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Biased Allelic Expression in Human Primary Fibroblast Single Cells

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The study of gene expression in mammalian single cells via genomic technologies now provides the possibility to investigate the patterns of allelic gene expression. We used single-cell RNA sequencing to detect the allele-specific mRNA level in 203 single human primary fibroblasts over 133,633 unique heterozygous single-nucleotide variants (hetSNVs). We observed that at the snapshot of analyses, each cell contained mostly transcripts from one allele from the majority of genes; indeed, 76.4% of the hetSNVs displayed stochastic monoallelic expression in single cells. Remarkably, adjacent hetSNVs exhibited a haplotype-consistent allelic ratio; in contrast, distant sites located in two different genes were independent of the haplotype structure. Moreover, the allele-specific expression in single cells correlated with the abundance of the cellular transcript. We observed that genes expressing both alleles in the majority of the single cells at a given time point were rare and enriched with highly expressed genes. The relative abundance of each allele in a cell was controlled by some regulatory mechanisms given that we observed related single-cell allelic profiles according to genes. Overall, these results have direct implications in cellular phenotypic variability.

Introduction

In diploid organisms, the mammalian transcription machinery has the choice of transcribing two alleles. Apart from well-known exceptions in which one allele is known to be exclusively expressed—such as in imprinted genes,^{1,2} X-linked genes,^{3,4} and genes with random "allelic exclusion"^{5–10}—it is unclear whether ongoing transcription of active genes in individual cells occurs simultaneously from two alleles and whether the allele-specific mRNA level is uniform in all cells.

Studies performed on multiple selected genes in various cell types via RNA fluorescence in situ hybridization suggest that only a fraction of alleles are actively transcribed and associated with RNA polymerase II transcription factories.^{11–17} Rare are the genes displaying two detectable transcription spots in a large fraction of the cells. Recent single-cell studies have described pervasive random monoallelic expression of autosomal genes in mouse embryonic progenitors and cultured adult murine fibroblasts.¹⁸ Allele-biased expression at the single-cell level in 15 single cells from Epstein-Barr-virus-transformed human lymphoblastoid GM12878 cells was also recently reported.¹⁹

To investigate the extent of allele-specific transcription of autosomal human protein-coding genes, we used single-cell RNA sequencing (RNA-seq) technology to study 203 single cells from two different human primary fibro-

blast cell lines. By analyzing informative single-nucleotide variants (SNVs), we determined the relative mRNA abundance of each of the two alleles. For most of the actively transcribed genes, our results revealed that one allele was predominantly detected in a single cell at a particular point in time, whereas the second allele was at low levels or undetectable. We observed a stochastic process given that equal numbers of single cells expressed one or the other allele and a minority of single cells expressed both alleles. Interestingly, we detected only a few genes with an equal mRNA level from both alleles in all single cells. Detailed genomic characterization of these "single-cell biallelic" genes revealed that they express high levels of mRNA in a large number of cells. Our study allowed us to explore the highly dynamic and stochastic nature of allele-specific transcription of human autosomal genes.

Material and Methods

Samples

Human newborn primary fibroblast culture (female, UCF1014, GenCord sample collection) was established from umbilical cord tissue obtained from newborns of western European origin.²⁰ Human fetal primary fibroblast culture (T2N) was derived from postmortem skin tissue obtained from "Twin 2 normal" fetuses (16 weeks of gestation, female); see Dahoun et al.²¹ for details. The study was approved by the ethics committee of the University Hospitals of Geneva, and written informed consent was obtained from both parents of each individual prior to the study.

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Cell Growth

Cells were cultured in Dulbecco's modified Eagle's medium Gluta-MAX (Life Technologies) supplemented with 10% fetal bovine serum (Life Technologies) and 1% penicillin-streptomycin-fungizone mix (Amimed, BioConcept) at 37°C in a 5% CO₂ atmosphere. The day before the single-cell-capture experiment, cells were trypsinized (0.05% trypsin-EDTA, Life Technologies) and replated at a density of 0.3 × 10⁶ cells per 100 mm dish.

Single-Cell Capture

Single-cell captures were performed on the C1 Single-Cell Auto Prep system (Fluidigm) with the cell load script 1772x/1773x. Trypsinized cells were counted and sized with the CASY 1 Cell Counter + Analyzer System (Shärfe System). The average size of human primary fibroblasts was 20 μ m (15–25 μ m). A total of 4,500–6,000 dissociated live cells were loaded into the assay well of a primed microfluidic array (C1 Single-Cell Auto Prep array for mRNA sequencing [mRNA-seq, 17–25 μ m], 96 chambers, Fluidigm) according to the manufacturer's protocol. After 30 min of capture procedure, we visualized one by one the 96 chambers by using an inverted phase contrast microscope to annotate the content of the chambers. Only the chambers containing one individual cell were selected. Chambers containing debris or damaged cells were excluded from this analysis.

cDNA Synthesis and Pre-amplification of Single Cells

We performed all cDNA preparations on the C1 single-cell array for mRNA-seq with the C1 Single-Cell Auto Prep system (Fluidigm). We used the SMARTer Ultra Low RNA Kit for Illumina Sequencing (Clontech) for the cell lysis and cDNA synthesis according to the manufacturer's procedure. As recommended, we used the oligo(dT) 3'SMART CDS primer IIA to select for polyA⁺ RNA in a single-cell sample. No RNA extraction was performed; cDNA synthesis was coupled to the cell-lysis procedure. cDNA from single cells was pre-amplified with the Advantage 2 PCR Kit (Clontech) according to the manufacturer's protocol. We used two different scripts: the standard mRNA-seq prep script (1772x/ 1773x, Fluidigm) and a modified version with 12 cycles for the PCR step instead of 22 cycles. The standard mRNA-seq prep script (22 cycles) was as follows: lysis at 72°C (3 min), 4°C (10 min), and 25°C (1 min); reverse transcription at 42°C (90 min) and 70°C (10 min); and PCR at 95°C (1 min), five cycles at 95°C (20 s), 58°C (4 min), and 68°C (6 min), nine cycles at 95°C (20 s), 64°C (30 s), and 68°C (6 min), seven cycles at 95°C (30 s), 64°C (30 s), and 68°C (7 min), and a hold at 72°C (10 min). The modified version with 12 cycles for the PCR step was as follows: lysis at 72°C (3 min), 4°C (10 min), and 25°C (1 min); reverse transcription at 42°C (90 min) and 70°C (10 min); and PCR at 95°C (1 min), two cycles at 95°C (20 s), 58°C (4 min), and 68°C (6 min), six cycles at 95°C (20 s), 64°C (30 s), and 68°C (6 min), four cycles at 95°C (30 s), 64°c (30 s), and 68°C (7 min), and a hold at 72°C (10 min). We harvested the 96 pre-amplified cDNAs from the C1 single-cell array (volume ~ 13 µl) and quantified the cDNA by using the Qubit dsDNA BR Assay Kit (Invitrogen). We assessed cDNA quality on the 2100 Bioanalyzer (Agilent) with the high-sensitivity DNA chips (Agilent). See Table S1 (available online) for details.

Total RNA Extraction from Bulk Cell Samples

On the day of the single-cell capture, 1.5×10^6 cells from the same culture were collected and stored in TRIzol reagent (Invitrogen) at

 $-80^\circ\mathrm{C}.$ Total RNA was isolated according to the manufacturer's protocol.

mRNA-Seq Library Preparation

Single Cells

We used the Nextera XT DNA Kit (Illumina) to prepare 223 mRNAseq libraries for 183 UCF1014 single cells and 40 T2N single cells with 0.3 ng of pre-amplified cDNA according to the manufacturer's instructions. For cDNA samples below the threshold of Qubit detection, the starting material for the library preparation was 1.25 μ l. Additionally, we included six samples from empty chambers and one sample of water instead of cDNA material. For those samples, we took 1.25 μ l. In total, 230 samples were library prepared. For this paper, we retained a total of 203 singlecell samples (163 UCF1014 and 40 T2N) for allele-specific expression (ASE) analysis (see "Gene Quantification and De Novo Assembly" below).

Pool of Single Cells

We prepared two RNA-seq libraries with 1 ng of pooled cDNA as described for the single cells. For the pre-amplified cDNA (12 cycles), we took 8 μ l of 78 single-cell cDNAs that we pooled. Because of the low concentration, we precipitated the cDNA pool with NaAc (3M [pH 5.2]) and 100% EtOH and then washed it with 70% EtOH. For the pre-amplified cDNA (22 cycles), we took 2 μ l of 78 single-cell cDNAs. No precipitation step was necessary because the cDNA concentration of this pool was sufficient enough for library preparation.

Bulk TruSeq

We prepared two libraries with 500 ng of total RNA by using the TruSeq RNA Kit (Illumina) according to the manufacturer's instructions.

Bulk Nextera

We reverse transcribed 10 ng of total RNA to cDNA by using the SMARTer Ultra Low RNA Kit for Illumina Sequencing (Clontech). The PCR amplification step was conducted with the Advantage 2 PCR Kit (Clontech) with 12 PCR cycles according to the manufacturer's instructions. Two libraries were prepared with 1 ng of pre-amplified cDNA with the Nextera XT DNA Kit (Illumina) according to the manufacturer's instructions.

Whole-Genome Sequencing

Library Preparation

Cells were harvested on the day of the single-cell capture. Genomic DNA was extracted with the QIAamp DNA Blood Mini Kit (QIAGEN) according to the manufacturer's instructions, including for the RNase treatment. Purified genomic DNA (100 ng) was electrophoresed on a 0.8% agarose gel for quality assessment. We quantified the genomic DNA concentration by using the Qubit dsDNA BR Assay Kit (Invitrogen). Genomic DNA libraries were prepared with the TruSeq DNA Kit (Illumina). The starting amount of material was 1 μ g of genomic DNA sheared with Covaris S2 to fragments 300–400 bp in size.

Sequencing

Libraries were sequenced on two lanes for UCF1014 samples and on three lanes for T2N samples. In brief, we used the Burrows-Wheeler Aligner (v.0.5.9-r16) to align the sequencing reads to the human reference genome (UCSC Genome Browser GRCh37/ hg19). We used SAMtools v.0.1.18 to remove paired-end duplicate reads and pile up the remaining reads. SNVs were called with BCFtools v.0.1.17.

RNA-Seq

Libraries were sequenced on an Illumina HiSeq2000 machine as paired-end 100 bp reads. Demultiplexed fastq files were obtained with the Illumina CASAVA v.1.8.2 software and processed by our in-house pipeline running at the Vital-IT High Performance Computing Center of the Swiss Institute of Bioinformatics.

The two bulk TruSeq libraries were run on one lane. The two bulk Nextera libraries were run on one lane. The two pools of single cells were run on one lane. The single-cell libraries were multiplexed 12 or 16 libraries per lane (see Table S1).

Spike-In Experiment

The spike-in mixture contained 92 External RNA Control Consortium (ERCC) synthesized RNAs (Ambion, Life Technologies). This mixture was added in the lysis buffer during a single-cell-capture preparation with a final dilution of 1:40,000. Both ERCC spike-ins and single-cell mRNA-seq libraries were sequenced simultaneously for 12 samples (50 bp, paired end). The absolute number of spike-in molecules was calculated according to the known concentration of each spike-in. Given that we knew the volume of the chamber (9–10 nl) and the dilution ($40,000\times$) of the spike-in molecules, we derived the expected number of spike-in molecules per chamber.

RPSM Calculation

RPSM stands for reads at a single-nucleotide position per sequencing read length (in kb) and per million mapped reads. The formula for RPSM is $(10^6 \times A) / (B \times C)$, where A is the number of mappable reads at a nucleotide position, B is the total number of mappable reads of the sample, and C is the sequencing read length (in kb; C = 0.199).

