

Correction

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Loss of *Parp-1* affects gene expression profile in a genome-wide manner in ES cells and liver cells

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Background

Following the publication of the paper 'Loss of *Parp-1* affects gene expression profile in a genome-wide manner in ES cells and liver cells' [1], we found an error in our data.

In the article, we used six replicates of microarray data of wild-type ES cells for comparison with the microarray data of *Parp-1* knockout ES cells. We found that three replicate data were carelessly included in the data for wild-type ES cells. The comparison should have been carried out between three replicates for the *Parp-1*^{+/+} ES cell line, J1, and three replicates for two *Parp-1*^{-/-} ES cell lines, 210-58 and 226-47, respectively.

Therefore, we re-analyzed the data in ES cells according to the same criteria. The consequences of this error are reflected in changes to our results although the conclusions we obtained in the study are not affected.

Corrected sentences in the Abstract

Here, we demonstrate that of the 9,640 genes analyzed, in *Parp-1*^{-/-} ES cells. 3.6% showed altered gene expression. Of these, 2.5% and 1.1% of the genes were down- or up-reg-

Table 1: Differential expression of genes between *Parp-1*^{+/+} and *Parp-1*^{-/-} ES cells, livers, and EFs

| p-value cut off ^a | No. of genes | | | | |
|------------------------------|--------------|-------------------------------------------------------------|-------------------|-------------------------------------------------------------|-------------------|
| | Total | <i>Parp-1</i> ^{-/-} < <i>Parp-1</i> ^{+/+} | | <i>Parp-1</i> ^{-/-} > <i>Parp-1</i> ^{+/+} | |
| | | Total | 2-fold or greater | Total | 2-fold or greater |
| ES cells^c | | | | | |
| Total ^b | 9,640 | 5,065 | 1,056 | 4,481 | 1,520 |
| p < 0.05 ^b | 893 | 663 | 238 | 230 | 106 |
| Livers^d | | | | | |
| Total ^b | 12,353 | 7,138 | 1,184 | 4,860 | 1,038 |
| p < 0.05 ^b | 1,616 | 1,190 | 253 | 426 | 158 |
| p < 0.01 ^b | 641 | 515 | 100 | 126 | 43 |
| EFs^e | | | | | |
| Total | 12,357 | 5,042 | 707 | 7,317 | 501 |
| p < 0.05 | 996 | 390 | 216 | 606 | 205 |

^aAnalyzed by One-Way ANOVA (non-parametric test known as the Mann-Whitney U test)

^bThese genes were presented in Fig. 1.

^c*Parp-1*^{+/+} ES cell clone, J1, and *Parp-1*^{-/-} ES cell clones, 210-58 and 226-47, were used.

^dTwo mice were used for each genotype.

^eThree EFs obtained from three embryos were analyzed as triplicate experiments.

