Identification of Genes That Promote or Inhibit Olfactory Memory Formation in *Drosophila*

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ABSTRACT Genetic screens in *Drosophila melanogaster* and other organisms have been pursued to filter the genome for genetic functions important for memory formation. Such screens have employed primarily chemical or transposon-mediated mutagenesis and have identified numerous mutants including classical memory mutants, *dunce* and *rutabaga*. Here, we report the results of a large screen using panneuronal RNAi expression to identify additional genes critical for memory formation. We identified >500 genes that compromise memory when inhibited (low hits), either by disrupting the development and normal function of the adult animal or by participating in the neurophysiological mechanisms underlying memory formation. We also identified >40 genes that enhance memory when inhibited (high hits). The *dunce* gene was identified as one of the low hits and further experiments were performed to map the effects of the *dunce* RNAi to the α/β and γ mushroom body neurons. Additional behavioral experiments suggest that *dunce* knockdown in the mushroom body neurons impairs memory without significantly affecting acquisition. We also characterized one high hit, *sickie*, to show that RNAi knockdown of this gene enhances memory through effects in dopaminergic neurons without apparent effects on acquisition. These studies further our understanding of two genes involved in memory formation, provide a valuable list of genes that impair memory that may be important for understanding the neurophysiology of memory or neurodevelopmental disorders, and offer a new resource of memory suppressor genes that will aid in understanding restraint mechanisms employed by the brain to optimize resources.

KEYWORDS RNAi screen; memory suppressor genes; *Drosophila*; memory

THE fruit fly, *Drosophila melanogaster*, is an ideal system for studying the genetic basis for memory formation. Flies exhibit robust memory formation in several different learning paradigms, with olfactory classical conditioning being the most intensively studied type of learning to date (Tully and Quinn 1985; Davis 2005; Tomchik and Davis 2013). The arsenal of tools that the researcher can bring to bear on memory formation and other biological problems using *Drosophila* is unparalleled (Venken *et al.* 2011). For instance, large collections of mutants exist harboring transposable elements that disrupt gene function (Bellen *et al.* 2011), or enhancer detector collections that provide a report on the expression pattern of nearby genes, and often disrupt the nearest gene (www.flybase.org), as well as RNAi collections (www.stockcenter.vdrc.at; www.flyrnai.org; www.shigen.nig.ac.jp/fly/nigfly/) that can be expressed using binary gene expression tools, such as the *gal4/uas* system (Brand and Perrimon 1993). Thousands of *gal4* driver lines are available that exhibit tissue-specific expression (www.janelia.org/team-project/fly-light) that afford the ability to drive transgene expression in virtually any group of cell types in the fly. Newer genome engineering techniques, like CRISPR, offer additional future promise for making directed mutations (Jinek *et al.* 2012; Sternberg *et al.* 2014). Approaches using the TARGET system, or Gene-Switch, offer the experimenter the ability to express *uas*-transgenes or *uas-RNAi* lines in both time and space (McGuire *et al.* 2004).

The genetic entrée to many biological problems is a large, forward genetic screen. Such screens are invaluable for several reasons. First, they identify the initial set of genes and gene functions involved in the biological process of interest when a saturation screen is completed. Second, they provide numerous genetic resources that are valuable for the study of

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individual genes, such as recessive, loss-of-function amorphic mutations, and dominant negative or hypermorphic mutations that produce a loss and gain of function, respectively.

Past genetic screens for olfactory memory using *Drosophila* have identified numerous genes important for the process as well as critical conceptual insights into the biology of memory formation. The initial screens employing chemical mutagenesis identified several mutants including *dunce* (*dnc*) and *rutabaga* (*rut*), which were subsequently found to encode cAMP phosphodiesterase and Ca^{++}/calmodulin-sensitive adenylyl cyclase, respectively (Dudai *et al.* 1976; Byers *et al.* 1981; Livingstone *et al.* 1984; Chen *et al.* 1986; Levin *et al.* 1992; Tomchik and Davis 2013) These and related observations with other organisms identified the critical role of cAMP metabolism in behavioral plasticity. Enhancer detector screens identified genes preferentially expressed in the mushroom bodies, a critical neural focus for olfactory learning (Han *et al.* 1996, and secondary behavioral screens on these collections pinpointed other important molecules for memory formation including cell adhesion receptors (Grotewiel *et al.* 1998; Cheng *et al.* 2001). *Drosophila* mutants have been identified that perturb different temporal forms of memory, including *amnesiac* (*amn*), which has a pronounced impairment of intermediate-term memory (Quinn *et al.* 1979), and mutants that have specific deficits in protein-synthesis-dependent long-term memory, many of the latter identified through P-factor-mediated mutagenesis (Dubnau *et al.* 2003).

We report here the results of a large, RNAi screen to identify genes important for memory formation. The RNAi approach is facilitated by existing libraries of transgenes that encode an RNAi molecule against one of the ~15,000 *Drosophila* genes. In addition, the RNAi approach facilitates mapping phenotypes to specific populations of neurons using a battery of spatially restricted *gal4* drivers, whereas genomic mutations require more difficult and less successful spatial rescue experiments. Our results identify a large collection of RNAi transgenes that impair olfactory memory and >40 RNAi transgenes that enhance memory.

Materials and Methods

Fly husbandry

Flies were raised on standard fly food at room temperature. The *uas-RNAi* stocks used for the RNAi screen were obtained from the Vienna *Drosophila* RNAi Center (http://stockcenter.vdrc.at/control/main). We employed the control line (*60100*) used to construct the *uas-RNAi* transgenic lines for some behavioral experiments. For the primary screen, secondary screen, and TriKinetics locomotor activity assay, we crossed *Nsyb-gal4* virgin females with males from individual *uas-RNAi* stocks. We conducted the initial screen using an $n = 4$ across the first 6 mo (1719 lines) and then changed to an $n = 3$ after pilot experiments showed that this had an insignificant effect on the number of false positives obtained. Other *gal4* driver lines used in this study include: *TH-gal4*, *238y-gal4*, *c772-gal4*, *NP2492-gal4*, *MZ604-gal4*, *VT64246-gal4*, *GH146-gal4*, *c739-gal4*, *R28-gal4*, *1471-gal4*, and *c305a-gal4*.

A recent letter to the editor included data showing that the KK RNAi library used in this study has a nonannotated docking site into which most RNAi integrations occurred (Green *et al.* 2014). All lines tested in that study (39) had RNAi insertion elements in the nonannotated site. Approximately 25% of the lines (9/39) also had an insertion element into the annotated docking site. Lines that contained insertions in the annotated site also exhibited a collapsed wing phenotype when crossed to the panneuronal *gal4* driver, *c155-gal4*, whereas lines without the insertion in the annotated site exhibited normal wings, even in the presence of the *gal4* driver.