Read Mapping for RNA-Seq Samples

We employed the RNA pipeline from gemtools v.1.6.2 to map RNA-seq reads. For alignment to the human reference genome sequence (GRCh37/hg19, including the herpes virus sequence), we used the GEM mapping suite²² to first map and subsequently split map all reads that did not map entirely. The mapping pipeline and settings can be found on the GitHub website (see Web Resources).

The GEM output format was converted to BAM format with the following mapping quality scores and flags. (For reference, MAPQ is the Phred-scaled mapping quality score, XT is the mapperdefined tag, U is the number of unique matches, R is a perfect tie, and NM is the number of total mismatches [read 1 + read 2]. See further details of flag information in the SAMtools documentation in the Web Resources.)

- 1. Matches that are unique and do not have any subdominant match: 251 \geq MAPQ \geq 255, XT = U
- 2. Matches that are unique and have subdominant matches but a different score: $175 \ge MAPQ \ge 181$, XT = U
- 3. Matches that are putatively unique (not unique but distinguishable by score): $119 \ge MAPQ \ge 127$, XT = U
- 4. Matches that are a perfect tie: $78 \ge MAPQ \ge 90$, XT = R

Furthermore, the NM flag contains the number of total mismatches (read 1 + read 2). In the analysis, we used reads in categories 1 and 2 (MAPQ \geq 150).

ASE Analysis

ASE analysis was performed as in Lappalainen et al.²³ In brief, we considered heterozygous sites obtained from wholegenome sequencing with DNA reads supporting both alleles. We used a minimum site quality call of 200. We excluded sites susceptible to allelic mapping bias, namely (1) sites with 50 bp mappability < 1 according to the UCSC mappability track (implying that the 50 bp flanking region of the site is not unique in the genome), and (2) sites where overlapping simulated RNAseq reads showed a >5% mapping difference between those that carried the reference allele and those that carried the non-reference allele (see the methods in Lappalainen et al.²³).

In all analyses, we only used uniquely mapped RNA-seq reads (GEM mapping quality > 150) and sites with base quality > 20 and support from at least 16 reads. Using information from SAMtools (v.0.1.19) mpileup,²⁴ we obtained for each site and each sample the number of reads mapping in the reference, the number of alternative alleles, and the sum of both. Each site was then annotated with the overlapped genomic feature in GENCODE annotation v.15 or the novel exons from the de novo assemblies of each sample. For each site, the number of single cells (and non-single cells) where the site was assessed was also counted. The distribution of allelic ratios for all samples is reported in Figure S9.

Gene Quantification and De Novo Assembly

We used the software Cufflinks (v.2.1.1)^{25,26} with default parameters and GENCODE v.12 as a reference annotation.²⁷ On the basis of Cufflinks transcript (170,086) quantifications, we selected for further analysis single cells that passed the arbitrary threshold of 12,000 transcripts expressed at FPKM (fragments per kilobase of exon per million reads mapped) > 0.3. We retained 163 UCF1014 single-cell samples expressing an average of 15,807 transcripts (the remaining samples expressed an average of 4,998 transcripts). Additionally, for each sample we performed de novo assembly to identify novel transcripts (Figure S4) without using the reference annotation. We then used the program cuffcompare to compare the assembled transcripts with the GENCODE reference annotation (v.15). Finally, for the four bulk RNA samples, we merged the four assemblies into a merged bulk RNA assembly. We compared each single-cell de novo assembly against the merged bulk RNA assembly to identify novel single-cell-specific transcripts. The program intersectBed from bedtools²⁸ was used for this last comparison.

Results

Human newborn primary fibroblasts (UCF1014, GenCord) and human fetal primary fibroblasts (T2N) were cultured, and hundreds of individual cells were captured with the C1 microfluidic system (Fluidigm). We conducted independent experiments that differed by the day of the cell capture and the number of PCR cycles used to pre-amplify the cDNA from individual cells (Figure 1; see Material and Methods). We performed 22 PCR cycles (standard) and 12 PCR cycles in order to test for PCR amplification bias. We sequenced RNA libraries from 163 UCF1014 single cells (98 bp, paired end) to an average depth of 36 million reads (22 PCR cycles) and 16 million reads (12 PCR cycles)



samples was on average 136 and 251 million reads, respectively (Table S1;

Figure S2).

To investigate the ASE at the singlecell level, we performed wholegenome sequencing of UCF1014 samples (26-fold coverage on average; Figure 1) in order to detect the majority of the heterozygous sites. After rigorous filtering, we calculated allelic ratios as the number of reads mapped to the reference allele divided by the total number of reads covering heterozygous SNVs. The main limitation of a single-cell RNA-seq approach is the accurate detection and quantification of two alleles for weakly transcribed genes.¹⁸ Thus, we devised a metric for the analysis by implementing a normalized read number at a nucleotide position, namely RPSM (see Material and Methods). This measure is preferable to RPKM (reads per kilobase of exon per million reads mapped) or FPKM measures because it is not dependent on the coverage of the transcript and it accurately reflects the abundance of the transcript at a specific nucleotide position and still allows comparison across samples.

Across 163 single cells from UCF1014, we analyzed 83,576 unique hetSNVs with a coverage \geq 16 reads at the SNV position. Interestingly, 7.46% of hetSNVs were located in intergenic regions, whereas 68.27% were found within annotated exons (Figure S4). We used Cufflinks to

(Table S1; Figures S1 and S3). In addition, 40 single cells from T2N were RNA sequenced to a similar depth and used as a replicate sample. We also sequenced four bulk RNA samples generated from 1.5 million cells and two in-vitro-pooled cDNA samples obtained from 78 singlecell cDNAs each (Figure 1). The four bulk RNA samples were prepared from the two different primary fibroblast lines (UCF1014 and T2N) according to two different library procedures: (1) SMARTer Ultra Low RNA Kit (Clontech) for cDNA synthesis followed by Nextera library construction (Illumina) and (2) TruSeq RNA Sample Preparation Kits (Illumina). Each in-vitro-pooled cDNA sample was made from 78 pre-amplified cDNAs (22 or 12 PCR cycles) obtained from 78 different single cells (Figure 1). The total number of reads obtained for the bulk RNA and pooled conduct a de novo assembly of transcripts (see Material and Methods) and revealed novel exons specific to single cells and not previously annotated. In total, we retained 9,154 GENCODE genes and 3,875 novel exons specific to single cells for further analysis.

A main challenge was to identify and control for technical noise that could mask genuine biological cell-to-cell allelic expression differences. We carried out a spike-in experiment to assess how our platform performed on synthetic control ERCC RNAs²⁹ to quantify the allelic amount at a single nucleotide position. We concluded that a sensitivity threshold set at 20 RPSM was appropriate for our study objectives (Figure S5). By filtering out sites with fewer than 20 RPSM, we set up the detection threshold at eight molecules per site with a sensitivity of 87%.



Figure 2. ASE in Single Cells

The histograms show the frequency distribution of the allelic ratio (reference reads per total reads) of 35,763 hetSNVs (\geq 20 RPSM) in 163 single cells (UCF1014 sample), bulk cell samples, and the pool of single-cell samples.

One Allele Is Predominantly Detected in Single Cells

We predominantly detected one transcribed allele per interrogated hetSNV of UCF1014 (n = 35,763, RPSM \geq 20); 76.4% of the hetSNVs displayed an allelic ratio between 0–0.2 and 0.8–1 in 163 single cells (Figure 2). The ratio of single cells expressing one allele to single cells expressing the second allele for all SNVs examined was 49:51. This suggests a stochastic allelic usage, which we confirmed by examining the bulk samples made of 1.5 million cells and samples obtained from an in vitro pool of 78 single cells. Indeed, bulk samples displayed biallelic expression (allelic ratio = 0.2-0.8) for 98.3% of the interrogated hetSNVs $(n = 545, RPSM \ge 20; Figure 2)$. We obtained the same results from an in vitro single-cell pool sample made of 78 individual cDNAs showing 97.7% of interrogated hetSNVs $(n = 480, RPSM \ge 20)$ with two transcribed alleles (Figure 2). The skewed monoallelic distribution observed in single cells in a given time point was independent of the number of reads per hetSNV (Figure 3A; Figure S6). Furthermore, our findings were apparently not affected by a bias introduced by the number of PCR cycles given that preparation of single-cell cDNAs with either 12 or 22 PCR cycles revealed

similar patterns (Figure 3B). Additionally, the results remained largely unchanged after we removed duplicate reads from the analysis (Figures S7 and S8).

We further compared our experimental data to an in-silico-pooled data set. For that, we created an in silico pooling that we derived by averaging the allelic ratios for hetSNVs detected in more than 82 cells (50%). This in silico pooling recapitulated the signal from the in vitro single-cell pool sample (Pearson correlation of 0.86, Figure 3C). Similar results were obtained when we compared the in silico pooling with the bulk sample (Pearson correlation of 0.72; Figure 3C).

In an attempt to validate our findings in a second individual, we used the same method to RNA sequence 40 single cells from another human primary fibroblast female cell line (T2N; Figure 3D). The allele-specific analysis revealed comparable results such that 65.8% of hetSNVs (n = 16,075) expressed only one detectable allele (allelic ratio = 0–0.2 and 0.8–1) and 34.2% of hetSNVs expressed two detectable alleles (allelic ratio = 0.2–0.8; Figure 3D). Our results, in agreement with others,^{18,19} reveal that snapshot detection of the majority of the protein-coding actively transcribed genes is skewed toward one allele per individual cell. We also describe a random (i.e., non-parental-origin-specific) allelic usage, supporting the stochastic nature of gene transcription.

Stochastic Allelic Expression of Adjacent hetSNV Pairs Is Highly Correlated

We investigated whether two adjacent hetSNVs (RPSM \geq 20) located in the same gene are likely to be transcribed from the same allele. To do so, we estimated the haplotypes of our sample with SHAPEIT³⁰ by using the phase information contained in sequencing reads and the 1000 Genomes phase 1 haplotypes as a reference.³¹ Then, we binned every pair of consecutive hetSNVs according to their physical distance (bp) and evaluated whether the allelic ratios agreed with their underlying haplotypes. The relationship between distance and allele expression is reported in Figure 4. We provide evidence that allele expression is highly correlated over the closest adjacent hetSNVs and that this correlation begins to drop from 1 kb to reach 0 at 100 kb. The 1 kb distance corresponds to the average size of cDNA products and might explain this sudden decline (data not shown). It follows that hetSNVs belonging to the same gene are transcribed from the same allele in a single cell. Inversely, it is likely that hetSNVs located on two consecutive genes are not transcribed from the same haplotype in a single cell. Remarkably, compared to hetSNVs in autosomal sites, hetSNVs located on the X chromosome exhibited a higher correlation over longer distances (Figure 4) and a random monoallelic pattern (Figure S10). These results are consistent with the process by which X chromosome inactivation leads to one transcriptionally silenced X chromosome in each 46,XX somatic cell and would thus result in higher allelic correlation across genes on the X chromosome.



Figure 3. Estimation of the Technical Biases

(A) Frequency-distribution histograms of the allelic ratio (reference reads per total reads) according to the read coverage at hetSNV position (35,763 hetSNVs, 163 UCF1014 single cells, \geq 20 RPSM).

(B) Frequency-distribution histograms of the allelic ratio of single cells (35,763 hetSNVs, UCF1014 single cells, \geq 20 RPSM), for which the cDNA pre-amplification was performed with 22 or 12 PCR cycles.

(C) Pairwise scatter plots for comparison of the allelic ratio between in silico pooling of single cells and experimental pooling (left panel) or bulk samples (right panel). Listed in the panel are the Pearson correlation coefficients (r) and the numbers of comparisons (n). The diagonal is plotted in red.

(D) Independent experimental replication. Frequency-distribution histograms of the allelic ratio of single cells from T2N single-cell samples (40 single cells, 16,075 hetSNVs, \geq 20 RPSM).