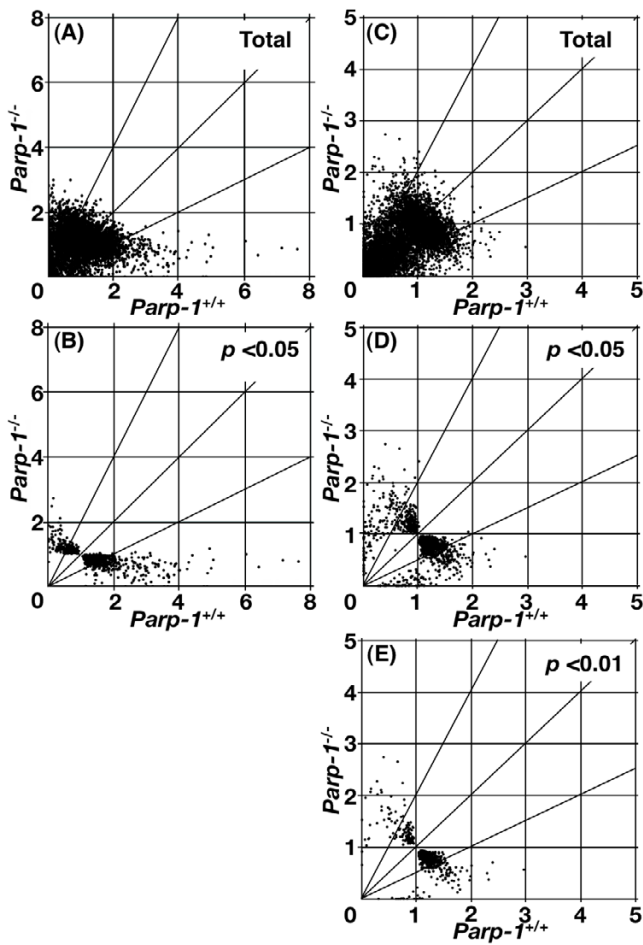


Figure 1
Effect of *Parp-1* deficiency on gene expression. Gene expression data from microarray analyses are plotted for *Parp-1*^{-/-} versus wild-type (*Parp-1*^{+/+}) ES cell lines (A) & (B). Horizontal and vertical axes represent expression levels normalized for an individual gene. Each point represents normalized expression data for an individual gene. The genes that showed standard deviation greater than 2.0 in the normalized data of both genotypes (A) were excluded and gene lists were constructed with $p < 0.05$ (B). Fig. 1D–F in the original article [1] remains unchanged and is presented as (C) – (E), respectively.

ulated by 2-fold or greater, respectively, compared with *Parp-1*^{+/+} ES cells ($p < 0.05$).

Corrected results in the text
Gene expression profile in *Parp-1*^{-/-} ES cells

A comparison of the basal gene expression profiles in *Parp-1*^{-/-} ES cells to their wild-type (*Parp-1*^{+/+}) counterparts, is presented in Fig. 1A & 1B (corrected) and Table 1 (corrected). We found the expression of (344/9,640) genes, namely 3.6%, was different by at least 2-fold between

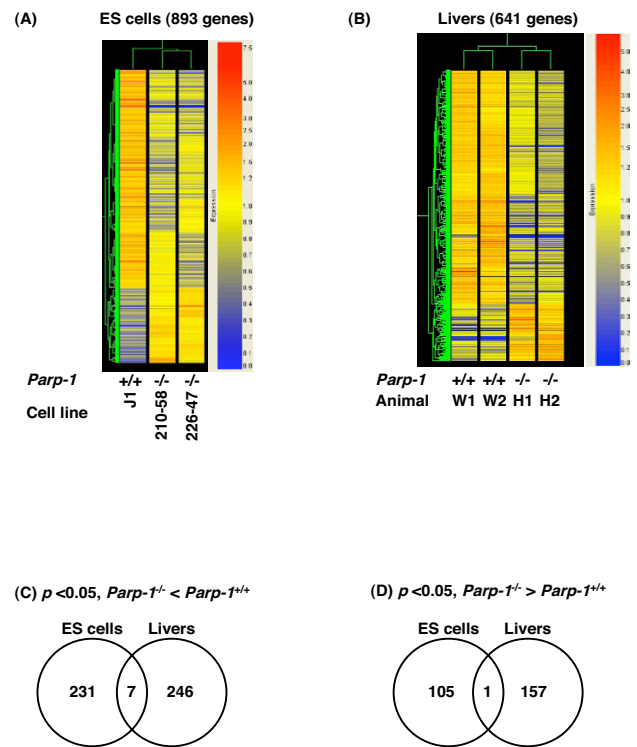


Figure 2
Comparison of gene expression profiles among cell lines or cell types. Heatmaps of gene expression profiles in ES cells (A). We constructed the heatmaps using the gene lists containing the genes that showed a difference at $p < 0.05$ in ES cells. Each heatmap is constructed using GeneSpring GX ver. 7.3.1. Numbers of genes down-(C) or up-(D) regulated in common between *Parp-1*^{-/-} ES cells and livers. The numbers of the genes are indicated in Venn diagrams. These genes showed the difference with at least 2-fold between *Parp-1*^{+/+} and *Parp-1*^{-/-} ($p < 0.05$). Fig. 2B in the original article [1] remains unchanged and is presented as (B). Fig. 2D & F in the original article [1] are removed and Fig. 2C & E were corrected in the original article [1] and are presented as (C) and (D).

Parp-1^{-/-} and *Parp-1*^{+/+} ES cells ($p < 0.05$) (Fig. 1B (corrected) and Table 1 (corrected)). Notably, a larger fraction of the genes, being 2.5% (238/9,640), was down-regulated, whereas only 1.1% (106/9,640) of the genes were up-regulated (see Table 1 (corrected)).

We also made the heatmaps using the gene lists containing the 893 genes that showed a difference at $p < 0.05$ in ES cells (Fig. 2A (corrected)). Although we used independently isolated *Parp-1*^{-/-} ES cell clones, a clear and common alteration in the gene expression profile was observed (see Fig. 2A (corrected), and Tables 2 (corrected) and 3 (corrected)).