We identified many lines with collapsed wings when crossed to *Nsyb-gal4* (Supporting Information, Table S2). Using PCR primers designed by Green *et al.* (2014), we assayed seven lines along with the control line, *60100*. The control line had neither site filled, as expected. Lines 100363 and 106641 (Table 2), with phenotypically normal wings, contain a filled nonannotated site and an empty annotated site. Neither of these lines exhibited collapsed wings. Five of the lines did exhibit collapsed wings in the presence of *Nsyb-gal4*: 108395, previously tested by Green *et al.* (2014), 110077, 110786, 108196, and 110518. Four of the five lines, 108395, 110077, 110786, and 108196, had integrations at both the annotated and nonannotated sites. One of the five, 110518, showed integration only at the annotated site and curiously, also exhibited collapsed wings.

Behavior

We used 1- to 4-day-old flies for all behavioral experiments. Flies were collected ~24 hr before experiments and were transferred to fresh food vials ~15 min before conditioning for equilibration to the experimental room conditions of 25° and ~70% humidity. Experiments were performed in a dark room under red filtered light. Standard aversive olfactory conditioning experiments were performed as described (Beck *et al.* 2000). Each experimental group of ~60 flies was loaded into a training tube where they received the following sequence of stimuli: 30 sec of air, 1 min of an odor paired with 12 pulses of 90 V electric shock (conditioned stimulus, CS^+), 30 sec of air, 1 min of a second odor with no electric shock (CS^-), and a final 30 sec of air. For conditioning odors, we bubbled fresh air through 3-octanol (OCT) or benzaldehyde (BEN) at concentrations in mineral oil that provided for optimal balance in the half performance index (PI) between odors. Optimal odor concentrations varied across time and between experimenters but were generally between 0.045 and 0.07% for benzaldehyde and between 0.14 and 0.165% for 3-octanol. After conditioning, flies were returned to a food vial to be tested at the 3-hr time point. Flies were allowed a 1-min resting period followed by a 2-min decision period to choose between a *T*-maze arm exposing the flies to the CS^+ odor and an arm exposing the flies to the CS^- odor. For all

experiments, two groups were trained and tested simultaneously. One group was trained with OCT as the conditioned stimulus paired with electric shock (CS^+) and BEN unpaired with electric shock (CS^-), while the other group was trained with BEN as CS^+ and OCT as CS^-. Each group tested provides a half PI: Half PI = [(no. flies in CS^- arm) − (no. flies in CS^+ arm)]/(no. flies in both arms). A final PI was calculated by averaging the two half PIs. Since the two groups were trained to opposite CS^+/CS^- odor pairs, this method balances out naive odor biases.

To test for odor avoidance, naive flies were allowed 2 min within the *T*-maze to choose between an arm with odor and an arm with fresh air. The odor avoidance index was calculated as the [(no. flies in fresh air arm) − (no. flies in odor arm)]/(no. flies in both arms). To test for shock avoidance, naive flies were allowed 2 min within the *T*-maze to choose between an arm with an electrified copper grid (same as used for conditioning above) and an arm with a nonelectrified copper grid. The side that is electrified was alternated to control for any side-to-side *T*-maze bias. The shock avoidance index was calculated as the [(no. flies in nonelectrified arm) − (no. flies in electrified arm)]/(no. flies in both arms).

For TriKinetics locomotor activity monitoring, 2- to 3-day-old flies were tested using the TriKinetics DAM5 Activity Monitor (www.trikinetics.com). In each experiment, eight flies of each genotype were randomly selected and placed into individual glass tubes. Eight flies of the control group, 60100, were assayed in parallel with approximately six different experimental groups. Flies selected were of both genders and tested at approximately the same time of day as the 3-hr memory experiments. Flies were raised on a 12:12 light:dark cycle. The flies were monitored for a 10-min period with the number of beam breaks recorded across 30-sec intervals. Activity scores were calculated by averaging the number of beam breaks per 30-sec epoch in the first 2 min. This experimental design was chosen to estimate the locomotor activity of the lines across the 2-min decision period that the flies have during testing in the *T*-maze after classical olfactory conditioning. The average activity score of each RNAi line tested was compared to the control line using one-way ANOVA followed by Dunnett's *post hoc* test.

Statistics

GraphPad Prism was used to analyze most of the data. The TriKinetics data were analyzed using the statistical package, R. PIs among experimenters followed a normal distribution (Figure 1). Therefore, we used a one-tailed Student *t*-test to compare the performance of an RNAi line to a control group in experiments that employed a control group tested in parallel, namely the characterization experiments of *sickie* and *dunce*. Significance was set at $\alpha = 0.05$. For all comparisons of the effect of genotype on memory retention across selected time points, we performed a two-way ANOVA with both genotype and time as factors. We followed the two-way ANOVA with a Bonferroni *post hoc* comparison among the relevant groups. Significance was set at $\alpha = 0.05$.

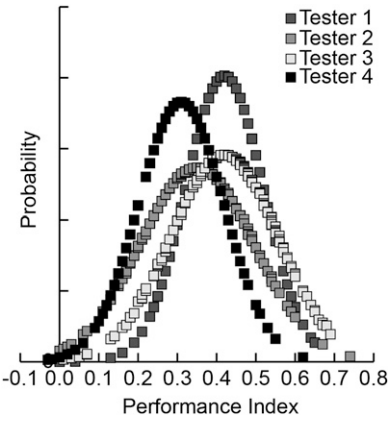

Figure 1 Performance indices for testers. Distribution of performance indices obtained by four testers involved in the screen for the first 200 lines screened by each tester using $n = 4$ for each line. Differences in the manual procedure and apparatuses (*T*-mazes, etc.) produce some variability between testers, with the average 3-hr PI ranging from 0.32 to 0.42. PIs for each tester were normally distributed.

Results

We obtained 3655 *uas-RNAi* lines (Table 1) for our screen from the Vienna Drosophila RNAi Center (http://stockcenter.vdrc.at/control/main) that were preselected for relevance to CNS development and function using bioinformatics criteria. The sources used to obtain this information and the filters used for selection included: (1) FlyBase (http://flybase.org/) listed genes that were selected from a query using gene ontology terms: (a) nervous system development, (b) neurological system process, (c) behavior, (d) neurophysiology defective, (e) neuroanatomy defective, (f) behavior defective, (g) adult brain, and (h) nervous system. (2) FlyAtlas (http://www.flyatlas.org/) listed genes with a preferential expression ratio of >1.5 in the brain and thoracicoabdominal ganglia compared to other nonneuronal tissues. (3) Fly genes whose mammalian orthologs are thought to be involved in neuronal processes from the literature (Cajigas *et al.* 2012; Hodas *et al.* 2012).