Distinct Single-Cell Allelic Pattern

To illustrate the diversity of allelic expression variation across single cells, we selected all genes (n = 568, detected in more than 40 cells) with at least one hetSNV located in coding regions and/or UTRs (RPSM \geq 20) (Figure 5; Figure S11). As anticipated, genes on the X chromosome (C1GALT1C1 [MIM 300611], ACOT9 [MIM 300862], ZFX [MIM 314980], LAMP2 [MIM 309060], RP11-622K12.1, and TSPAN6 [MIM 300191]) exhibited monoallelic expression in single cells. As a result of lyonization of gene expression,³² cells randomly express only one allele because the second allele is silenced. Consequently, a subset of the cells expressed one allele, and the other subset expressed the second allele. We detected only one or very few cells expressing both alleles. A similar feature was observed for three autosomal genes (RAD52 [MIM 600392], BCLAF1 [MIM 612588], TRBC2 [MIM 615445]), for which fewer than 5% of cells displayed biallelic expression (allelic

ratio = 0.2-0.8). Interestingly, we observed 32 autosomal genes with a stochastic single-cell skewed allelic expression, i.e., for which fewer than 10% of cells expressed one type of allele and the remaining cells expressed either the second allele or both alleles (<80% of cells with allelic ratio = 0.2-0.8). As an example, Figure 5 schematically shows the profile of some of those genes (VAMP3 [MIM 603657], CNN3 [MIM 602374], RP11-166D19.1, ATL3 [MIM 609369], RAD52 [MIM 600392], C12orf75, FAM101B [MIM 615928], CCDC80, SPCS3, WDR36 [MIM 609669], BCLAF1 [MIM 612588], and TRBC2 [MIM 615445]). Next, we observed a class of 16 genes (MINOS1, CAP1, ITGB1 [MIM 135630], CD44 [MIM 107269], NACA [MIM 601234], DAD1 [MIM 600243], UQCR11, PPP1CB [MIM 600590], SRSF6 [MIM 601944], RPS21 [MIM 180477], SSR3 [MIM 606213], SPARC [MIM 182120], SRSF3 [MIM 603364], CALU [MIM 603420], TOMM7 [MIM 607980], and COL1A2 [MIM 120160]) for which



Figure 4. Relationship between hetSNVs Located within Genes or in Two Different Genes

Scatter plots of allelic-ratio correlation versus genomic distance between two adjacent hetSNVs. hetSNVs located in the same autosomal genes are in green, hetSNVs located in different autosomal genes are in orange, and hetSNVs located on the X chromosome are in blue.

more than 90% of cells expressed both alleles (allelic ratio = 0.2-0.8). We termed those genes "single-cell biallelic genes" because both alleles were expressed in almost all individual cells.

Transcription Rate and ASE in Single Cells

We asked whether the total transcript level could correlate with ASE in single cells. We quantified the steadystate mRNA level of detectable genes in 163 single cells from UCF1014 by averaging the RPSM values for the hetSNVs located in coding regions and/or UTRs. We plotted the minimum allelic ratio against mRNA level (RPSM average) for all detectable genes (Figure 6A). The results indicated that genes with higher mRNA levels were enriched in the single-cell biallelic genes described above (see Figure 6A). Analysis of functional-pathway enrichment was performed with DAVID (Database for Annotation, Visualization, and Integrated Discovery)³³ on genes with high mRNA levels (average RPSM per gene > 90). Genes associated with cellular function and maintenance were enriched with gene-ontology terms related to response to nutrients, protein-complex assembly, the ER, organelle membranes, catalytic activities, and others (modified Fisher exact p value < 0.05; Figure 6A). This is consistent with the fact that constitutively expressed genes, essential for the maintenance of basic cellular functions, generally maintain constantly high mRNA levels across cells.

Because steady-state mRNA abundance is determined by both the rate of transcription and mRNA decay, we used

published RNA half-life data from HeLa cells to examine the relationship between the single-cell allelic ratio of gene expression and the half-life of these transcripts.³⁴ Tani et al. developed an inhibitor-free method named BRIC-seq (5'-bromo-uridine-immunoprecipitation chasedeep sequencing) to determine mRNA decay. We selected the genes commonly expressed by the two different data sets and further divided the sites into three groups according to their single-cell allelic ratio. Compared to the single-cell biallelic group (allelic ratio = 0.2-0.8), the single-cell monoallelic group (allelic ratio <0.2 or >0.8) contained sites with significantly shorter half-lives (p value $< 2 \times 10^{-16}$, ANOVA; Figure 6B). This finding suggests that genes detected as biallelic in single cells are more likely to have a longer RNA half-life. We then tested the relationship between transcriptional initiation rates of genes in single cells. Thus, we introduced in our analysis Cap Analysis of Gene Expression (CAGE³⁵) sequencing data from nuclear-enriched RNAs of human dermal fibroblasts of fetal origin (HDF-f).³⁶ CAGE technology on nuclear-enriched RNA allows reliable transcription start site (TSS) identification and transcript quantification of mostly nascent messenger RNAs. We identified 2,572 nuclear CAGE clusters from HDF-f overlapping TSSs of proteincoding genes expressed in our single-cell RNA-seq data. Figure 6B shows a correlation between the initiation rate (determined by nuclear CAGE tags) and ASE. Sites with monoallelic expression show a lower initiation rate than do biallelic sites (p value $< 2 \times 10^{-16}$, ANOVA).

Discussion

The transcriptional activity of alleles is of interest because it determines the steady-state level of mRNA of the cell and the nature of transcripts available for translation. By analyzing single-cell transcriptomes, we and others have confirmed that gene transcription is stochastic and extremely variable among cells.^{18,19,37,38} Our main observation suggests that, at any point in time, a cell contains mostly transcripts from one allele (76.4% of hetSNVs with >20 RPSM). This stochastic monoallelic expression at the single-cell level is independent of the parent of origin of the allele, given that we randomly detected one or the other allele in each single cell. Our results are in agreement with recent studies in human lymphoblastoid lines and mouse embryonic progenitors and cultured fibroblasts,^{18,19} confirming the existence of an essential process of eukaryotic cells.

Does this necessarily mean that the cellular machinery transcribes one allele at a time? Transcription occurs as either a constitutive or an episodic bursty mode.^{39,40} For most eukaryotic genes, transcription in mammals is discontinuous and occurs in transcriptional bursts interspersed by refractory periods of gene inactivity.^{41–43} It has been demonstrated that transcriptional bursting is gene specific, and thus the frequency and amplitude of the bursts



Figure 5. Pattern of Allelic Expression in Single Cells

We selected genes for a representative view of the allelic expression in single cells. A complete overview is given in Figure S11. The index bar indicates the color coding for the allelic-ratio values (reference reads per total reads). Vertical dashed lines delineate a set of 20 single cells.

and intervals of gene inactivity modulate the extent of temporal variations in mRNA in a cell.⁴⁴ Two main alternative scenarios could explain the observation of stochastic monoallelic expression in single cells. In the first scenario, a single cell transcribes one allele at a time. The transcription machinery could switch from one allele to the second. This requires the assembly of the pre-initiation complex on one allele and the subsequent dissociation of the complex and clearance of the promoter region before the next round of transcription initiation.⁴⁵ This model of transcription was previously referred to as the dynamic flip-flop transcription cycle model with a long period of gene inactivity and suggests a cross-talk between the two alleles.^{11,46–49} This model could predict heterogeneity within a population of cells expressing one allele at a time. In the second scenario, we hypothesized that the cellular machinery simultaneously transcribes both alleles of all autosomal genes, with the exception of the imprinted genes. The first alternative explanation of our results is that transcription is indeed biallelic but asynchronous, i.e., the transcription machinery is associated with both alleles, but the bursts of transcription of each allele are not synchronous. In such a

scenario, in a single cell at a particular point in time, the allelic transcription appears biallelic if the mRNA half-life is very long, i.e., longer than the refractory period of gene inactivity. Conversely, the allelic transcription appears random and monoallelic for a gene that is poorly transcribed (below the threshold of detection) with a long refractory period of gene inactivity and/or for genes with very short half-lives. Our findings are compatible with this scenario because we revealed that monoallelic transcripts in single cells are short lived and less actively transcribed and that biallelic transcripts are long lived and more actively transcribed.

The stochastic monoallelic expression in single cells could be theoretically linked to phenotypic variability in humans; examples of this include (1) penetrance of a dominant developmental disorder, (2) expressivity of a dominant disorder, (3) cellular or tissue phenotype in carriers of recessive disorders, (4) cellular heterogeneity in cancers, (5) differential cellular response to environmental agents, (6) predisposition to a complex phenotype, and (7) phenotypic variability in monozygotic twins.



Figure 6. Relationship of mRNA Level and Allelic Ratio in Single Cells

(A) A composite figure made of a scatter plot and a table. The scatter plot represents the mRNA level from single-cell RNA-seq data (UCF1014) against the minimum allelic ratio. The minimum allelic ratio is the absolute value of the difference between 0.5 and the allelic ratio (reference reads per total reads). For each gene, the average of RPSM values (coding regions and UTRs) for all single cells was calculated, log transformed (log₂), and plotted on the y axis. Each data point represents one gene. Genes located on the X chromosome are included. The table on the right is the list of enriched gene-ontology (GO) terms with their respective p values (DAVID) for genes with RPSM values > 90.

(B) Box plots of RNA half-life (left) or CAGE nuclear RNA (right) in three different groups of sites with variable allelic ratio (AR). tpm stands for the normalized raw CAGE tag count per million.

In conclusion, the allelic expression of single cells might be an important determinant of the developmental fate and specific function of each cell and might contribute to the phenotypic variability of the organism.

Accession Numbers

RNA and DNA sequencing data have been deposited in the European Genome-phenome Archive for controlled accesses under accession number EGAS00001001009.

Supplemental Data

Supplemental Data include 11 figures and one table and can be found with this article online at http://dx.doi.org/10.1016/j. ajhg.2014.12.001.

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Web Resources

The URLs for data presented herein are as follows:

European Genome-phenome Archive, https://www.ebi.ac.uk/ega/ Gemtools, http://github.com/gemtools Online Mendelian Inheritance in Man (OMIM), http://omim.org/ SAMtools, http://samtools.sourceforge.net/ UCSC Genome Browser, http://genome.ucsc.edu/ Vital-IT, http://www.vital-it.ch

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The American Journal of Human Genetics, Volume 96 Supplemental Data

Biased Allelic Expression in Human Primary

Fibroblast Single Cells

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Histograms displayed read distribution per sample (y-axis, number of reads or percentage of reads). We used color code to differentiate single-cell samples amplified with 12 PCR cycles (blue) or with 22 PCR cycles (grey, standard protocol). We included one sample containing water instead of pre-amplified cDNA and samples from empty capture chamber, i.e chambers containing no cell after single-cell capture procedure (red). Samples colored in green are single-cell samples from T2N fibroblasts, whereas all the other single-cell samples have been prepared from UCF1014 fibroblasts.

Figure S2.



Figure S2. Read distribution for bulk of cells and pool of single-cells (UCF1014).

Histograms displayed read distribution per sample (y-axis, number of reads or percentage of reads). We used color code to differentiate samples. See Figure 1 and method section summarizing the experimental workflow and describing the different types of samples.

Figure S3.



Figure S3. Read duplicates (UCF1014).

(a) Read duplicate refers to reads with identical coordinates. We determined read duplicates for all the samples and we depicted their proportion. Single-cell samples have an average of 73.2% of non-duplicated reads and standard deviation of 5.6%.

(b) Frequency graph shows the distribution of the % of read duplicates across the single-cell samples.





Figure S4. Genomic annotation of 83576 hetSNVs (UCF1014) (>16 reads at position) after cufflinks novel assembly. The pie chart shows the percentage of hetSNVs classified in each Cufflinks class code described by Cuffcompare.