Table 2: Genes down-regulated in *Parp-1*^{-/-} ES cells

| Accession No. | Fold change ^{a)} | | | Symbol | Chromosome | Gene description |
|-------------------------------------------------|---------------------------|--------------|--------------|---------------------|------------|---------------------------------------------------------|
| | W vs H | J1 vs 210-58 | J1 vs 226-47 | | | |
| Cell cycle/cell proliferation/cell death | | | | | | |
| AW122355 | 3.2 | 5.2 | 2.3 | <i>Prkcbp1</i> | 2 | Protein kinase C binding protein 1 |
| AF067395 | 2.9 | 2.9 | 2.9 | <i>Bnip3l</i> | 14 | BCL2/adenovirus E1B 19 kDa-interacting protein |
| AI842277 | 2.7 | 2.3 | 3.2 | <i>Igfbp3</i> | 11 | Insulin-like growth factor binding protein 3 |
| U95826 | 2.2 | 2.5 | 1.9 | <i>Ccng2</i> | 5 | Cyclin G2 |
| Cell structure/cell adhesion | | | | | | |
| UI6741 | 4.1 | 6.3 | 3.1 | <i>Capza2</i> | 6 | Capping protein (actin filament) muscle Z-line, alpha 2 |
| AI132380 | 3.6 | 3.1 | 4.3 | <i>Fndc3a</i> | 14 | Fibronectin type III domain containing 3a |
| AI505453 | 2.9 | 2.5 | 3.4 | <i>Myh9</i> | 15 | Myosin, heavy polypeptide 9, non-muscle |
| AW208938 | 2.4 | 3.2 | 2.0 | <i>Pkp2</i> | 16 | Plakophilin 2 |
| M76124 | 2.4 | 2.2 | 2.6 | <i>Tacstd1</i> | 17 | Tumor-associated calcium signal transducer 1 |
| Metabolism | | | | | | |
| U73820 | 5.5 | 5.2 | 5.8 | <i>Galnt1</i> | 18 | Polypeptide GalNAc transferase-T1 (ppGaNTase-T1) |
| AI841270 | 3.4 | 2.4 | 6.4 | <i>Gstm1</i> | 3 | Glutathione S-transferase, mu 1 |
| AV308550 | 2.6 | 4.1 | 1.9 | <i>Piga</i> | x | Phosphatidylinositol glycan, class A |
| AI851912 | 2.3 | 2.2 | 2.5 | <i>Rps27</i> | 3 | Ribosomal protein S27 |
| AI852144 | 2.1 | 2.9 | 1.7 | <i>Pbef-pending</i> | 12 | Pre-B-cell colony-enhancing factor |
| U65986 | 2.1 | 1.9 | 2.5 | <i>Anxa11</i> | 14 | Annexin A11 |
| D50264 | 2.1 | 1.4 | 4.1 | <i>Pigf</i> | 17 | Phosphatidylinositol glycan, class F |
| AF031486 | 2.0 | 2.0 | 2.0 | <i>Sms</i> | x | Spermidine synthase |
| AI845882 | 2.0 | 2.5 | 1.7 | <i>Acypl</i> | 12 | Acylphosphatase I, erythrocyte (common) type |
| Protein biosynthesis/degradation | | | | | | |
| AI852581 | 3.0 | 3.0 | 3.1 | <i>Ide</i> | 19 | Insulin degrading enzyme |
| AI414051 | 3.0 | 1.8 | 9.1 | <i>Usp24</i> | 4 | Ubiquitin specific protease 24 |
| AW121012 | 2.9 | 2.8 | 3.0 | <i>Rnf19</i> | 15 | Ring finger protein 19 |
| X92665 | 2.9 | 2.5 | 3.4 | <i>Ube2e1</i> | 14 | Ubiquitin-conjugating enzyme UbcM3 |
| AW048882 | 2.2 | 2.8 | 1.8 | <i>Iars</i> | 13 | Isoleucine-tRNA synthetase |
| AA867340 | 2.2 | 1.9 | 2.6 | <i>Psme4</i> | 11 | Proteasome (prosome, macropain) activator subunit |
| AB024427 | 2.2 | 2.3 | 2.1 | <i>Rnf11</i> | 4 | Ring finger protein 11 |
| Signaling | | | | | | |
| AI846023 | 4.6 | 2.8 | 13.1 | <i>Arl7</i> | 1 | ADP-ribosylation factor-like 7 |
| AA260005 | 2.8 | 2.7 | 2.8 | <i>Pawr</i> | 10 | PPKC, apoptosis, WT1, regulator |
| AI317205 | 2.6 | 2.4 | 2.7 | <i>Map3kl</i> | 13 | Mitogen activated protein kinase kinase 1 |
| AF035644 | 2.3 | 2.0 | 2.7 | <i>Ptp4a2</i> | 4 | Protein tyrosine phosphatase 4a2 |
| M21019 | 2.3 | 1.9 | 2.9 | <i>Rras</i> | 7 | Harvey rat sarcoma oncogene, subgroup R |
| AI194248 | 2.2 | 2.5 | 1.9 | <i>Csnk2a1</i> | 2 | Casein kinase II, alpha 1 polypeptide |