We used 3-hr memory as the critical time point for screening, since this time point after conditioning allows hits to be identified that affect acquisition (learning), memory stability, memory consolidation, forgetting, and/or retrieval. We anticipated that hits affecting acquisition might alter the processing of the CS signal, the unconditioned stimulus (US) signal, or the integration of the CS and US. Hits that alter memory stability may alter general mechanisms that promote memory stabilization that are not yet well defined, consolidation of memories into a form resistance to experimental insults, or forgetting (Dudai *et al.* 1976; Tully *et al.* 1994; Shuai *et al.* 2010; Berry *et al.* 2012). Within the first few hours after conditioning, *Drosophila* olfactory memories are known to consist of anesthesia sensitive memory (ASM), a form disruptable with cold anesthesia, and anesthesia resistant memory (ARM), a consolidated form of memory that is resistant to this treatment (Folkers *et al.* 1993). Our strategy utilized the

Table 1 Outlier selections from primary and secondary screens

Lines obtained	Lines screened	Primary screen hits	Secondary screen hits
3655	3207	964	600

Outliers from the primary and secondary screen of the KK RNAi library were made based on the distribution of performance index scores of the population shown in Figure 1. The average PI of the first 800 lines, 200 tested by each experimenter, was 0.38 with a standard deviation of 0.14. Lines deviating by ~1 standard deviation from the mean (0.24< and >0.52) were kept as putative hits.

CNS-wide *gal4* driver, *Nsyb-gal4*, to identify as many cellular players as possible, anticipating that further studies would identify the cell types in the brain that require the function of any identified gene.

Each individual *uas-RNAi* line was crossed with *Nsyb-gal4* and the F_1 progeny collected and tested for 3-hr memory after olfactory classical conditioning. Of the 3655 lines obtained, 3207 produced F_1 progeny in sufficient numbers for conditioning and testing (Table 1; Table S1). The screen employed four laboratory testers that produced population PIs that followed a normal distribution (Figure 1). A total of 964 outliers, or hits, were selected from the primary screen using soft floor and ceiling thresholds that approximated ±1 standard deviation from the population mean (Table 1). Thus, lines producing scores above ~0.52 were kept as high performers, and lines producing scores below ~0.24 were kept as low performers. The mean 3-hr PI across the complete screen was 0.34. The 964 primary hits were rescreened, again using the population mean as a control. In this secondary screen, 600 hits were confirmed (Table 1). Five hundred and fifty seven of these lines performed with a reduced PI (Table S2). Forty-two lines exhibited an increased PI (Table 2).

About half of the lines (264) identified as low performers (Table S2) emerged with physical abnormalities using *Nsyb-gal4* as a driver, the most common of which was misshapen wings. In addition, locomotor assays were performed for 362 of the lines and 213 exhibited a significant difference in locomotor activity. These observations suggest that a large fraction of the low performing lines were recovered due to associated developmental defects, rather than specific impairments in the molecular machinery underlying memory formation. This is also suggested by the nature of many of the genes identified. For instance, 18 of the low performing lines expressed RNAi's to mitochondrial ribosomal proteins, consistent with a general developmental disability due to poor calcium homeostasis or energy supply. The low hit list is also populated with genes with known general developmental roles, such as *folded gastrulation*, *prospero*, *faint sausage*, *gooseberry neuro*, and others. Many of the low hits with obvious developmental abnormalities may be important for furthering our understanding of intellectual disabilities. The uncharacterized genes (CGXXXX) without obvious developmental issues will be of future importance in dissecting the genetic basis for memory formation.

Importantly, many of the genes already known to function in olfactory memory formation were identified in the RNAi screen, providing internal validation of the effectiveness of the screen (Table 3). A recent review (Tomchik and Davis 2013) listed 30 genes that have been reported to be involved in olfactory memory acquisition, short-term memory, or intermediate-term memory, processes and phases that would have been captured in our 3-hr memory screen. Eight of the 30 identified genes reported in Tomchik and Davis (2013) were recaptured in the RNAi screen, including the classical mutants *dunce* and *rutabaga* (Dudai *et al.* 1976; Tempel *et al.* 1983; Livingstone *et al.* 1984; Folkers *et al.* 1993; Connolly *et al.* 1996; Moreau-Fauvarque *et al.* 2002; Ho *et al.* 2007; Knapek *et al.* 2010; Madalan *et al.* 2011). It was not expected that all known genes would be reidentified, since only a fraction of the genome was screened, some RNAi transgenes may not be functional, and the degree of knockdown by RNAi for some involved genes may be too slight to produce a phenotype.

Remarkably, the secondary screen identified 42 RNAi transgenes whose expression improved 3-hr olfactory memory! These genes thus belong to the general category of memory suppressor genes, genes whose normal function is to suppress memory, analogous to the normal role for tumor suppressor genes in the suppression of tumor growth (Abel *et al.* 1998). There are several ways that gene knockdown could enhance memory. It may be that the knockdown increases the salience of the environmental stimuli (odor and shock) used for conditioning. The gene product may function to suppress the integration of the two stimuli, *i.e.*, suppress the process of acquisition. Memory tested at 3 hr also reflects the stability of the memory produced by acquisition, such that processes that increase (for instance, consolidation) or decrease memory stability (*i.e.*, forgetting), would be captured. Nevertheless, given the paucity of memory suppressor genes, this set offers an extremely valuable group for further study.

The *dnc* gene, the prototypic memory formation gene, was identified among the low hits using RNAi line, *uas-RNAi*^{107967}. The gene encodes the enzyme cAMP phosphodiesterase (Byers *et al.* 1981; Chen *et al.* 1986), is preferentially expressed in the mushroom bodies (Nighorn *et al.* 1991), and exhibits remarkable gene structure and RNA complexity (Davis and Davidson 1986; Qiu *et al.* 1991). Surprisingly, although *dnc* was the first memory gene characterized with beautiful expression in the mushroom bodies, numerous questions remain regarding its function in different types of neurons that can be dissected using an RNAi approach.