Figure S5. Spike-in experiment

During a single-cell capture experiment, we added to the lysis mix 92 ERCC synthetic spike-in controls at known concentrations. The lysis mix is then uniformly distributed in every chambers. We sequenced 12 spiked fibroblasts from 12 different chambers. (a) The plot shows the number of predicted ERCC spike-in molecule number (see methods) versus the observed normalized read number expressed in RPSM units for a nucleotide located in the middle of the spike sequence (* RPSM, reads at a single nucleotide position per sequencing read length (in kb) and per million mapped reads). Additionally, we calculated the sensitivity and specificity for 4 spike-in molecules (b) and for 8 spike-in molecules (c) at different RPSM levels.

Figure S6.



Figure S6. Allelic ratio and read coverage at hetSNV position (UCF1014).

Frequency distribution histograms of the allelic ratio (reference reads / total reads) according to the read coverage at hetSNVs position (RPSM>20, 163 UCF1014 single cells).

Figure S7.



Figure S7. Effect of duplicates reads on allelic ratio.

Pairwise comparison of the allelic ratio after removing the duplicate reads (Y-axis) and all the reads (X-axis). Pearson coefficient of correlation is indicated at the top of the scatter plot. Points are color coded according to the read coverage at hetSNVs position. (RPSM threshold is not applied; 163 UCF1014 single cells).





B



Figure S8. Allelic ratio and read coverage at hetSNV position (UCF1014) after removing duplicate reads. (a) Frequency distribution histogram of the allelic ratio of single cells (reference reads/ total reads) after removing duplicate reads. (b) Frequency distribution according to the read coverage. (RPSM threshold is not applied; 163 UCF1014 single cells).





Figure S9. Distribution of minimum allelic ratio across the samples. The minimum allelic ratio is the absolute value of the difference between 0.5 and the allelic ratio (reference reads / total reads). Graph is made of side-by-side boxplots (x-axis, samples). RPSM threshold is not applied.

Figure S10.



Figure S10. Allelic ratio in single cells on chromosome X (UCF1014). Frequency distribution histograms of the allelic ratio (reference reads / total reads) for hetSNVs located on chromosome X (RPSM>20, 163 UCF1014 single cells). As expected, due to X-inactivation, the transcription is random (one allele or the other with no specification of the parental origin) and monoallelic across all the single cells.

Figure S11.



27.66 93.17 58.62 84.05 85.28 61.17 22.92 35.90 75.68 61.74 35.71 72.09 86.99 33.85 30.56 41.89 55.93 41.18 25.86 25.80 39.71 100.00 29.17 51.55 44.44 52.59 19.05 37.89 36.36 26.00 48.86 46.67 38.64 15.79 9.43 81.29 68.13 41.82 47.46 52.08 51.33 45.13 67.78 34.48 51.47 38.30 55.41 35.71 46.85 96.20 82.58 67.96 64.77 48.60 50.65 51.32 52.94 44.23 26.09 37.50 77.14 53.06 49.15 22.92 40.79 52.48 57.03 54.62 65.22 40.68 65.22 26.09 27.91 28.85 10.00

AR [0.2, 0.8] 53.49

25.49

70.97

23.64 33.33 31.82 76.52

29.09 44.74

44.74 48.10 47.44

41.84

26.56 67.59 22.22 67.82

57.53

14.63

AR [0.8, 1]

33.33

18.06

30.91 35.56 25.76 9.09

40.00 25.00 25.32 25.64

22.45

42.19 25.00 44.44 17.24

16.44

51.22 40.43 3.11

18.10 7.36 8.59

16.50 31.25 38.46

16.22

19.46 38.10 8.53

6.16

30.77 54.63 35.14

22.88

16.67

36.21 32.35 0.00 43.75

25.77 27.78 25.00 40.48

44.21

47.73 30.00 23.86 35.56

29.55

78.95

78.93 86.79 12.90 19.38

38.18

28.81

23.96 23.01 24.78

4.44

32.76 23.53 17.02 18.24

30.95

30.95 32.43 2.53 10.32

16.50 17.05

16.82 18.18 17.11

23.53

23.08

47.83 47.50 11.43

14.29

22.03 29.17 23.68

12.06 17.97 21.85

20.87 27.12 19.57

36.96 30.23 30.77 24.00

26.53

20.33 56.82 30.43 21.01 16.90

10.20

13.64 58.70 56.30 61.27

DPAGT1	chr11_118967291	34	.00	38.00
DPAGT1	chr11_118967758	30	.36	35.71
USP47	chr11_11976628	33.	.90	35.59
RP11-166D19.1	chr11_121960257	55.	.83	43.56
CLMP	chr11_122943495	34.	.88	13.95
CLMP	chr11_122943802	24.	.32	31.08
SRPR	chr11_126133208	24.	.29	31.43
CD44	chi11_35252920	3.	09	95.85
RRM1	chr11_33233272	27	63	44 74
ATL3	chr11_63393243	4.	17	29.17
ATL3	chr11_63395639	2.	91	24.27
NEATI	chr11 65205958	32	.56	39.53
CCND1	chr11 69466737	36	.07	32.79
RAB6A	chr11 73388363	36	.59	24.39
MRPL48	chr11_73575499	41	.56	35.06
MRPL48	chr11_73575504	42	.86	33.77
PRCP	chr11_82535461	36	.07	40.98
EED	chr11_85968623	47	.62	21.43
IPO7	chr11_9468367	17.	.57	59.46
RAD52	chr12_1021557	73	.81	2.38
NT5DC3	chr12_104167185	28	.00	34.00
NT5DC3	chr12_104167404	27.	.08	33.33
NT5DC3	chr12_104168087	24.	.44	35.56
C12orf75	chr12_105764984	4.	20	61.34
C12orf23	chr12_107367224	11.	.95	81.76
C12orf23	chr12_10/36/225	11.	.95	81.76
MACOUR	chi12_107507439 chr12_10758703	7	22	64.81
MAGOHB	chr12_10753705	18	07	66.27
CSDA	chr12_10851772	18	26	68 70
WSB2	chr12_10851772 chr12_118471760	21	.74	26.09
TRIAP1	chr12_120882112	22	.55	43.14
TRIAP1	chr12 120882217	23	.08	43.27
POP5	chr12_121017171	21	.74	51.30
GPRC5A	chr12 13069410	34	.62	38.46
GPRC5A	chr12 13070752	34	.09	47.73
RAN	chr12_131361241	30	.00	40.00
EMP1	chr12_13369574	25	.81	38.71
MGST1	chr12_16516994	20	.00	52.14
GOLT1B	chr12_21669996	19	.18	50.68
GOLT1B	chr12_21670020	31	.82	51.52
MRPS35	chr12_27867727	31	.91	38.30
MRPS35	chr12_27908603	20	.00	45.00
C12orf5	chr12_4462040	28	.81	37.29
ARID2	chr12_46300100	22	.14	58.57
AMIGO2	chr12_47471439	32	.00	26.00
TMEM106C	chr12_48359984	39.	.08	36.78
IMEM106C	chr12_48362412 shr12_50570127	35.	.57	42.68
LIMAT	chr12_50570127 chr12_50570510	30.	.69 45	47.97
LIMAT	chr12_50570519 chr12_50616346	20.	.45 77	42.03
CBY5	chr12_50010540	13.	96	17.12
NACA	chr12_54025516	1.	84	96.93
USP15	chr12_62696599	19	.35	50.54
HMGA2	chr12 66358347	35	.29	27.45
HMGA2	chr12_66359752	24	.36	37.18
COPS7A	chr12_6840371	28	.26	36.96
KRR1	chr12_75893486	0.0	D0	7.58
KRR1	chr12_75900588	26	.32	43.86
C12orf29	chr12_88440676	25	.45	23.64
DCN	chr12_91539687	27.	.66	46.81
EEA1	chr12_93166538	39	.33	32.58
EEAI	chr12_9316/435	24.	.62	40.00
TMDO	clil12_95802989	19.	.10	69.22
CDC16	chr12_96945365	12.	17	12.50
EXOSC8	chr13_37580130	10	87	70.29
GTF2F2	chr13_45841502	47	27	27.27
RBM26	chr13_79894736	24	.69	50.62
STK24	chr13_99104689	40	.43	40.43
PPP2R5C	chr14_102323093	19	.33	57.14
ZFYVE21	chr14_104199580	45.	.24	26.19
DAD1	chr14_23033838	0.4	61	96.93
C14orf119	chr14_23567369	19	.44	57.64
PSME1	chr14_24606928	25	.00	53.00
SEC23A	chr14_39517925	36	.99	38.36
FKMD6	cnr14_52196115 abr14_54804204	24	.//	50.40
DI GAP5	chr14_54654290 chr14_55655602	18	18	69.12
KTN1	chr14 56078730	10.	31	69.23
JKAMP	chr14 59971039	16	.20	59.15
DHRS7	chr14 60611648	18	.84	53.62
DHRS7	chr14_60611675	16	.46	55.70
ELMSAN1	chr14_74182810	13	.53	55.64
EIF2B2	chr14_75476071	57.	.78	20.00
GPATCH2L	chr14_76645514	37.	.78	17.78
RP11-66B24.4	chr15_101455840	40	.00	44.71
CHSY1	chr15_101716583	36	.36	44.32
CHSY1	chr15_101717065	38	.27	39.51
NDUFAF1	chr15_41679685	40	.00	20.00
TMEM87A	chr15_42529665	46	.51	23.26
FBN1	chr15_48702457	13	.79	63.45
FBN1	chr15_48702873	20	.45	51.52
USP8	chr15_50769520	39	.58	25.00
AKPP19 DNID2	cnr15_52843442 abr15_50051572	38.	.3U 75	38.30 26.25
BNIP2 BNIP2	chr15_59951575	43	33	20.23
BNIP2 BNIP2	chr15_59957997	41.	 44	27.55
BNIP2	chr15 59952341	47.	.15	24.69
	· _ · · · · · · · · · · · ·	+0.	-	

28,00 33,93 30,51 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 51,16 52,27 53,00 52,37 53,81 52,97 53,81 52,97 53,81 52,97 53,97 53,97 54,97 54,97 54,97 54,97 54,97 54,97 54,97 55

