broadly map promoters (and enhancers) → 5' UTRs

- Precise identification of TSSs.
- Quantitative analysis of TSS activity and promoter maps
- Genome-wide

CAGE

Cap Analysis of Gene Expression



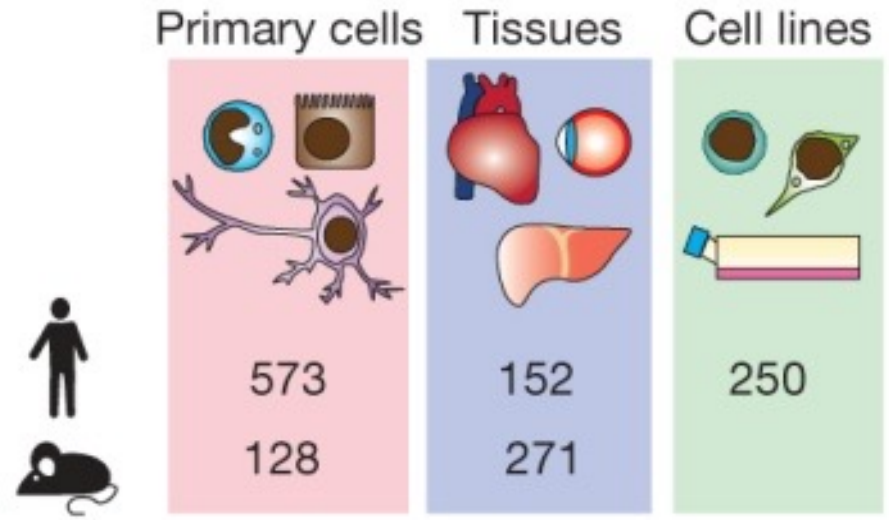


FANTOM5: *Regulatory elements in most primary cell types*

- 261 authors
- 120 international collaborators
- 19 countries

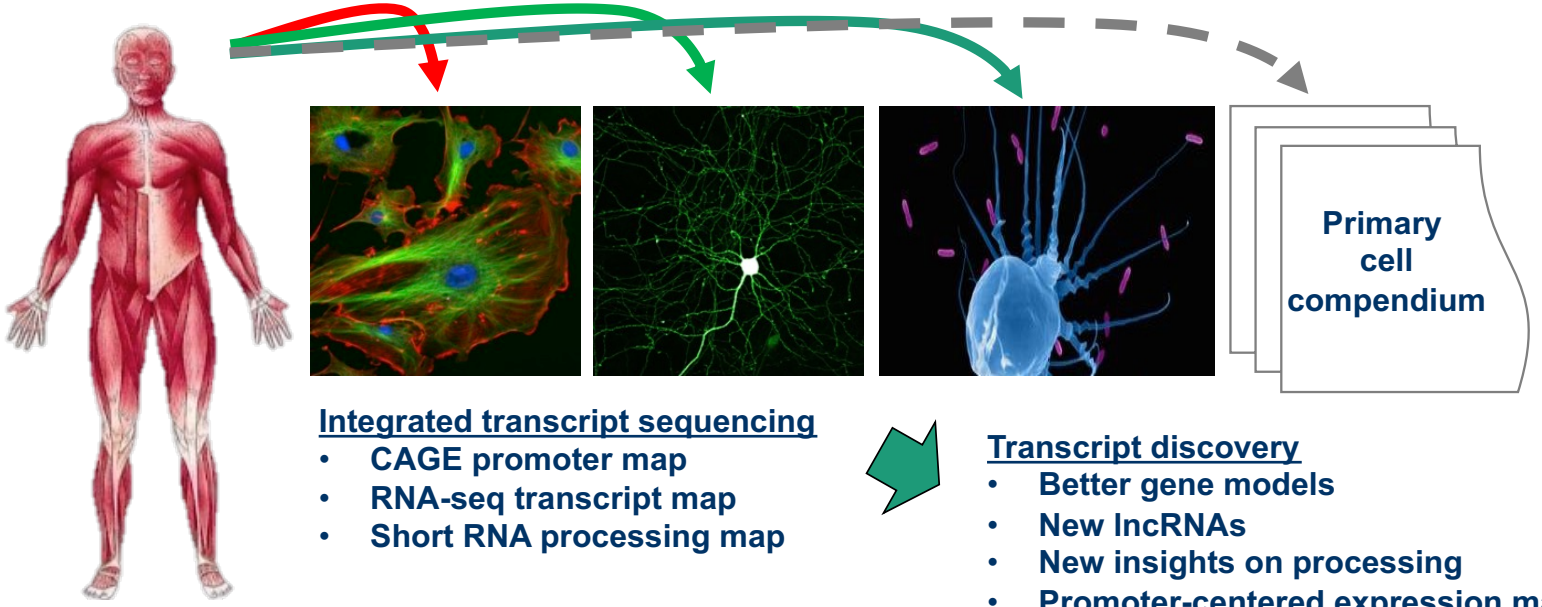
Samples: *Variety of cells*

~3,000 human and mouse libraries in total



Forrest *et al. Nature* 507, 462 (2014)

Overview of approaches; 3000 libraries

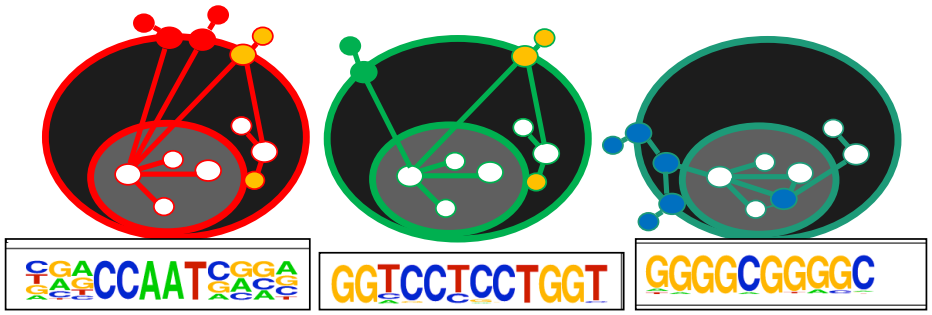


Integrated transcript sequencing

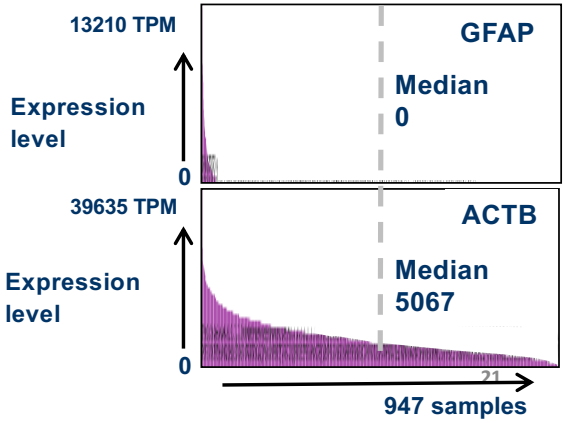
- CAGE promoter map
- RNA-seq transcript map
- Short RNA processing map

Transcript discovery

- Better gene models
- New lncRNAs
- New insights on processing
- Promoter-centered expression map



Cell specific network models
Key transcription factors, Key motifs



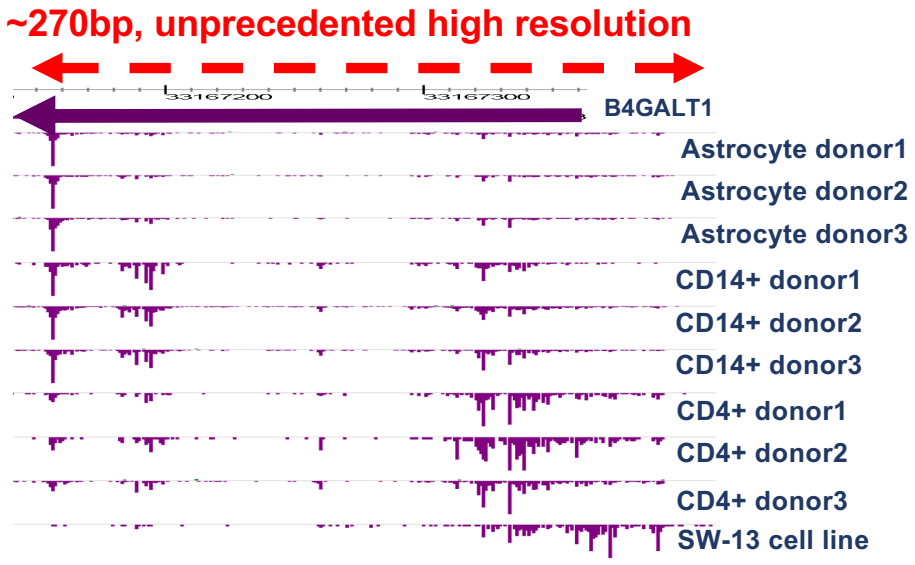
Forrest *et al. Nature* 507, 462 (2014)

Expected/unexpected results

- Measure gene expression
- Infer networks globally
- Map promoters

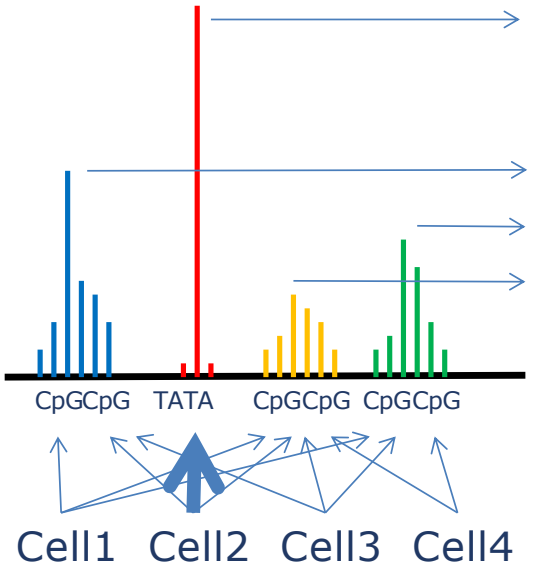
- Surprises?

FANTOM5: *Promoter architectures differ in different cells*



TSS preferences:

- **B4GALT1 core promoter**
- **Primary Astrocytes**
- **CD14+ monocytes**
- **CD4+ T-cells**



- **Blue, yellow and green: Broadly used**
- **Red: Cell2 specific and highly expressed**

223,428 in human and 162,264 in mouse of reference TSS

Forrest *et al. Nature* 507, 462 (2014)

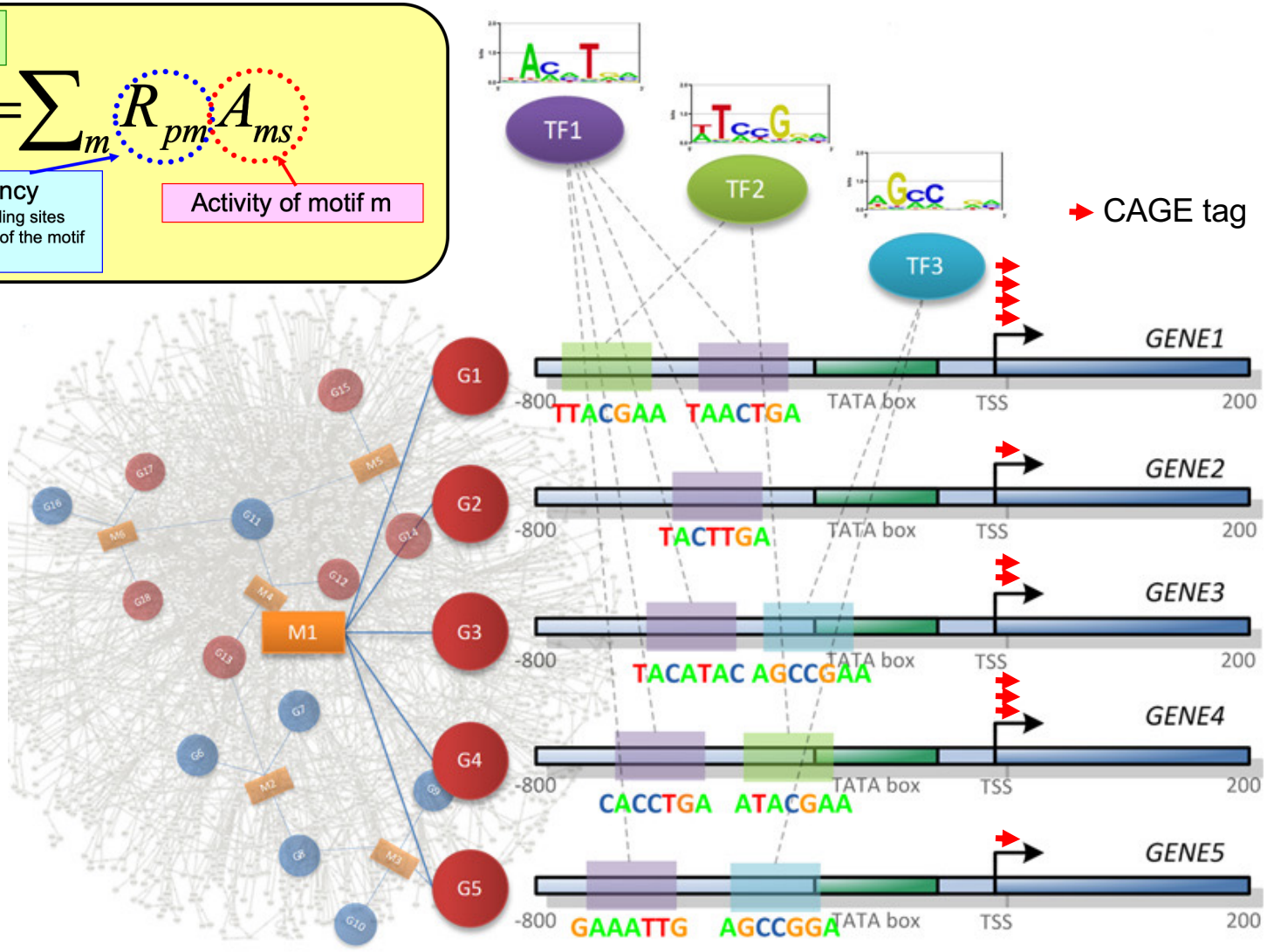
Regulatory network analysis. Why using CAGE?

Number of CAGE tags that mapped on the same site

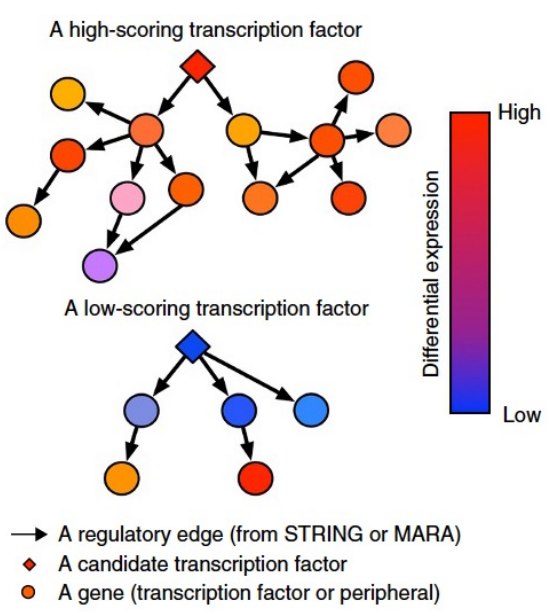
$$e_{ps} = \sum_m R_{pm} A_{ms}$$

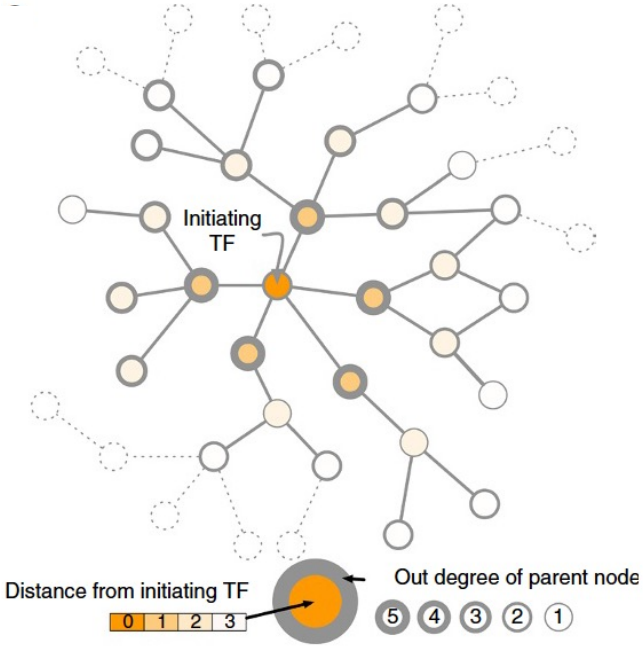
Reaction efficiency
- Number of possible binding sites
- Degree of conservation of the motif
- Chromatin status