We crossed the *dnc*^{RNAi} to a battery of *gal4* drivers known to express in different compartments of the brain and measured 3-hr memory to map the spatial requirement for *dnc* function (Figure 2A). In this experiment, the *gal4* > *RNAi* genotype was compared to *gal4* > *60100*, *60100* being the host genotype for producing the RNAi transgenics (see *Materials and Methods*). Expression of the *dnc*^{RNAi} with most drivers was without effect, but a significant impairment in 3-hr memory was observed with *Nsyb-gal4*, *c772-gal4*, *238y-gal4*, *c739-gal4*, and *1471-gal4*. The *c772-gal4* and *238y-gal4* drivers provide strong and preferential expression in the mushroom bodies (Aso *et al.* 2009). The

Table 2 Outliers from the secondary screen with an increased PI

Transformant ID	CG no.	*Drosophila* gene	Primary PI and SEM line	Secondary PI and SEM line	Physical abnormality	Mean activity difference	Act. sig.
100151	CG10483	CG10483	0.64 ± 0.10	0.62 ± 0.03	—	−11.66	
100363	CG42614	scribble	0.85 ± 0.04	0.63 ± 0.04	—	7.40	
100624	CG13521	roundabout	0.55 ± 0.06	0.61 ± 0.06	—	−3.13	
100706	CG1470	Guanylyl cyclase β-subunit at 100B	0.62 ± 0.07	0.61 ± 0.02	—	−4.07	
100721	CG11326	Thrombospondin	0.65 ± 0.07	0.53 ± 0.10	—	4.62	
100727	CG8715	lingerer	0.65 ± 0.12	0.54 ± 0.03	—	29.81	***
101189	CG42244	Octβ3R	0.67 ± 0.03	0.6 ± 0.08	—	−0.38	
102058	CG1128	α-Esterase-9	0.65 ± 0.04	0.60 ± 0.04	—	2.12	
102373	CG3217	CKII-α subunit interactor-3	0.66 ± 0.12	0.60 ± 0.02	—	1.53	
102563	CR17025	CR17025	0.56 ± 0.10	0.70 ± 0.05	—	1.65	
102816	CG12806	tipE homolog 1	0.63 ± 0.08	0.62 ± 0.03	—	19.09	***
103625	CG6746	CG6746	0.61 ± 0.07	0.53 ± 0.02	—	−5.76	
103767	CG13387	embargoed	0.74 ± 0.03	0.64 ± 0.07	—	15.15	**
104255	CG6800	N/A	0.65 ± 0.09	0.63 ± 0.06	—	−3.04	
104262	CG6658	Ugt86Di	0.63 ± 0.01	0.61 ± 0.06	—	−7.79	
104763	CG10251	portabella	0.57 ± 0.06	0.72 ± 0.02	—	5.78	
104782	CG8418	Ras which interacts with calmodulin	0.68 ± 0.06	0.65 ± 0.07	—	1.40	
104796	CG5036	CG5036	0.60 ± 0.06	0.52 ± 0.04	—	8.90	
105374	CG11734	HERC2	0.62 ± 0.07	0.60 ± 0.08	—	2.37	
105624	CG42783	atypical protein kinase C	0.67 ± 0.07	0.59 ± 0.07	—	4.53	
105996	CG14015	CG14015	0.65 ± 0.03	0.60 ± 0.09	—	2.37	
106046	CG3423	Stromalin	0.72 ± 0.04	0.61 ± 0.02	—	4.09	
106248	CG10238	Molybdopterin synthase 2	0.66 ± 0.05	0.48 ± 0.01	—	−4.19	
106255	CG7125	Protein Kinase D	0.65 ± 0.03	0.6 ± 0.02	—	2.09	
106555	CG7442	CG7442	0.74 ± 0.07	0.6 ± 0.05	—	13.75	*
106641	CG8808	Pyruvate dehydrogenase kinase	0.59 ± 0.09	0.63 ± 0.07	—	5.43	
106642	CG9375	Ras oncogene at 85D	0.56 ± 0.07	0.53 ± 0.05	—	8.06	
106805	CG9044	CG9044	0.58 ± 0.17	0.56 ± 0.11	—	6.12	
107037	CG43720	sickie	0.67 ± 0.03	0.61 ± 0.06	—	6.90	
107047	CG6860	Leucine-rich-repeats and calponin homology domain protein	0.62 ± 0.04	0.58 ± 0.06	—	7.18	
107297	CG5941	CG5941	0.63 ± 0.07	0.64 ± 0.06	—	12.78	
107725	CG9481	UDP-glycosyltransferase 37b1	0.6 ± 0.06	0.5 ± 0.03	—	−1.88	
108011	CG13893	CG13893	0.58 ± 0.11	0.6 ± 0.06	—	−0.16	
108453	CG1657	CG1657	0.60 ± 0.02	0.67 ± 0.06	—	10.90	
108694	CG6384	Centrosomal protein 190kD	0.58 ± 0.11	0.69 ± 0.06	—	−2.63	
108836	CG1989	Yippee	0.56 ± 0.09	0.55 ± 0.06	—	5.93	
109290	CG3654	Jumonji, AT rich interactive domain 2	0.61 ± 0.04	0.63 ± 0.01	—	5.40	
110045	CG30443	Optix-binding protein	0.65 ± 0.06	0.61 ± 0.14	—	−0.91	
110197	CG5429	Autophagy-specific gene 6	0.63 ± 0.07	0.54 ± 0.11	—	−2.79	
110205	CG12178	$Na^+/H+$ hydrogen exchanger 1	0.62 ± 0.13	0.60 ± 0.08	—	−4.72	
110310	CG11072	Maternal gene required for meiosis	0.53 ± 0.02	0.58 ± 0.02	—	8.84	
110788	CG6438	amontillado	0.59 ± 0.05	0.54 ± 0.09	—	2.87	

The performance index (PI) was calculated as the number of flies avoiding the CS^+ minus those avoiding the CS^- over the total in both *T*-maze arms $[(CS^-) - (CS^+)]/[(CS^-) + (CS^+)]$. The primary screen was performed with $n = 3$ or 4, the secondary screen at a later date with $n = 4$. Physical abnormalities, such as misshapen wings or lethargic behavior, are noted by (+) in companion Table S2. Mean activity difference for the 2-min window simulating the decision period during testing was calculated from the TriKinetics Monitoring System (mean activity score 60100) − (mean activity score experimental line). The mean activity score for the 60100 control line was 44.43 ± 0.42 (n = 552). Differences in activity (act. sig.) were determined using ANOVA followed by Dunnett's *post hoc* test. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

c739-gal4 driver is specific to α/β-mushroom body neurons; *1471-gal4* is relatively specific to γ-mushroom body neurons. The impairments observed in 3-hr memory when the dnc^{RNAi} was driven by mushroom body *gal4* drivers are not attributable to impairments in odor or shock sensitivity (Figure 2, B and C). These data map *dnc* function in memory to both the α/β- and γ-mushroom body neurons.