DINIF 2	chr15_59952905	29.58 20	ó.76
TIPIN	chr15_66629403	42.50 35	5.00
SMAD3 WDR61	chr15_6/48684/	34.78 40	J.58 6.61
PSMA4	chr15_78837262	6.17 8	3.01 8.27
PSMA4	chr15_78841220	2.52 89	9.31
FAH	chr15_80472561	47.89 23	3.94
MESDC2	chr15_81270754	41.82 25	5.45
MESDC2	chr15_81270816	38.00 20	5.00
AC068851.8 RSI 1D1	chr15_91525197 chr16_11940390	5.01 81 8.18 81	1.95
GSPT1	chr16 11969724	33.77 31	1.17
BFAR	chr16_14762586	25.76 42	2.42
FOPNL	chr16_15960226	25.40 39	Э.68
XYLT1	chr16_17196433	23.19 42	2.03
GDE1 THUMPD1	chr16_19513167 abr16_20747104	42.00 16	5.00 1.84
USP31	chr16_20747104	35.29 23	7.45
MT1L	chr16 56652635	29.09 58	8.18
MT1L	chr16_56652655	29.55 59	9.09
KARS	chr16_75675609	24.00 42	2.00
CDH13	chr16_83065664	25.00 25	5.00
FOXF1	chr16_85846041 chr16_86547838	40 00 40	5.04 6.67
RPA1	chr17 1801189	33.75 38	8.75
RPA1	chr17_1801263	26.67 43	3.33
USP22	chr17_20902959	17.97 60	0.16
FAM101B	chr17_290362	5.93 37	7.04
FAMIUIB	chr17_290370 abr17_200552	5.80 30	J.43 6.02
CCL2	chr17_290332 chr17_32583269	18.84 31	1.88
CCL2	chr17_32583911	17.19 32	2.81
TOP2A	chr17_38545193	12.12 68	3.18
GOSR2	chr17_45008570	30.30 50	0.00
LRRC59	chr17_48458924 abr17_48458925	28.57 42	2.86
RP11-294122.6	chr17_48458525	637 75	8 34
SKA2	chr17_57187729	5.26 84	4.21
SMURF2	chr17_62541309	39.66 30	δ.21
PRKAR1A	chr17_66528778	20.63 53	3.97
BIRC5	chr17_76221428	45.90 44	4.26
TTC39C	chr18_21/14/91 chr18_21714934	32.91 30	J.38 2.08
AC015933.2	chr18_25543387	32.71 43	3.93
DSG2	chr18_29128572	40.00 35	5.56
TPGS2	chr18_34398914	25.58 27	7.91
SMAD2	chr18_45362721	28.00 28	3.00
SMAD2	chr18_45363289	28.00 28	3.00
TWSG1	chr18_30993390	23 73 34	1.75 5.59
1001	01110 /100122		
TWSG1	chr18 9402174	22.86 55	5.71
TWSG1 VAPA	chr18_9402174 chr18_9955849	22.86 55 55.56 15	5.71 5.56
TWSG1 VAPA UQCR11	chr18_9402174 chr18_9955849 chr19_1598203	22.86 55 55.56 15 3.07 92	5.71 5.56 3.25
TWSG1 VAPA UQCR11 CTD-2231E14.8	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056	22.86 55 55.56 11 3.07 92 26.92 34	5.71 5.56 3.25 1.62
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16302087 chr19_17603206	22.86 55 55.56 11 3.07 92 26.92 32 45.33 17	5.71 5.56 3.25 4.62 7.33
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16302087 chr19_17693206 chr19_7116283	20.73 22.86 55.55 3.07 26.92 3.07 45.33 17 12.42 88 27.72 44	5.71 5.56 3.25 4.62 7.33).12 5.53
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16302087 chr19_17693206 chr19_7116283 chr2_10271196	20.73 22.86 55.55 19 3.07 26.92 3.07 45.33 17 12.42 84 27.72 44 10.10 76	5.71 5.56 3.25 4.62 7.33 0.12 5.53 5.77
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16244056 chr19_16302087 chr19_17693206 chr19_7116283 chr2_10271196 chr2_113287964	22.86 55 55.56 15 3.07 99 26.92 34 45.33 17 1.2.42 88 27.72 44 10.10 76 32.31 22	5.71 5.56 3.25 4.62 7.33 0.12 5.53 5.77 7.69
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DD14	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16244056 chr19_16244057 chr19_7116283 chr2_10271196 chr2_113287964 chr2_151325303	20.85 55 55.56 11 3.07 99 26.92 34 45.33 17 12.42 88 27.72 46 10.10 77 32.31 22 15.07 57	5.71 5.56 3.25 4.62 7.33 0.12 5.53 5.77 7.69 5.16
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MAPCH7	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16320087 chr19_17693206 chr19_7116283 chr2_113287964 chr2_113287964 chr2_1532503 chr2_15735648 chr2_16744152	22.86 55 55.56 11 3.07 99 26.92 33 45.33 11 12.42 86 27.72 44 10.10 77 32.31 22 15.07 56 9.38 77	5.71 5.56 3.25 4.62 7.33 0.12 5.53 5.77 7.69 5.16 5.00
TWSG1 VAPA UQCR11 CTD-2231E14.8 FAM32A GL725D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN	ch18_9402174 ch18_9955849 ch19_1598203 ch19_16244058 ch19_16302087 ch19_16302087 ch19_1793206 ch19_7116283 ch2_10271196 ch2_113287964 ch2_151325033 ch2_15735648 ch2_160604452 ch2_1677011	22.86 55 55.56 11 3.07 99 26.99 34 45.33 11 12.42 84 10.10 76 32.31 27.72 44 10.10 76 32.31 27.75 9.38 75 46.51 33 17.48 55	5.71 5.56 3.25 4.62 7.33 0.12 5.53 5.77 7.69 5.16 5.00 2.56 5.31
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PXDN	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_16302087 chr19_17693206 chr19_7116283 chr2_0271196 chr2_113287964 chr2_151325648 chr2_1637201 chr2_1637201 chr2_1637201	22.88 55 55.56 15 3.07 99 26.92 34 45.33 17 12.44 88 27.72 44 10.10 76 32.31 22 15.07 55 9.38 77 46.51 32 17.48 56 15.00 44	5.71 5.56 3.25 4.62 7.33 0.12 6.53 5.77 7.69 5.16 5.00 2.56 5.31 5.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PXDN PXDN PPIG	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16320087 chr19_17693206 chr29_7116283 chr2_10271196 chr2_113287964 chr2_15735648 chr2_1637201 chr2_1637201 chr2_1637648 chr2_1637648 chr2_1637648	22.88 55 55.56 11 3.07 99 26.92 34 45.33 11 12.44 88 27.72 44 10.10 75 32.31 22 15.07 55 9.38 75 46.51 33 17.48 55 15.00 45 29.89 44	5.71 5.56 3.25 4.62 7.33 0.12 6.53 5.77 7.69 5.16 5.00 2.56 5.31 5.00 4.83
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16320087 chr19_1763206 chr19_7116283 chr2_10271196 chr2_113287964 chr2_113287964 chr2_16375648 chr2_16377648 chr2_1637648 chr2_1637648 chr2_1642574 chr2_182401752	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 5.16 5.00 2.56 5.31 5.00 4.83 5.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PYIG CERKL NCKAP1 EAM171P	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1624050 chr19_16302087 chr19_16302087 chr19_17093206 chr19_7116283 chr2_1073201 chr2_113287964 chr2_113287964 chr2_15132503 chr2_16375648 chr2_1637648 chr2_170462574 chr2_183799558 chr2_183799558	$\begin{array}{c} 22.86 \\ 55.56 \\ 3.07 \\ 92.692 \\ 3.07 \\ 92.692 \\ 3.07 \\ 92.692 \\ 3.07 \\ 92.692 \\ 3.07 \\ 12.42 \\ 8.0 \\ 27.72 \\ 4.0 \\ 10.10 \\ 7.72 \\ 4.0 \\ 10.10 \\ 7.72 \\ 4.0 \\ 10.07 \\ 5.68 \\ 29.89 \\ 4.0 \\ 15.00 \\ 4.0 \\ 29.89 \\ 4.0 \\ 29.80 \\ 29.8 \\ 20.8$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 5.16 5.00 2.56 5.31 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 4.83 5.00 5.00 4.83 5.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RRM3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B FAM171B FAM171B FAM171B	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_17693206 chr2_102307 chr2_102307 chr2_103201 chr2_113287964 chr2_151325303 chr2_15735648 chr2_1637648 chr2_170462574 chr2_1637648 chr2_1737648 chr2_1737648 chr2_1737648 chr2_183799558 chr2_1837699558 chr2_1837697631	22.88 55 55.56 15 3.07 99 26.92 34 45.33 17 1.2.42 88 27.72 44 10.10 77 32.31 22 15.07 56 9.38 77 46.51 32 17.48 56 42.9.89 44 56.82 22 40.00 33 14.07 77 5.08 77	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 5.16 5.00 2.56 5.31 5.00 4.83 5.00 4.83 5.00 7.78 7.78 7.78 7.12
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B COL5A2 ORMDL1	chr18_9402174 chr18_9402174 chr19_1598203 chr19_16244056 chr19_1632087 chr19_17693206 chr2_07116283 chr2_10271196 chr2_113287964 chr2_113287964 chr2_151325703 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_182401752 chr2_187629495 chr2_187629495 chr2_189897631 chr2_189897631	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.53 6.77 7.69 6.16 5.00 2.56 5.31 5.00 2.56 5.31 5.00 3.00 7.78 3.00 7.712 7.61
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PXDN PXDN PPIG CERKL NCKAP1 FAM171B COI5A2 ORMDL1 STK17B	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_16320087 chr19_17693206 chr29_7116283 chr2_10271196 chr2_113287964 chr2_1513287964 chr2_1513287964 chr2_15735648 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_182401752 chr2_188997638 chr2_1899588 chr2_1899588 chr2_189636411 chr2_196999139	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.53 6.77 7.69 6.16 5.00 2.56 5.31 5.00 2.56 5.31 5.00 3.00 7.78 3.00 7.78 3.00 7.712 7.61 3.98
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN CERKL NCKAP1 FAM171B COL5A2 ORMDL1 STK17B STK17B	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1624056 chr19_16302087 chr19_16302087 chr19_17193206 chr19_7116283 chr2_1071196 chr2_113287964 chr2_15132503 chr2_15735648 chr2_1637648 chr2_1637648 chr2_170462574 chr2_183799558 chr2_18762940 chr2_18762945 chr2_18762945 chr2_188796531 chr2_190636411 chr2_190699139 chr2_196999139	22.88 55.56 13.07 26.92 3.07 12.42 84 27.72 44 10.10 77 32.31 12.42 88 27.72 44 10.10 77 46.51 32 15.07 56 9.38 17.48 56 15.00 44 51.82 22 40.00 33 17.48 56 15.00 46 51 32 17.48 56 15.07 56 9.38 17.48 56 15.07 56 9.38 17.48 56 15.07 56 9.38 17.48 56 15.00 46 51 32 17.48 56 15.07 56 9.38 17.48 56 15.00 46 51 32 17.48 56 15.00 32 17.48 56 15.00 32 14.57 50 17.48 56 15.00 32 14.57 50 15.07 56 15.00 32 17.48 56 15.00 32 14.57 15.07 56 15.07 56 17.48 56 15.00 32 14.57 15.07 56 15.07 57 57 20.39 32 22.83 33 22.83 33 15.07 56 15.07	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 5.00 2.56 5.31 5.00 4.83 5.00 7.78 7.12 7.61 3.98 5.96
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B FAM171B FAM171B FAM171B STK17B STK17B STK17B	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16302087 chr19_17693206 chr19_17693206 chr19_71032306 chr2_1021196 chr2_113287964 chr2_1131287964 chr2_151325303 chr2_15735648 chr2_1637648 chr2_170462574 chr2_1837648 chr2_170462574 chr2_1837648 chr2_170462574 chr2_1837699558 chr2_187629495 chr2_187629495 chr2_190636411 chr2_106999139 chr2_1999306	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 5.31 5.00 2.56 5.31 5.00 7.78 7.12 7.12 7.12 7.12 7.12 7.12 5.96 3.81 5.96
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B COL5A2 ORMDL1 STK17B STSB1 SF3B1 SF3B1	chr18_9402174 chr18_9402174 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_17693206 chr2_10271196 chr2_113287964 chr2_1131287964 chr2_1513287964 chr2_160604452 chr2_1607048 chr2_1677648 chr2_1677648 chr2_170462574 chr2_18740752 chr2_187629495 chr2_18799558 chr2_187629495 chr2_189897631 chr2_196999130 chr2_19699910 chr2_198265526 chr2_198283305 chr2_198265526	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 5.31 5.00 2.56 5.31 5.00 3.00 7.78 7.712 7.61 3.98 3.99 3.81 5.99 5.96
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PXDN PYDN PPIG CERKL NCKAP1 FAM171B CO15A2 ORMDL1 STK17B STSB1 SF3B1 CLK1 NIF3L1	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16244056 chr19_1632087 chr19_17693206 chr19_7116283 chr2_10271196 chr2_113287964 chr2_113287964 chr2_1513287964 chr2_1513287964 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_188997631 chr2_189897631 chr2_196999139 chr2_196999139 chr2_19625526 chr2_19828305 chr2_0171910 chr2_01768238	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 5.00 2.56 6.31 5.00 2.56 6.31 5.00 7.78 7.12 3.98 5.90 7.74 3.98 5.99 5.96 5.90 2.54 1.41
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN PXDN	chr18_94/02174 chr18_9955849 chr19_1598203 chr19_16302087 chr19_16302087 chr19_17693206 chr19_7116283 chr2_0171196 chr2_01196 chr2_01735648 chr2_15132503 chr2_15735648 chr2_1637648 chr2_1637648 chr2_1637648 chr2_170462574 chr2_183709558 chr2_18870751 chr2_18870751 chr2_19805651 chr2_19805526 chr2_198265526 chr2_198265526 chr2_198265526 chr2_01717910 chr2_017910 chr2_017823305 chr2_20178238	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 2.56 6.31 5.00 3.00 7.78 7.12 7.61 3.98 5.99 5.06 2.41 3.19
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 PXDN PPIG CCU5A2 ORMDL1 STK17B STSB1 SF3B1 SF3B1 SF3B1 SF3B1 CLK1 NIF5L1 LAPTM4A FN1	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_1632087 chr19_17693206 chr19_7103230 chr21021196 chr2_113287964 chr2_113287964 chr2_151325303 chr2_15735648 chr2_1607604452 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_187029495 chr2_187029495 chr2_187029495 chr2_187029495 chr2_198265326 chr2_198283305 chr2_198283305 chr2_01717910 chr2_201768238 chr2_201717910 chr2_201708238	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 5.00 2.56 5.00 7.78 5.00 7.78 5.00 7.712 7.61 3.98 5.96 3.81 5.99 5.06 5.42 7.12 7.12 7.12 7.12 7.12 7.12 7.12 7.1
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B COL5A2 ORMDL1 STK17B STK17B STK17B STK17B STK17B STK17B STSB1 CLK1 NIF3L1 LAPTM4A FN1 XRCC5 STEDBUTD	chr18_9402174 chr18_9955849 chr19_159203 chr19_1632036 chr19_1632036 chr19_17693206 chr19_17693206 chr19_17693206 chr2_10271196 chr2_113287964 chr2_151325303 chr2_160604452 chr2_160604452 chr2_1607048 chr2_170462574 chr2_1677648 chr2_170462574 chr2_187629495 chr2_187629495 chr2_18799558 chr2_187699310 chr2_19699310 chr2_196265526 chr2_198283305 chr2_198283305 chr2_198283305 chr2_198283305 chr2_198284526 chr2_198283305 chr2_0178238 chr2_01768238 chr2_0170766	$\begin{array}{c} 2.7.35 \\ 2.2.86 \\ 55.56 \\ 13.07 \\ 92.692 \\ 3.47 \\ 12.42 \\ 84 \\ 27.72 \\ 44 \\ 10.10 \\ 77.2 \\ 44 \\ 10.10 \\ 77.2 \\ 44 \\ 10.10 \\ 77.5 \\ 9.38 \\ 75 \\ 46.51 \\ 33 \\ 17.48 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 20.87 \\ 57.5 \\ 20.37 \\ 59.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 50.82 \\ 20.37 \\ 20$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 2.56 3.00 7.78 9.00 3.00 7.78 9.00 3.00 7.78 9.00 3.81 3.98 3.81 3.99 3.81 3.99 3.00 7.41 3.98 3.81 3.99 3.00 7.41 3.98 3.81 3.99 3.00 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.41 7.42 7.44 7.42 7.44
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN PXDN	cht 8 9402174 cht 8 9402174 cht 8 9955849 cht 9_1598203 cht 9_16244056 cht 9_16302087 cht 9_16302087 cht 9_1793206 cht 9_1793206 cht 9_1793206 cht 9_1793206 cht 9_17935648 cht 9_1735648 cht 9_1735648 cht 9_1735648 cht 9_1735648 cht 9_1735648 cht 9_170462574 cht 9_18379958 cht 9_18379558 cht 9_18379568 cht	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 2.56 6.31 5.00 7.78 7.12 7.69 5.00 7.78 7.61 5.00 7.78 7.61 5.00 7.78 7.61 5.00 7.78 5.96 5.00 7.78 5.96 5.00 7.74 7.61 5.00 7.78 5.96 5.00 7.78 5.96 5.00 7.78 5.96 5.00 7.78 5.99 5.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN PXDN	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16302087 chr19_16302087 chr19_16302087 chr19_17093206 chr19_7116283 chr2_10121196 chr2_113287964 chr2_151325033 chr2_15735648 chr2_1637648 chr2_1637648 chr2_1637648 chr2_170462574 chr2_183709558 chr2_188705731 chr2_190636411 chr2_190636411 chr2_196999130 chr2_198265526 chr2_1888205526 chr2_201719710 chr2_198265526 chr2_201749030 chr2_20176823305 chr2_20176823305 chr2_20176823305 chr2_2017682305	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 5.25 4.62 7.33 0.12 5.30 0.12 5.50 6.16 6.31 5.00 2.56 6.31 5.00 3.00 7.78 7.69 3.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PYDN PYDN PYDN PYDN PYDN PYDN PYDN PY	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16302087 chr19_17693206 chr19_17693206 chr19_7116283 chr210721196 chr2_113287964 chr2_151325303 chr2_15735648 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_18376949588 chr2_18376949588 chr2_18376949588 chr2_190636411 chr2_10699139 chr2_19099310 chr2_19099310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_190899310 chr2_1917910 chr2_201768288 chr2_216249587 chr2_221682422 chr2_231685198 chr2_231685105	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 5.30 5.00 7.78 5.00 7.78 5.00 7.712 7.61 3.98 5.99 5.06 9.41 5.99 5.06 9.41 5.99 5.06 9.41 5.99 5.06 5.41 5.99 5.06 5.41 5.99 5.06 5.41 5.99 5.06 5.41 5.99 5.06 5.41 5.99 5.06 5.41 5.99 5.00 5.41 5.99 5.10 5.11 5.90 5.12 5.12 5.12 5.12 5.12 5.12 5.12 5.12
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B COL5A2 ORMDL1 STK17B SF3B1 SF	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_17693206 chr2_071196 chr2_103287964 chr2_113287964 chr2_113287964 chr2_113287964 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637648 chr2_170462574 chr2_170462574 chr2_187629495 chr2_187629495 chr2_187899588 chr2_187699310 chr2_19699310 chr2_19699310 chr2_19828526 chr2_19828305 chr2_0178238 chr2_1070768238 chr2_1070766 chr2_021078238 chr2_1070766 chr2_217070766 chr2_21685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 7.78 8.00 7.78 8.00 7.712 7.61 3.98 5.99 3.81 5.99 3.81 3.19 3.51 2.26 5.20 7.61 9.25 5.22 7.62 7.61 9.25 5.22 7.61 7.61 9.25 5.22 7.61 7.62 7.61 7.62 7.62 7.63 7.69 7.69 7.69 7.69 7.69 7.69 7.69 7.69