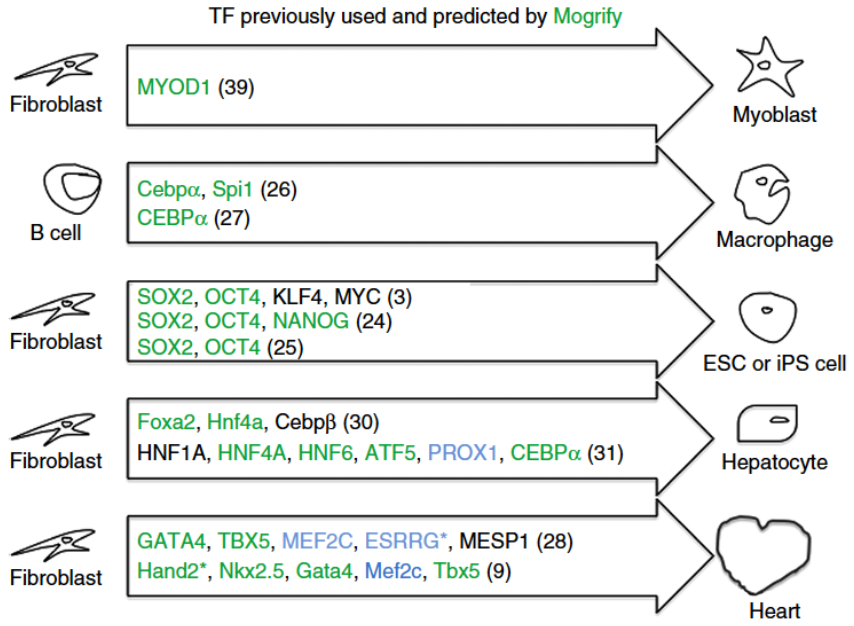
Activity of motif m

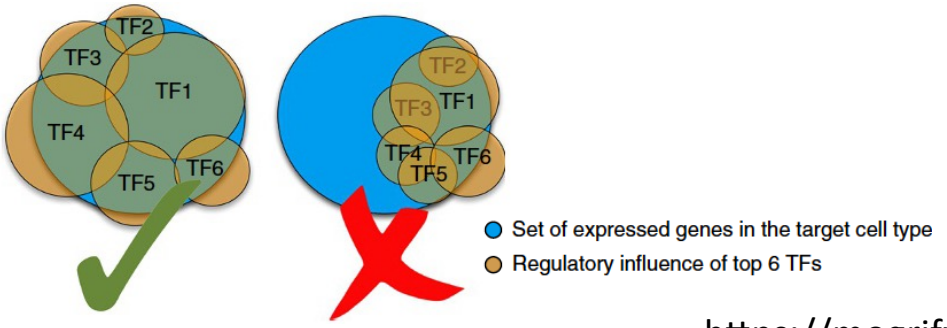


MOGRIFY: direct cellular reprogramming







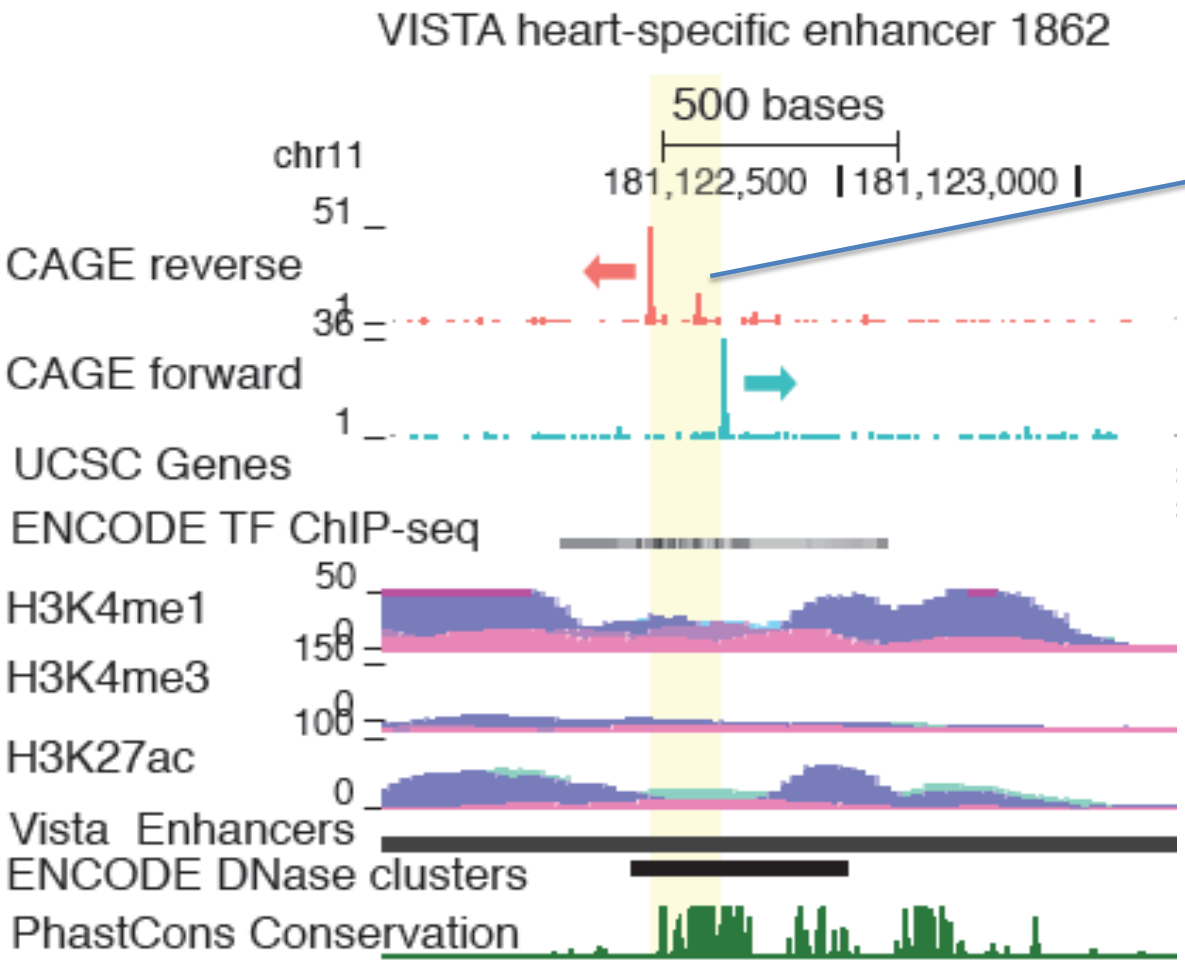


Rackham *et al.* **A predictive computational framework for direct reprogramming between human cell types,** *Nature Genetics*, 2016

https://mogrify.co.uk/ , a FANTOM5 spinoff

More surprises

Bidirectional transcription identifies cell specific enhancers



Enhancers have bidirectional CAGE transcription.

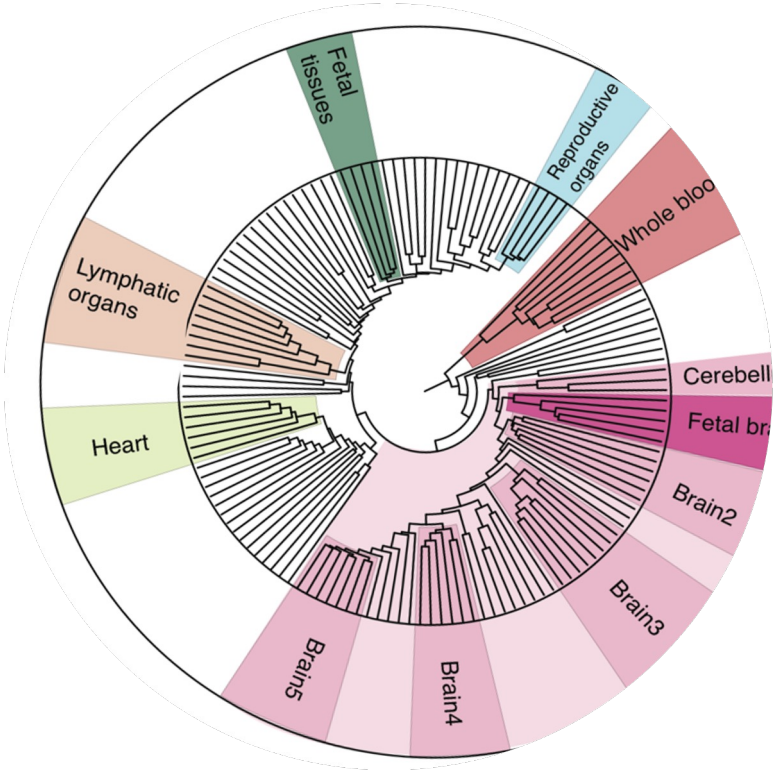
Bidirectional transcription identifies the nucleosome boundary.

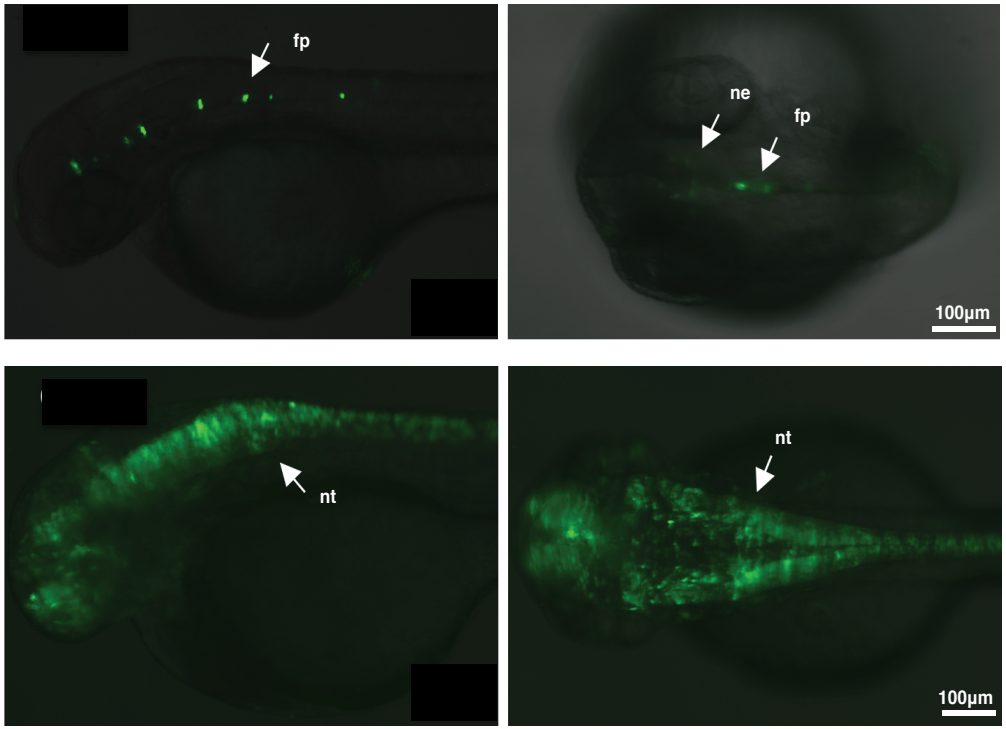
Based on this, we make a rule to locate novel transcribed enhancers over the whole FANTOM collection.

Andersson *et al. Nature* 507, 455 (2014)

Systematic in vivo characterization of active enhancers across the human body

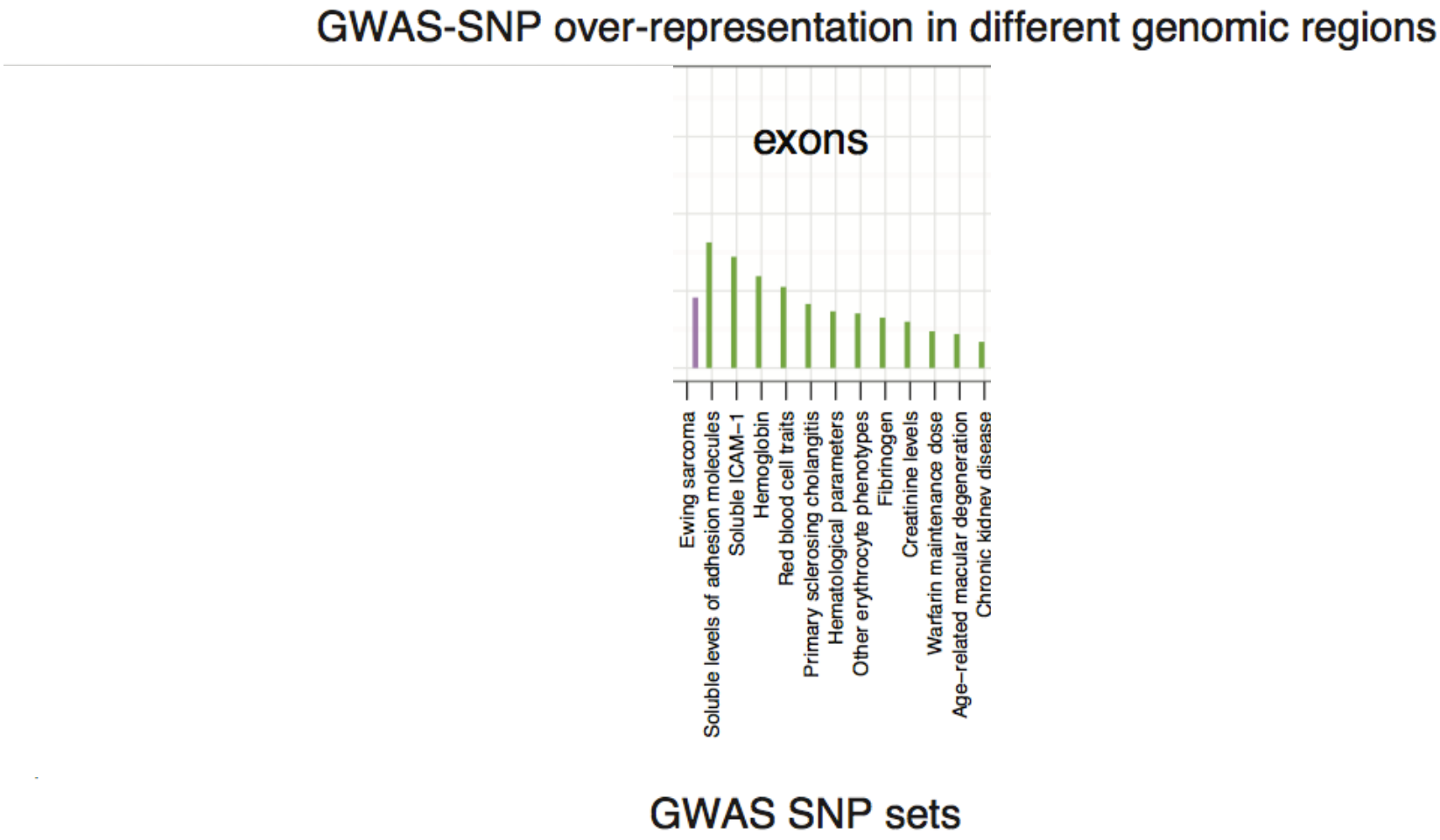
- identified 65,423 and 44,459 enhancers in human and mouse.
- 60% are over-represented in one cell/tissue group.
- Human GWAS SNPs map often on enhancers and promoters (less frequently on coding exons).
- Promoter and enhancer usage and QTL analysis. *Garieri et al. Nat Commun.* (2017)





Andersson *et al. Nature* 507, 455 (2014)

Disease-associated SNPs are enriched in enhancers

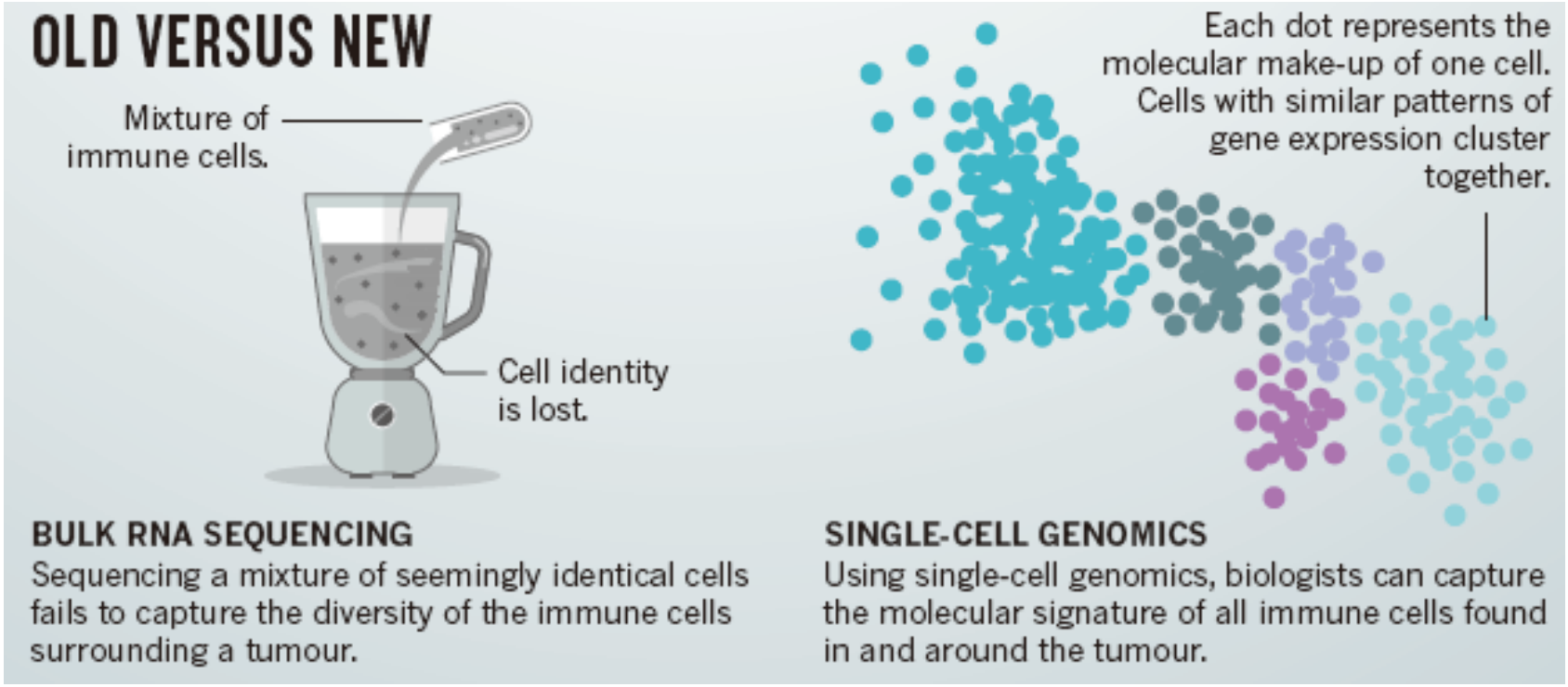


Mapping the genome regions that regulate gene activity in diseases

Andersson *et al. Nature* 507, 455 (2014)

Transcriptome for ALL human cells

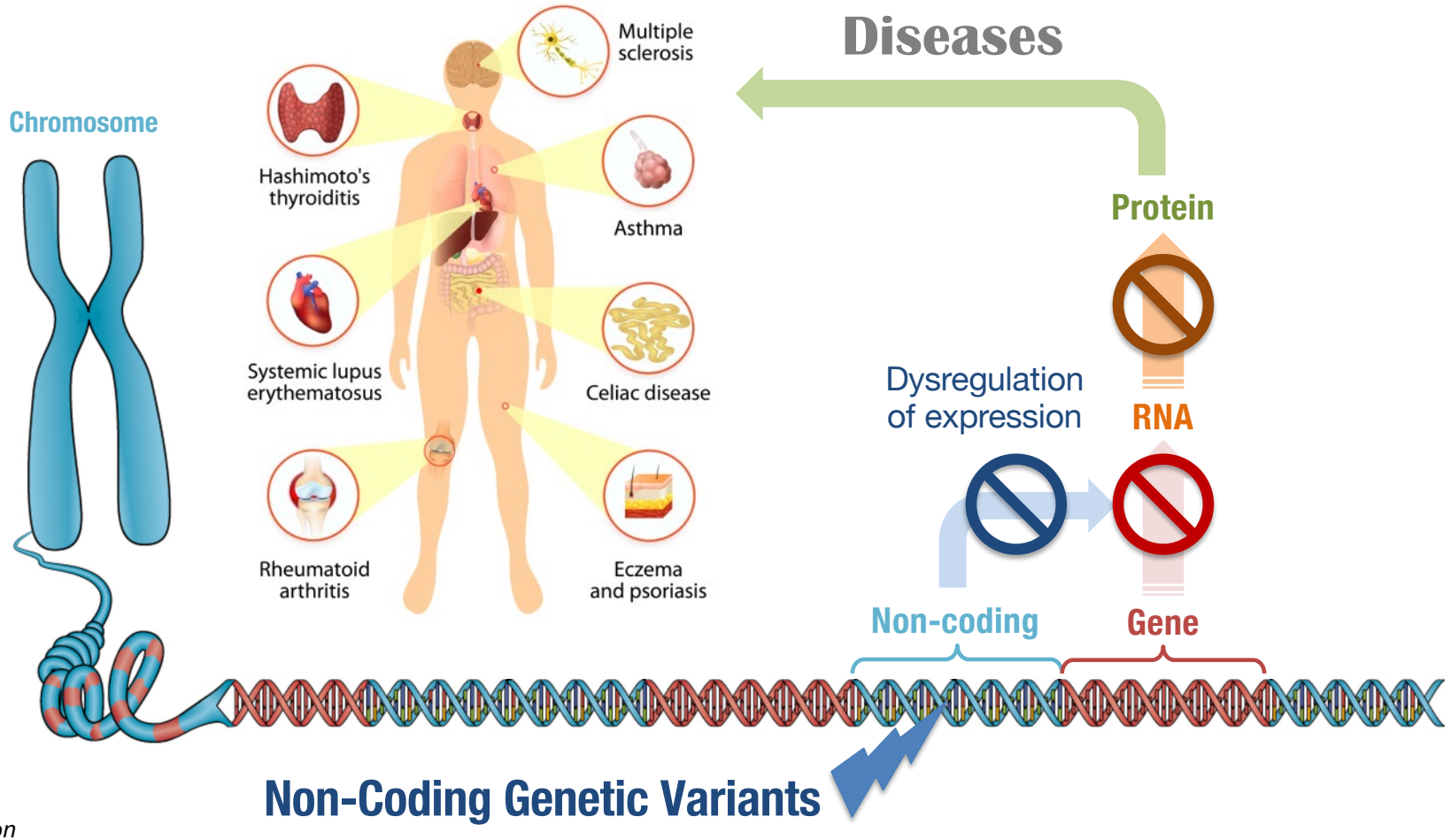
- Promoters, enhancers, lncRNAs as FANTOM5 but in “single cells”: from cell classification to precision genomics