Table 2: Genes down-regulated in *Parp-1*^{-/-} ES cells (Continued)

| | | | | | | |
|----------------------------------|-----|-----|------|----------------------|----|----------------------------------------------------|
| AI854006 | 2.0 | 2.0 | 2.1 | <i>Set</i> | 2 | SET translocation |
| D83921 | 2.0 | 1.9 | 2.1 | <i>Ebaf</i> | 1 | Endometrial bleeding associated factor |
| Transcription/replication | | | | | | |
| XI4206 | 9.9 | 8.4 | 11.9 | <i>Adprt1</i> | 1 | Poly(ADP-ribose) polymerase I |
| M99167 | 3.0 | 6.2 | 2.0 | <i>Hnrpa1</i> | 15 | Heterogeneous nuclear ribonucleoprotein A1 |
| AW107922 | 2.8 | 3.7 | 2.2 | <i>Sox11</i> | 12 | SRY-box containing gene 11 |
| AI849135 | 2.5 | 2.5 | 2.5 | <i>Foxo3a</i> | 10 | Forkhead box 03a |
| Y07836 | 2.5 | 2.3 | 2.8 | <i>Bhlhb2</i> | 6 | Basic-helix-loop-helix domain containing, class B2 |
| X74760 | 2.5 | 2.3 | 2.7 | <i>Notch3</i> | 17 | Notch gene homolog 3, (Drosophila) |
| AI447783 | 2.1 | 2.4 | 1.9 | <i>Helb</i> | 10 | Helicase (DNA) B |
| X94694 | 2.1 | 2.7 | 1.7 | <i>Tcfap2c</i> | 2 | Transcription factor AP-2, gamma |
| AF077861 | 2.1 | 2.2 | 2.1 | <i>Id2</i> | 12 | Inhibitor of DNA binding 2 |
| AI605405 | 2.0 | 1.9 | 2.3 | <i>Phf13</i> | 4 | PHD finger protein 13 |
| D78382 | 2.0 | 1.7 | 2.6 | <i>Tob1</i> | 11 | Transducer of ErbB2.1 |
| Transport | | | | | | |
| AV356315 | 4.1 | 5.5 | 3.3 | <i>Lman1</i> | 18 | Lectin, mannose-binding, 1 |
| AV298789 | 2.9 | 2.6 | 3.2 | <i>Ranbp5</i> | 14 | Ran binding protein 5 |
| D88315 | 2.2 | 2.2 | 2.2 | <i>Hiat1</i> | 3 | Hippocampus abundant gene transcript 1 |
| Unknown | | | | | | |
| AI845617 | 3.5 | 3.5 | 3.4 | <i>2610019A05Rik</i> | 11 | Hypothetical protein |
| AI852287 | 3.2 | 3.3 | 3.2 | <i>Ankrd28</i> | 14 | Ankyrin repeat domain 28 |
| AI836771 | 3.0 | 2.8 | 3.3 | <i>2900008M13Rik</i> | 15 | Unknown EST |
| AA684456 | 2.9 | 2.1 | 4.5 | <i>2310015N07Rik</i> | 7 | Hypothetical protein |
| AI848435 | 2.8 | 1.9 | 4.8 | <i>C78339</i> | 13 | Unknown EST |
| AW123157 | 2.8 | 2.5 | 3.1 | <i>1700051E09Rik</i> | 11 | Hypothetical protein |
| AW124843 | 2.6 | 3.1 | 2.3 | <i>C85108</i> | 4 | Unknown EST |
| AA710439 | 2.6 | 2.0 | 3.6 | <i>6230421P05Rik</i> | 16 | Unknown EST |
| AI853444 | 2.5 | 1.8 | 3.9 | <i>2610042L04Rik</i> | 14 | Hypothetical protein |
| AI853444 | 2.2 | 2.1 | 2.3 | <i>2610042L04Rik</i> | 14 | Hypothetical protein |
| AW121353 | 2.1 | 1.6 | 3.1 | <i>Lrrc8</i> | 2 | Lucine rich repeat containing 8 |
| AI037493 | 2.1 | 1.5 | 3.4 | <i>Tbcd15</i> | 10 | TBC1 domain family, member 15 |
| AI461803 | 2.1 | 2.2 | 1.9 | <i>1300006C19Rik</i> | 9 | Hypothetical protein |
| AW049969 | 2.0 | 2.0 | 2.1 | <i>C330005L02Rik</i> | 9 | Hypothetical protein |
| AI847483 | 2.0 | 2.0 | 2.0 | <i>Tmem41b</i> | 7 | Transmembrane protein 41B |