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN CERKL CCERKL CCL5A2 ORMDL1 STK17B	ch 18 9402174 ch 18 9402174 ch 18 9955849 ch 19_1598203 ch 19_1624056 ch 19_1630087 ch 19_17693206 ch 19_17693206 ch 19_1716283 ch 2_1071196 ch 2_113287964 ch 2_151325303 ch 2_151325303 ch 2_151325303 ch 2_151325303 ch 2_1637648 ch 2_1637648 ch 2_170462574 ch 2_18379958 ch 2_18379958 ch 2_18379958 ch 2_196094139 ch 2_196094139 ch 2_196094310 ch 2_196094310 ch 2_19609530 ch 2_1076238 ch 2_20240668 ch 2_2162823305 ch 2_216295526 ch 2_2163828305 ch 2_21639585 ch 2_216382842 ch 2_216385805 ch 2_231685205 ch 2_231685205 ch 2_232035429 ch 2_231685205 ch 2_232035429 ch 2_23008277 ch 2_240040707 ch 2_2400470706 ch 2_2400470706 ch 2_224004707 ch 2_2400470706 ch 2_224004707 ch 2_2400470706 ch 2_224004707 ch 2_2400470706 ch 2_224004707 ch 2_2400470706 ch 2_224004707 ch 2_2400470706 ch 2_224004707 ch 2_24004707 ch 2_24004707 ch 2_24004707 ch 2_24004707 ch 2_4004707 ch	22.88 55.56 3.07 26.92 3.4 45.33 11.2.42 88 27.72 44 10.10 77 9.38 17.48 56.82 29.89 44 56.82 29.89 44 56.82 29.89 44 56.82 29.89 44 56.82 29.89 44 56.82 20.39 33 22.83 35 24.24 55 24.24 55 24.24 55 24.24 55 25 25 20.39 33 22.83 35 24.24 55 24.24 55 24.24 55 25 25 25 25 20.39 33 22.83 35 24.24 55 25 25 25 25 20.39 33 22.83 35 24.24 35 25 25 25 25 25 25 25 25 25 2	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 4.83 5.00 5.00 4.83 5.00 5.00 4.83 5.00 5.00 5.00 4.83 5.00
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT2501 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 DDX1 DDX1 DDX1 MARCH7 PXDN PYGD CERKL NCKAP1 PXDN PYGG CERKL NCKAP1 PXDN PYGG CERKL NCKAP1 FAM171B CCI5A2 ORMDL1 STK17B SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 XRCC5 SERPINE2 CAB39 CAB39 FMD1 NDUFA10 DNUTA10	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_7116283 chr2_0171196 chr2_011196 chr2_01196 chr2_01735648 chr2_01735648 chr2_01735648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_017648 chr2_0176320 chr2_0176320 chr2_0178230 chr2_00068 chr2_0179006 chr2_017666 chr2_224862842 chr2_017666 chr2_0176766 chr2_0176766 chr2_0176766 chr2_0177766 chr2_01777766 chr2_01777766 chr2_01777766 chr2_01777766 chr2_017777766 chr2_017777766 chr2_01777777777777777777777777777777777777	$\begin{array}{c} 2.7.35 \\ 2.2.86 \\ 55.56 \\ 13.07 \\ 9.26.92 \\ 3.47 \\ 12.42 \\ 84 \\ 27.72 \\ 44 \\ 10.10 \\ 77 \\ 32.31 \\ 27 \\ 15.07 \\ 56 \\ 15.00 \\ 44 \\ 29.89 \\ 44.651 \\ 32.4 \\ 29.89 \\ 44.651 \\ 37.48 \\ 56.82 \\ 22 \\ 40.00 \\ 33 \\ 14.07 \\ 77 \\ 19.57 \\ 56 \\ 20.39 \\ 33 \\ 14.07 \\ 77 \\ 19.57 \\ 57 \\ 20.39 \\ 32.48 \\ 32.44 \\ 56.82 \\ 22 \\ 40.00 \\ 33 \\ 14.07 \\ 77 \\ 19.57 \\ 57 \\ 20.39 \\ 33 \\ 22.83 \\ 33 \\ 45.24 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.28 \\ 37.25 \\ 22.28 \\ 33 \\ 45.24 \\ 22.26 \\ 33 \\ 40.48 \\ 9 \\ 9 \\ 90 \\ 25.00 \\ 51 \\ 15.38 \\ 57 \\ 22.58 \\ 39.39 \\ 42 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 22.54 \\ 35.79 \\ 35.7$	5.71 5.56 5.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 8.00 7.78 7.69 8.00 7.78 7.69 8.00 8.00 7.78 7.12 7.61 8.59 5.00 3.81 5.59 5.09 5.09 3.81 5.99 5.06 3.19 4.29 5.26 5.27 7.61 5.39 5.99 5.09 5.10 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.12 7.61 5.99 5.00 7.78 7.72 7.61 5.99 5.00 7.78 7.72 7.61 5.99 5.00 7.78 7.72 7.61 5.99 5.00 7.76 7.79 5.99 5.00 7.76 7.70 7.70 7.71 7.71 7.71 7.71 7.71 7.71 7.71 7.72 7.71 7.72 7.71 7.72 7.74 7.72 7.74 7.72 7.74 7.72 7.74 7.72 7.76 7.72 7.76 7.72 7.76 7.79 7.22 7.76 7.76 7.79 7.22 7.76 7.76 7.79 7.22 7.76 7.76 7.76 7.76 7.77
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 PXDN PPIG CERKL NCKAP1 FAM171B CCN52 ORMDL1 STK17B SF3B1 SF3B	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_1793206 chr19_1793206 chr210_7793206 chr210_7793206 chr210_711083 chr2107375648 chr2113287964 chr21131287964 chr21131287964 chr21637648 chr21637648 chr21737648 chr2170462574 chr2183709558 chr2183769958 chr2183769958 chr2190636411 chr21909310 chr219099310 chr219828305 chr2201717910 chr220178238 chr2217070766 chr2231685198 chr2213185205 chr2231885198 chr2231685205 chr223185205 chr223185205 chr223185205 chr223185205	22.86 55.56 3.07 26.92 3.4 45.33 11.2.42 88 27.72 44. 10.10 76 9.38 77 46.51 32. 17.48 56.82 22.89 44. 56.82 22. 40.00 33 14.07 508 77 508 50 20.39 33 22.83 33 45.24 52 23.40 64 52.25 20.39 33 22.83 33 45.24 55 57 20.39 57 57 57 20.39 57 57 20.39 57 57 20.39 57 57 20.39 57 57 20.39 57 57 57 20.39 57 57 57 57 57 57 57 57 57 57	5.71 5.56 5.25 5.25 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 7.78 5.00 7.78 5.00 7.78 5.00 7.712 7.61 3.98 5.99 5.06 3.81 5.99 5.06 3.19 4.29 3.51 5.99 5.06 3.19 4.29 3.51 5.22 5.22 7.73 3.19 4.29 3.51 5.22 5.22 7.73 5.00 7.72 7.61 3.39 5.00 7.72 7.61 7.72 7.72 7.72 7.72 7.72 7.72 7.72 7.7
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPIG CERKL NCKAP1 FAM171B COL5A2 ORMDL1 STK17B SF3B1 SF	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_17693206 chr210_7116283 chr2_101287 chr2_113287964 chr2_113287964 chr2_113287964 chr2_151325303 chr2_160604452 chr2_1607048 chr2_170462574 chr2_167201 chr2_1677648 chr2_170462574 chr2_187629495 chr2_187629495 chr2_187899588 chr2_187629495 chr2_198987631 chr2_10609310 chr2_109699310 chr2_109699310 chr2_109699310 chr2_109828305 chr2_211717010 chr2_00768238 chr2_217070766 chr2_217070766 chr2_213685198 chr2_213685198 chr2_231685295 chr2_231685198 chr2_231685295 chr2_231685198 chr2_231685295 chr2_231685198 chr2_231685295 chr2_231685198 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685295 chr2_231685198 chr2_23	22.86 55 55.56 11 3.07 99 26.92 34 45.33 11 1.2.42 88 27.72 44 10.10 77 9.38 75 46.51 33 17.48 56 15.00 44 29.89 44 56.82 22 40.00 33 14.07 77 5.08 777 19.57 55 20.39 32 22.83 36 45.24 22 16.13 55 37.25 29 23.40 55 24.24 56 37.25 29 23.40 56 24.24 56 37.25 29 23.40 56 39.39 44 32.26 35 39.39 44 35.79 22 22.54 49 0.00 10 16.30 77	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.99 5.381 5.99 5.36 5.41 3.19 3.51 2.52 5.52 7.76 1.77 1.22 7.61 1.52 5.52 5.50 2.41 3.19 3.51 2.52 5.52 7.76 1.77 7.79 5.52 7.76 2.52 5.52 5.50 2.41 5.52 7.76 1.779 1.92 5.52 7.76 1.779 1.92 5.52 7.76 1.779 1.92 5.52 7.76 1.779 1.92 5.42 5.42 5.42 5.59 5.52 7.76 1.779 1.92 5.42 5.42 5.42 5.52 7.76 1.779 1.92 5.42 5.42 5.42 5.42 5.52 7.76 1.779 1.92 5.45
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN PXDN	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16240056 chr19_16302087 chr19_17093206 chr19_17093206 chr19_7116283 chr2_1071196 chr2_113287964 chr2_151325303 chr2_15735648 chr2_1607604452 chr2_1637648 chr2_170462574 chr2_183799558 chr2_183799558 chr2_183799558 chr2_183799558 chr2_183799558 chr2_183799558 chr2_198265526 chr2_198265526 chr2_1982305 chr2_20171910 chr2_109238305 chr2_201749818 chr2_201768238 chr2_201768238 chr2_2017668 chr2_218485105 chr2_3240667 chr2_2340667 chr2_2340667 chr2_23406766 chr2_234946766 chr2_234946766 chr2_23405155	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 5.25 4.62 7.33 0.12 5.50 0.12 5.67 7.69 5.00 2.56 6.31 5.00 2.56 6.31 5.00 4.83 5.00 4.83 5.00 7.78 7.61 5.00 4.83 5.90 5.00 3.81 5.99 5.06 3.81 2.26 5.31 2.26 5.31 2.26 5.31 2.26 5.32 5.99 5.00 2.51 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.51 2.52 5.99 5.00 2.51 5.00 2.52 5.00 2.51 5.00 2.51 5.00 7.78 7.71 2.52 5.00 7.78 7.71 2.52 5.00 7.78 7.71 2.52 5.00 7.78 7.71 2.52 5.00 7.78 7.71 2.52 5.00 7.71 2.52 5.00 7.78 7.71 2.56 3.81 5.99 5.00 7.78 7.71 2.56 3.81 5.99 5.00 7.78 7.71 2.56 3.81 5.99 5.00 7.78 7.71 2.56 3.81 5.99 5.99 5.00 2.56 3.81 5.99 5.99 5.26 5.50 2.52 5.99 5.99 5.99 5.90 5.52 5.52 5.52 5.52 5.52 5.52 5.52 5.5
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT2501 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PP1G CERKL NCKAP1 PXDN PP1G CERKL NCKAP1 FAM171B CCK4 CCI5A2 ORMDL1 STK17B SF3B1 SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 XRCC5 SF3B1 SF3B1 SCK17B SF3B1 SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 XRC5 SF3B1 SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 XRC5 SF3B1 SF3B1 CLK1 NIF3L1 CLA7 NUFA10 NUF410 NUF410 DNMT3A GPN1 PP91CB PP91CB PP91CB PP91CB	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16302087 chr19_17993206 chr19_17993206 chr19_7116283 chr21071196 chr2_113287964 chr2_151325303 chr2_15735648 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1837698 chr2_170462574 chr2_183769958 chr2_1837699958 chr2_1837699958 chr2_190636411 chr2_190636411 chr2_190639310 chr2_196999310 chr2_196999310 chr2_201761208 chr2_2179100 chr2_201761238 chr2_2179100 chr2_201768238 chr2_217010766 chr2_224652842 chr2_231685198 chr2_231685198 chr2_231684766 chr2_24467666 chr2_2446766 chr2_234515 chr2_20023749 chr2_20023749 chr2_20023749 chr2_20023749 chr2_2003748	$\begin{array}{c} 2.1.3 \\ 2.2.86 \\ 55.56 \\ 13.07 \\ 9.26.92 \\ 3.4 \\ 45.33 \\ 17.12.44 \\ 10.10 \\ 77 \\ 32.31 \\ 22 \\ 15.07 \\ 56 \\ 15.00 \\ 44 \\ 29.89 \\ 44.51 \\ 32.2 \\ 15.07 \\ 56 \\ 29.38 \\ 77 \\ 46.51 \\ 32.3 \\ 17.48 \\ 56.82 \\ 22.4 \\ 40.00 \\ 33 \\ 14.07 \\ 77 \\ 5.08 \\ 77 \\ 19.57 \\ 57 \\ 20.39 \\ 33 \\ 22.83 \\ 33 \\ 45.24 \\ 22 \\ 23.40 \\ 55 \\ 20.39 \\ 33 \\ 22.83 \\ 33 \\ 45.24 \\ 22 \\ 23.40 \\ 55 \\ 20.39 \\ 33 \\ 22.83 \\ 33 \\ 45.24 \\ 22 \\ 23.40 \\ 55 \\ 20.39 \\ 33 \\ 22.83 \\ 33 \\ 45.24 \\ 22 \\ 23.40 \\ 55 \\ 20.39 \\ 39.02 \\ 9 \\ 39.02 \\ 9 \\ 39.00 \\ 9 \\ 39.02 \\ 9 \\ 39.02 \\ 9 \\ 39.02 \\ 9 \\ 39.02 \\ 9 \\ 25.00 \\ 55 \\ 15.38 \\ 35.79 \\ 22.54 \\ 44 \\ 35.79 \\ 35.79 \\ 35.79 \\ 35.79 \\ 35.79 \\ 35.70 $	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 8.00 8.00 8.00 8.00 8.00 8.00 8.00
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TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN PXDN CERKL CCERKL CCL5A2 ORMDL1 STK17B SF3B1 STK17B SF3B1 SF3B1 CLK1 NUF3L1 LAPTM4A FN1 XRCC5 SFRPNE2 CAB39 PSMD1 NUF410 N	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_17693206 chr19_17693206 chr19_17693206 chr210_7116283 chr2_101283 chr2_101287 chr2_113287964 chr2_113287964 chr2_113287964 chr2_113287964 chr2_113287964 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_1637201 chr2_170462574 chr2_170462574 chr2_187629495 chr2_187629495 chr2_187629495 chr2_187629495 chr2_187629495 chr2_198987631 chr2_10609310 chr2_10969310 chr2_109828305 chr2_01768238 chr2_1017910 chr2_0216686 chr2_11249587 chr2_21685198 chr2_216349587 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685198 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_231685109 chr2_338505 chr2_3085048 chr2_47132529 chr2_3085048 chr2_4713259 chr2_3085048 chr2_4713259	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 5.57 5.56 5.25 4.62 7.33 6.77 7.69 6.16 6.77 7.69 6.16 6.77 7.69 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 5.02 5.22 5.22 5.22 5.24 5.42
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TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 MARCH7 PXDN PPD0 CERKL NCKAP1 PXDN PPGG CERKL NCKAP1 NCKAP1 PXDN PPGG CCIS52 ORMDL1 STK17B SF3B1 CLK1 NUFA10 NDUFA10 NDUFA10 NDUFA10 NDUFA10 NDUFA10 NDUFA10 NDUFA10 NDUFA10 SMNT3A GPN1 PPP1CB PPP1CB PPP1CB SC2Ca774 USP34 GFPT1 AC114772.1	chr18_9402174 chr18_9955849 chr19_1598203 chr19_1632087 chr19_1793206 chr19_1793206 chr19_1793206 chr210_7793206 chr210_711083 chr210735648 chr2113287964 chr21131287964 chr21131287964 chr21131287964 chr21131287064 chr211372648 chr2170462574 chr21870748 chr2170462574 chr2187079588 chr2187029495 chr2187029495 chr2198263205 chr2198263205 chr22198263205 chr22198263205 chr22198263205 chr22198263205 chr22198263205 chr2210717910 chr2207076668 chr2216249587 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685198 chr2231685195 chr2231685195 chr2231685195 chr2231685195 chr2231685195 chr2231797 chr223035429 chr2240946766 chr2245456100 chr227873415 chr229025479 chr223035429 chr223035429 chr223035429 chr2240946766 chr2245521 chr22905479 chr230381529 chr226172298 chr26167731	$\begin{array}{c} 2.1.3 \\ 2.2.86 \\ 55.56 \\ 13.07 \\ 9.26.92 \\ 3.4 \\ 45.33 \\ 11.2.42 \\ 88 \\ 27.72 \\ 44 \\ 10.10 \\ 77 \\ 32.31 \\ 22 \\ 15.07 \\ 50 \\ 9.38 \\ 77 \\ 46.51 \\ 32 \\ 17.48 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 56.82 \\ 29.89 \\ 44 \\ 40.00 \\ 33 \\ 14.07 \\ 77 \\ 5.08 \\ 37.25 \\ 22.33 \\ 33 \\ 39.39 \\ 45.24 \\ 52 \\ 22.54 \\ 40.48 \\ 9 \\ 39.02 \\ 9 \\ 39.02 \\ 51 \\ 15.38 \\ 51 \\ 39.39 \\ 40.48 \\ 9 \\ 39.02 \\ 50 \\ 15.38 \\ 51 \\ 39.39 \\ 40.48 \\ 9 \\ 39.00 \\ 21 \\ 31.34 \\ 45 \\ 22 \\ 28.57 \\ 33 \\ 13.46 \\ 57 \\ 22 \\ 28.57 \\ 37.21 \\ 20 \\ 20 \\ 27 \\ 37.21 \\ 20 \\ 20 \\ 27 \\ 37.21 \\ 20 \\ 20 \\ 37.21 \\ 20 \\ 37.21 \\ 37.21 \\ 20 \\ 37.21 \\ 37.21 \\ 20 \\ 37$	5.71 5.56 5.25 4.62 7.33 0.12 6.53 7.769 6.16 6.77 7.769 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 2.56 5.00 7.78 5.00 7.78 7.61 3.98 5.00 7.712 7.61 3.98 5.00 7.712 7.61 3.98 5.00 3.81 3.99 5.06 5.22 5.22 7.76 5.22 5.22 7.76 5.22 5.22 7.76 5.22 5.22 7.75 5.22 5.22 5.22 7.75 5.22 5.22
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 MARCH7 PXDN PXDN PXDN PXDN PXDN PXDN CERKL CCERKL CCL5A2 ORMDL1 STK17B SF3B1 STK17B SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 XRCC5 SERPINE2 CAB39 CAB39 CKS SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 SF3B1 CLK1 NIF3L1 LAPTM4A FN1 NIF3L1 CAB39 CAB39 CAB39 FNDI NUF3L0 NDUFA10 DNU	ch 18 9402174 ch 18 9402174 ch 18 9955849 ch 19 1598203 ch 19 16244056 ch 19 1630267 ch 19 1630267 ch 19 1630267 ch 19 1630267 ch 19 1735648 ch 2 10121196 ch 2 113287964 ch 2 113287964 ch 2 113287964 ch 2 113287964 ch 2 113287964 ch 2 113287964 ch 2 1132879658 ch 2 13735648 ch 2 170462574 ch 2 183799558 ch 2 183799558 ch 2 183799558 ch 2 183799558 ch 2 190636411 ch 2 190639411 ch 2 196999139 ch 2 19699139 ch 2 196392526 ch 2 31858205 ch 2 231685205 ch 2 3318505 ch 2 30856048 ch 2 47132529 ch 2 61372298 ch 2 6137298 ch 2 61372298 ch 2 6137239 ch 2 6137239 c	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.71 5.56 3.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 5.00 2.56 6.31 5.00 2.56 6.31 5.00 7.78 7.61 5.00 7.78 7.61 5.00 7.78 7.712 7.61 3.89 8.696 3.81 3.19 4.29 5.06 5.20 5.26 5.31 5.00 8.00 7.78 7.12 7.61 3.39 8.50 5.20 5.20 5.20 5.20 5.20 5.20 5.20 5
TWSGI VAPA UQCR11 CTD-2231E14.8 FAM32A GLT25D1 INSR RRM2 TTL RND3 DDX1 DDX1 DDX1 DDX1 MARCH7 PXDN PYDN PYDN PCC CERKL NCKAP1 FAM171B CCI5A2 ORMDL1 STK17B STS3B1 SF3B1 CLK1 NIF3L1 CLK1 NIF3L1 LAPTM4A FN1 XRCC5 SERPINE2 CAB39 CAB39 CAB39 FSMD1 NDUFA10 DNUF	chr18_9402174 chr18_9955849 chr19_1598203 chr19_16240565 chr19_16302087 chr19_17992006 chr19_7116283 chr2_071196 chr2_071196 chr2_071196 chr2_07196 chr2_07196 chr2_07196 chr2_07196 chr2_071970 chr2_07111 chr2_07111 chr2_071711 chr2_07	$\begin{array}{c} 2.1.3 \\ 2.2.86 \\ 55.56 \\ 13.07 \\ 9.26.92 \\ 3.45.33 \\ 11.2.42 \\ 18.42 \\ 10.10 \\ 77.72 \\ 46.51 \\ 13.231 \\ 27.72 \\ 46.51 \\ 15.07 \\ 50.8 \\ 77 \\ 46.51 \\ 32.31 \\ 27.8 \\ 46.51 \\ 33.2 \\ 17.48 \\ 56.82 \\ 22 \\ 40.00 \\ 38 \\ 14.07 \\ 75.08 \\ 77 \\ 19.57 \\ 50.8 \\ 77 \\ 19.57 \\ 50.8 \\ 77 \\ 19.57 \\ 50.8 \\ 77 \\ 19.57 \\ 50.8 \\ 77 \\ 19.57 \\ 50.8 \\ 77 \\ 19.57 \\ 20.39 \\ 32.28 \\ 37.25 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.340 \\ 55 \\ 22.26 \\ 37.25 \\ 22.340 \\ 55 \\ 23.40 \\ 55 \\ 23.40 \\ 55 \\ 23.26 \\ 37.25 \\ 22.55 \\ 40.48 \\ 39.02 \\ 99 \\ 25.00 \\ 51 \\ 39.39 \\ 44 \\ 35.79 \\ 22.54 \\ 44 \\ 35.79 \\ 22.54 \\ 44 \\ 35.79 \\ 22.54 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 39.39 \\ 44 \\ 35.77 \\ 31.34 \\ 86 \\ 64.29 \\ 22.55 \\ 37.21 \\ 20.00 \\ 37.14 \\ 20.00 \\ 37.14 \\ 37.1$	5.71 5.56 5.25 4.62 7.33 0.12 6.53 6.77 7.69 6.16 6.31 5.00 2.56 6.31 5.00 2.56 6.31 5.00 8.00 7.78 7.69 6.30 5.00 8.00 7.78 7.61 6.31 5.00 8.00 7.78 7.61 6.31 5.00 8.01 8.51 8.22 8.42 9.30 8.00 8.242 8.33 8.38 8.33 8.55 8.53 8.55