Giladi *et al. Nature* (2017)

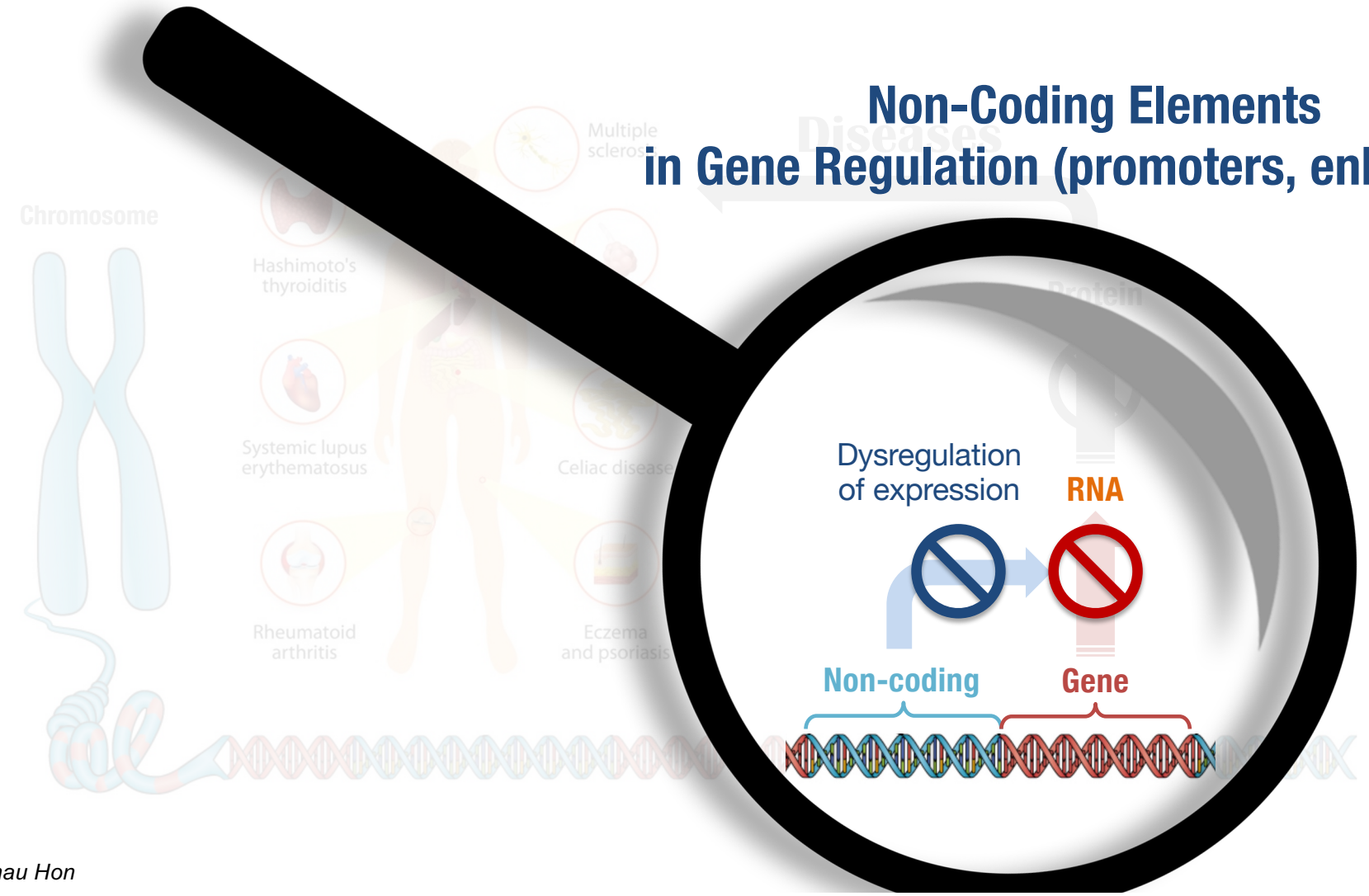
Taking advantage of single cell work- single cell CAGE

CAGE approach to map regulatory elements and map Predispositions to Diseases



Slide, Chung Chau Hon

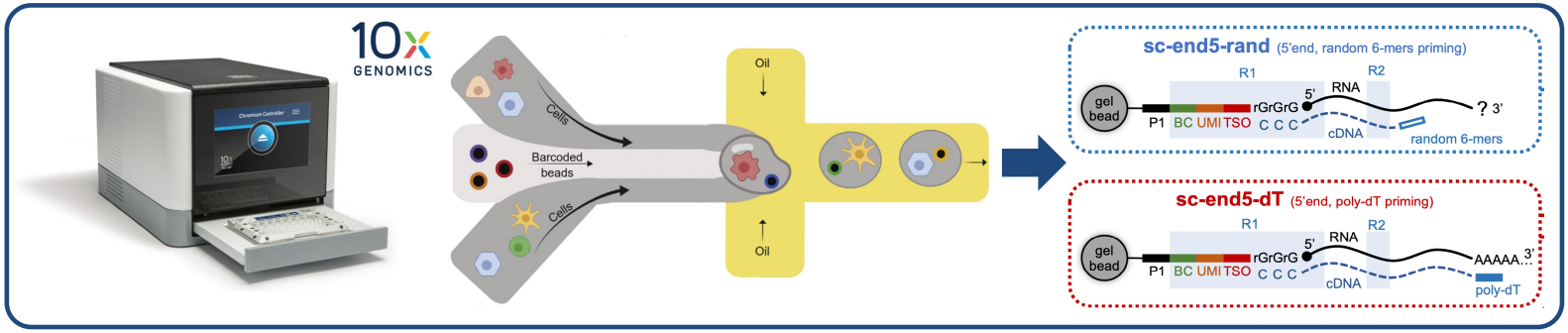
The Focus : Cis-Regulatory Elements **(CRE) at SINGLE CELL**



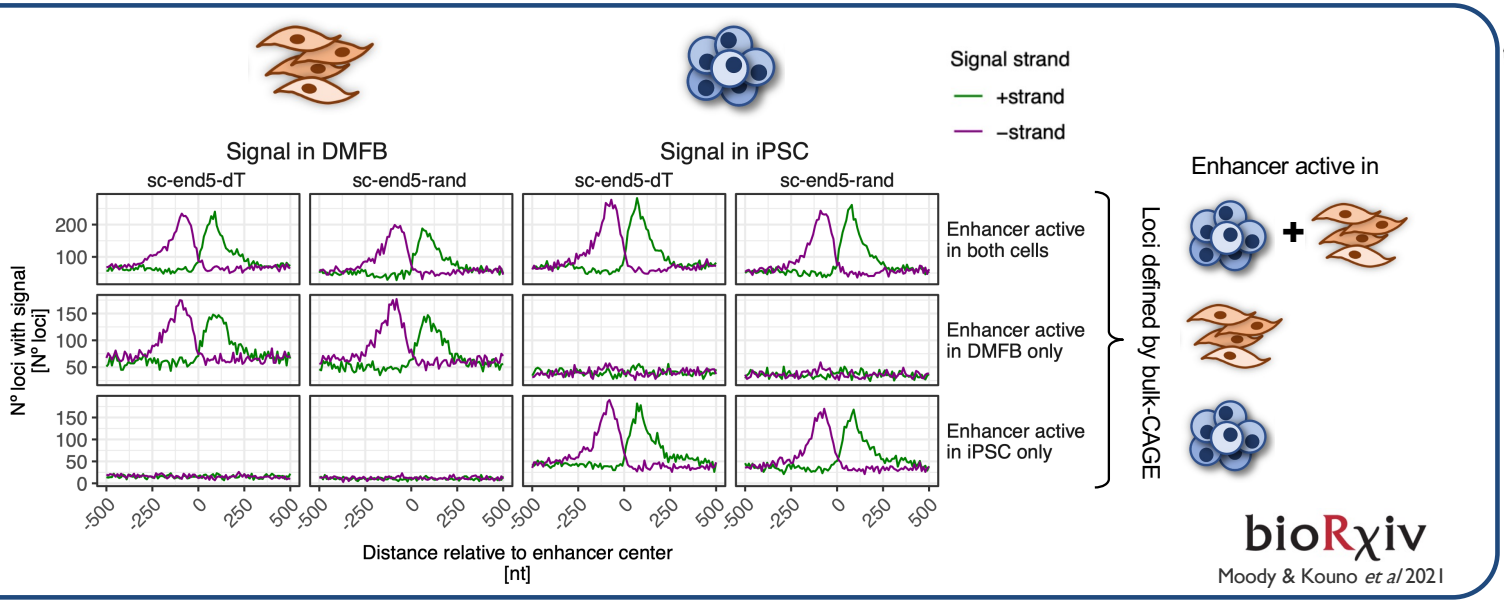
Slide, Chung Chau Hon

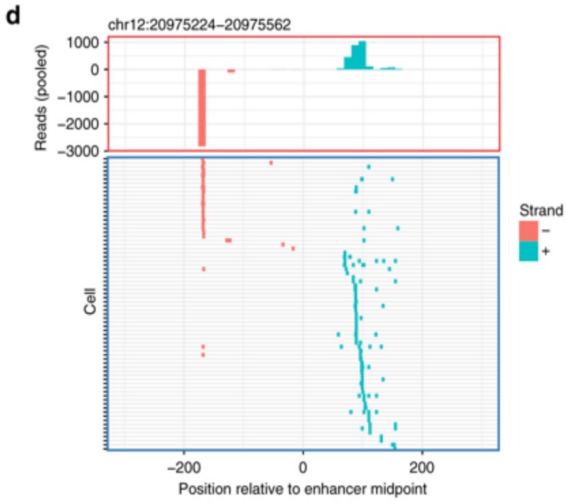
We can now profile transcription and regulatory elements in single cells

5'end sc-RNA-Seq : Testing random and oligo-dT priming on 10X Genomics Chromium



Enhancers : Both random and oligo-dT priming detects eRNA in single cells

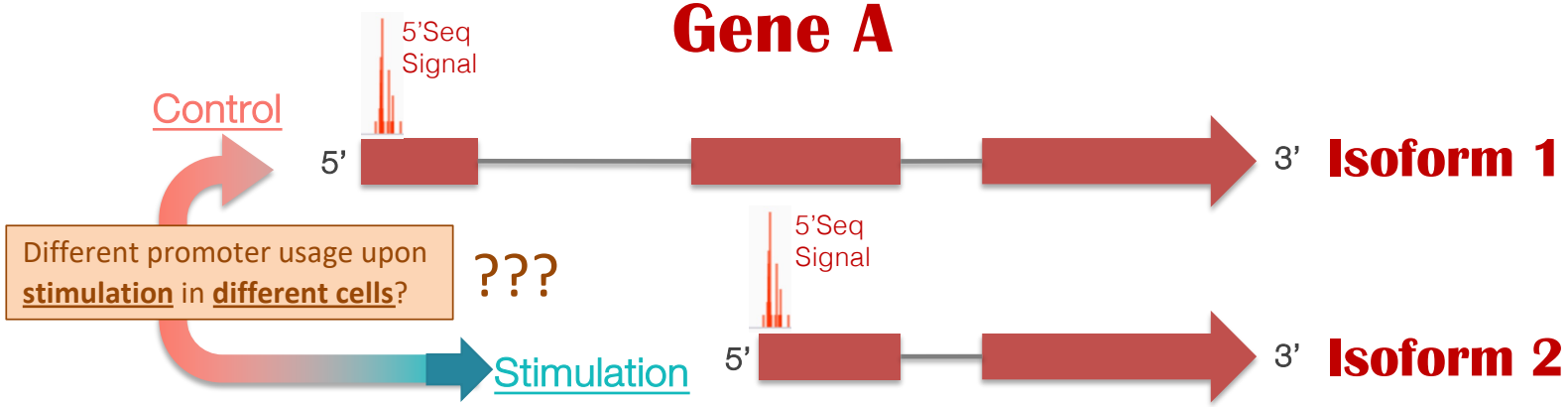


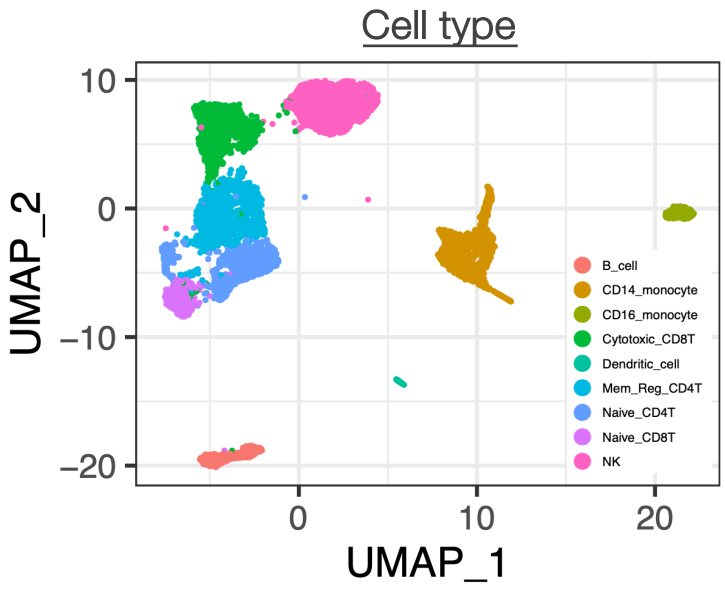


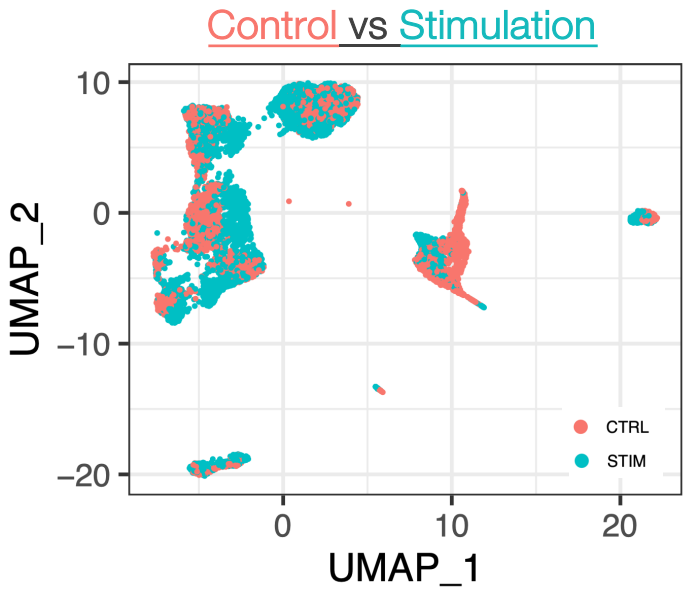
Enhancer RNAs at single base resolution in single cells

From Kouno T., Moody J., Kwon AT, et al. *Nature Communications* 2019

Technology: *to identify regulatory elements in genome*





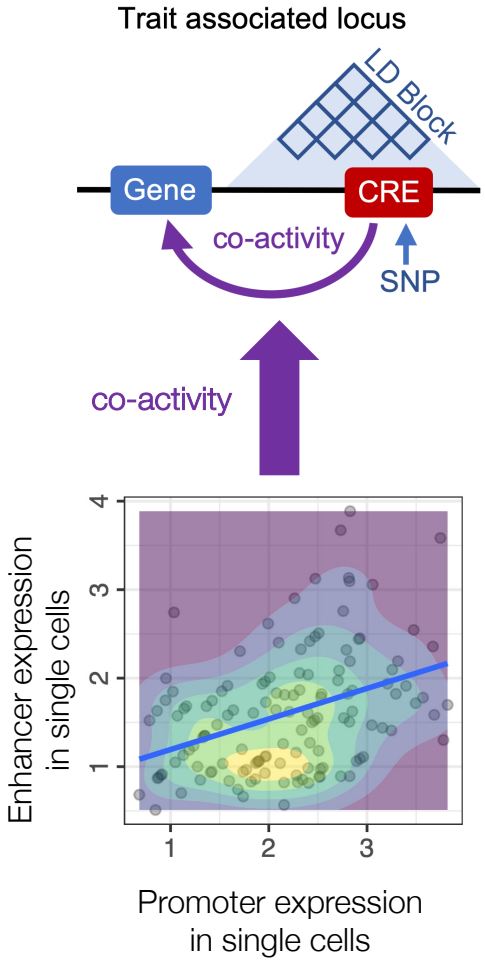


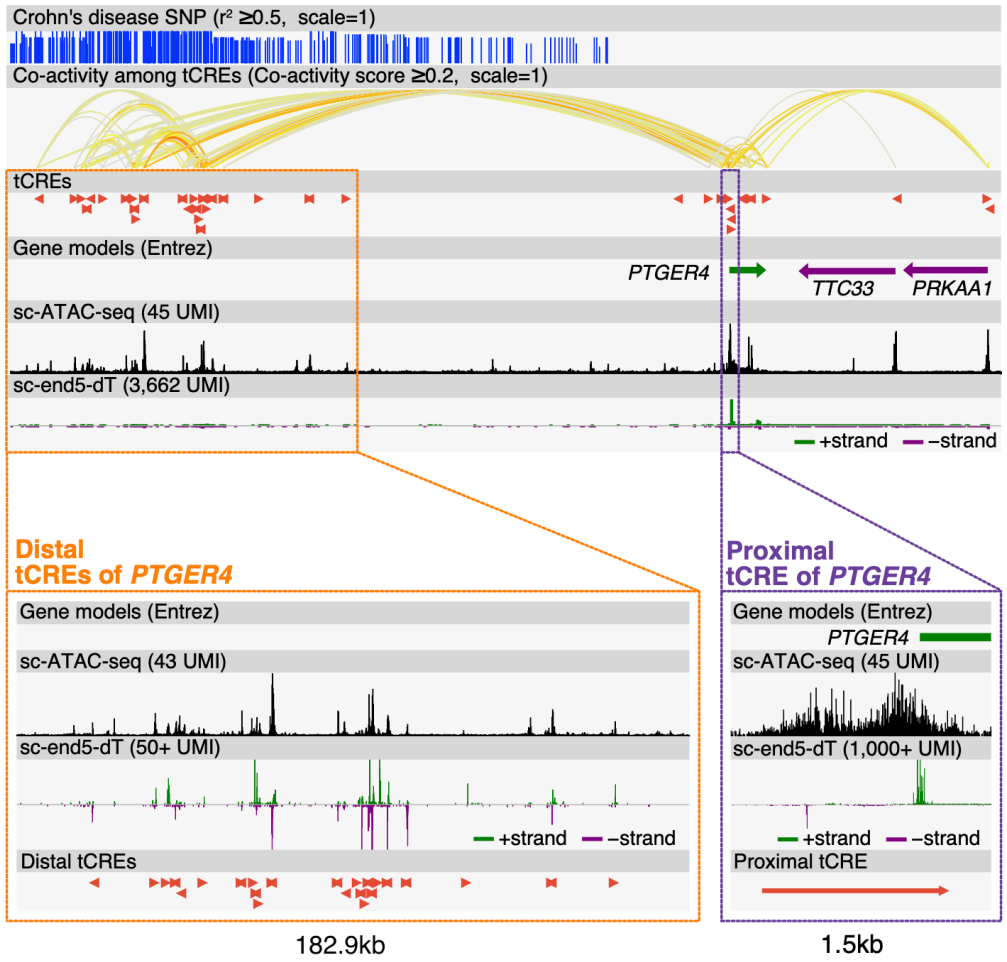
Yes CAGE works at single cell, can detect expression, promoters, enhancers, lncRNAs…

