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Summary Report

Analysis of Zebra Fish Microarray Data

Prepared by
Rachel M. Rohde, Edward V. Thomas, and Jerilyn A. Timlin
Sandia National Laboratories
PO Box 5800
Albuquerque, NM 87185-0895

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Primary EPA contacts: David Bencic, Ph.D. and RongLin Wang, Ph.D.

Abstract

Commercial Zebra fish (*D. rerio*) microarrays were manufactured by Agilent Technologies and hybridized and scanned by ParadigmArrayLabs (PAL), a service unit of Icoria, Inc. These arrays were obtained from the Environmental Protection Agency's (EPA) toxicology research. Data from EPA toxicology microarrays were analyzed to assess the degree of photobleaching, slide reproducibility, and effect of treatments (versus control) on gene expression. Inference regarding the overall treatment effect (across replicate arrays) for a given gene was made via a modified t-statistic. The analysis was performed with and without the dye swap slides included. Genes that were identified as significantly up and down regulated as a result of the treatment are given as well as a brief discussion on the applicability of these methods for future investigations.

Introduction

The study presented in this report is part of a larger collaboration between the Environmental Protection Agency and Sandia National Laboratories (SNL) to develop and apply improved methods for microarray science for the purpose of increasing the reliability of microarray data used for toxicology studies at the EPA. In this report expression data from commercial Zebra fish microarrays manufactured by Agilent Technologies and hybridized and scanned by ParadigmArrayLabs (PAL), a service unit of Icoria, Inc., were analyzed to assess the degree of photobleaching, slide reproducibility, and to test the utility of SNL developed microarray analysis methods based on a modified t-statistic[1] to determine effect of treatments (versus control) on gene expression. This report is a formal communication of the results of the microarray data analysis efforts.

Experimental

The microarray slides investigated contained 21,000+ predicted *D. rerio* genes in a 22k slide format using Agilent's 60-mer SurePrint Technology. This format contains only one representation of each gene on the array. Hybridization was performed by PAL in a 64 slide experiment to compare three different chemical effects on brain and reproductive organs at two time points. The details of the larger experiment were not the focus of this current study and thus are not given in this report. Following hybridization these arrays were scanned by PAL three times in rapid succession using the same scan settings. Data from these three repeat scans on each of 5 randomly selected slides were used in this current investigation to assess photobleaching behavior.

In addition, a subset of 12 of the 64 arrays were selected for further statistical analysis. There were 6 arrays (5 + a dye swap) comparing RNA from female brain tissue (treatment and control) at the 48 hr time point and 6 arrays (5 + a dye swap) comparing male brain tissue (treatment and control) at the 96 hr time point. See Results and Discussion for a more complete discussion of the experimental detail of the arrays used. Spot finding and background subtraction was performed using GenePix 5.1 and statistical analysis was performed using custom scripts written for Matlab R2006b.

Although PAL calculated spot intensities for the first scan for each array we chose to recalculate those values using GenePix in order to avoid potential incompatibilities between the two software packages and to guarantee full understanding of what was being calculated. Global background subtraction was performed for each channel using the mean of the local background means for that channel and then treatment vs. control ratios (FAD/CTL) were calculated. Spots were visually inspected and those with poor quality (compromised by a spill, scratch, large dust particle, etc. or completely missing) were omitted from all analyses. In addition the data was also further trimmed for statistical analysis so that all spots had a median of at least 440 counts in the green channel and at least 120 counts in the red channel to create a “thresholded” data subset. These limits were determined from the standard deviation of the background multiplied by three to ensure accuracy in the analysis. Background values for the red channel were estimated from the glass background and values for the green channel were estimated from the glass plus contaminant levels. Contaminant levels were determined from hyperspectral imaging results. (see report titled “Hyperspectral Imaging of Zebra Fish Microarrays, Sept. 20, 2006”)

Analysis was performed on either 1) the full data set (21,000+ genes minus those with poor quality due to spatial anomalies) or 2) the reduced, “thresholded” data set that excluded spots as described above and with or without the dye swap slide included. Table 3 notes the number of spots included in each analysis variant. The $\log_2$ intensity medians (Y) were normalized by array and the t-statistics were determined by the following equation for each Y:

$$t_Y=\surd(\#\text{Slides})*Y_{mean}/\max(L,S_y);$$

where S_y is the standard deviation of Y and L was determined by rounding the lowest point of the V-shaped median fit of Y vs. S_y. Using $\max(L,S_y)$ in the denominator prevents the magnitude of the t-statistic from being unrealistically large. Significance t-values came from a random matrix of simulated modified t-statistics.

Results and Discussion 1: Photobleaching behavior

Figure 1 shows the photobleaching results for one of the slides investigated. Statistics for this slide and the additional four slides investigated are shown in Table 1. The percent loss is calculated as the (Scan 1 background subtracted spot intensity – the Scan 3 background subtracted spot intensity) divided by the Scan1 spot intensity *100. The values in Table 1 were calculated using only spots with intensities < 60000 counts and > 150 for the green channel and > 180 for the red channel to ensure reliability. The extent of photobleaching in three successive scans was determined to be minor under the conditions used for this analysis. Specific values for the degree of photobleaching were variable: 0 to ~3.6 % for the Cy3 and ~1.5 to ~6.0 % for Cy5 after three scans. The values are in agreement with the limited literature reports and as expected the Cy5 dye photobleaches to a higher degree in all cases.[2, 3] The slight negative losses and moderate variability reported in Table 2 are most likely a result of instrument noise on the measurements.

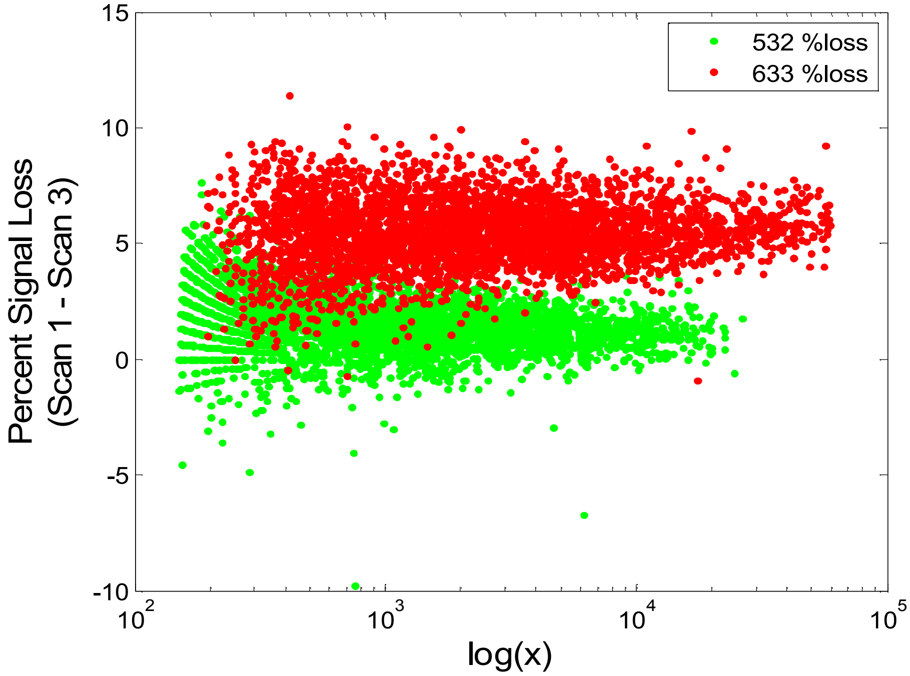

Figure 1: Percent Signal loss from Scan1 to Scan3 for slide # US23502387_251322310605