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IMP3	1 22 420
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CDCP1	chr3_2396 chr3_2396 chr3_4512
DCP1 YCO1	chr3_2396 chr3_2396 chr3_4512 chr3_4595
PLIS DCP1 PYCO1 AAP4	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795
PLIS CDCP1 VYCO1 MAP4 SAM208A	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795 chr3_5665
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PL15 CDCP1 YCO1 MAP4 SAM208A MRF4 DDHB	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795 chr3_5665 chr3_5755 chr3_5841
IPL15 CDCP1 YCC01 MAP4 SAM208A ARF4 PDHB DDHB	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795 chr3_5665 chr3_5755 chr3_5841 chr3_5841
IPLIS CDCP1 YCC01 MAP4 SAM208A MRF4 DHB DHB HUMPD3	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795 chr3_5665 chr3_5755 chr3_5841 chr3_5841 chr3_5841
APLIS 2DCP1 YCC01 AAP4 AAP4 AAP4 AAP4 AAP4 AAP4 AAP4 AAP	chr3_2396 chr3_2396 chr3_4512 chr3_4595 chr3_4795 chr3_5665 chr3_5755 chr3_5841 chr3_5841 chr3_9425
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42/15 50CP1 57CO1 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4AP4 4DPB 4DPB 4DPB 4AP5 4AP	chr3_2396 chr3_2396 chr3_4512 chr3_4512 chr3_4595 chr3_5665 chr3_5755 chr3_5755 chr3_5841 chr3_5841 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9426 chr4_1143 chr4_1202 chr4_1143 chr4_1209 chr4_1669 chr4_1669 chr4_1669 chr4_1688 chr4_1838 chr4_1845 chr4_1845 chr4_1856 chr4_1850 chr4_3950 chr4_751 chr4_950 chr4_
42/15 5DCP1 5DCP1 4AP4 4AP4 4AP2 4AP2 4AP2 4AP2 4AP2 4AP2 4AP2 4AP2 4AP2 4AP2 4DHB 4DHB 4HUMPD3 HUMPD3 HUMPD3 4HUMPD3 4CVF12 4AP3 4AP2 4AP2 4AP2 4AF3 4AP2 4AF3 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58 4AP2 4AM58	chr3_2396 chr3_2396 chr3_4512 chr3_4512 chr3_4512 chr3_4595 chr3_5655 chr3_5655 chr3_5755 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9425 chr3_9426 chr3_9425 chr3_9426 chr3_9425 chr3_9426 chr3_9
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37 31	29.85
91.41	4.29
90.80	4.91
38.16	22.37
84.44	8.89
40.78	28.16
53.21	23.85
43.48	28.26
43.07	25.94
45.00	26.67
20.55	75.34
26.67	33.33
44.44	26.26
65.52	15.52
63.78	20.47
38.46	17.31
35.62	42.47
74.36	9.62
39.29	35./1
03.83	0.62
70.33	15.38
25.00	36.54
30.30	48.48
37.29	38.98
49.53	24.30
61.36	19.70
52.13	28.72
70.47	16.11
66.67	17.36
45.45	27.27
20.83	39.02 27.25
22.99	21.55
18.60	46.51
43.10	29.31
46.00	26.00
68.75	16.67
64.20	14.81
40.68	28.81
71.33	17.33
37.21	27.91
38.89	27.78
38.10	23.81
40.50	22.22
43.90	25.61
46.81	19.15
31.11	33.33
32.91	25.32
0.00	100.00
0.00	100.00
29.63	38.89
18.33	30.00
25.58	27.91
34.88	37.21
68.55	10.00
69.57	18.12
54.55	24.24
26.42	33.96
41.46	34.15
40.28	36.11
92.64	4.29
54.84	28.23
62.12	21.97
67.27	15.45
25.00	28.13
41.38	31.03
47.06	27.45
28.57	40.48
18.37	36.73
35.71	28.57
40.00	26.67
58.02	24.43
58.06	17.74
48.25	32.46
59.48	10.58
21.43	21.01
48.72	31.62
31.25	27.08
48.15	25.93
42.31	26.92
43.42	30.26
32.18	43.68
51.11	26.67
32.39	38.03
30.14	38.36
55.55 64 59	15 07
70.97	12.97
93.87	1.23
36.59	36.59
19.67	49.18
50.98	22.55
50.98 0.00	22.55 100.00