Slide, Chung Chau Hon and Jonathan Moody

GWAS interpretation : Linking GWAS variants to candidate genes

We infer how genome sequence variants influence gene expression, in health and diseases, in all human cells

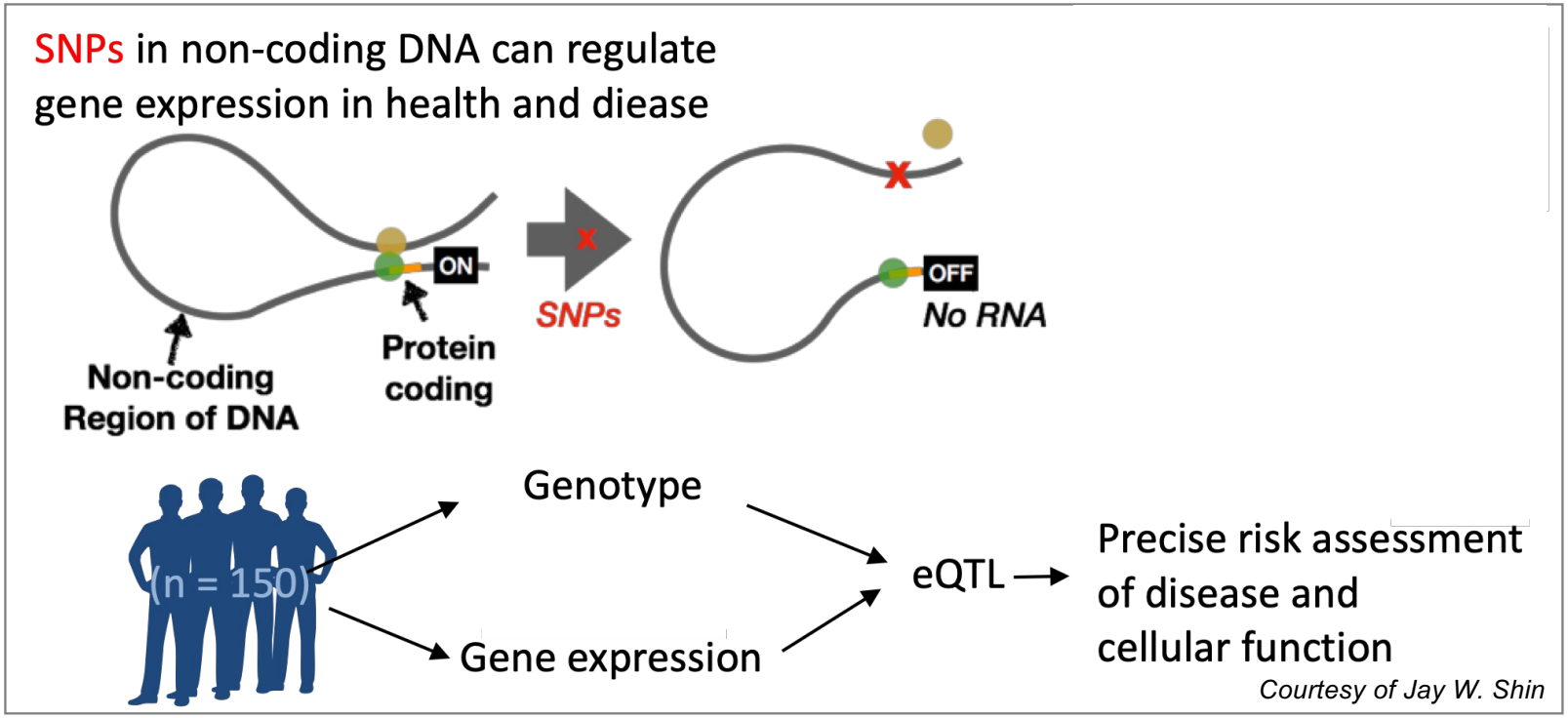




Chung Chau Hon

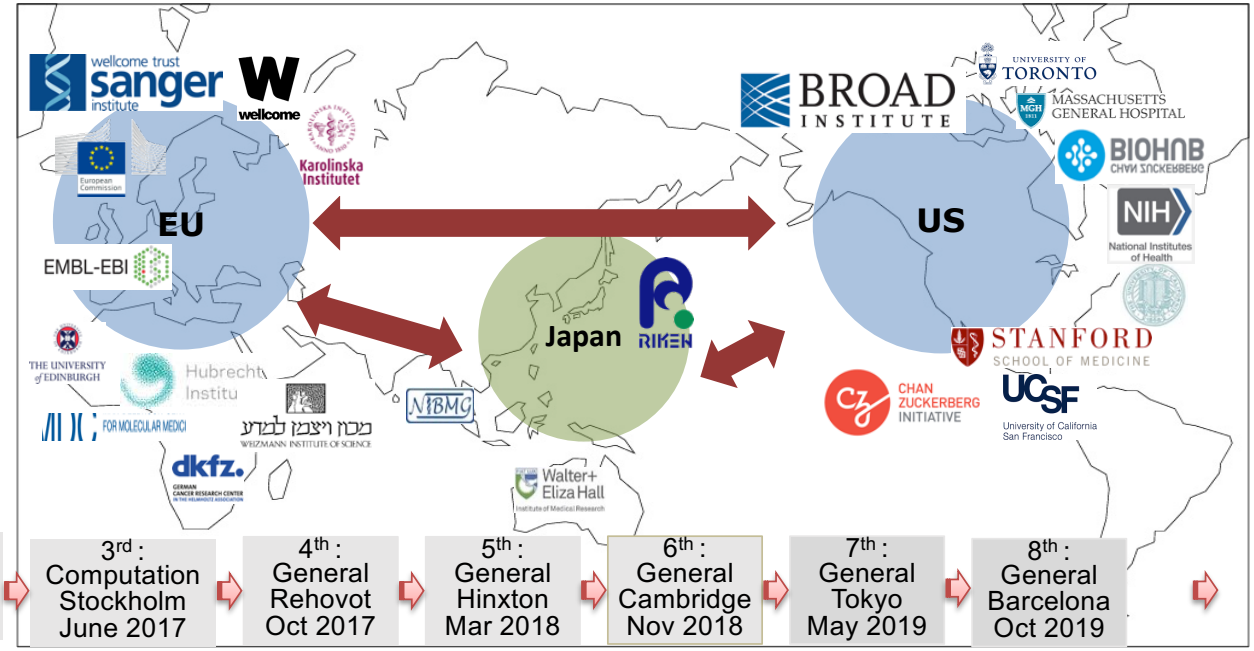
Comprehensively linking gene expression to human genetics

- eQTL with much higher resolution at single cell level
- unbiased cell-type specific expression controlled by genomic elements
- easier to understand if a given genome variation is responsible for the onset/progression of a disease
- eQTL needs ~100 individuals for each cell type to be profiled



Human Cell Atlas (HCA)

Comprehensive reference maps of all human cells at single cell level



HCA meetings

- 1st: Launch London Oct 2016
- 2nd: Technology Stanford Feb 2017
- 3rd: Computation Stockholm June 2017
- 4th: General Rehovot Oct 2017
- 5th: General Hinxton Mar 2018
- 6th: General Cambridge Nov 2018
- 7th: General Tokyo May 2019
- 8th: General Barcelona Oct 2019
- 9th: General Virtual June 2021 … …

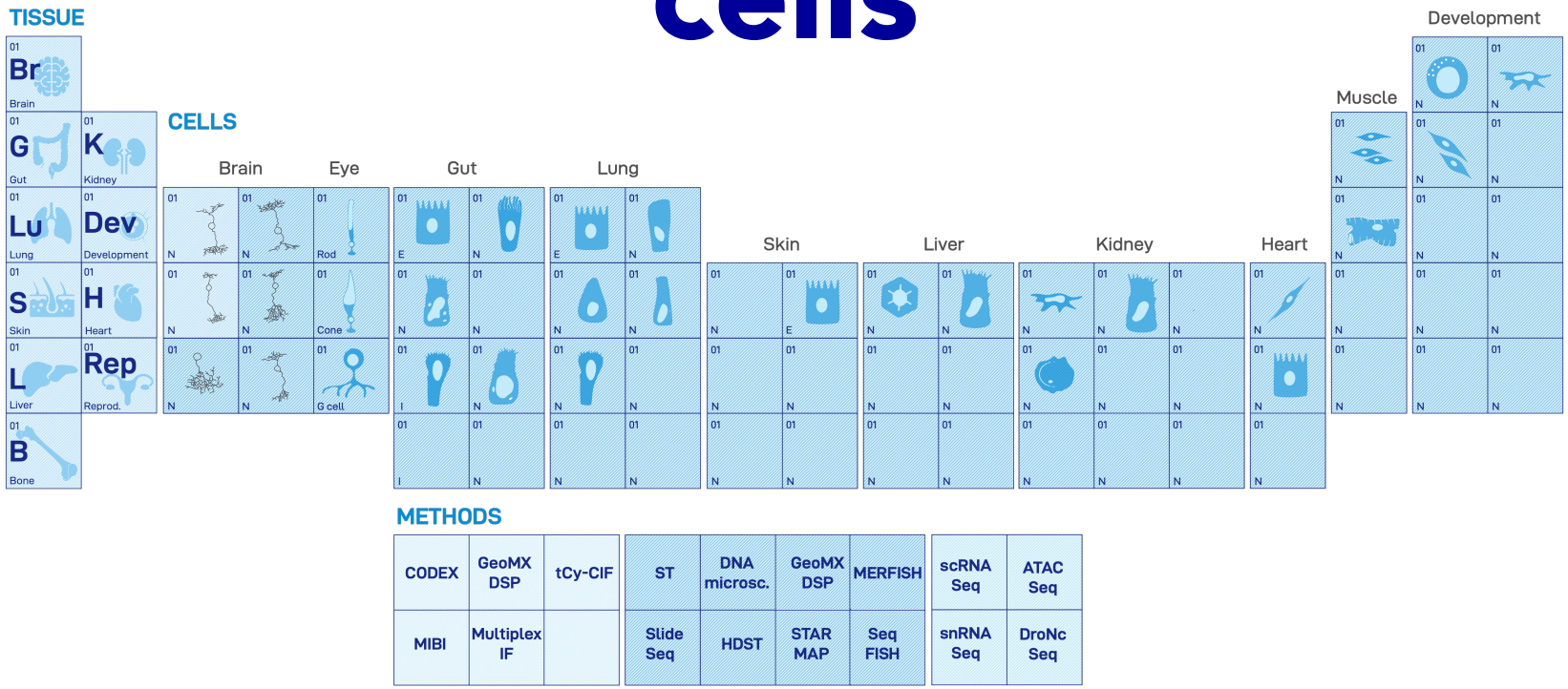
- 1st: Asia Okinawa Nov 2017
- 2nd: Asia Jeju Nov 2018
- 3rd: Asia Singapore Nov 2019
- 4th: Asia Virtual Oct 2020
- 5th: Asia Virtual Nov 2021 … …

- Single cell genomics
- High-resolution 3D imaging analysis
- Bioinformatics

➢ Reformulate our fundamental definition of cell types/development & human biology.

➢ Understand health & diseases at high-resolution.

A periodic table of our cells



Graphics credit: Ania Hupalowska

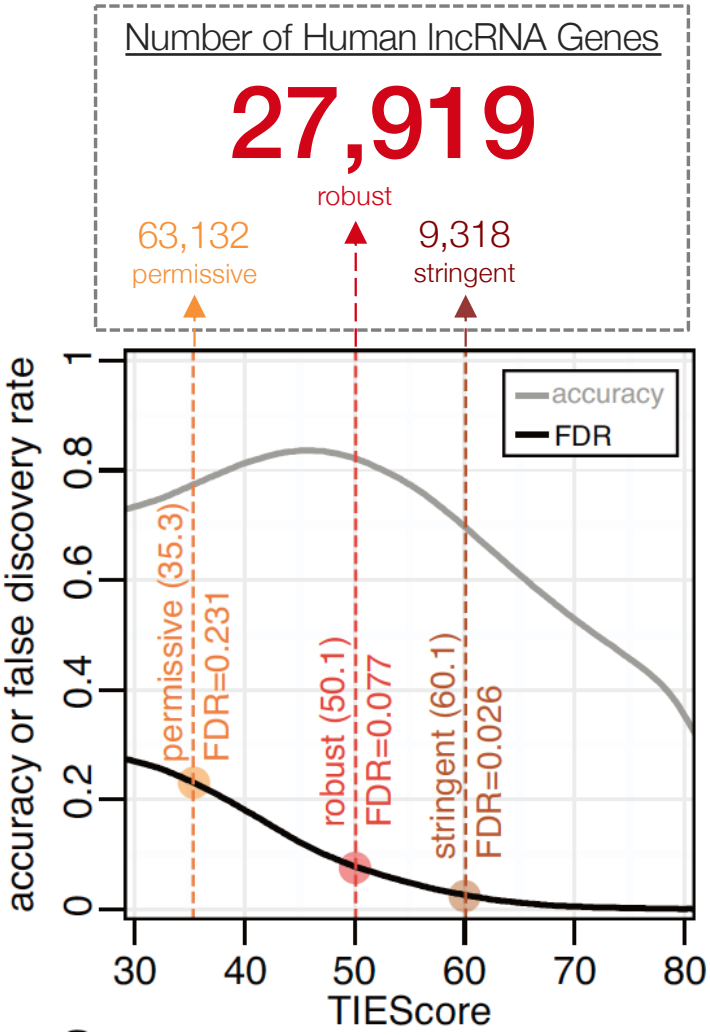
The 7th HCA General Meeting in Japan

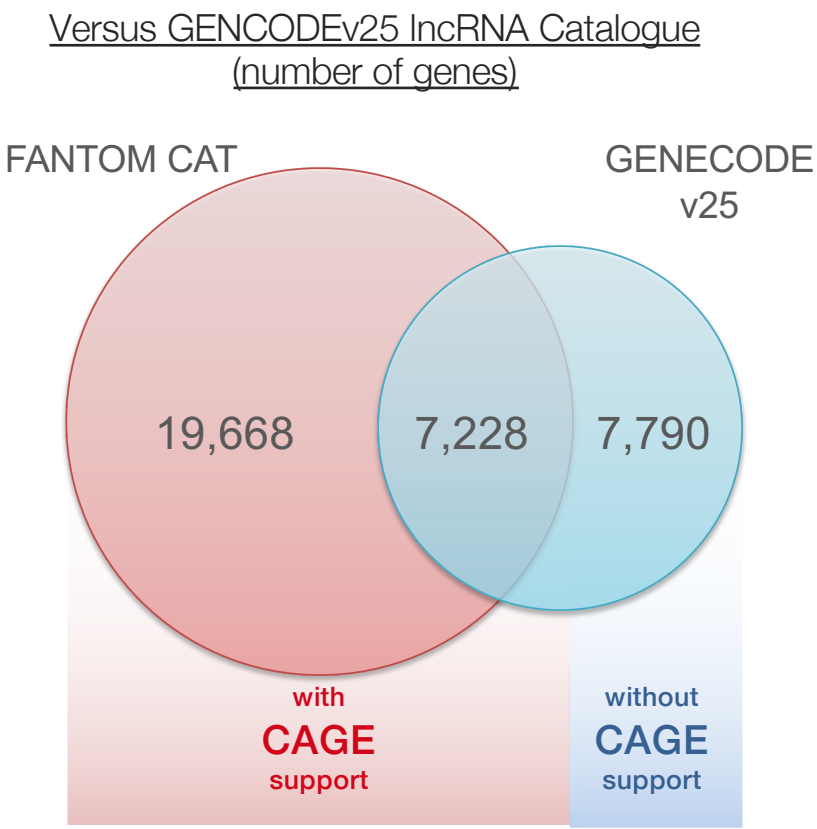
Coordination of HCA in Japan and in Asia (HCA executive office at RIKEN)

Back to the non-coding RNAs
(Is this a good name?)

CAGE to recount number of lncRNAs

Recounting lncRNAs





Hon *et al.*, *Nature* 543, 199 (2017)

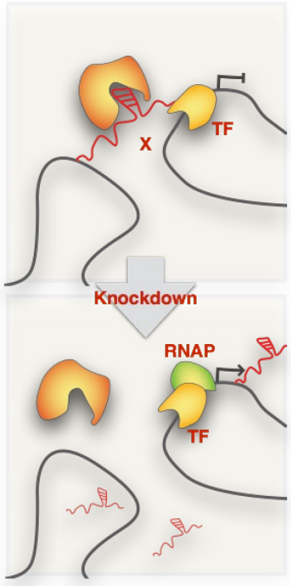
Function:

Do we need experimental evidence?