Table 1: Photobleaching behavior of 5 select slides

Slide Identifier	532 % Loss Median	532 % Loss Standard Deviation	633 % Loss Median	633 % Loss Standard Deviation
US23502387_251322310635	-0.07%	1.7662	1.50%	1.352
US23502387_251322310598	3.59%	1.5573	6.05%	1.6301
US23502387_251322310605	1.47%	1.2147	5.43%	1.3621
US23502387_251322310618	-0.40%	1.3533	1.81%	1.3726
US23502387_251322310665	-0.03%	2.1684	3.16%	2.3495

Results and Discussion 2: Reproducibility, Gene Expression and Analysis

Twelve arrays comparing gene expression in brain tissue from control and FAD exposed Zebra fish were selected for further investigation. The experimental details of these arrays are summarized in Table 2. There were 6 arrays (5 + a dye swap) comparing RNA from female brain tissue at the 48 hr time point and 6 arrays (5 + a dye swap) comparing male brain tissue at the 96 hr time point. These arrays were chosen for several reasons. First, they included dye swaps which permitted us to assess possible red-green bias that is often seen. Second, there were a sufficient number of replicate slides to permit the use of the t-statistic methods. Also, this particular grouping of slides potentially can give information about the effect of treatment on brain tissue in each sex and in general without confounding of additional variables such as tissue type, time point, etc.

Reproducibility: Reproducibility across slides within an experiment was assessed visually using a scatterplot matrix of the log$_2$(FAD/CTL) for all slides in the each experiment (Figures 2 and 3). For these figures the values for each slide were normalized such that the median value of log$_2$(FAD/CTL) is equal to 0 for that slide. Ideally, if two slides were perfectly reproducible the scatterplot for those two slides would have all the data points falling on a perfect diagonal line centered on 0. It is clear from figures 2 and 3 that there are substantial deviations from ideality and these differences can be used to gain some insight into the reproducibility of the slides and possible problems with the data. There are several trends apparent that are not well understood at this point. For example, in Figure 2 slide 40 appears to have a small cluster of "outlier" points and in Figure 3 several of the comparisons result in negative slopes instead of positive ones.

It should be noted that the microarray experiment we are investigating does not assess solely slide-to-slide variation but rather slide-to-slide plus biological variation, due the nature of the experimental design (RNA hybridized to each array was from a different biological replicate, except in the case of the dye swap). This effect can be seen in the results if you compare distribution of points of the subplots in Figure 2 for slides 44/45 vs. slide 44/any other slide and in Figure 3 slide 08/09 vs. slide 08/any other slide. It is clear that when the same RNA is used for the dye swaps (i.e. no biological variation introduced) there is a tighter distribution of points around the diagonal, indicating lower variability in gene expression. Though both of the dye swaps (slides 44 and 45 in Figure 2 and slides 08 and 09 in Figure 3) have an unusual bivariate distribution and this warrants further investigation.

Table 2: Details of slides analyzed

Slide #	Channel 1 - Cy3 (Sample ID – experiment)	Channel 2 - Cy5 (Sample ID – experiment)
251322310640	23085 – 48 h female brain – CTL	23077 – 48 h female brain – FAD
251322310641	23050 – 48 h female brain – CTL	23090 – 48 h female brain – FAD
251322310644	**23073** – 48 h female brain – CTL	**23053** – 48 h female brain – FAD
251322310645	**23053** – 48 h female brain – FAD	**23073** – 48 h female brain – CTL
251322310646	23061 – 48 h female brain – CTL	23065 – 48 h female brain – FAD
251322310647	23086 – 48 h female brain - CTL	23089 – 48 h female brain – FAD
251322310608	**23136** - 96 h male brain - CTL	**23115** - 96 h male brain - FAD
251322310609	**23115** - 96 h male brain - FAD	**23136** - 96 h male brain - CTL
251322310610	23099 - 96 h male brain - CTL	23103 - 96 h male brain - FAD
251322310611	23124 - 96 h male brain - CTL	23128 - 96 h male brain - FAD
251322310661	23112 - 96 h male brain - CTL	23140 - 96 h male brain - FAD
251322310663	23135 - 96 h male brain - CTL	23104 - 96 h male brain - FAD

Bold sample IDs are dye swaps

Slides will be referred to by underlined portion of slide number throughout this report

Overall, the variation seen in both the female brain microarray slides and the male brain microarray slides was moderate, compared to other microarray data this lab has analyzed. While this is in part due to the innate biological variation in the experiment, it could adversely affect the reliability of gene lists generated from this expression data.

Significantly Expressed Genes:

Expression data was analyzed to determine genes that were significantly up and down regulated with respect to FAD treatment in 4 ways -- with and without the dye swap data included and with and without a threshold applied to exclude spots that could potential be impacted by the presence of contaminant emissions. The analysis was performed such that a positive t-value corresponds to an increase in expression of that gene in the treatment vs. control (up-regulated), whereas a negative t-value corresponds to a decrease in expression of that gene in treatment vs. control (down-regulated). The results of these analyses with a stringent (t(0.999975)) and more relaxed (t(0.999900)) t-statistic criterion are summarized in Table 3. In addition, Appendix A lists the up and down regulated genes identified for the male and female brain tissue experiments thresholded to exclude spots that could be affected by contaminant emission, with and without the inclusion of the dye flip. The gene lists are not given for the analysis without the threshold applied because this analysis generated a large number of significant genes (See Table 3), but the list can be made available. With this adjusted t-statistic method, t(0.999975) implies that the likelihood of one or more false positives is 0.05 for the thresholded analysis with about 2000 spots included.

It was clear from these analyses that the inclusion of the dye swap resulted in a smaller number of genes being significantly expressed, however it was encouraging that a modest number of the genes identified in both the female and male experiments with the dye flip included were also present when the dye flip was not included (7/14 for female, 4/7 for male). It should be noted however that there was no overlap between genes identified using the thresholded data subset and the full set of spots for either the female or male brain experiment with the dye swap included. This is concerning and warrants further investigation as to the appropriateness of the dye swap and the thresholding methods applied. Also, if the dye swap was included there was no overlap between the genes identified in the male brain tissue and female brain tissue experiment; however there was slight overlap (17 genes out of 55 (female) and 122 (male)) between these experiments if the analysis was performed without the dye swap. This might be of biological significance, but cannot be confirmed without further experimentation, due to the apparent discrepancy with the inclusion of the dye swap.