^{a)}W, wild-type cells (J1); H, *Parp-1*^{-/-} ES cells (210–58 and 226–47).

Table 3: Genes up-regulated in *Parp-1*^{-/-} ES cells

| Accession No. | Fold change ^{a)} | | | Symbol | Chromosome | Gene description |
|-------------------------------------------------|---------------------------|--------------|--------------|---------------------------------|------------|-------------------------------------------------------------------------|
| | H vs W | 210–58 vs J1 | 226–47 vs J1 | | | |
| Cell cycle/cell proliferation/cell death | | | | | | |
| X58196 | 3.1 | 3.3 | 2.9 | <i>H19</i> | 7 | H19 non-coding RNA |
| AI842665 | 3.0 | 3.1 | 2.8 | <i>Tax1bp3</i> | 11 | Human T-cell leukemia virus type I binding protein 3 |
| Cell structure/cell adhesion | | | | | | |
| X04017 | 2.3 | 2.3 | 2.3 | <i>Sparc</i> | 11 | Cysteine-rich glycoprotein SPARC |
| M26071 | 2.1 | 2.5 | 1.8 | <i>F3</i> | 3 | Coagulation factor III |
| M91236 | 2.1 | 2.1 | 2.1 | <i>Gjb5</i> | 4 | Gap junction membrane channel protein beta 5 |
| Immune response | | | | | | |
| U13705 | 2.3 | 2.1 | 2.4 | <i>Gpx3</i> | 11 | Glutathione peroxidase 3 |
| Metabolism | | | | | | |
| AW120625 | 2.3 | 1.9 | 2.7 | <i>Pgd</i> | 4 | Phosphogluconate dehydrogenase |
| M64782 | 2.2 | 1.9 | 2.5 | <i>Folr1</i> | 7 | Folate-binding protein 1 (FBP1) |
| X97755 | 2.0 | 2.1 | 2.0 | <i>Ebp</i> | x | Phenylalkylamine Ca ²⁺ antagonist (emopamil) binding protein |
| Protein biosynthesis/degradation | | | | | | |
| W71352 | 3.9 | 4.2 | 3.6 | <i>Bag2</i> | 1 | Bcl2-associated athanogene 2 |
| AI844175 | 3.4 | 3.4 | 3.4 | <i>Mrps11</i> | 7 | Mitochondrial ribosomal protein S11 |
| U16163 | 2.9 | 2.9 | 2.8 | <i>P4ha2</i> | 11 | Prolyl 4-hydroxylase alpha(II)-subunit |
| D00622 | 2.5 | 2.0 | 3.0 | <i>Lrpap1</i> | 5 | Low density lipoprotein receptor related protein, associated protein 1 |
| X60676 | 2.3 | 2.4 | 2.2 | <i>Serpinh1</i> | 7 | HSP47 |
| AW124432 | 2.1 | 1.8 | 2.5 | <i>Mrpl12</i> | 11 | Mitochondrial ribosomal protein L12 |
| AI839392 | 2.0 | 2.0 | 2.1 | <i>Aars</i> | 8 | Alanyl-tRNA syntase |
| Transcription/replication | | | | | | |
| D49473 | 3.4 | 3.0 | 3.7 | <i>Sox17</i> | 1 | SRY-box containing gene 17 |
| U51335 | 2.5 | 2.5 | 2.6 | <i>Gata6</i> | 18 | GATA-binding protein 6 |
| U79962 | 2.4 | 2.1 | 2.6 | <i>Tarbp2</i> | 15 | TAR (HIV) RNA binding protein 2 |
| D49473 | 2.1 | 1.9 | 2.3 | <i>Sox17</i> | 1 | SRY-box containing gene 17 |
| Transport | | | | | | |
| D14077 | 2.2 | 2.1 | 2.3 | <i>Clu</i> | 14 | Clusterin |
| Others | | | | | | |
| M34603 | 2.6 | 2.3 | 3.0 | <i>Prg</i> | 10 | Proteoglycan core protein |
| AA793009 | 2.3 | 2.0 | 2.7 | <i>Tex19</i> | 11 | Testis expressed gene 19 |
| Unknown | | | | | | |
| AI846553 | 3.2 | 3.0 | 3.3 | <i>I11002</i> <i>OC13Rik</i> | 15 | Hypothetical protein |
| AI845664 | 2.1 | 2.0 | 2.2 | <i>Grwd</i> | 7 | Glutamate-rich WD repeat containing 1 |