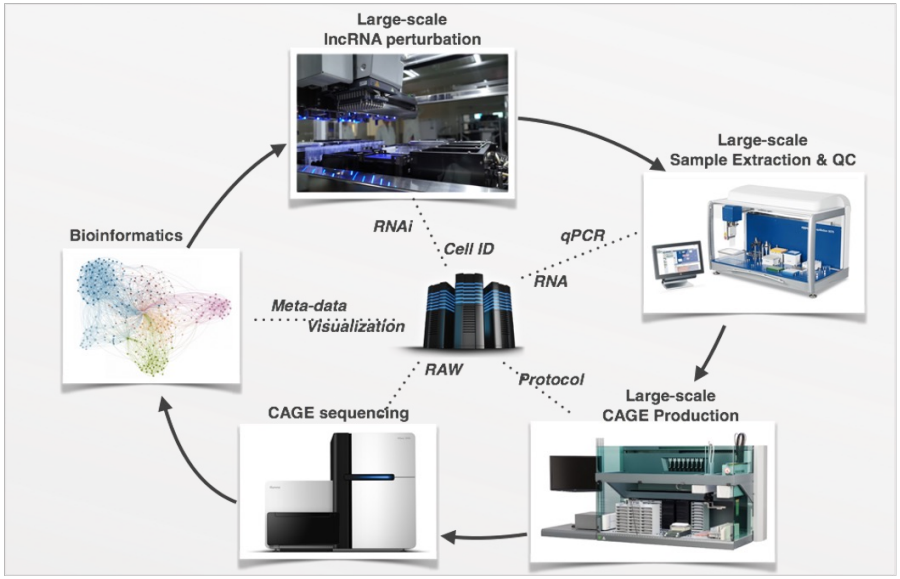
FANTOM6: *Functional lncRNA catalogue*

Measuring transcriptional phenotypes

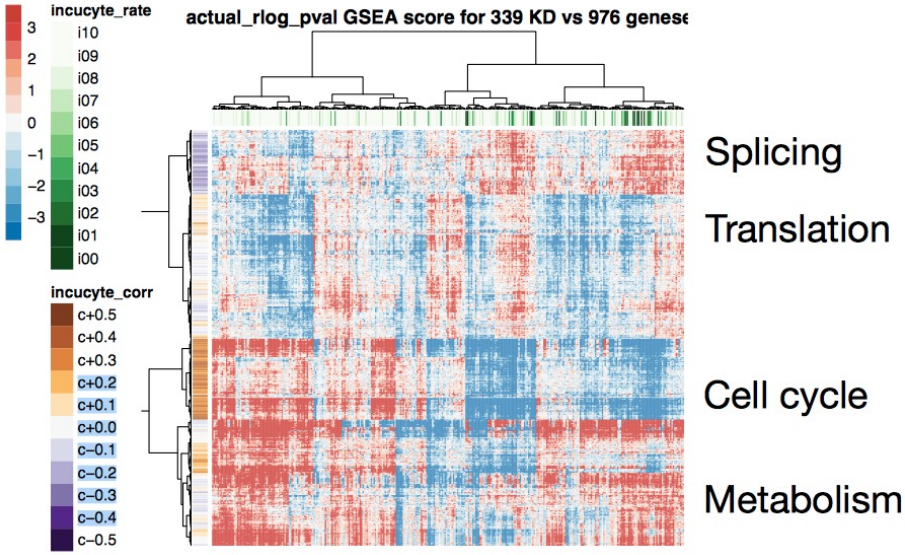
Principle



Systematic pipeline

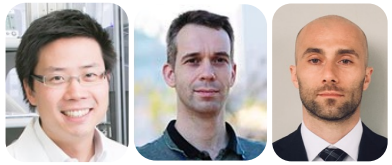


Molecular phenotype induced by lncRNA KD



Characterization of the “new continent” of lncRNA:

- lncRNA functional
- Regulatory role among others
- Many genes with natural antisense RNAs

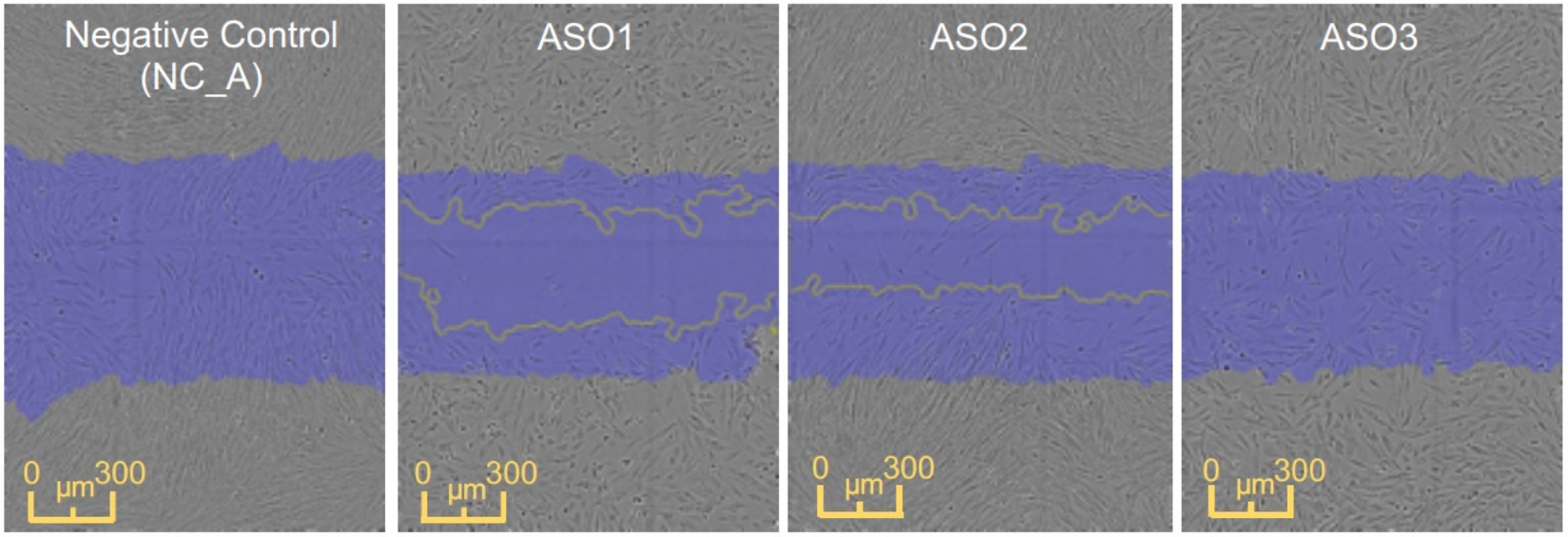


Jay W. Shin, Michiel de Hoon, Jordan Ramilowski

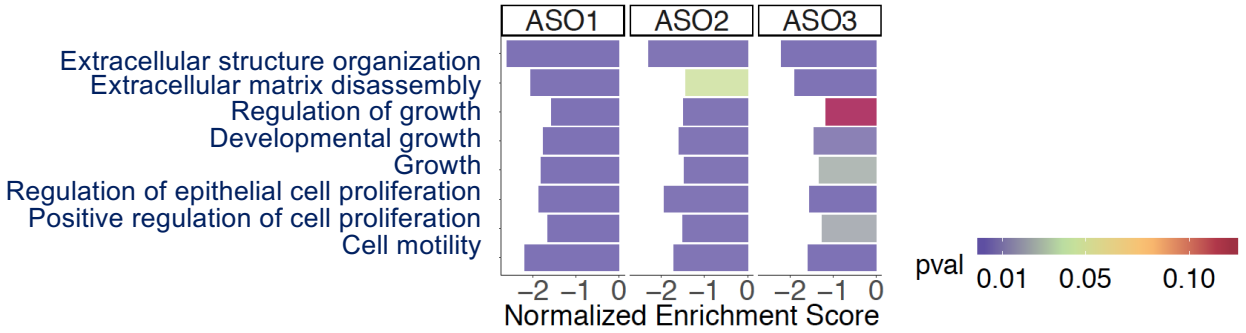
Ramilowski *et al. Genome Res.* 30, 1060 (2020)

Example: KD of ZNF213-AS1 impacts cell growth and migration

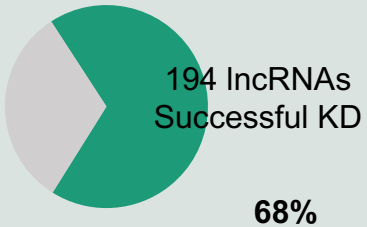
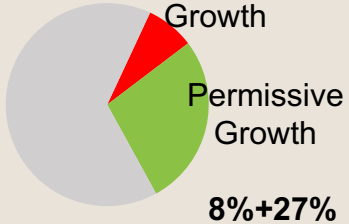
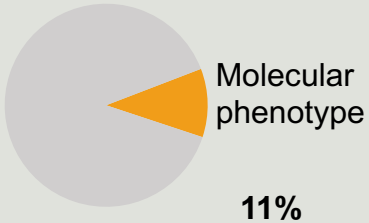
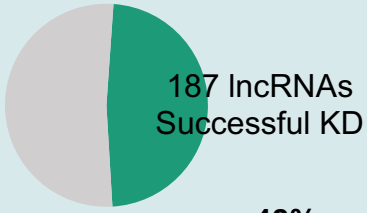
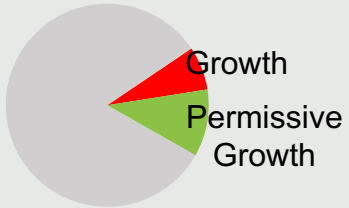
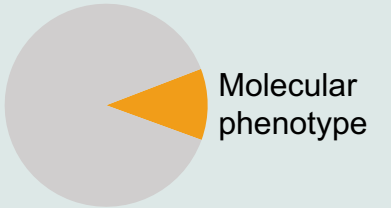
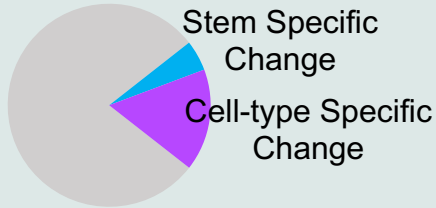
Wound healing assay for ASOs targeting ZNF213-AS1
35-73% impairment of wound-closure in fibroblasts lacked ZNF213-AS1



Selected enriched biological pathways



After thousands of experiments: many lncRNAs have function

	Knockdown	Cell Phenotype	LQ-CAGE Transcriptomic Profiling
			
HDF	**285 lncRNAs**  **68%**	**194 lncRNAs**  **8%+27%**	**119 lncRNAs**  **11%**
iPSC	**390 lncRNAs**  **48%**	**187 lncRNAs**  **6%+12%**	**123 lncRNAs**   **11%** **5%+16%**

Ramilowki JA, Yip CW. Genome Research 2019

Note: lncRNAs may be functional in another cell type or assay

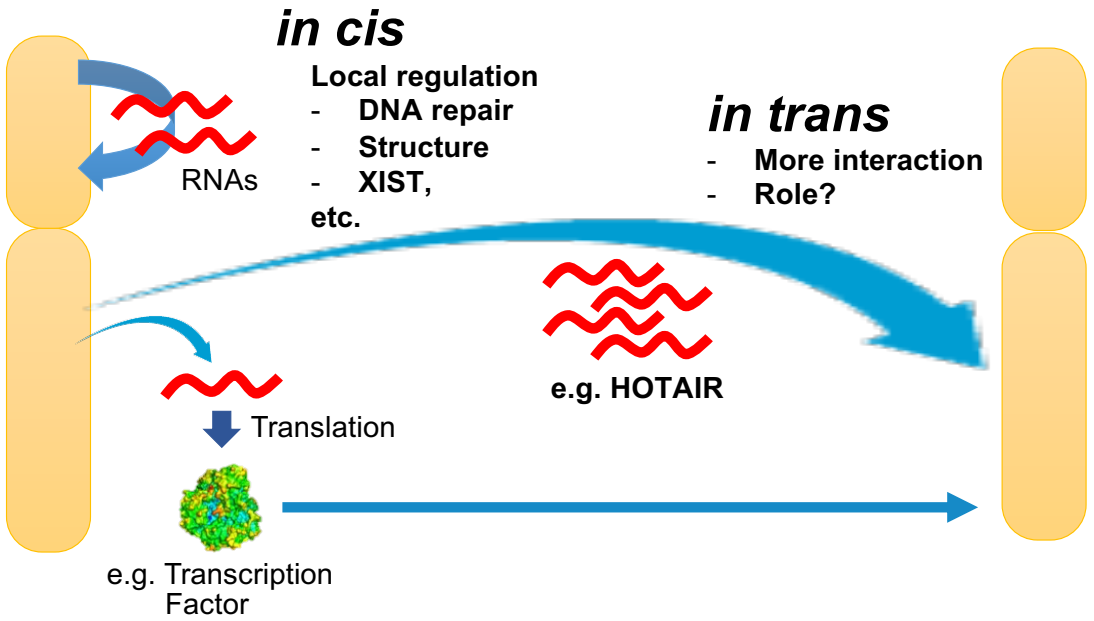
Slide courtesy of Jay Shin and Chi Wai Yip

How to collect information about lncRNAs,

faster?

Can we collect how and where lncRNAs interact, their “interactome”?

RNA-DNA interactions affect epigenome and gene regulation



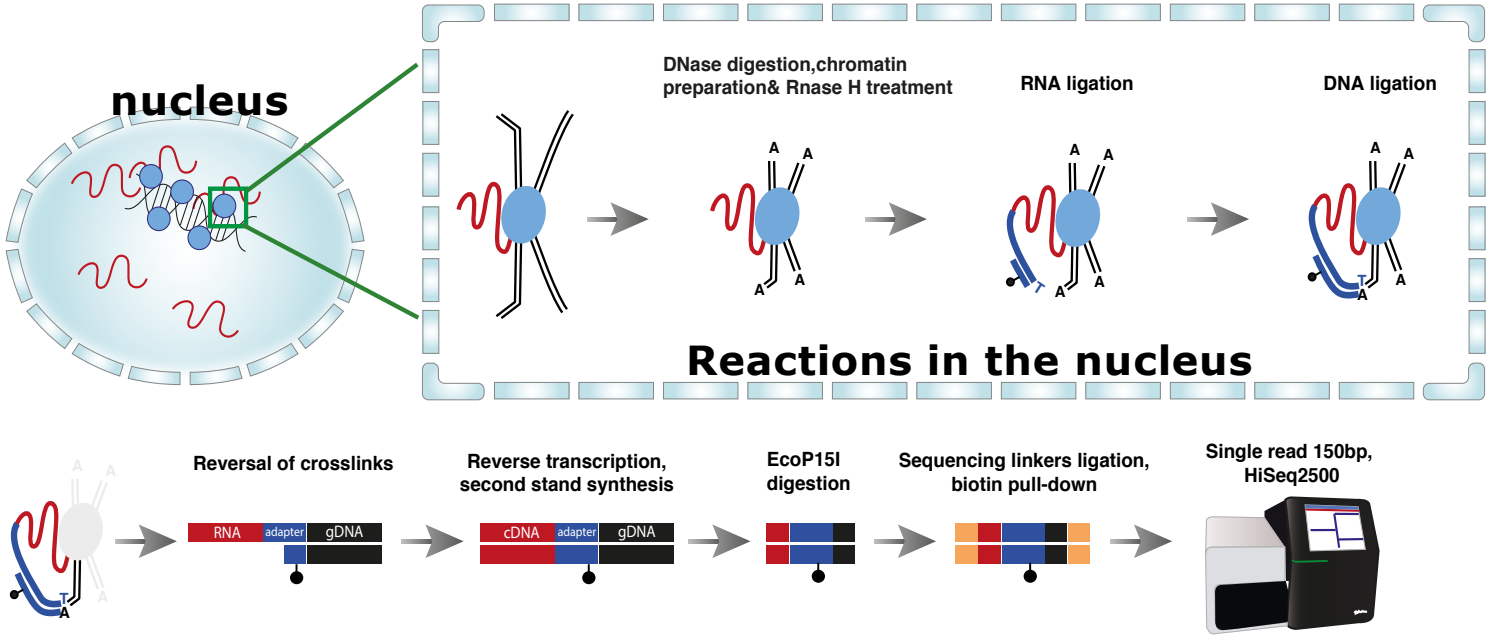
37% of lncRNAs chromatin-bound

What is the role of RNA-chromatin interaction *in cis* and *in trans* ?

- **Activate genes? Promoter? Enhancer?**
- **Repress genes? Insulator?**

RADICL-seq captures RNA-DNA interactions in intact crosslinked nuclei

mESCs, crosslinked with Formaldehyde.



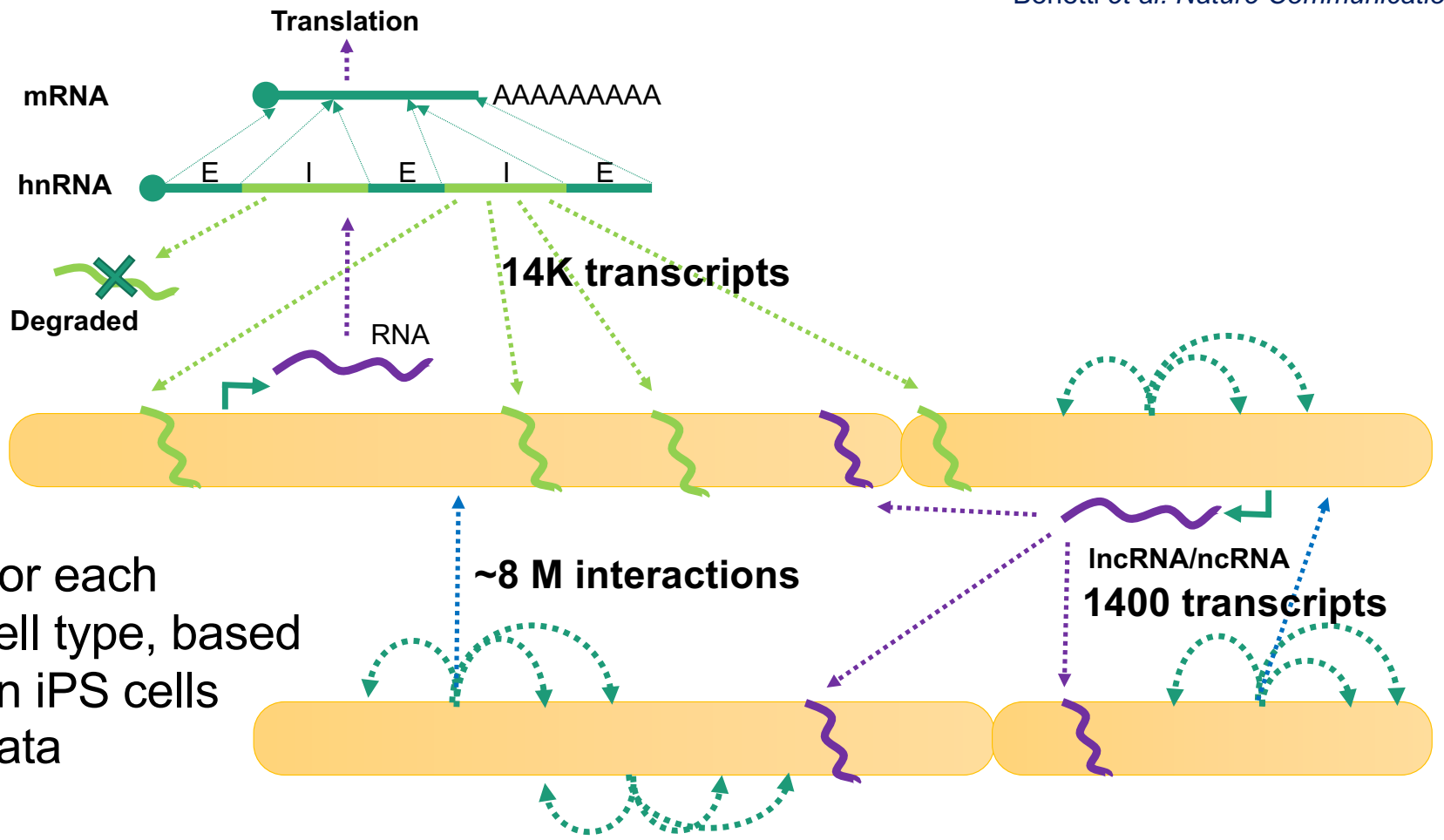
Other cell types that have been successfully tested with RADICL seq: miPSCs, mMEF, mOPC.
Typical seq. depth: 1 lane HiSeq2500/each replica.