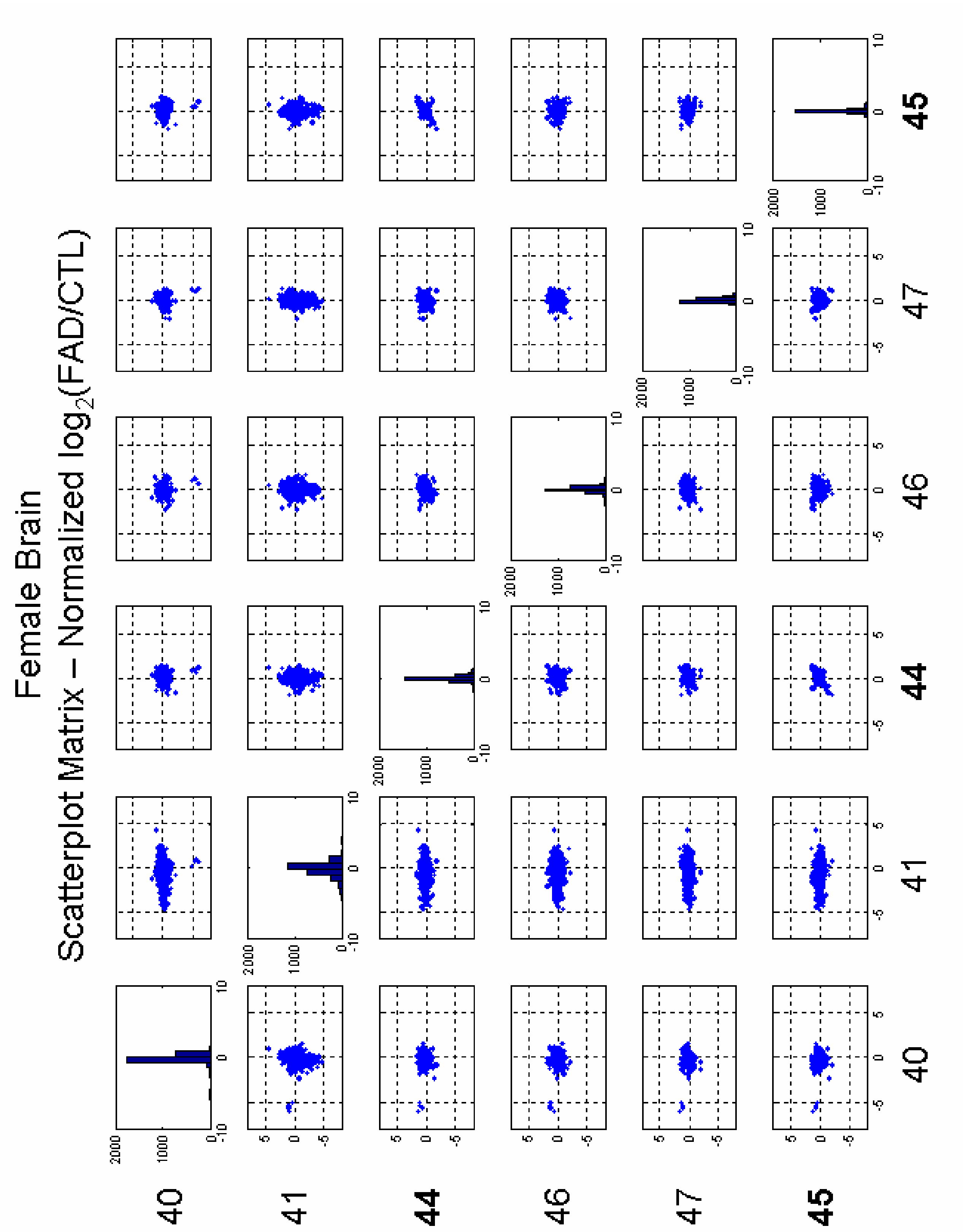

Figure 2: Scatterplot matrix of gene expression experiment with FAD exposure in female brain tissue. Dye swaps are slide 44 and 45.

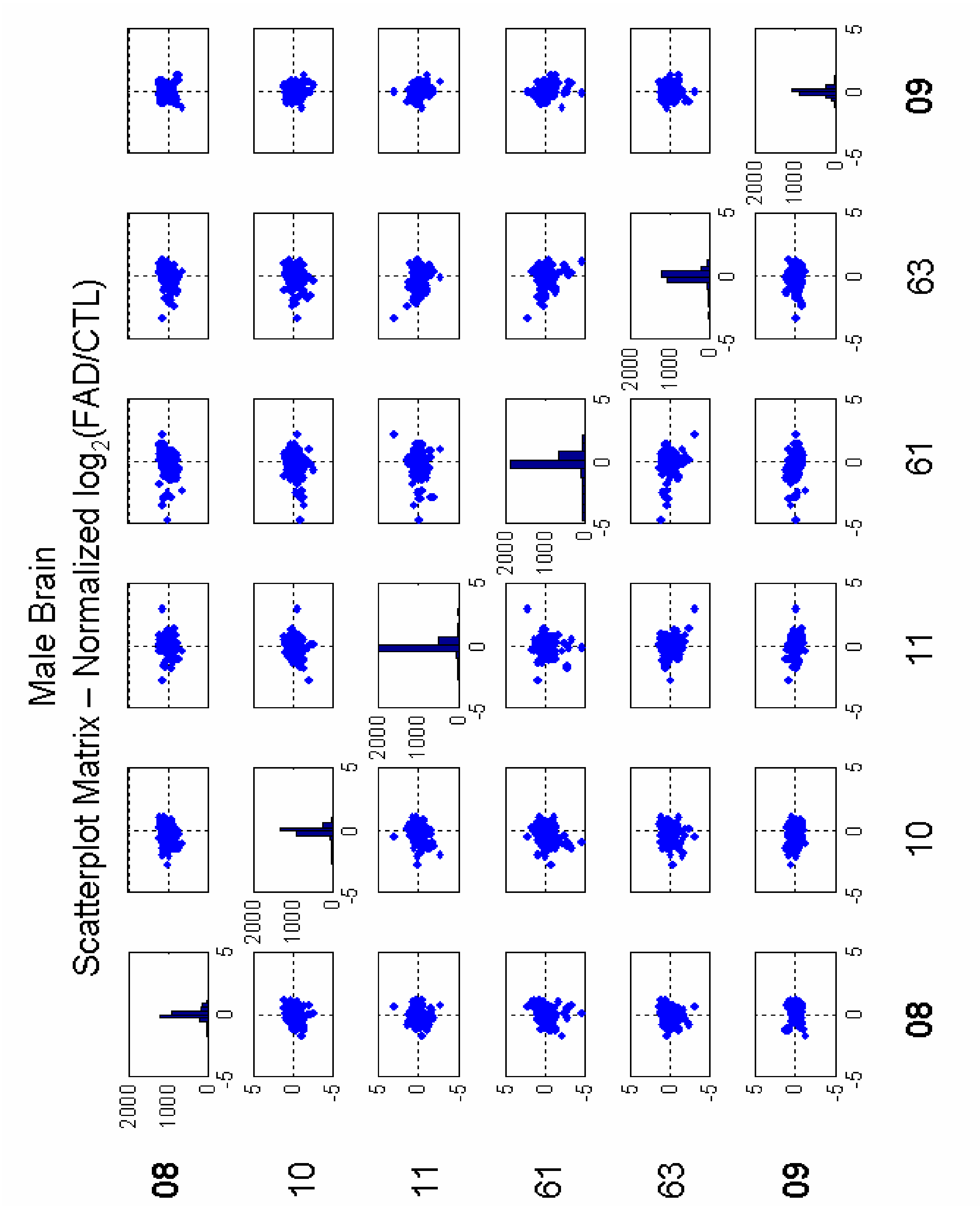

Figure 3: Scatterplot matrix of gene expression data of FAD exposure in male brain tissue. Dye swaps are slides 08 and 09.