We also measured memory in control and experimental flies expressing dnc^{RNAi} in the mushroom bodies at various times after conditioning, to probe the kinetics of memory decay (Figure 2D). No significant difference in performance was observed between the two groups at 3 min after conditioning, the earliest time point that can be measured. A significant difference in performance was observed at 1 hr after conditioning and strong trends toward performance impairments were observed in the experimental flies at 3 and 6 hr after conditioning. We also measured the rate of acquisition by varying the number of shock pulses presented to the flies during conditioning (Figure 2E). Interestingly, no significant differences were observed with 1, 2, 3, 6, or 12

Table 3 Known memory genes identified from the RNAi screen

Transformant ID	CG no.	*Drosophila* gene	Reference
19124	CG2204	G protein oα 47A	Madalan *et al.* (2011)
100039	CG17348	derailed	Moreau-Fauvarque *et al.* (2002)
101759	CG9533	rutabaga	Livingstone *et al.* (1984)
101811	CG15720	radish	Folkers *et al.* (1993)
104422	CG42344	bruchpilot	Knapek *et al.* (2010)
105485	CG2835	G protein sα 60A	Connolly *et al.* (1996)
107967	CG32498	dunce	Dudai *et al.* (1976)
109637	CG8318	Neurofibromin 1	Ho *et al.* (2007)
109881	CG10697	Dopa decarboxylase	Tempel *et al.* (1983)
110606	CG3985	Synapsin	Knapek *et al.* (2010)

The subset of lines from Table S2 representing genes that have already been reported to be involved in memory formation.

shocks between the two groups, suggesting that acquisition processes are not significantly impaired in the dnc^{RNAi} knockdown. The conclusions must remain provisional, since RNAi knockdown is seldom complete in its effects, and acquisition experiments do not provide a perfect and uncontaminated measure of acquisition processes. Nevertheless, the results are compatible with the model that *dnc* provides a function in the mushroom body neurons required for maintaining the stability of memory after conditioning.

Table 2 lists the interesting set of RNAi lines that improve memory when expressed with *Nsyb-gal4*. The list contains genes with a remarkably diverse set of cellular functions, with no one biochemical pathway or cellular process appearing to dominate memory suppressor functions. We selected one gene, *sickie*, for further characterization to illustrate an effective path to gain further insights into the mechanisms underlying memory suppressor genes. This gene was selected because of its interesting role in the regulation of the NF-κB signaling pathway and function in immunity (Foley and O'Farrell 2004), offering an entrée to exploring the relationship between innate immunity and memory functions (see *Discussion*).

We crossed the $sickie^{RNAi}$ to a battery of *gal4* drivers to map the spatial effect of the RNAi. None of the *gal4* drivers with expression in specific regions or cell types were with effect, except for *TH-gal4* (Figure 3A), a tyrosine hydroxylase promoter-based *gal4* that drives expression in the vast majority of dopaminergic neurons (Friggi-Grelin *et al.* 2003; Mao and Davis 2009). Odor and shock avoidance were not significantly different from the control using *TH-gal4* (Figure 3C), although the broader expression with *Nsyb-gal4* produced impairment in benzaldehyde avoidance (Figure 2B). A second *sickie* RNAi line was tested and found to enhance 3-hr memory (Figure 3F), dramatically reducing the possibility that the memory enhancement was due to off-target effects.

An acquisition profile constructed using varying shock numbers during training revealed no difference between the control group and the $sickie^{RNAi}$ knockdown (Figure 3E). A memory curve constructed after the normal 12-shock learning paradigm revealed significantly enhanced performance at 3 and 6 hr after conditioning, although no significant difference was observed at 3 min after training (Figure 3D), confirming the results of the 12-shock portion of the acquisition profile (Figure 3E). The combined data suggest that *sickie* knockdown has no effect on the acquisition of information, but is involved in subsequent memory stability. Since dopaminergic neurons have been proposed to chronically release dopamine after learning to promote forgetting (Berry *et al.* 2012), an attractive working hypothesis is that *sickie* RNAi reduces the dopaminergic forgetting signal.

Discussion

The results of the large RNAi screen for memory genes reported here offer a valuable resource for the future study of three different classes of genes that alter memory formation: (1) genes that are required for normal development of the nervous system and produce a memory impairment when their expression is reduced, (2) genes that encode products that have a role in the neural physiology of memory formation and impair memory when their expression is reduced, and (3) genes that normally function as memory suppressor genes.

The delineation of genes with developmental roles from those that impair memory formation through neurophysiological mechanisms requires further experimentation using TARGET or Gene-Switch strategies to map the RNAi effects to the temporal domain of development or adulthood (McGuire *et al.* 2004). Nevertheless, the identification of both classes is extremely valuable: genes with specific developmental roles for nervous system that alter memory processing when defective may provide insights into the developmental routines required for constructing portions of the nervous system necessary for olfactory memory. In this sense, some of these may offer models for human intellectual disabilities (IDs). For instance, several genes representing the low hits show high similarities to mammalian genes that cause ID, such as *armadillo* (β-catenin), *little imaginal discs* (lysine-specific demethylase 5c), *Klp31E* (kinesin-like protein KIF4A), and *mushroom bodies tiny* (serine/threonine-protein kinase PAK 3). β-Catenin is critical for embryonic and craniofacial development through the WNT signaling pathway and serves as an intracellular anchor for the cadherin family of cell adhesion receptors. Two recent studies found that dominant β-catenin mutations resulted in syndromic intellectual disability (Dubruc *et al.* 2014; Tucci *et al.* 2014). Lysine-specific demethylase 5c (also known as