Bonetti *et al. Nature Communications* 11, 1018 (2020)

Alessandro Bonetti

Interactome analysis: *mostly introns in cis; lncRNAs interact more often in trans*

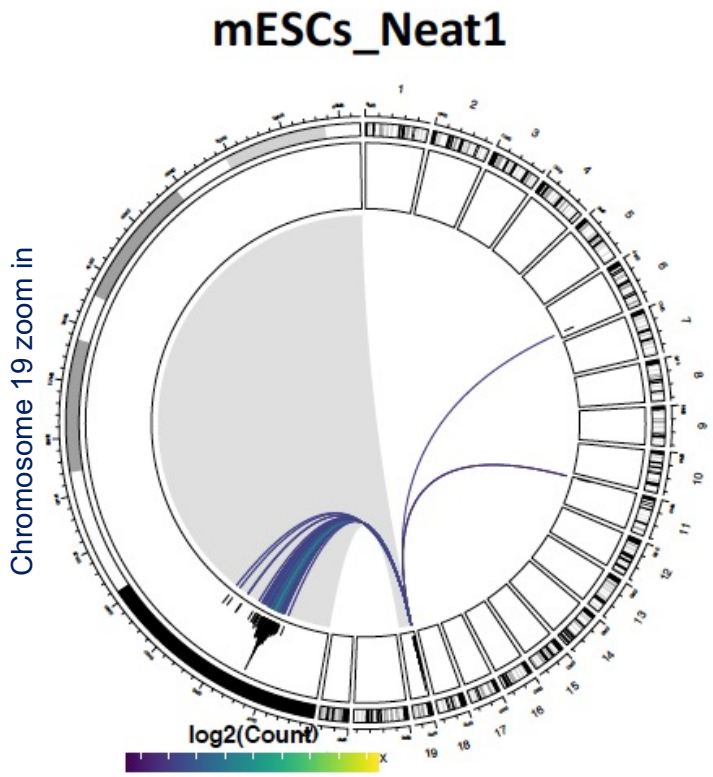
Bonetti *et al. Nature Communications* 11, 1018 (2020)



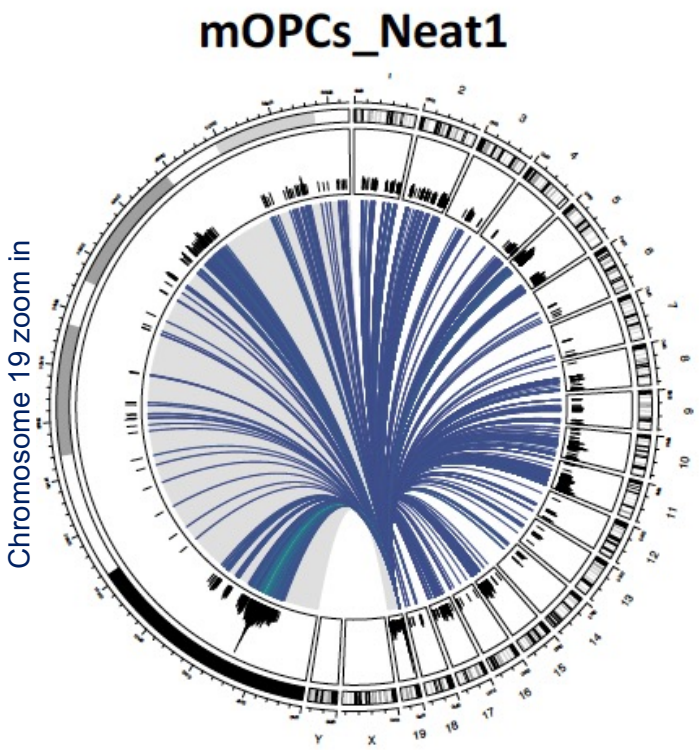
For each cell type, based on iPS cells data

➡ RNA sequence and structure unknown, need full-length RNA seq

Different cell types with different interactions patterns of lncRNAs in trans



mouse embryonic stem cells



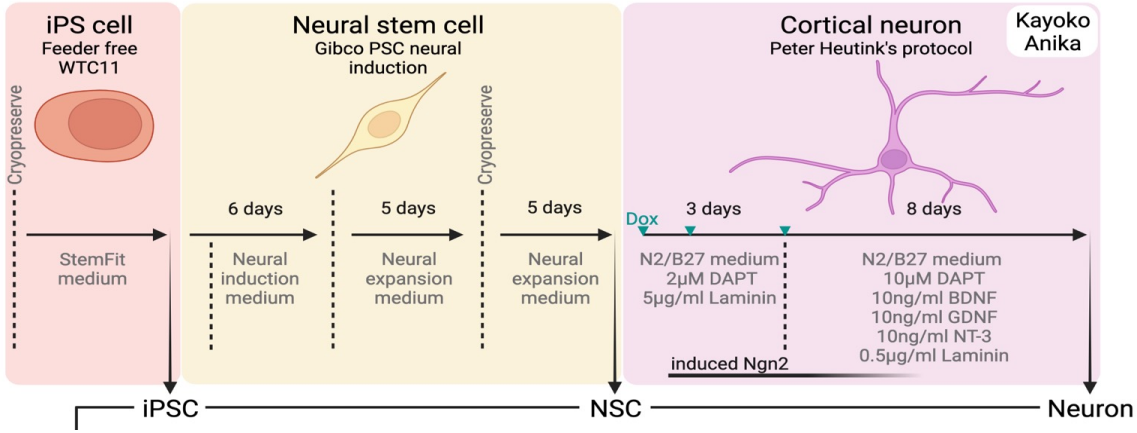
mouse oligodendrocyte progenitor cells

Slide courtesy of Alessandro Bonetti

Bonetti *et al. Nature Communications* 11, 1018 (2020)

Cell models and FANTOM6 RADICL libraries (~15 cell types)

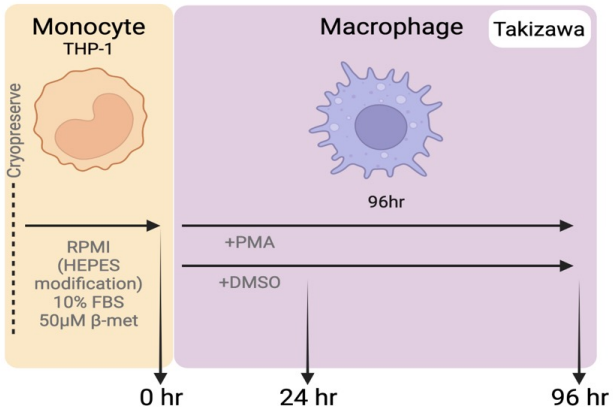
iPSC-Neuron series (2 reps each): iPS to neurons



iPSC-mNGN2 / NSC from iPSC-mNGN2 / Neuron from iPSC-mNGN2

Each rep 120~240 M(mapq10)

THP-1 series: THP-1 monocyte to macrophage



THP-1 (DMSO, PMA 24h, 96h)

Each rep 80~120 M(mapq10)

Pre F6 cell lines

iPSC (F6)
(3 reps)
Each rep ~200 M (mapq10)

HDF
(human dermal fibroblast)
(2 reps)
Each rep ~130 M (mapq10)

ENCODE cell lines

MCF7
(breast cancer cell line)
(2 reps)
Each rep ~80 M (mapq10)

MCF10A
(mammary gland, non-tumorigenic epithelial) (2 reps)

K562
(chronic myeloid leukemia (CML) cell line) (2 reps)

HCT116
(colorectal carcinoma cell line)
(2 reps)

Each rep ~120 M(mapq10)

T cell CD4+

(naïve and active(Th1))
(Beatrice Bodega lab)
(2 donors each)

Each rep 22~33 M (mapq10)

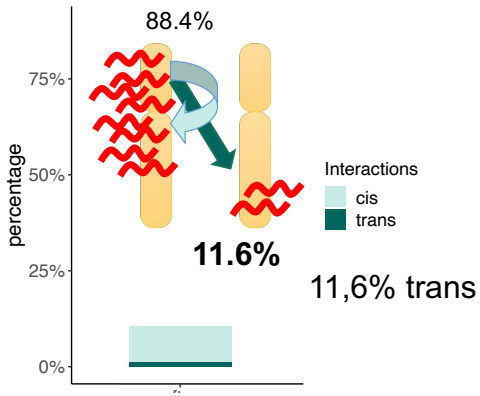
AML samples from patients

(acute myeloid leukemia)
(Andreas Lennartsson lab) (2 donors)

Each rep ~15 M (mapq10)

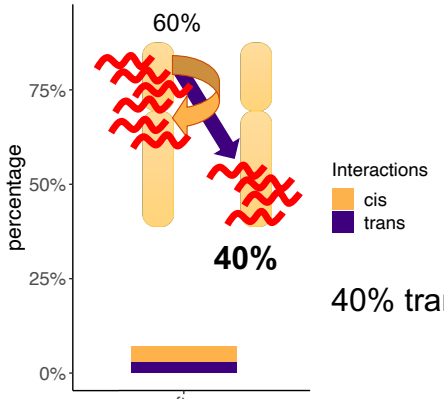
In trans interactions increase along differentiation process; lncRNAs and intronic RNAs have different targets

Type of interactions- initial



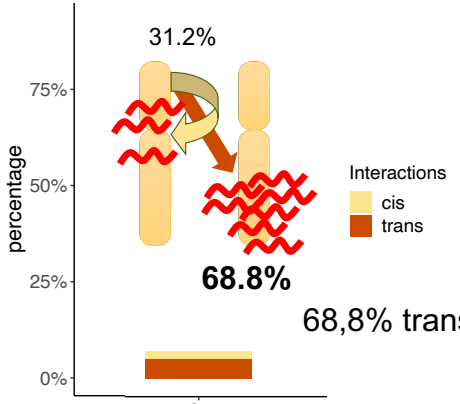
11,6% trans

Type of interactions in stimulation PMA 24 h

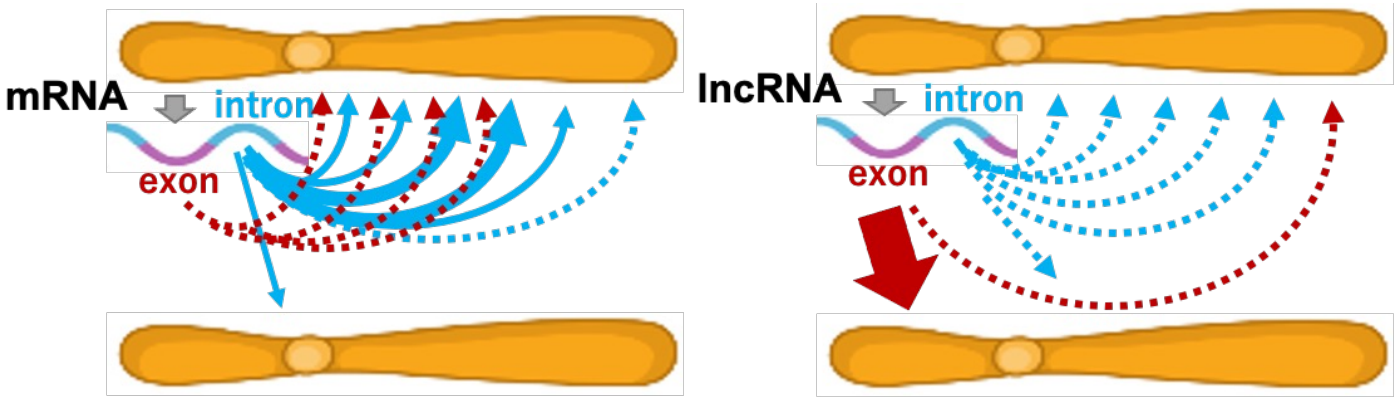


40% trans

Type of interactions in PMA 96 h



68,8% trans



Signals sent through RNAs from gene to other genesand regulatory elements?

Laura Carpen,
Aslihan Karabakack Calvielllo
Rodrigo Pracana, HT

A new type of crosstalk: RNA - genome in the nuclei

Further characterization of functions:
- structural?
- (epi)genome control?

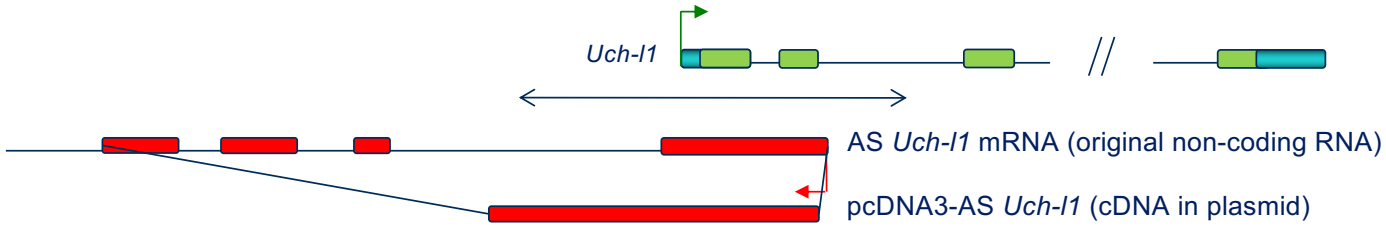
SINEUPs

More unexpected function of lncRNAs and repetitive elements

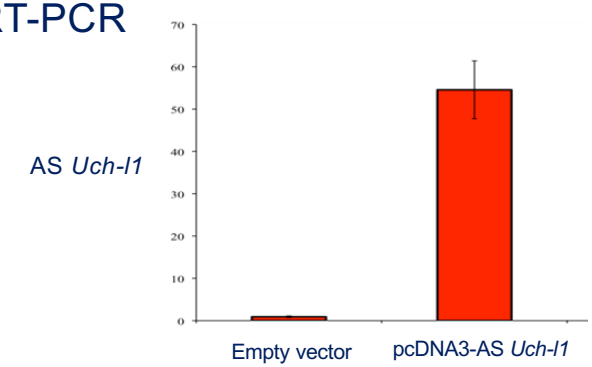
- *COI disclosure*
- *I am co-founder of Transine Therapeutics, a UK company that aims to develop therapeutics based on the SINEUP technology discussed in the presentation. https://www.transinetx.com/*

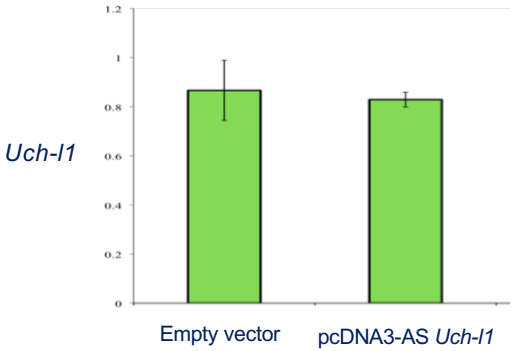
SINEUPs: an important example of antisense RNA function

AS Uch-l1 regulates endogenous UCH-L1 protein expression

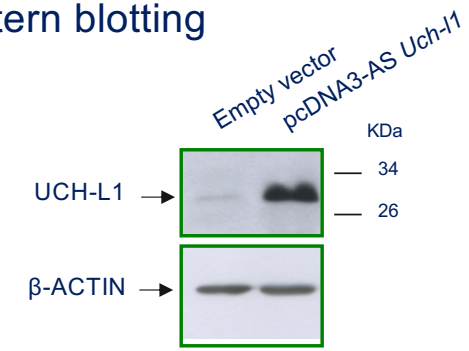


qRT-PCR





Western blotting



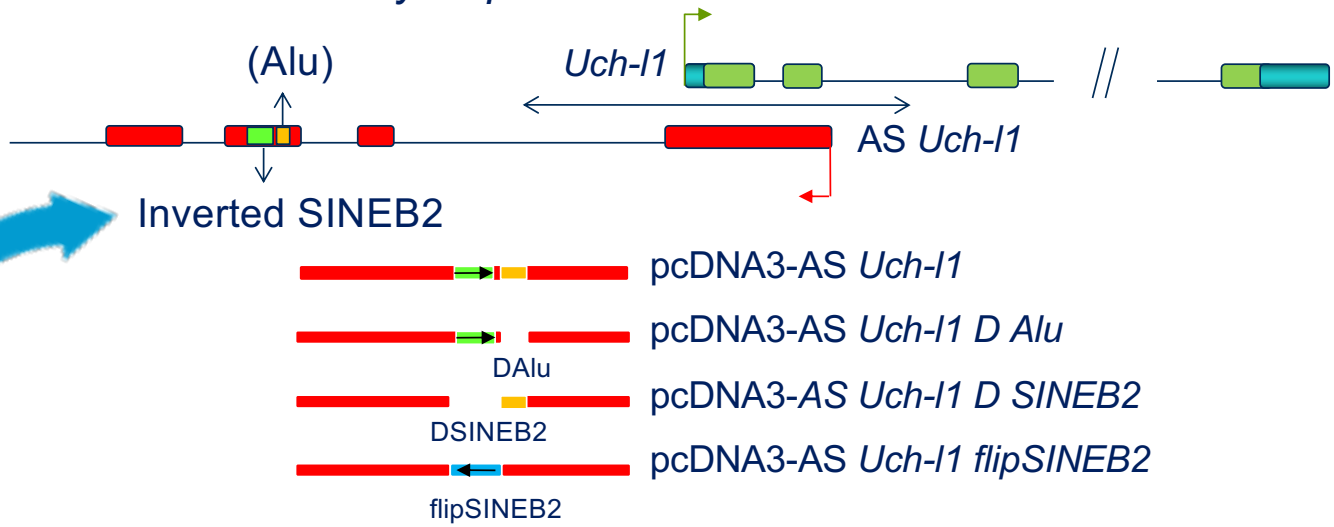
No changes at RNA level

Protein level:
dramatically enhanced!!

Carrieri *et al, Nature* 491, 454 (2012)

SINEUPs: an important example of antisense RNA function

AS Uch-l1 activity requires the inverted SINEB2



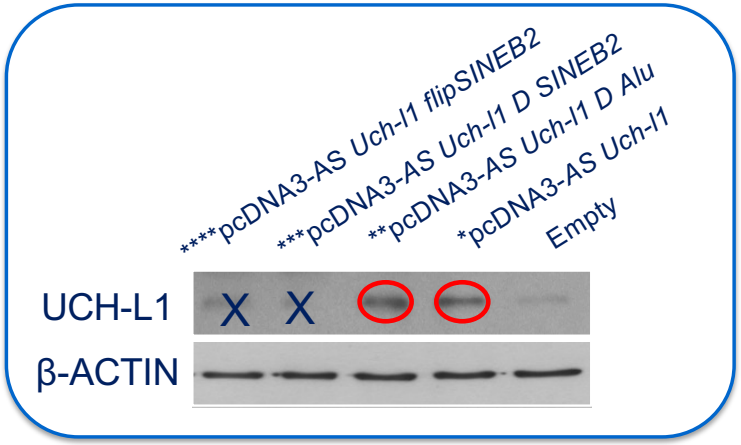
REPEAT MASKER analysis of AS *Uch-l1* sequence

```
  UnnamedSequen      765 GTGC--AGTGCTAGAGGAGGTCAGAAGAGGGCATTGGATCCCCCAGAACT 812
                           --i    iv v     i          i i        ii
C B3#SINE/B2         156 GTGCCTGGTGCCCGCGGAGGCCAGAAGAGGGCGTCGGATCCCCTGGAACT 107

  UnnamedSequen      813 GGAGTTATACGGTAACCTCGTGGTGGTTGTGAACCACCATGTGGATGGAT 862
                           i ------------ i        i  i        i  ---
C B3#SINE/B2         106 GGAGTTACA------------GATGGTTGTGAGCCGCCATGTGGGTG--- 72

  UnnamedSequen      863 ATTGAGTTCCAAACACTGGTCCTGTGCAAGAGCATCCAGTGCTCTTAAGT 912
                         -i  i vvi i   v v      v  v       v             vi
C B3#SINE/B2          71 -CTGGGAATCGAACCCGGGTCCTCTGGAAGAGCAGCCAGTGCTCTTAACC 23

  UnnamedSequen      913 GCTGAGCCATCTCTTTAGCTCC 934
                             ii   i
C B3#SINE/B2          22 GCTGAGCCATCTCTCCAGCCCC 1
```

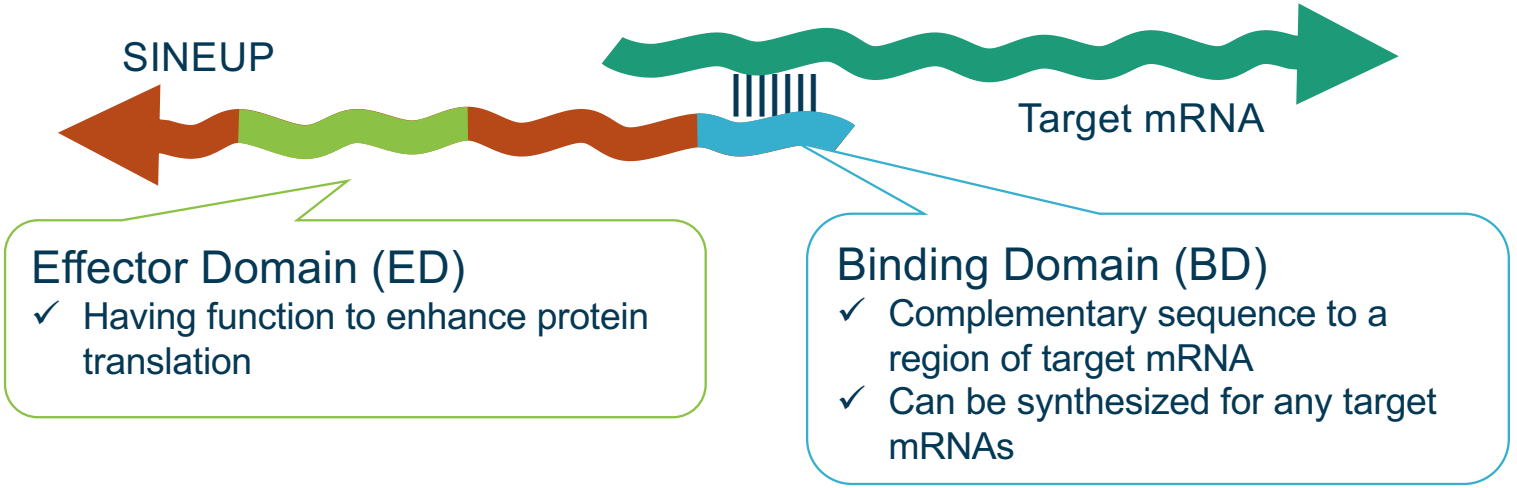


Carrieri *et al, Nature* 491, 454 (2012)