Table 3: Summary of results of gene expression analysis

		t-statistic	# spots	total # of significant genes	# upregulated	# downregulated
Female Brain w/ dye swap						
Threshold Applied	t(.999975)	3.86	2581	14	8	6
	t(.999900)	3.6175	2581	19	9	10
All Spots Included	t(.999975)	3.942	22467	106	91	15
	t(.999900)	3.5778	22467	164	135	29
Female Brain w/o dye swap						
Threshold Applied	t(.999975)	3.94	2628	55	37	18
	t(.999900)	3.5939	2628	83	55	28
All Spots Included	t(.999975)	3.9017	22470	9279	5734	3545
	t(.999900)	3.5916	22470	10438	6101	4337
Male Brain w/ dye swap						
Threshold Applied	t(.999975)	3.917	2585	7	1	6
	t(.999900)	3.5843	2585	14	2	12
All Spots Included	t(.999975)	4.0207	22529	35	19	16
	t(.999900)	3.6308	22529	65	41	24
Male Brain w/o dye swap						
Threshold Applied	t(.999975)	3.9601	2641	122	87	35
	t(.999900)	3.6032	2641	171	106	65
All Spots Included	t(.999975)	3.8973	22532	17456	8577	8879
	t(.999900)	3.6375	22532	17837	8804	9033

Conclusions and Recommendations for Future Work

The results of the analysis of the three successive microarray scans indicate a minimal amount of photobleaching. The low levels of signal degradation coupled with their consistency to previous observations of the photobleaching behavior in these dyes contribute to assuring stable microarrays under the scanning conditions used. However, since the photobleaching phenomenon depends on many factors including the number of scans, intensity of laser, scan dwell times, scan speeds, and potentially sample age, there is no guarantee that these findings can be applied to other circumstances, such as a different instrument or scan parameters.

When analyzing gene expression data from microarrays one of the most important characteristics is to assess the variability and reproducibility of the data. This is typically done in three levels: technical replication, biological replication, and experiment/treatment replication, although there are variants on this process. The technical and biological replication experiments set the baseline levels of variance. In order for genes to be identified as significantly expressed as a result of a treatment they must be significant above this baseline. For this reason it is desirable to assess and subsequently minimize the variation introduced from technical and biological variation. In this experiment as designed there are no technical replicates available. It would be useful to study the variation introduced simply as a result of the technique. It is also possible that techniques such as pooling the RNA from multiple fish could potentially reduce the levels of biological variation. Overall, the female brain microarray slides and the male brain microarray slides lacked reproducibility compared to other microarray experiments this lab has analyzed. It was also discomforting that the analysis with and without the thresholding applied lead to such drastically varying results and this warrants further investigation, perhaps by comparing gene lists generated via other analysis methods.

In addition to slide replicates, replicate spots within an array would also be helpful. In the case of the modified t-statistic used in this analysis, the algorithm was designed to operate with 4-6 replicate spots within an array. Such a format offers a robust method to handle data with spatial variations that are prevalent in microarrays due to printing and hybridization defects.

On the basis of this analysis, we would strongly recommend moving to an array platform that includes replicate spots on the same arrays, and performing additional hybridizations including dye swaps to more fully characterize the levels of technical and biological variation and thus allow more confidence in gene lists generated as a result of the treatment.

Acknowledgements

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References

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3. J. Malicka, I. Gryczynski, J. Fang, J. Kusba, and J. R. Lakowicz, "Photostability of Cy3 and Cy5-labeled DNA in the presence of metallic silver particles," Journal of Fluorescence 12, 439-447 (2002).

Appendix A: Gene lists

Female Brain with Dye Swap

t(.999975)=3.86

row	col	t(adj)	ProbeName	GeneName	SystematicName	Description
34	85	-5.04	A_15_P118659	zgc:103772	NM_001006005	Danio rerio zgc:103772 (zgc:103772), mRNA [NM_001006005]
32	70	-4.97	A_15_P101310	BC056779	BC056779	Danio rerio cDNA clone IMAGE:3816160, partial cds. [BC056779]
18	177	-4.93	A_15_P119155	sepp1a	NM_178297	Danio rerio selenoprotein P, plasma, 1a (sepp1a), mRNA [NM_178297]
94	81	-4.64	A_15_P112610	zgc:77063	NM_212704	Danio rerio zgc:77063 (zgc:77063), mRNA [NM_212704]
60	156	-4.61	A_15_P105537	TC279930	TC279930	Unknown
12	209	-4.04	A_15_P114734	bsg	NM_198142	Danio rerio basigin (bsg), mRNA [NM_198142]
93	203	3.92	A_15_P102146	BM181130	BM181130	fv94f05.y1 Zebrafish SJD adult male II Danio rerio cDNA clone IMAGE:5544729 5', mRNA sequence [BM181130
14	115	4.00	A_15_P106603	zgc:73292	NM_212661	Danio rerio zgc:73292 (zgc:73292), mRNA [NM_212661]
34	178	4.20	A_15_P104306	cd9l	NM_213428	Danio rerio CD9 antigen, like (cd9l), mRNA [NM_213428]
56	113	4.28	A_15_P101154	zgc:55427	NM_199865	Danio rerio zgc:55427 (zgc:55427), mRNA [NM_199865]
61	105	4.50	A_15_P106181	TC279012	TC279012	SYU_TORCA (P37379) Synuclein, partial (66%) [TC279012]
37	125	4.50	A_15_P107634	ddx5	NM_212612	Danio rerio DEAD (Asp-Glu-Ala-Asp) box polypeptide 5 (ddx5), mRNA [NM_212612]
93	35	4.98	A_15_P115542	neurod	NM_130978	Danio rerio neurogenic differentiation (neurod), mRNA [NM_130978]
100	136	5.06	A_15_P109741	tuba8l3	NM_001003558	Danio rerio tubulin, alpha 8 like 3 (tuba8l3), mRNA [NM_001003558]