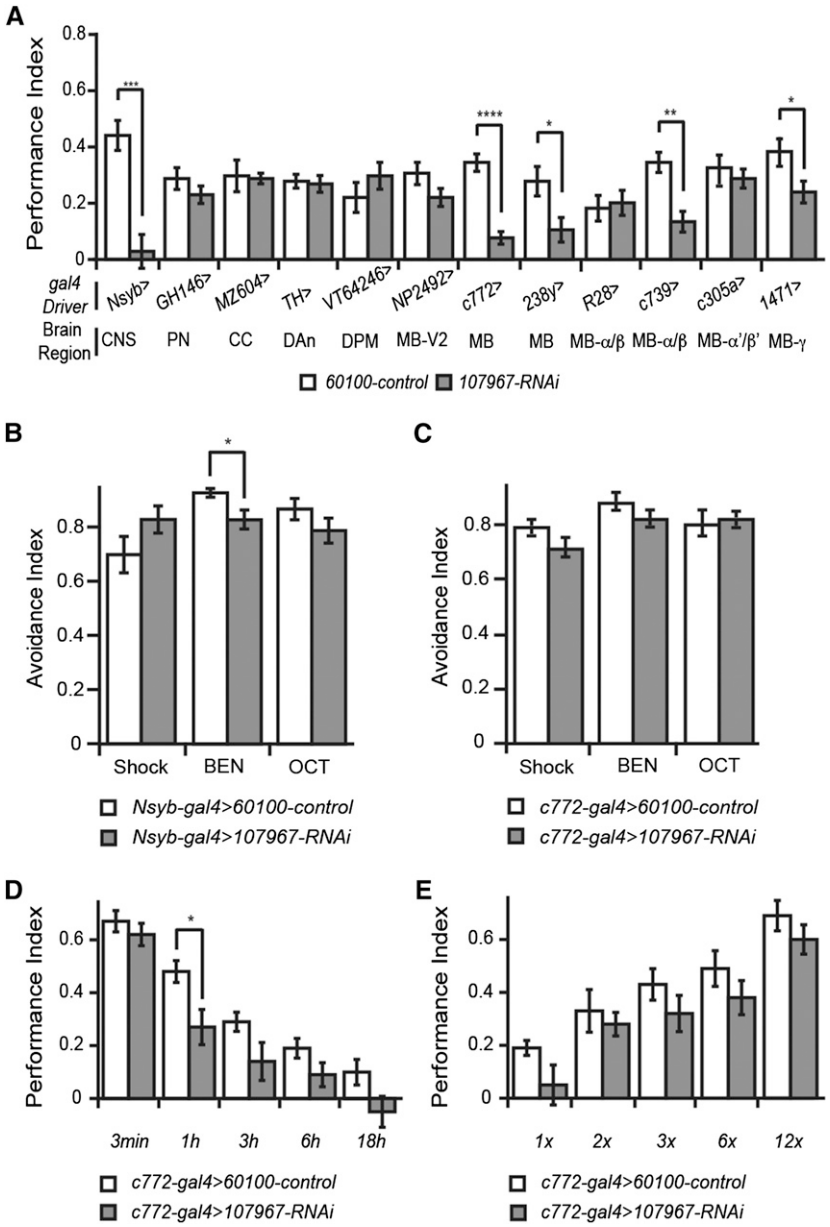

Figure 2 RNAi analysis of dnc function in memory formation. (A) Spatial mapping of the memory impairment produced by expression of dncRNAi-107967. Twelve different gal4 drivers were employed to promote RNAi expression in different sets of brain neurons. The parental line for the RNAi transgenic lines, 60100, was crossed to the same set of gal4 drivers and used as the control. The PIs for the various gal4 driver lines were variable due to genetic background. Comparisons made were therefore between each individual gal4 driver and its paired experimental group. CNS, all neurons; PN, projection neurons; CC, central complex; DAn, dopamine neurons; DPM, dorsal paired medial neurons; MB-V2, mushroom body V2 output neurons; MB, mushroom body neurons; MB-a/b, alpha/beta lobes of the mushroom body; MB-a'/b', alpha'/beta' lobes of the mushroom body; MB-g, gamma lobe of the mushroom body. (B) Odor and shock avoidance of the control and RNAi crossed to the panneuronal driver, Nsyb-gal4. The dncRNAi line exhibited a significantly reduced avoidance to benzaldehyde (BEN) compared to the control. No differences were observed with shock or the odorant 3-octanol, OCT. (C) Odor and shock avoidance of the control and RNAi crossed to the mushroom body driver, c772-gal4. No significant differences between the dncRNAi line and control were observed. (D) Performance indices of memory measured at multiple times after conditioning for the dncRNAi line compared to the control. A significant difference was detected at 1 hr after conditioning in this experiment, although trends toward reduced performance were observed at 3 and 6 hr as well. (E) Memory acquisition curve of dncRNAi-107967. Performance indices for acquisition using 1, 2, 3, 6, and 12 shock pulses measured for the dncRNAi line compared to the control. No significant differences were observed between the RNAi line and the control.

JARID1C) is an X-linked intellectual disability gene and participates in neural development by regulating chromatin remodeling (Jensen *et al.* 2005; Najmabadi *et al.* 2011). KIF4A was identified as an intellectual disability factor through next-generation sequencing of families segregating intellectual disability (Willemsen *et al.* 2014). PAK3, too, is an X-linked intellectual disability gene (Magini *et al.* 2014). Those genes identified that underlie the neurophysiology of memory formation provide a resource for dissecting memory mechanisms, as well as perhaps providing insights into the genetics of neuropsychiatric disorders (McDonald *et al.* 2012), since most neuropsychiatric disorders alter memory processing. For instance, 18 of the *Drosophila* genes listed in Table 2 and Table S2 are homologs of the 351 putative, schizophrenia-associated genes linked to the known 108 human schizophrenia-associated loci mapped from genome-wide association studies (Schizophrenia Working Group of the Psychiatric Genomics Consortium 2014). Furthermore, the novel genes identified (CGXXXX) offer a very exciting resource, given their unrecognized character and involvement in memory processing.

Lee (2014) provided a list of 26 genes whose classical or conditional knockout in the mouse enhances memory. Remarkably, there is no overlap between this list of memory suppressor genes in the mouse and those in *Drosophila* (Table 2). However, studies using the mouse have generally employed behavioral tests that quantify long-term memory, such as contextual fear conditioning or water maze learning. Our studies employed a single olfactory training session that generates short- and intermediate-term memory, but not protein synthesis-dependent, long-term memory. In addition, the failure to find overlap despite the general conservation in cellular mechanisms for learning and memory (Davis 2005) is likely also due to the fact that saturation