^{a)}H, *Parp-1*^{-/-} ES cells (210–58 and 226–47); W, wild-type cells (J1).

We further selected the genes that showed relatively high expression levels (the "Flag value" in GeneSpring ver. 6.1 of the genes should be either "Present" (high level of expression) or "Marginal" (moderate level of expression) in all replicates of the genotype within the 893 genes that showed a difference at $p < 0.05$, see Table 1 (corrected)). Among the 85 genes selected by this analysis, there were 61 genes, obviously including the *Parp-1* (*Adprt1*) gene itself, that were down-regulated and 24 genes up-regulated, as listed in Tables 2 (corrected) and 3 (corrected).

Gene expression profile of the livers and EF cells

In the livers, 3.3% (411/12,353) of genes showed a significant difference in expression level ($p < 0.05$) between the *Parp-1* genotypes. In the livers of *Parp-1*^{-/-} mice, 2.0% (253/12,353) of the genes were down-regulated and 1.3% (158/12,353) of the genes were up-regulated ($p < 0.05$). Similar to *Parp-1*^{-/-} ES cells, a higher percentage of the genes, 62% (253/411), were down-regulated and the remaining 38% were up-regulated (Fig. 1C–E in the original article [1], and Table 1 (corrected)). The expression of representative marker genes of the liver, including *albumin* (*Alb1*) and *phosphoenolpyruvate carboxykinase* (*Pepck*), was similarly high in both *Parp-1* genotypes.

The heatmaps were constructed using the gene lists containing the 641 genes that showed a difference at $p < 0.01$ in livers (Fig. 2B). *Parp-1* deficiency commonly altered gene expression profiles in the livers of two mice analyzed (Fig. 2B, and Table 4 in the original article [1]).

Comparison of the profiles among different cell types

We compared gene expression profiles between *Parp-1*^{-/-} ES cells and the livers. There were no genes commonly up- or down-regulated as summarized in Tables 2 (corrected), 3 (corrected), and 4 in the original article [1], namely in the genes showing relatively high expression levels selected by Flag values, although we observed that 7 genes, including *Eif2s2* (*eukaryotic translation initiation factor 2 subunit 2 beta*), *Parp-1*, and 1 gene *Crygs* (*crystallin gamma S*), were commonly down- and up-regulated in the ES cells and livers ($p < 0.05$), respectively (Fig. 2C (corrected) & 2D (corrected)).

Corrected methods in the text

Data analysis

Data analysis was performed with the GeneSpring® software ver. 6.1 and ver. 7.3.1 (the latest version). For statistical analyses, the fluorescence intensity (raw signal) was normalized to the 50th percentile reading per chip, and then normalized to the median reading per gene. We performed the non-parametric tests with the cross-gene error model being inactive. In the case of *Parp-1*^{-/-} ES cells, 6 replicates consisting of triplicate microarray results from two *Parp-1*^{-/-} ES cell lines were used. We used the triplicate

microarray results from the *Parp-1*^{+/+} ES cell line, J1. We excluded genes that showed a standard deviation greater than 2.0 in the normalized data of both genotypes, and we started analysis with 9,640 genes and ESTs for ES cells (Table 1 (corrected)). We constructed gene lists only with the genes that showed statistical differences ($p < 0.05$) and 2-fold or greater differences in normalized expression levels between *Parp-1* genotypes. To construct heatmaps, we used GeneSpring® GX ver. 7.3.1 (the latest version).

We regret that this error occurred in the phase of generating the data set in our paper may have caused any inconvenience. In the process of making these corrections, the microarray data were submitted to the gene expression database CIBEX [2] with the following accession number: CBX22.

References

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