Female Brain without Dye Swap

t(.999975)=3.94

row	col	t(adj)	ProbeName	GeneName	SystematicName	Description
8	193	-14.23	A_15_P118764	TC282169	TC282169	Q7SYV3 (Q7SYV3) MGC64464 protein, partial (59%) [TC282169]
46	72	-13	A_15_P117498	zgc:91997	NM_001004113	Danio rerio zgc:91997 (zgc:91997), mRNA [NM_001004113]
4	184	-12.19	A_15_P117601	TC296972	TC296972	Q8BU53 (Q8BU53) Mus musculus 2 days pregnant adult female oviduct cDNA, RIKEN full-length enriched library
36	113	-10.34	A_15_P120936	zgc:76908	NM_213094	Danio rerio zgc:76908 (zgc:76908), mRNA [NM_213094]
58	205	-7.31	A_15_P103908	zgc:101069	NM_001003570	Danio rerio zgc:101069 (zgc:101069), mRNA [NM_001003570]
94	81	-5.2	A_15_P112610	zgc:77063	NM_212704	Danio rerio zgc:77063 (zgc:77063), mRNA [NM_212704]
32	70	-4.77	A_15_P101310	BC056779	BC056779	Danio rerio cDNA clone IMAGE:3816160, partial cds. [BC056779]
31	144	-4.53	A_15_P101052	TC294969	TC294969	Unknown
34	85	-4.52	A_15_P118659	zgc:103772	NM_001006005	Danio rerio zgc:103772 (zgc:103772), mRNA [NM_001006005]
39	157	-4.46	A_15_P121437	zgc:92472	NM_001002304	Danio rerio zgc:92472 (zgc:92472), mRNA [NM_001002304]
37	157	-4.42	A_15_P111989	zgc:92425	NM_001002180	Danio rerio zgc:92425 (zgc:92425), mRNA [NM_001002180]
49	27	-4.35	A_15_P109354	BM316955	BM316955	fw77d06.y1 Gong zebrafish testis Danio rerio cDNA clone IMAGE:5616419 5', mRNA sequence [BM316955]
60	156	-4.31	A_15_P105537	TC279930	TC279930	Unknown
45	197	-4.24	A_15_P101340	tcea1	NM_199994	Danio rerio transcription elongation factor A (SII), 1 (tcea1), mRNA [NM_199994]
101	4	-4.16	A_15_P119998	TC268844	TC268844	Q6PBZ5 (Q6PBZ5) Zgc:73179, complete [TC268844]
84	83	-4.13	A_15_P111755	rbp1b	NM_212895	Danio rerio cellular retinol-binding protein type 1b (rbp1b), mRNA [NM_212895]
76	153	-4.01	A_15_P120694	rbp1b	NM_212895	Danio rerio cellular retinol-binding protein type 1b (rbp1b), mRNA [NM_212895]
40	32	-3.99	A_15_P119438	bckdk	NM_213060	Danio rerio branched chain alpha-ketoacid dehydrogenase kinase (bckdk), mRNA [NM_213060]
98	160	3.96	A_15_P115681	zgc:65770	NM_001001889	Danio rerio zgc:65770 (zgc:65770), mRNA [NM_001001889]
60	25	3.97	A_15_P116526	kbtbd10	NM_198979	Danio rerio kelch repeat and BTB (POZ) domain containing 10 (kbtbd10), mRNA [NM_198979]
52	23	4.01	A_15_P115019	zgc:66325	NM_201041	Danio rerio zgc:66325 (zgc:66325), mRNA [NM_201041]
78	189	4.02	A_15_P100153	zgc:73358	NM_213045	Danio rerio zgc:73358 (zgc:73358), mRNA [NM_213045]
29	49	4.05	A_15_P100582	sox9b	NM_131644	Danio rerio SRY-box containing gene 9b (sox9b), mRNA [NM_131644]
32	64	4.09	A_15_P105570	atp5g	NM_131761	Danio rerio ATP synthase, H+ transporting, mitochondrial F0 complex, subunit c (subunit 9) (atp5g), mRNA [NM_
102	202	4.10	A_15_P111800	atp6v1g1	NM_199934	Danio rerio ATPase, H+ transporting, V1 subunit G isoform 1 (atp6v1g1), mRNA [NM_199934]
76	107	4.12	A_15_P103678	zgc:63840	NM_200626	Danio rerio zgc:63840 (zgc:63840), mRNA [NM_200626]
100	136	4.13	A_15_P109741	tuba8l3	NM_001003558	Danio rerio tubulin, alpha 8 like 3 (tuba8l3), mRNA [NM_001003558]
67	186	4.13	A_15_P113269	zgc:101811	NM_001006049	Danio rerio zgc:101811 (zgc:101811), mRNA [NM_001006049]
32	45	4.16	A_15_P106713	TC271072	TC271072	BC020113 TRAP/Mediator complex component TRAP25 {Mus musculus;} , partial (85%) [TC271072]
24	147	4.18	A_15_P103858	TC276758	TC276758	BC014455 NEDD5 protein {Homo sapiens;} , partial (55%) [TC276758]
44	157	4.18	A_15_P118089	zgc:92784	NM_001002548	Danio rerio zgc:92784 (zgc:92784), mRNA [NM_001002548]
90	27	4.22	A_15_P101626	pkm2	NM_199333	Danio rerio pyruvate kinase, muscle (pkm2), mRNA [NM_199333]
37	125	4.23	A_15_P107634	ddx5	NM_212612	Danio rerio DEAD (Asp-Glu-Ala-Asp) box polypeptide 5 (ddx5), mRNA [NM_212612]
93	32	4.37	A_15_P114731	CF550364	CF550364	AGENCOURT_15592276 NIH_ZGC_4 Danio rerio cDNA clone IMAGE:7012619 5', mRNA sequence [CF550364
49	18	4.43	A_15_P117539	TC291339	TC291339	Unknown
28	190	4.43	A_15_P110225	wu:fk66c03	BE016624	fk66c03.y1 Zebrafish Research Genetics C32 fin Danio rerio cDNA 5', mRNA sequence [BE016624]
62	147	4.48	A_15_P116828	zgc:65873	NM_200542	Danio rerio zgc:65873 (zgc:65873), mRNA [NM_200542]
7	183	4.51	A_15_P113966	bactin1	NM_131031	Danio rerio bactin1 (bactin1), mRNA [NM_131031]
1	149	4.59	A_15_P109432	TC287937	TC287937	Q9W3T5 (Q9W3T5) CG32736-PA (Cg32736-pb) (RE60462p), partial (35%) [TC287937]
20	53	4.64	A_15_P112458	BM530212	BM530212	fw73d08.x1 Gong zebrafish testis Danio rerio cDNA clone IMAGE:5616039 3' similar to SW:DUS3_HUMAN P514
78	166	4.71	A_15_P119226	zgc:73107	NM_200714	Danio rerio zgc:73107 (zgc:73107), mRNA [NM_200714]
52	215	4.71	A_15_P112465	ndufa6	NM_200968	Danio rerio NADH dehydrogenase (ubiquinone) 1 alpha subcomplex, 6, 14kDa (ndufa6), mRNA [NM_200968]
13	89	4.75	A_15_P110494	zgc:55970	NM_201176	Danio rerio zgc:55970 (zgc:55970), mRNA [NM_201176]
81	126	4.78	A_15_P100096	zgc:73358	NM_213045	Danio rerio zgc:73358 (zgc:73358), mRNA [NM_213045]
57	69	4.88	A_15_P105561	TC297159	TC297159	Q6T937 (Q6T937) Gremlin, complete [TC297159]
5	152	4.92	A_15_P111082	TC290463	TC290463	Q9PUK9 (Q9PUK9) High mobility group protein HMG1, partial (22%) [TC290463]
93	35	4.97	A_15_P115542	neurod	NM_130978	Danio rerio neurogenic differentiation (neurod), mRNA [NM_130978]
20	65	5.35	A_15_P117740	arl6ip	NM_201112	Danio rerio ADP-ribosylation factor-like 6 interacting protein (arl6ip), mRNA [NM_201112]
98	134	5.44	A_15_P103611	TC291559	TC291559	Q6PBN6 (Q6PBN6) Inositol hexaphosphate kinase 2, complete [TC291559]
61	105	5.95	A_15_P106181	TC279012	TC279012	SYU_TORCA (P37379) Synuclein, partial (66%) [TC279012]
105	195	6.03	A_15_P117718	TC290034	TC290034	Q9PTT9 (Q9PTT9) Homeobox protein, partial (39%) [TC290034]
52	193	6.05	A_15_P112106	ldb4	NM_131316	Danio rerio LIM-domain binding factor 4 (ldb4), mRNA [NM_131316]
90	78	6.13	A_15_P115226	ldhb	BC068981	Danio rerio lactate dehydrogenase B4, mRNA (cDNA clone MGC:76941 IMAGE:6524932), complete cds. [BC068
34	84	6.56	A_15_P108328	TC281215	TC281215	Unknown
25	205	6.96	A_15_P112313	ENSDART00000005670	ENSDART00000005670	DHS7_MOUSE (Q9CXR1) Dehydrogenase/reductase SDR family member 7 precursor (Retinal short-chain dehy