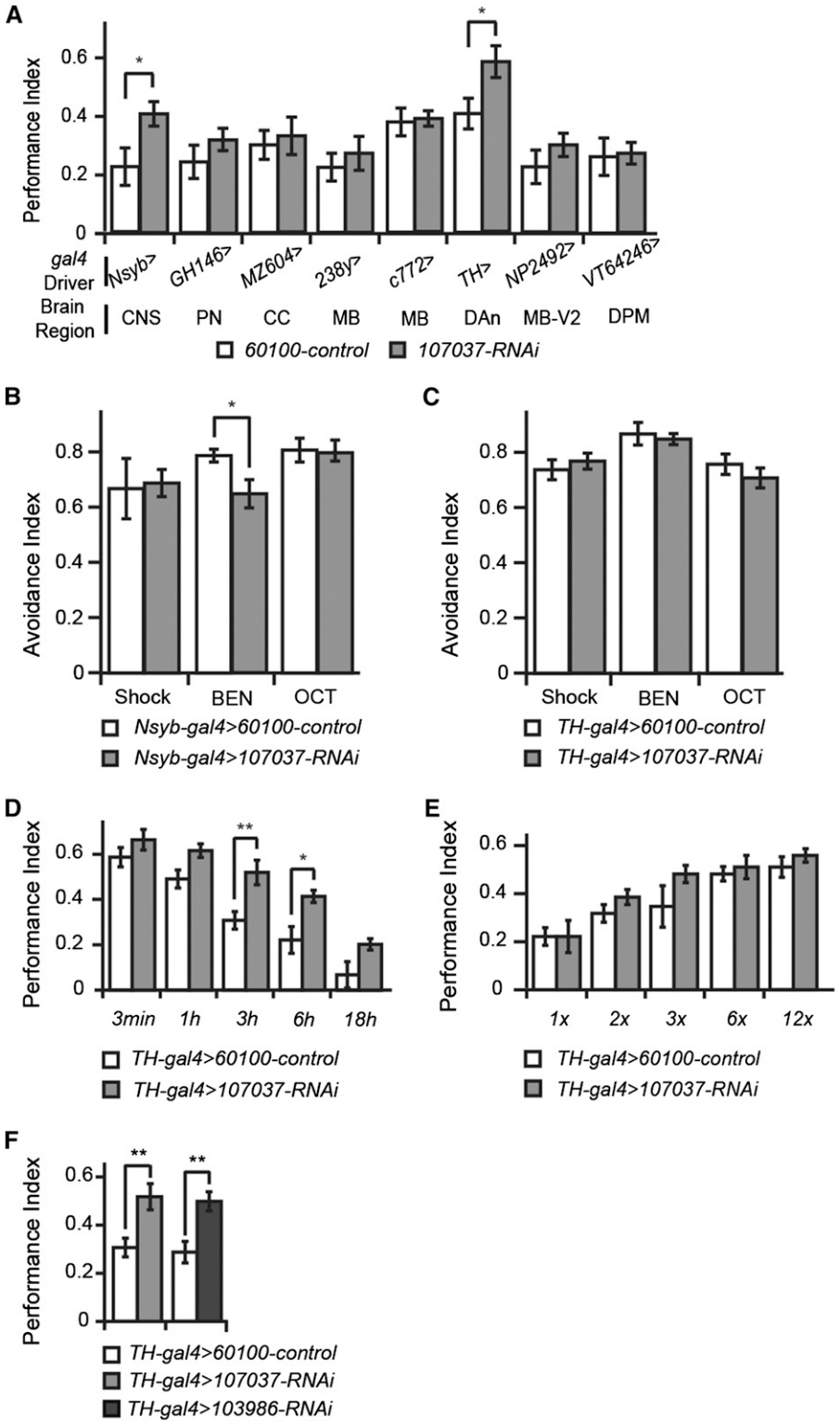

Figure 3 RNAi analysis of sickie function in memory formation. (A) Spatial mapping of the memory enhancement produced by expression of sickieRNAi-107037. Eight different gal4 drivers were employed to promote RNAi expression in different sets of brain neurons. The parental line for the RNAi transgenic lines, 60100, was crossed to the same set of gal4 drivers and used as the control. The PIs for the various gal4 driver lines were variable due to genetic background. Comparisons made were therefore between each individual gal4 driver and its paired experimental group. CNS, all neurons; PN, projection neurons; CC, central complex; MB, mushroom body neurons; DAn, dopamine neurons; MB-V2, mushroom body V2 output neurons; DPM, dorsal paired medial neurons. (B) Odor and shock avoidance of the control and RNAi crossed to the panneuronal driver, Nsyb-gal4. The sickieRNAi line exhibited a significantly reduced avoidance to benzaldehyde (BEN) compared to the control. No differences were observed with shock or the odorant 3-octanol, OCT. (C) Odor and shock avoidance of the control and RNAi crossed to the mushroom body driver, TH-gal4. No significant differences between the sickieRNAi line and control were observed. (D) Performance indices of memory measured at multiple times after conditioning for the sickieRNAi line compared to the control. A significant difference was detected at 3 hr and 6 hr after conditioning in this experiment, although trends toward enhanced performance were observed at 18 hr as well. (E) Memory acquisition curve of sickieRNAi-107037. Performance indices for acquisition using 1, 2, 3, 6, and 12 shock pulses measured for the sickieRNAi line compared to the control. No significant differences were observed between the RNAi line and the control. (F) Comparison of performance indices of memory of additional RNAi constructs for sickie. SickieRNAi-107037 and sickieRNAi-103986 both demonstrated significantly enhanced memory compared to the control.

screens have not been completed. We screened ~25% of the *Drosophila* genome using an RNAi approach; memory suppressor genes in the mouse have been identified through candidate gene approaches rather than forward genetic screens.

Our screen led us to further dissect *dnc*, the first memory mutant isolated in any organism (Dudai *et al.* 1976). Our results indicate that the *dnc* gene product, cAMP phosphodiesterase, is required in the mushroom body neurons for normal memory. This coincides with its preferential expression in these neurons (Nighorn *et al.* 1991). In addition, our results are consistent with the hypothesis that *dnc* functions within these neurons for memory stability, rather than in

acquisition processes, *per se*. Prior studies have assigned to *dnc* a function in acquisition, based on poor mutant performance immediately after conditioning (Dudai *et al.* 1976; Tully and Quinn 1985). However, this mutant phenotype may be due to a requirement for *dnc* function in another node of the olfactory nervous system, a hypothesis consistent with data claiming poor immediate performance with loss of function in the antennal lobe (Scheunemann *et al.* 2012). Nevertheless, a caveat to our provisional conclusion that dnc mediates memory stability through roles in the mushroom body neurons is that RNAi expression is likely to produce a partial loss of function (Figure 2E). A complete loss of function in the mushroom bodies might produce impairments during acquisition tests, as well as subsequent memory tests.