SINEUPs

Antisense lncRNAs for therapy

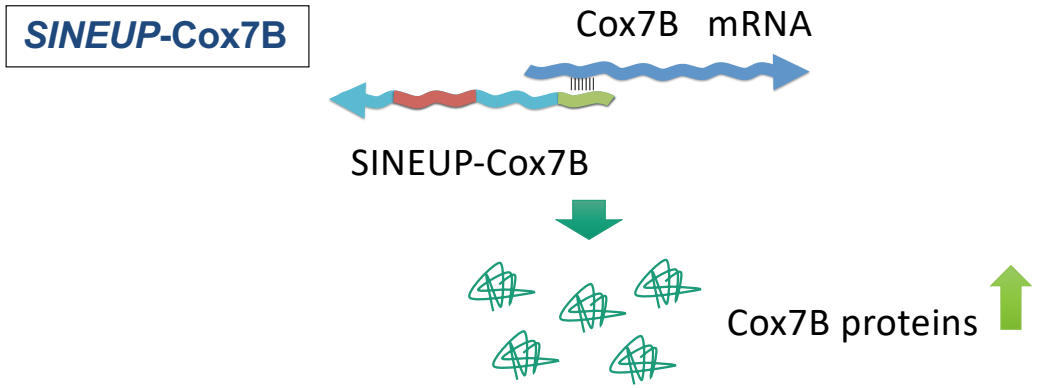
Using SINEUPs (antisense lncRNAs)

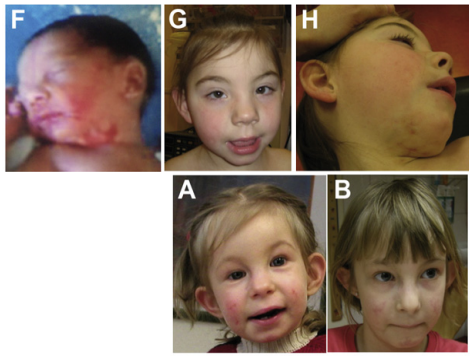


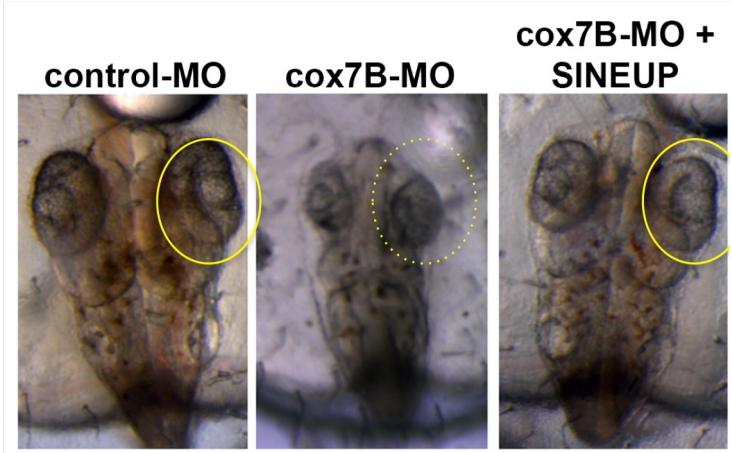
- Customizable design for any proteins
- Up-regulates protein synthesis 2-5 folds (physiological range)
- Acts on endogenous mRNA and exogenous targets

SINEUPs: *in vivo* model of human diseases in Medaka

Microphtalmia with Linear Skin Lesions (MLS)







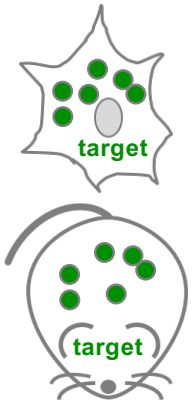
Embryo:	WT	MLS	MLS + SINEUP
Eye:	Normal	Diseased	Rescued ~50%

Indrieri A. *et al.*, *Scientific Reports*, 2016

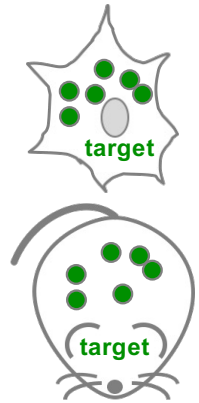
SINEUPs Therapeutics – haploinsufficiencies & others

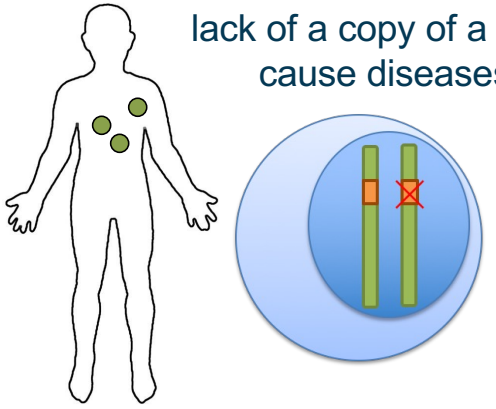
At least 300 haploinsufficiency genes known

(Dang *et al*., European Journal of Human Genetics, DOI: 10.1038/ejhg.2008.111, 2008)

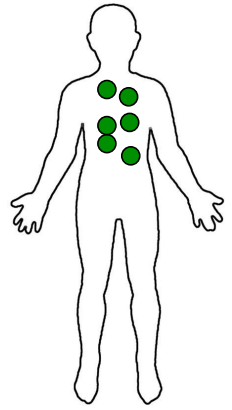


SINEUP-Target





lack of a copy of a gene cause diseases



Healthy

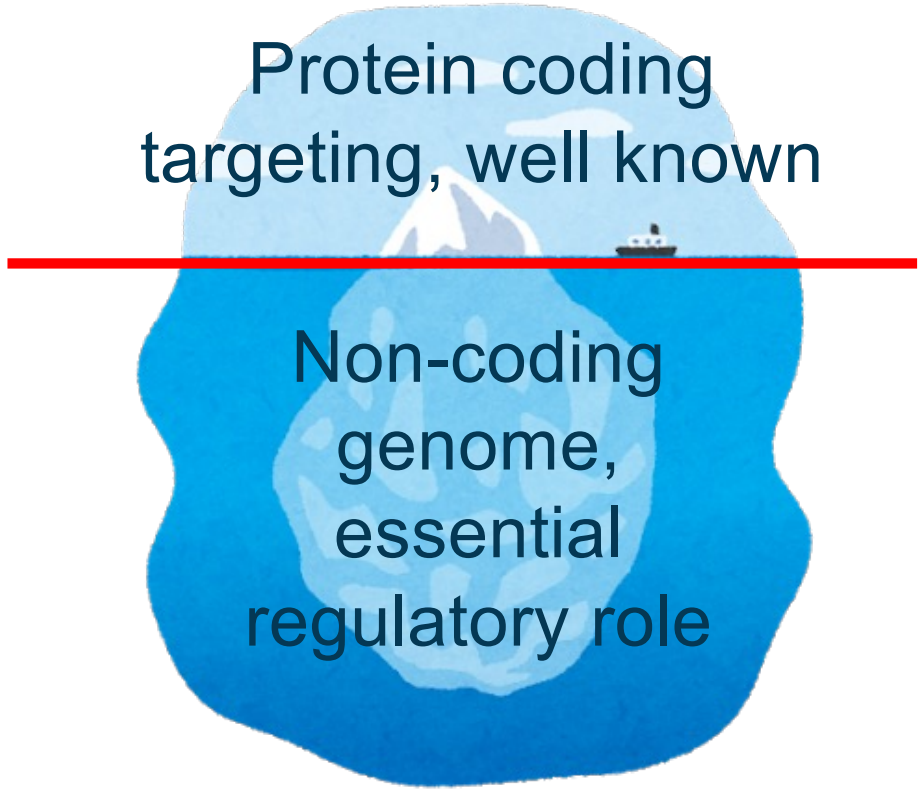
Haploinsufficiencies

Or conditions that require more protein

Therapeutic SINEUPs

Regulating genome activity

- Many lncRNAs have regulatory + structural role, sometimes other functions.
  - Large scale ahead
- We always need novel technologies to answer new questions in gene regulation
  - Including computational approaches to measure large networks
- Common diseases are caused by small unbalances of gene regulation for long time. lncRNA are the new frontier for drug development.



Future opportunities in gene regulation

https://humantechnopole.it/en/

Piero Carninci

Genomics Research Center, Human Technopole, Milan, Italy

RIKEN IMS, Yokohama

- Creating bridges between Japanese and Italian science
- New positions and chances to collaborate

Special thanks to:

RIKEN
Michiel de Hoon
Chung Chau Hon
Jonathan Moody
Takeya Kasukawa
Tsukasa Kouno
Jessica Severin
Masayoshi Itoh
Harukazu Suzuki
Hazuki Takahashi
Harshita Sharma
Masaki Kato
Naoko Toki
Erik Arner
Alessandro Bonetti
Jay W. Shin
Chi Wai (Wallace) Yip
Matthew Valentine
Xufeng Shu
Lokesh Tripathi

Human Technopole
Yoshimi Inaba
Laura Carpen
Marco Gaviraghi
Ilaria Nisoli
Chiara Medaglia
Aslihan Karabacak
Rodrigo Pracana
Magda Bienko
Lorenzo Calviello

Tokyo Metropolitan Institute of Medical Science
Hideya Kawaji

Yokohama City University
Jordan Ramilowski

Harry Perkins Institute of Medical Research
Alistair Forrest

Telethon Kids Institute
Timo Lassmann

Karolinska Institutet
Carsten Daub
Andreas Lennartsson

Univ. Copenhagen
Albin Sandelin
Robin Andersson
Kristoffer Vitting-Seerup

The Roslin Institute
Kenneth Baillie
Tom Freeman
Kim Summers

Univ. Edinburgh
Martin Taylor

Birmingham Univ.
Ferenc Mueller

Imperial College London
Boris Lenhard

Univ. Hosp Regensburg
Michael Rehli

DZNE
Peter Heutink

KAUST
Valerio Orlando

Univ. Melbourne
Christine Wells

Univ. Piedmont
Claudio Santoro
Diego Cotella

TIGEM
Alessia Indrieri
Brunella Franco

Universitá degli Studi di Milano
Beatrice Bodega

IIT Istituto Italiano di Tecnologia
Stefano Gustincich

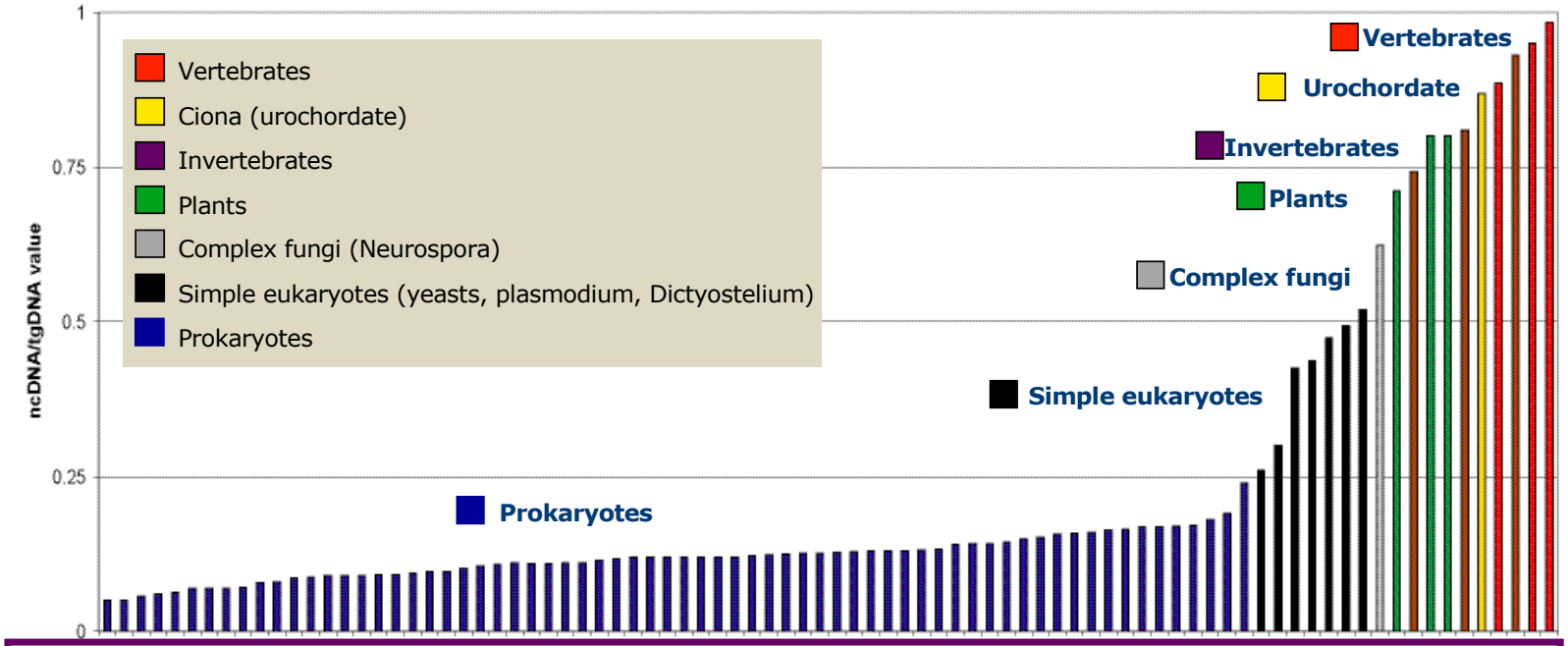
Funding
- Horizon2020,
- ZENCODE-ITN
- MEXT, Japan
- AMED, Japan

Institutional funding
- RIKEN
- Human Technopole

And to many more FANTOM Consortium members, lab members, students, historical collaborators…

Thank you

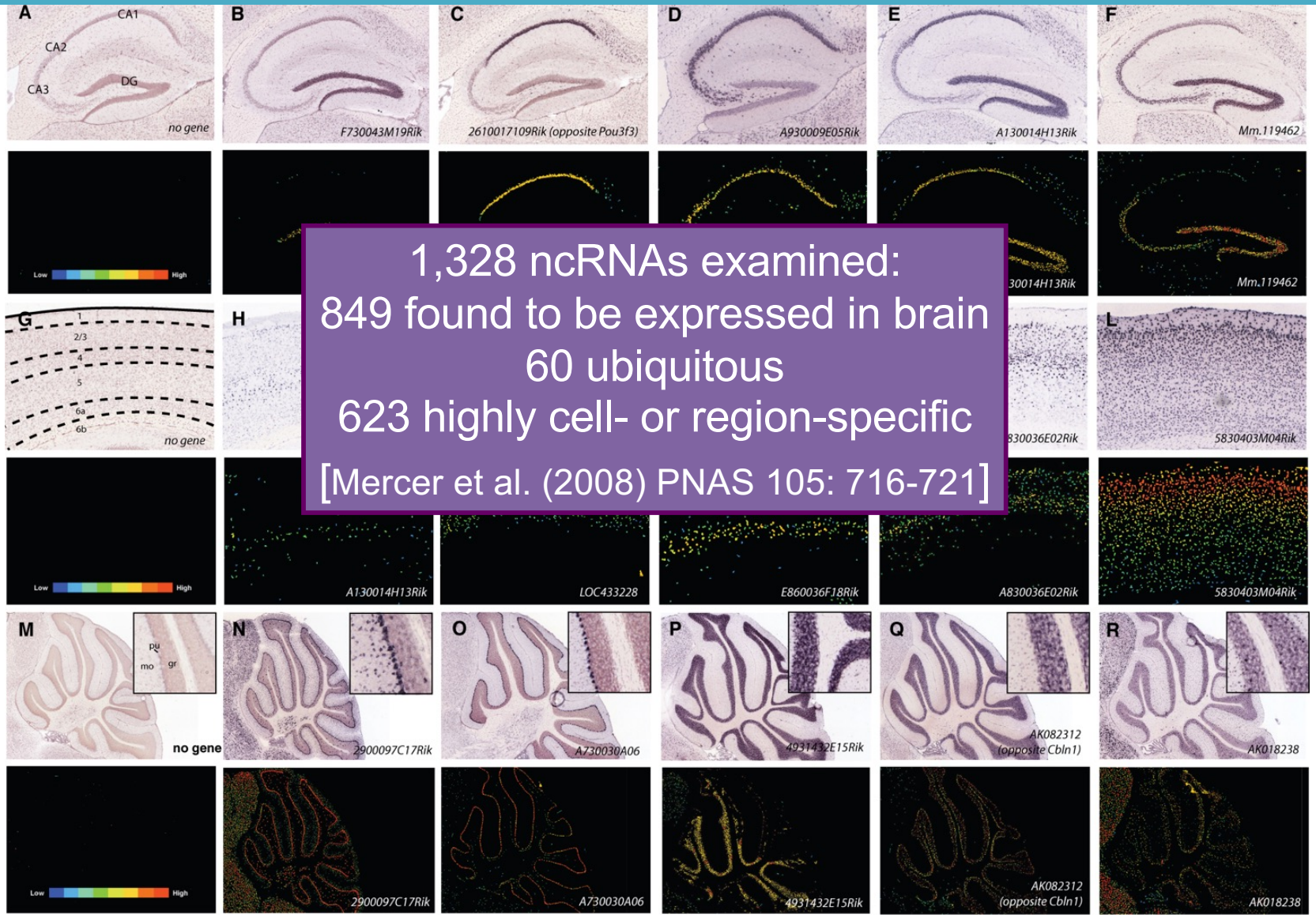
The proportion of noncoding DNA broadly increases with developmental complexity



Irrespective of the extent of non-coding sequences, it is now evident that the vast majority of the genomes of all organisms is transcribed in a dynamic manner in different cells and tissues at different developmental stages.