Male Brain with Dye Swap

t(.999975)=3.917

row	col	t(adj)	ProbeName	GeneName	SystematicName	Description
28	9	-5.08	A_15_P110418	zgc:85951	NM_213233	Danio rerio zgc:85951 (zgc:85951), mRNA [NM_213233]
88	32	-4.27	A_15_P105922	TC270239	TC270239	SA2_XENLA (Q9DGN0) Cohesin subunit SA-2 (XSA-2) (Stromal antigen 2 homolog) (SCC3 homolog 2), partial
94	93	-4.16	A_15_P116273	zgc:56334	NM_199568	Danio rerio zgc:56334 (zgc:56334), mRNA [NM_199568]
96	22	-4.09	A_15_P116657	zgc:56334	NM_199568	Danio rerio zgc:56334 (zgc:56334), mRNA [NM_199568]
40	116	-4.05	A_15_P100648	BC050162	BC050162	Danio rerio, clone IMAGE:5612092, mRNA. [BC050162]
16	94	-4.03	A_15_P103983	LOC402823	BC056279	Danio rerio hypothetical protein LOC402823, mRNA (cDNA clone IMAGE:6789379), partial cds. [BC056279]
79	95	4.51	A_15_P104141	rbp4	NM_130920	Danio rerio retinol binding protein 4, plasma (rbp4), mRNA [NM_130920]

Male Brain without Dye Swap

t(.999975)=3.94

row	col	t(adj)	ProbeName	GeneName	SystematicName	Description
8	193	-18.25	A_15_P118764	TC282169	TC282169	Q7SYV3 (Q7SYV3) MGC64464 protein, partial (59%) [TC282169]
46	72	-17.31	A_15_P117498	zgc:91997	NM_001004113	Danio rerio zgc:91997 (zgc:91997), mRNA [NM_001004113]
4	184	-17.30	A_15_P117601	TC296972	TC296972	Q8BU53 (Q8BU53) Mus musculus 2 days pregnant adult female oviduct cDNA, RIKEN full-length enriched library
41	36	-17.02	A_15_P118783	wu:fk34f03	AW595834	fk34f03.y1 zebrafish fin day1 regeneration Danio rerio cDNA 5' similar to SW:COX1_CYPCA P24985 CYTOCHR
36	113	-16.34	A_15_P120936	zgc:76908	NM_213094	Danio rerio zgc:76908 (zgc:76908), mRNA [NM_213094]
58	205	-15.34	A_15_P103908	zgc:101069	NM_001003570	Danio rerio zgc:101069 (zgc:101069), mRNA [NM_001003570]
101	4	-12.71	A_15_P119998	TC268844	TC268844	Q6PBZ5 (Q6PBZ5) Zgc:73179, complete [TC268844]
93	164	-8.62	A_15_P100556	zgc:86773	NM_001002129	Danio rerio zgc:86773 (zgc:86773), mRNA [NM_001002129]
31	144	-8.13	A_15_P101052	TC294969	TC294969	Unknown
28	9	-7.79	A_15_P110418	zgc:85951	NM_213233	Danio rerio zgc:85951 (zgc:85951), mRNA [NM_213233]
88	32	-6.91	A_15_P105922	TC270239	TC270239	SA2_XENLA (Q9DGN0) Cohesin subunit SA-2 (XSA-2) (Stromal antigen 2 homolog) (SCC3 homolog 2), partial
37	157	-6.56	A_15_P111989	zgc:92425	NM_001002180	Danio rerio zgc:92425 (zgc:92425), mRNA [NM_001002180]
84	68	-5.95	A_15_P109119	TC271723	TC271723	Q7ZWJ8 (Q7ZWJ8) LOC402796 protein (Fragment), complete [TC271723]
45	24	-5.92	A_15_P100132	epd	NM_131005	Danio rerio ependymin (epd), mRNA [NM_131005]
39	167	-5.76	A_15_P110649	rrm1	ENSDART00000012091	ribonucleotide reductase M1 polypeptide [Source:ZFIN;Acc:ZDB-GENE-990415-247] [ENSDART00000012091]
17	177	-5.33	A_15_P105415	CO916998	CO916998	AGENCOURT_30539697 NIH_ZGC_19 Danio rerio cDNA clone IMAGE:7427508 5', mRNA sequence [CO91699
94	93	-5.21	A_15_P116273	zgc:56334	NM_199568	Danio rerio zgc:56334 (zgc:56334), mRNA [NM_199568]
58	161	-5.12	A_15_P119715	LOC407698	BC067697	Danio rerio hypothetical protein LOC407698, mRNA (cDNA clone IMAGE:6960793), partial cds. [BC067697]
41	133	-4.95	A_15_P112548	zgc:55291	NM_213294	Danio rerio zgc:55291 (zgc:55291), mRNA [NM_213294]
47	135	-4.91	A_15_P101842	ktn1	NM_200081	Danio rerio kinectin 1 (ktn1), mRNA [NM_200081]
68	52	-4.85	A_15_P117399	TC270733	TC270733	N107_RAT (P52590) Nuclear pore complex protein Nup107 (Nucleoporin Nup107) (107 kDa nucleoporin) (p105),
50	170	-4.78	A_15_P107724	ktn1	NM_200081	Danio rerio kinectin 1 (ktn1), mRNA [NM_200081]
3	116	-4.69	A_15_P104196	tial1	NM_201132	Danio rerio TIA1 cytotoxic granule-associated RNA binding protein-like 1 (tial1), mRNA [NM_201132]
22	125	-4.46	A_15_P102627	TC274714	TC274714	Q8R3Q5 (Q8R3Q5) BC024868 protein, partial (18%) [TC274714]
9	117	-4.44	A_15_P109350	AW077980	AW077980	fj01g12.y1 Zebrafish adult olfactory Danio rerio cDNA 5', mRNA sequence [AW077980]
75	43	-4.29	A_15_P114812	zgc:63812	NM_201109	Danio rerio zgc:63812 (zgc:63812), mRNA [NM_201109]
40	116	-4.26	A_15_P100648	BC050162	BC050162	Danio rerio, clone IMAGE:5612092, mRNA. [BC050162]
54	185	-4.25	A_15_P108151	BC091544	BC091544	AGENCOURT_30542737 NIH_ZGC_19 Danio rerio cDNA clone IMAGE:7430194 5', mRNA sequence [CO91408
14	202	-4.19	A_15_P109077	zgc:56178	NM_200204	Danio rerio zgc:56178 (zgc:56178), mRNA [NM_200204]
23	167	-4.19	A_15_P118118	zgc:77760	NM_200859	Danio rerio zgc:77760 (zgc:77760), mRNA [NM_200859]
40	32	-4.06	A_15_P119438	bckdk	NM_213060	Danio rerio branched chain alpha-ketoacid dehydrogenase kinase (bckdk), mRNA [NM_213060]
23	172	-4.04	A_15_P116710	spon1b	NM_131517	Danio rerio spondin 1b (spon1b), mRNA [NM_131517]
44	154	-4.03	A_15_P112751	zgc:73200	NM_199952	Danio rerio zgc:73200 (zgc:73200), mRNA [NM_199952]
7	203	-4.03	A_15_P118047	uxs1	BC074058	Danio rerio UDP-glucuronic acid decarboxylase 1, mRNA (cDNA clone MGC:91980 IMAGE:7042298), complete
97	26	-3.98	A_15_P120494	zgc:63812	NM_201109	Danio rerio zgc:63812 (zgc:63812), mRNA [NM_201109]