32.84 4.29 39.47 6.67 30.99 38.81 4.10 40.09 38.81 4.11 40.00 38.82 4.23 21.92 32.55 44.23 21.92 32.617 18.94 8.86 6.21.21 32.73 32.50 14.29 21.92 32.617 18.94 8.86 6.21.21 32.727 34.15 19.66 42.22 34.88 8.80 42.22 34.88 8.80 42.22 34.88 33.33 34.82 34.83 34.82 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.83 34.84 35.56 41.77 9.66 42.22 34.88 35.10 31.42 21.99 22.09 30.51 17.37 34.55 35.09 30.41 31.42 21.27 21.17 34.15 35.60 31.48 8.80 41.77 40.00 31.48 8.25 41.77 40.00 31.48 8.25 41.77 40.00 31.48 8.25 41.77 40.00 31.47 45.75 30.77 40.00 31.67 45.75 30.77 40.00 31.67 45.75 30.77 40.00 31.67 45.75 30.77 40.00 31.67 45.75 30.77 40.00 31.67 45.75 30.77 40.00 31.67 45.75 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 30.77 40.00 24.14 40.10 24.14 24.22 24.15 24.14 24.22 24.14 24.22 24.22 24.22 24.23 24.14 24.24 2



0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 Allelic ratio (ref/total)

Figure S11. Single-cell allelic ratio distribution per detected genes (UCF1014).

We selected 568 genes for a representative view of the allelic expression in single cells. Index bar indicates the color-coded for the allelic ratio values (reference reads/ total reads). The columns are the gene name, the genomic coordinate of the hetSNV, the color coded column are the single cells, the three last columns are the percentage of cells with an allelic ratio between [0, 0.2], [0.2, 0.8] and [0.8, 1]. We subselected 60 genes out of 568 genes to make the figure 5.