J.S. Mattick *Nature Reviews Genetics* 5, 316-323 (2004)
R.J. Taft, M. Pheasant and J.S. Mattick, *Bioessays* 29, 288-299 (2007)

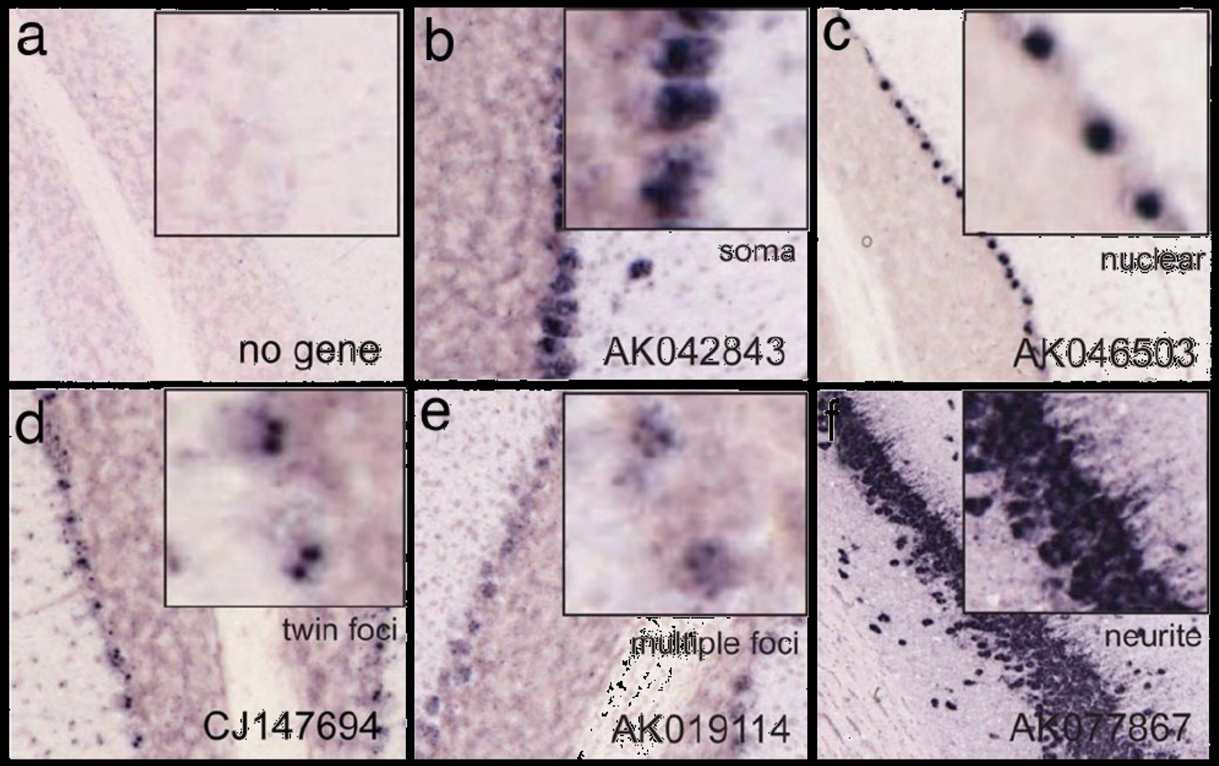
Non-coding RNA expression in mouse brain



1,328 ncRNAs examined:
849 found to be expressed in brain
60 ubiquitous
623 highly cell- or region-specific

[Mercer et al. (2008) PNAS 105: 716-721]

Subcellular localization of ncRNAs



Subcellular localisation of long ncRNAs in Purkinje cells
Subcellular localization ~ putative function

The mRNA-like noncoding RNA Gomafu constitutes a novel nuclear domain in a subset of neurons

Masamitsu Sone[1,2,3], Tetsutaro Hayashi[2], Hiroshi Tarui[2], Kiyokazu Agata[2], Masatoshi Takeichi[2,3] and Shinichi Nakagawa[1,2,*]

[1]Nakagawa Initiative Research Unit, RIKEN, 2-1 Hirosawa, Wako 351-0198, Japan
[2]RIKEN Center for Developmental Biology, 2-2-3 Minatojima Minamimachi, Chuo-ku, Kobe 650-0047, Japan
[3]Department of Cell and Developmental Biology, Graduate School of Biostudies, Kyoto University, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan
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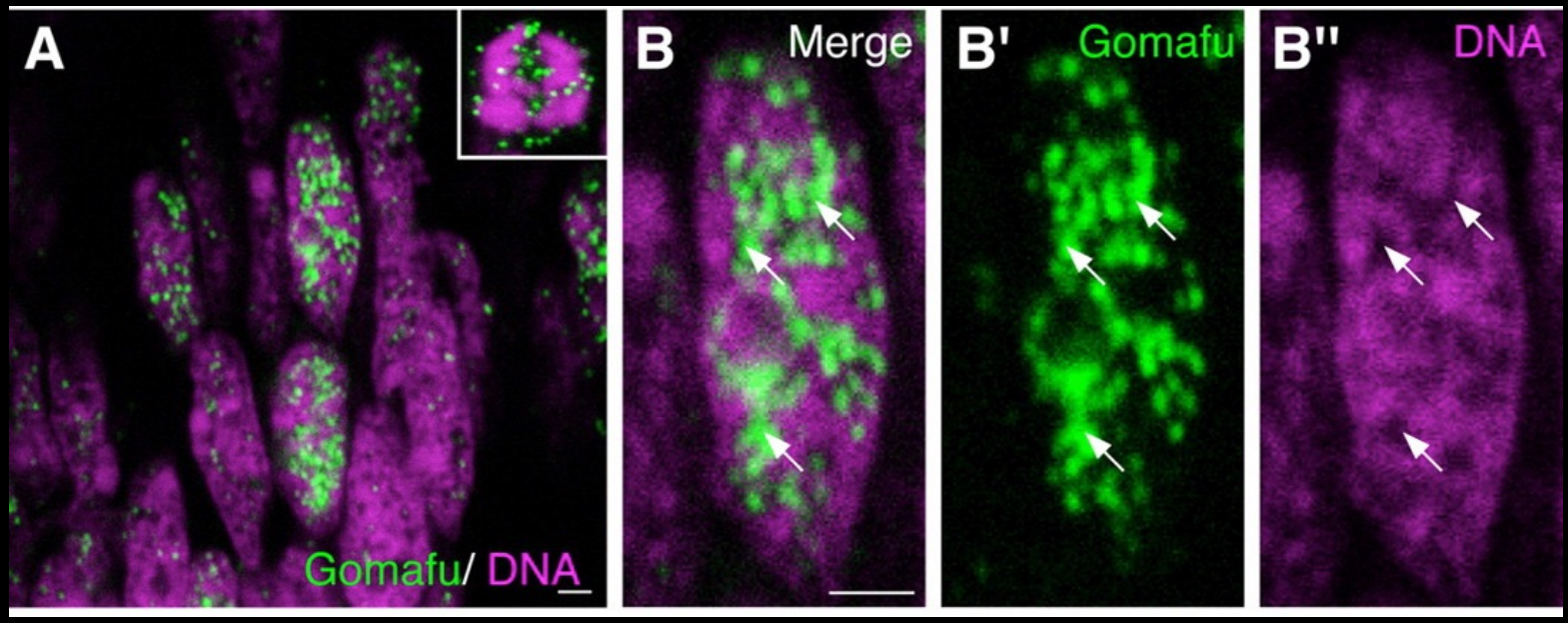
Accepted 21 May 2007
Journal of Cell Science 120, 2498-2506 Published by The Company of Biologists 2007
doi:10.1242/jcs.009357

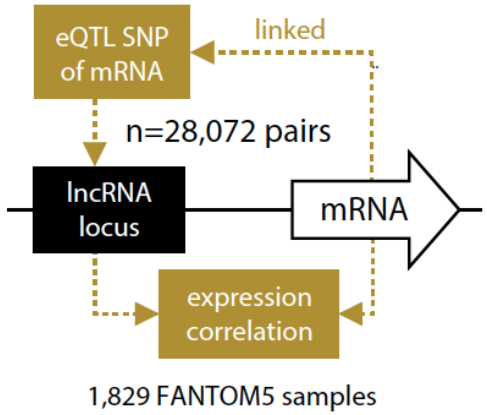


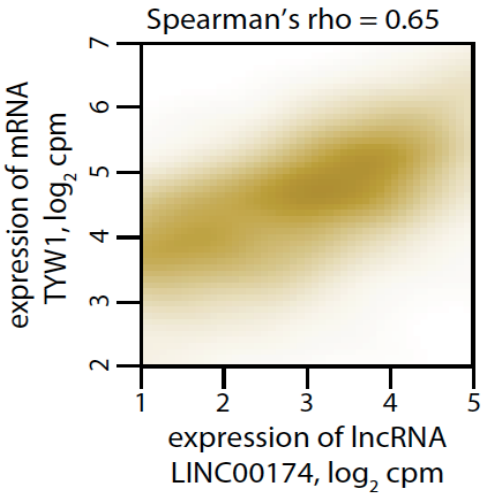
Cell-type-specific lncRNAs implicated in GWAS traits

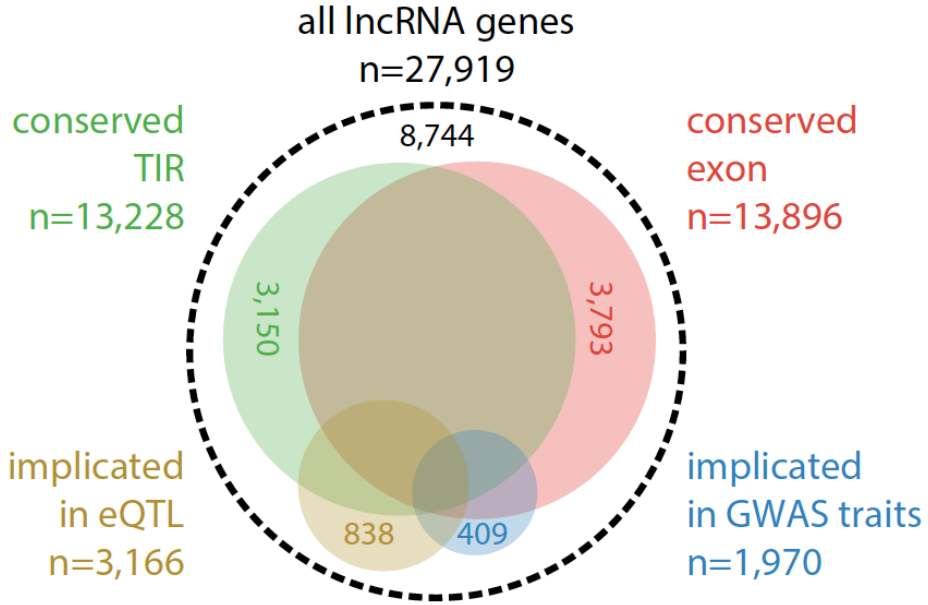
Hon *et al*., *Nature* 543, 199 (2017)

Many lncRNAs with potential function

Co-expression of lncRNA-mRNA pairs linked by eQTL



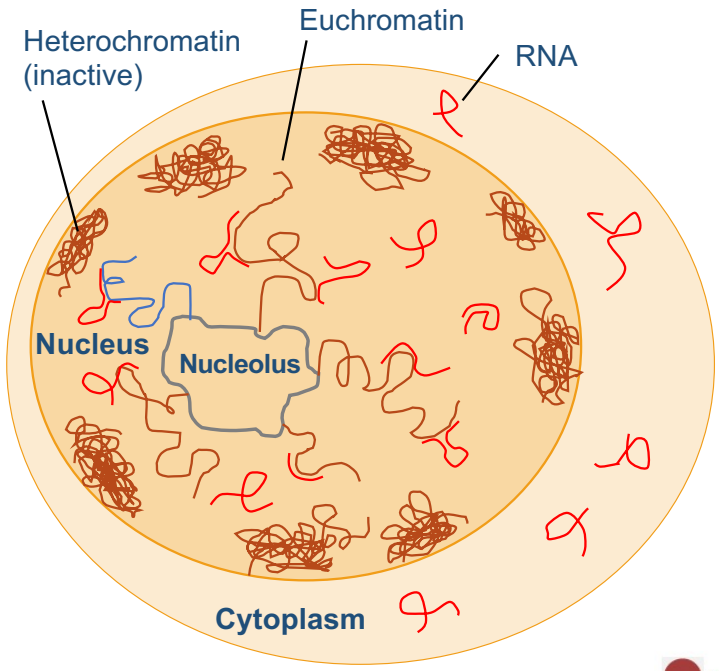


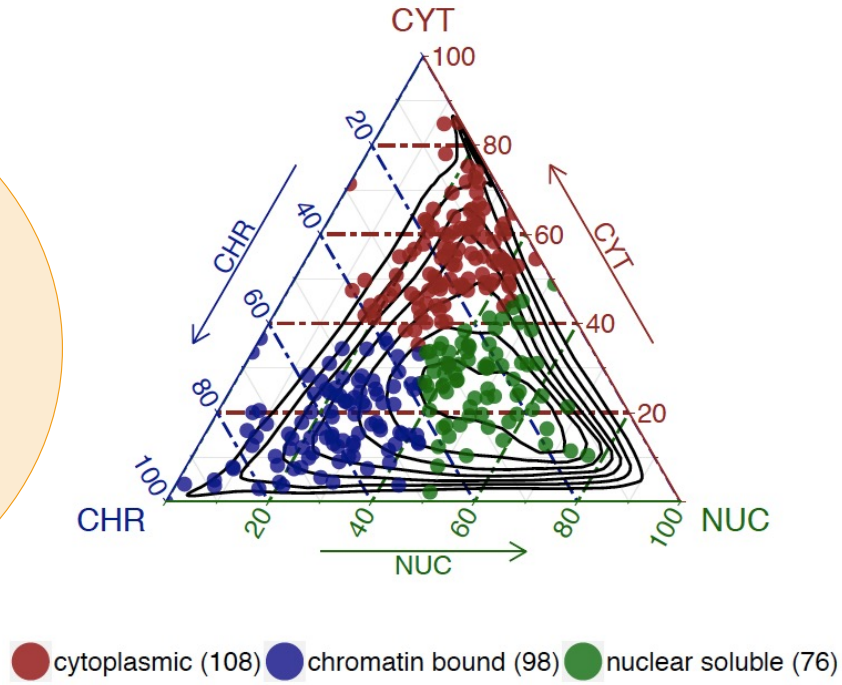


Identified 19,175 potentially functional lncRNAs in human

Hon *et al.*, *Nature* 543, 199 (2017)

Considerations: localization of lncRNAs
And functional interactions





- 64% in the nucleus
  - 37% in chromatin-bound
  - 27% in the nuclear soluble fraction
- 36% in the cytoplasm

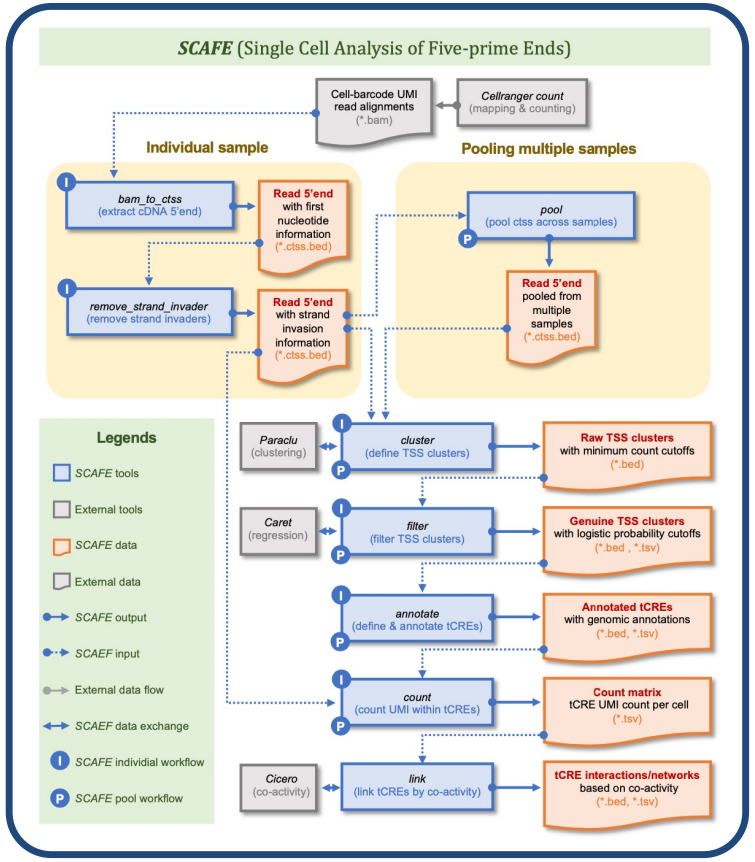
Analyzing tCREs : Gene expression + enhancer activity in one assay

SCAFE : Software to define, quantify and link tCREs from 10x 5'data

Make the most of your 10x 5'data…..for **FREE**!

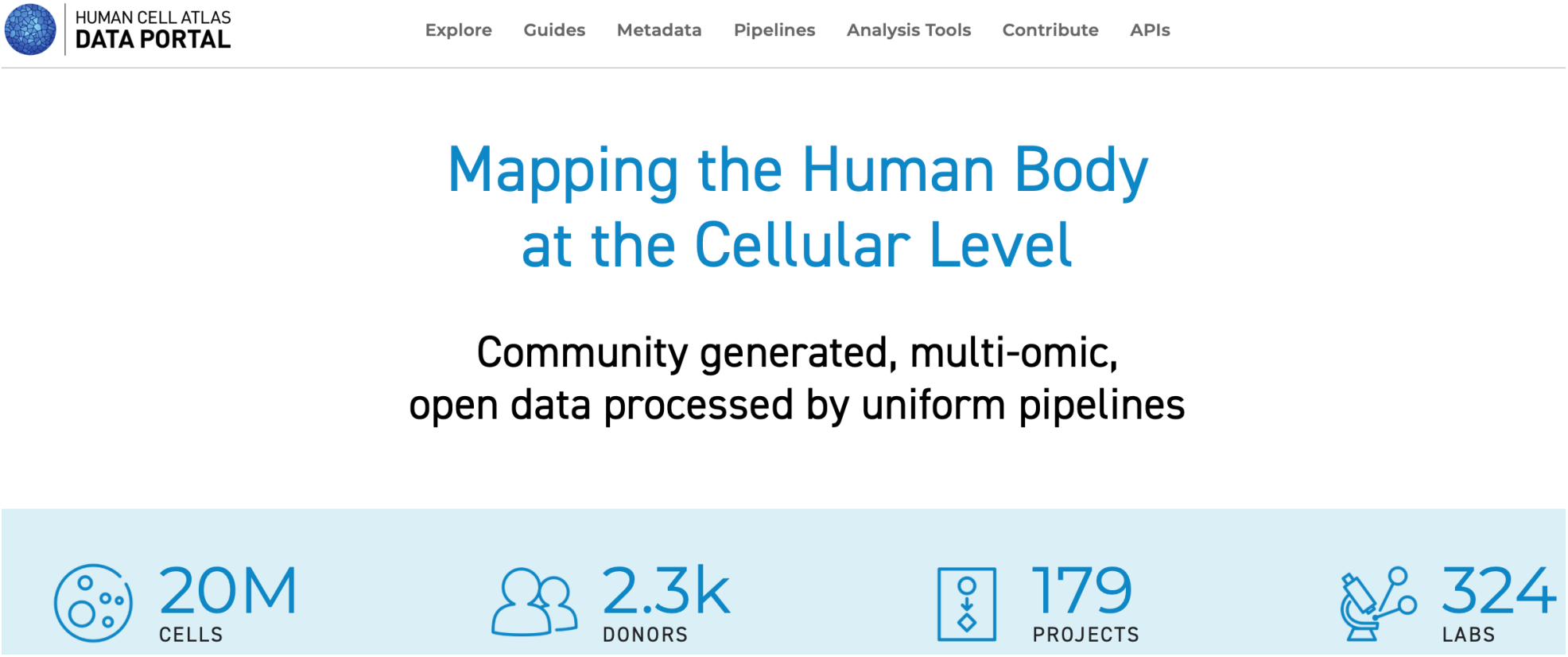
https://github.com/chung-lab/scafe

End-to-end solution for 10x 5'data



Slide courtesy of Chung Chau Hon

Progress in HCA



e.g. Brain: 172 Donors, 466 specimens, 9.9M Estimated cells

Blood: 664 Donors, 2.5k specimens, 2.2M Estimated cells

Immune: 9 Donors, 69 specimens, 274.2k Estimated cells

As of December 1, 2021, https://data.humancellatlas.org