Table continued on next page

Male Brain without Dye Swap

t(.999975)=3.94

row	col	t(adj)	ProbeName	GeneName	SystematicName	Description
81	126	3.98	A_15_P100096	zgc:73358	NM_213045	Danio rerio zgc:73358 (zgc:73358), mRNA [NM_213045]
22	108	3.99	A_15_P108412	zgc:101887	NM_001005960	Danio rerio zgc:101887 (zgc:101887), mRNA [NM_001005960]
69	31	4.00	A_15_P116587	zgc:73152	NM_212722	Danio rerio zgc:73152 (zgc:73152), mRNA [NM_212722]
30	11	4.03	A_15_P115211	zgc:56380	NM_200951	Danio rerio zgc:56380 (zgc:56380), mRNA [NM_200951]
52	179	4.04	A_15_P115161	zgc:92859	NM_001002487	Danio rerio zgc:92859 (zgc:92859), mRNA [NM_001002487]
87	214	4.09	A_15_P101191	yes1	AJ620749	Danio rerio mRNA for protein-tyrosine kinase (c-yes gene). [AJ620749]
38	181	4.15	A_15_P121146	ENSDART00000002187	ENSDART00000002187	fd05d01.y1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3729985 5' similar to SW:IATP_PIG
10	74	4.16	A_15_P108288	zgc:56140	NM_213005	Danio rerio zgc:56140 (zgc:56140), mRNA [NM_213005]
47	186	4.17	A_15_P105209	zgc:73144	NM_200729	Danio rerio zgc:73144 (zgc:73144), mRNA [NM_200729]
86	69	4.18	A_15_P119876	zgc:92891	NM_001002468	Danio rerio zgc:92891 (zgc:92891), mRNA [NM_001002468]
20	45	4.21	A_15_P107320	sb:cb890	NM_198824	Danio rerio sb:cb890 (sb:cb890), mRNA [NM_198824]
2	165	4.22	A_15_P119250	wu:fj43h11	CA476850	AGENCOURT_10702377 NCI_CGAP_ZEmb3 Danio rerio cDNA clone IMAGE:6800332 5', mRNA sequence [CA
81	150	4.25	A_15_P110420	zgc:55762	NM_201015	Danio rerio zgc:55762 (zgc:55762), mRNA [NM_201015]
41	138	4.31	A_15_P120271	zgc:76914	NM_213088	Danio rerio zgc:76914 (zgc:76914), mRNA [NM_213088]
54	150	4.31	A_15_P102274	rpl8	NM_200713	Danio rerio ribosomal protein L8 (rpl8), mRNA [NM_200713]
92	97	4.32	A_15_P105025	zgc:73340	NM_199743	Danio rerio zgc:73340 (zgc:73340), mRNA [NM_199743]
13	126	4.38	A_15_P104005	wu:fi32a10	CO810652	AGENCOURT_30335145 NIH_ZGC_5 Danio rerio cDNA clone IMAGE:7398230 5', mRNA sequence [CO810652
28	190	4.39	A_15_P110225	wu:fk66c03	BE016624	fk66c03.y1 Zebrafish Research Genetics C32 fin Danio rerio cDNA 5', mRNA sequence [BE016624]
13	184	4.40	A_15_P105299	zgc:77784	NM_205649	Danio rerio zgc:77784 (zgc:77784), mRNA [NM_205649]
31	48	4.40	A_15_P104002	aldoc	NM_194384	Danio rerio aldolase c, fructose-bisphosphate (aldoc), mRNA [NM_194384]
3	166	4.44	A_15_P100475	wu:fc23d08	AI641743	fc23d08.x1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3722223 3', mRNA sequence [AI6417
77	136	4.45	A_15_P102674	bactin2	NM_181601	Danio rerio bactin2 (bactin2), mRNA [NM_181601]
100	64	4.51	A_15_P116639	zgc:65895	NM_200574	Danio rerio zgc:65895 (zgc:65895), mRNA [NM_200574]
32	64	4.52	A_15_P105570	atp5g	NM_131761	Danio rerio ATP synthase, H+ transporting, mitochondrial F0 complex, subunit c (subunit 9) (atp5g), mRNA [NM_
3	156	4.54	A_15_P117544	cx43	NM_131038	Danio rerio gap junction protein, alpha 1 (gja1), mRNA [NM_131038]
91	144	4.61	A_15_P120439	htatip2	NM_131681	Danio rerio HIV-1 Tat interactive protein 2 (htatip2), mRNA [NM_131681]
90	27	4.61	A_15_P101626	pkm2	NM_199333	Danio rerio pyruvate kinase, muscle (pkm2), mRNA [NM_199333]
65	125	4.73	A_15_P108711	TC291740	TC291740	Unknown
55	157	4.75	A_15_P111266	zgc:92775	NM_001003424	Danio rerio zgc:92775 (zgc:92775), mRNA [NM_001003424]
10	156	4.78	A_15_P102200	cav1	NM_212651	Danio rerio caveolin 1 (cav1), mRNA [NM_212651]
62	147	4.78	A_15_P116828	zgc:65873	NM_200542	Danio rerio zgc:65873 (zgc:65873), mRNA [NM_200542]
103	91	4.83	A_15_P113999	tra2a	NM_200416	Danio rerio transformer-2 alpha (tra2a), mRNA [NM_200416]
16	182	4.83	A_15_P116956	AW018582	AW018582	fd48f12.y1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3733007 5', mRNA sequence [AW018
5	152	4.84	A_15_P111082	TC290463	TC290463	Q9PUK9 (Q9PUK9) High mobility group protein HMG1, partial (22%) [TC290463]
100	47	4.84	A_15_P112667	ENSDART00000036759	ENSDART00000036759	BC021603 D11Bwg0434e protein {Mus musculus;} , partial (82%) [TC292445]
104	27	4.86	A_15_P107868	zgc:73337	NM_200795	Danio rerio zgc:73337 (zgc:73337), mRNA [NM_200795]
30	157	4.88	A_15_P118346	hfe2	NM_213643	Danio rerio hemochromatosis type 2 (hfe2), mRNA [NM_213643]
60	207	4.89	A_15_P119206	TC279995	TC279995	Unknown
25	14	4.90	A_15_P112973	TC292239	TC292239	Q6ZQ58 (Q6ZQ58) MKIAA0731 protein (Fragment), partial (71%) [TC292239]
70	82	4.90	A_15_P119606	atp6v1bb	NM_182879	Danio rerio ATPase, H+ transporting, lysosomal, V1 subunit B, member b (atp6v1bb), mRNA [NM_182879]
81	82	4.92	A_15_P108939	atp6v1bb	NM_182879	Danio rerio ATPase, H+ transporting, lysosomal, V1 subunit B, member b (atp6v1bb), mRNA [NM_182879]
62	200	4.95	A_15_P111429	wu:fc64d11	AI883459	fc64d11.y1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3726165 5', mRNA sequence [AI8834
37	81	4.96	A_15_P118109	mtch2	NM_131382	Danio rerio mitochondrial carrier homolog 2 (mtch2), mRNA [NM_131382]
97	100	4.96	A_15_P101470	zgc:103765	NM_001004652	Danio rerio zgc:103765 (zgc:103765), mRNA [NM_001004652]
50	26	4.98	A_15_P121423	zgc:103765	NM_001004652	Danio rerio zgc:103765 (zgc:103765), mRNA [NM_001004652]
38	85	5.06	A_15_P112426	eef2l	NM_200458	Danio rerio eukaryotic translation elongation factor 2, like (eef2l), mRNA [NM_200458]
18	104	5.08	A_15_P120262	cav1	ENSDART00000014154	caveolin 1 [Source:ZFIN;Acc:ZDB-GENE-030131-2415] [ENSDART00000014154]
38	51	5.08	A_15_P100737	zgc:73139	CN020873	AGENCOURT_21030048 NIH_ZGC_17 Danio rerio cDNA clone IMAGE:7232668 5', mRNA sequence [CN02087
90	25	5.09	A_15_P106460	BI866471	BI866471	ft20a08.y1 Zebrafish neuronal Danio rerio cDNA clone IMAGE:5081775 5', mRNA sequence [BI866471]
82	113	5.11	A_15_P104928	zgc:56140	NM_213005	Danio rerio zgc:56140 (zgc:56140), mRNA [NM_213005]
16	178	5.27	A_15_P112898	TC268354	TC268354	Q8JH37 (Q8JH37) Vitellogenin 1 (Fragment), partial (22%) [TC268354]
96	67	5.38	A_15_P105842	TC282550	TC282550	CUL5_HUMAN (Q93034) Cullin homolog 5 (CUL-5) (Vasopressin-activated calcium-mobilizing receptor) (VACM-
78	166	5.40	A_15_P119226	zgc:73107	NM_200714	Danio rerio zgc:73107 (zgc:73107), mRNA [NM_200714]
67	72	5.41	A_15_P104937	rbm5	BC057427	Danio rerio RNA binding motif protein 5, mRNA (cDNA clone IMAGE:6793537), partial cds. [BC057427]
13	89	5.53	A_15_P110494	zgc:55970	NM_201176	Danio rerio zgc:55970 (zgc:55970), mRNA [NM_201176]
35	114	5.55	A_15_P114289	ndpkz2	NM_130927	Danio rerio nucleoside diphosphate kinase-Z2 (ndpkz2), mRNA [NM_130927]
63	179	5.57	A_15_P101202	BQ259479	BQ259479	fz99f04.y1 zebrafish fin day1 regeneration Danio rerio cDNA clone IMAGE:5908734 5' similar to contains elemen
29	149	5.57	A_15_P115552	zgc:92777	NM_001002551	Danio rerio zgc:92777 (zgc:92777), mRNA [NM_001002551]
34	93	5.60	A_15_P103309	TC291802	TC291802	Q90W08 (Q90W08) IFR1 protein (Interferon-related protein), partial (86%) [TC291802]
3	92	5.77	A_15_P111174	htatip2	NM_131681	Danio rerio HIV-1 Tat interactive protein 2 (htatip2), mRNA [NM_131681]
90	78	5.78	A_15_P115226	ldhb	BC068981	Danio rerio lactate dehydrogenase B4, mRNA (cDNA clone MGC:76941 IMAGE:6524932), complete cds. [BC068
72	99	5.79	A_15_P102363	TC295968	TC295968	BC031471 WDR26 protein {Homo sapiens;} , partial (61%) [TC295968]
101	180	5.95	A_15_P111633	NM_205554	NM_205554	Danio rerio zgc:77708 (zgc:77708), mRNA [NM_205554]
23	80	6.00	A_15_P100610	txnip	NM_200087	Danio rerio thioredoxin interacting protein (txnip), mRNA [NM_200087]
85	43	6.05	A_15_P100156	ddx54	NM_173268	Danio rerio DEAD (Asp-Glu-Ala-Asp) box polypeptide 54 (ddx54), mRNA [NM_173268]
51	98	6.10	A_15_P119430	CD283307	CD283307	G38814.76 NCI_CGAP_ZKid1 Danio rerio cDNA clone IMAGE:6524011 3', mRNA sequence [CD283307]
49	18	6.14	A_15_P117539	TC291339	TC291339	Unknown
57	191	6.14	A_15_P121058	ngfb	NM_199210	Danio rerio nerve growth factor, beta polypeptide (ngfb), mRNA [NM_199210]
80	100	6.17	A_15_P119135	BC090902	BC090902	BC003266 cDNA sequence BC003266 {Mus musculus;} , partial (95%) [TC280527]
20	200	6.27	A_15_P103041	TC269675	TC269675	DYR2_HUMAN (Q92630) Dual-specificity tyrosine-phosphorylation regulated kinase 2 , partial (75%) [TC26967
23	191	6.28	A_15_P108645	BI475369	BI475369	fq31f12.y3 zebrafish adult brain Danio rerio cDNA clone IMAGE:4833167 5', mRNA sequence [BI475369]
21	41	6.30	A_15_P111444	blnk	NM_212838	Danio rerio B-cell linker (blnk), mRNA [NM_212838]
37	108	6.33	A_15_P103830	TC279991	TC279991	Q7ZVX9 (Q7ZVX9) ATP binding protein associated with cell differentiation, complete [TC279991]
62	2	6.34	A_15_P114374	wu:fc89h05	AI958031	fc89h05.y1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3728601 5', mRNA sequence [AI9580
30	215	6.36	A_15_P110370	A_15_P110370	A_15_P110370	Unknown
101	117	6.38	A_15_P102164	zgc:56140	ENSDART00000014098	BC045940 zgc:56140 {Danio rerio;} , complete [TC279427]
6	206	6.39	A_15_P102378	gad1	NM_194419	Danio rerio glutamate decarboxylase 1 (gad1), mRNA [NM_194419]
17	198	6.50	A_15_P100646	si:ch211-51e12.6	CK400164	AGENCOURT_17517127 NIH_ZGC_4 Danio rerio cDNA clone IMAGE:7120349 5', mRNA sequence [CK400164]
80	68	6.53	A_15_P110639	BG305603	BG305603	fm06d06.x1 Zebrafish adult retina cDNA Danio rerio cDNA clone IMAGE:4145339 3', mRNA sequence [BG30560
68	162	6.62	A_15_P118878	gstm	NM_212676	Danio rerio glutathione S-transferase M (gstm), mRNA [NM_212676]
82	120	6.68	A_15_P120523	tcf7l1a	NM_131269	Danio rerio transcription factor 7-like 1a (T-cell specific, HMG-box) (tcf7l1a), mRNA [NM_131269]
1	129	6.69	A_15_P104027	wu:fq40e10	AI722667	fc30b01.y1 Zebrafish WashU MPIMG EST Danio rerio cDNA clone IMAGE:3722857 5', mRNA sequence [AI7226
58	189	6.78	A_15_P111576	BM036600	BM036600	fu79h07.y1 Gong zebrafish testis Danio rerio cDNA clone IMAGE:5377381 5', mRNA sequence [BM036600]
102	202	6.83	A_15_P111800	atp6v1g1	NM_199934	Danio rerio ATPase, H+ transporting, V1 subunit G isoform 1 (atp6v1g1), mRNA [NM_199934]
6	153	6.85	A_15_P119153	TC281397	TC281397	JJAZ_MOUSE (Q80U70) Polycomb protein Suz12 (Suppressor of zeste 12 protein homolog), partial (74%) [TC28
87	200	6.86	A_15_P117366	cacna1c	NM_131900	Danio rerio calcium channel, voltage-dependent, L type, alpha 1C subunit (cacna1c), mRNA [NM_131900]
78	64	7.01	A_15_P110956	zgc:56708	NM_200310	Danio rerio zgc:56708 (zgc:56708), mRNA [NM_200310]