We also performed a partial characterization of one new memory suppressor gene, *sickie*. *Sickie* was identified originally in an RNAi screen for immune system molecules that regulate the activation of the NF-κB family member *Relish* by the caspase-8 homolog *Dredd* (Foley and O'Farrell 2004). *Sickie* gene function is required for the translocation of Relish from the cytoplasm to the nucleus in response to the detection of gram-negative bacteria. If the many signaling molecules involved in the immune deficiency pathway (Foley and O'Farrell 2004) are conserved in general function in dopaminergic neurons for normal memory functions, then one might have expected these to also have been identified from our RNAi screen (Figure 3A). The fact that they were not may indicate that *sickie* has a unique function in dopaminergic neurons, or that our partial loss-of-function screen of only a portion of the genome simply failed to identify the other players. Structural analysis of the predicted *sickie* amino acid sequence indicates a relationship with the AAA+ ATPase family of proteins.

Acknowledgments

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GENETICS

Supporting Information
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Identification of Genes That Promote or Inhibit Olfactory Memory Formation in *Drosophila*

Erica Walkinshaw, Yunchao Gai, Caitlin Farkas, Daniel Richter, Eric Nicholas, Krystyna Keleman, and Ronald L. Davis

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Table S1 is available for download as an Excel file at

http://www.genetics.org/lookup/suppl/doi:10.1534/genetics.114.173575/-/DC1

Table S2 Outliers from the secondary screen with a reduced PI. The Performance Index (PI) was calculated as the number of flies avoiding the CS+ minus those avoiding the CS- over the total in both T-maze arms [(CS-)-(CS+)]/ [(CS-)+(CS+)]. The primary screen was performed with 3 or 4n; the secondary screen at a later date with 4n. Physical abnormalities, such as misshapen wings or lethargic behavior, are noted by (+). Mean Activity Difference for the two-minute window simulating the decision period during testing was calculated from the Trikinetics Monitoring System (Mean Activity Score 60100)-(Mean Activity Score Experimental Line). The Mean Activity Score for the 60100 control line was 44.43 +/- 0.42 (n=552). Differences in activity (Act. Sig.) were determined using ANOVA followed by Dunnett's Post-Hoc test. **P* < 0.05, ***P* < 0.01, ****P* < 0.001. NT indicates the line was not tested.

TRANSFORMANT ID	CG NUMBER	*DROSOPHILA* GENE	PRIMARY PI & SEM LINE	SECONDARY PI & SEM LINE	PHYSICAL ABNORM.	MEAN ACTIVITY DIFF.	ACT. SIG.
11471	CG33517	Dopamine 2-like receptor	0.16 ± 0.09	0.13 ± 0.10	-	-5.63	
11817	CG42260	CG42260	0.05 ± 0.16	0.15 ± 0.13	+	NT	
13140	CG31546	CG31546	0.21 ± 0.15	0.15 ± 0.04	-	NT	
19124	CG2204	G protein oα 47A	-0.12 ± 0.08	0.15 ± 0.06	+	NT	
26876	CG7485	Octopamine-Tyramine receptor	0.25 ± 0.07	0.19 ± 0.14	-	NT	
37549	CG6711	TBP-associated factor 2	0.15 ± 0.05	0.24 ± 0.14	-	NT	
46757	CG3977	Copper transporter 1A	0.23 ± 0.04	0.18 ± 0.03	-	11.51	***
48984	CG8451	CG8451	0.10 ± 0.17	0.22 ± 0.10	-	NT	
100010	CG7595	crinkled	0.10 ± 0.12	0.03 ± 0.05	-	25.68	***
100029	CG15390	CG15390	0.17 ± 0.05	0.17 ± 0.05	-	22.06	***
100032	CG14925	Osiris 21	0.24 ± 0.02	0.14 ± 0.10	+	33.73	***
100039	CG17348	derailed	0.00 ± 0.05	0.07 ± 0.03	+	22.93	***
100067	CG7354	mitochondrial	0.01 ± 0.04	0.13 ± 0.05	-	20.37	***

		ribosomal protein S26					
100084	CG4790	female sterile (1) M3	0.14 ± 0.10	0.25 ± 0.05	-	NT	
100122	CG31256	Brf	0.07 ± 0.04	0.04 ± 0.05	+	NT	
100123	CG31811	centaurin gamma 1A	0.17 ± 0.05	0.19 ± 0.08	-	12.78	
100170	CG9674	CG9674	0.10 ± 0.08	0.24 ± 0.08	+	NT	
100189	CG4058	Neprilysin 4	0.06 ± 0.08	0.28 ± 0.05	+	12.96	
100196	CG14491	CG14491	0.16 ± 0.05	0.24 ± 0.06	-	5.46	
100213	CG18262	CG18262	0.15 ± 0.11	0.06 ± 0.09	+	13.80	***
100226	CG10203	CG10203	0.12 ± 0.12	0.18 ± 0.14	-	NT	
100276	CG1939	Dephospho-CoA kinase	0.13 ± 0.03	0.21 ± 0.04	+	28.65	***
100295	CG9779	Charged multivesicular body protein 3	0.16 ± 0.16	0.15 ± 0.10	+	NT	
100400	CG10804	CG10804	0.09 ± 0.07	0.15 ± 0.07	-	20.93	***
100404	CG2969	ABC transporter expressed in trachea	0.19 ± 0.07	0.30 ± 0.07	-	12.34	
100432	CG4922	spalt-adjacent	0.18 ± 0.03	0.11 ± 0.05	-	6.03	
100438	CG15529	CG15529	0.18 ± 0.06	0.13 ± 0.04	+	13.90	*
100439	CG13602	CG43999	0.25 ± 0.09	0.22 ± 0.04	+	NT	
100458	CG15585	Osiris 1	0.09 ± 0.07	0.17 ± 0.08	-	20.40	***
100466	CG5611	CG5611	0.25 ± 0.02	0.20 ± 0.04	-	20.18	***
100494	CG7135	CG7135	0.24 ± 0.05	0.31 ± 0.02	-	3.62	
100539	CG18467	CG18467	0.27 ± 0.05	0.26 ± 0.05	-	1.84	

100588	CG6251	Nucleoporin 62	0.03 ± 0.09	0.18 ± 0.07	-	-16.41	***
100593	CG9238	CG9238	0.10 ± 0.07	0.03 ± 0.03	-	4.40	
100598	CG3578	bifid	0.21 ± 0.08	0.12 ± 0.02	+	NT	
100618	CG8372	CG8372	0.14 ± 0.07	0.16 ± 0.01	-	20.18	***
100652	CG32017	CG32017	0.18 ± 0.05	0.13 ± 0.04	-	-2.76	
100691	CG9949	seven in absentia	0.25 ± 0.03	0.25 ± 0.02	-	14.65	**
100710	CG14407	CG14407	0.25 ± 0.01	0.24 ± 0.03	-	1.21	
100719	CG8295	Myelodysplasia/myeloid leukemia factor	0.19 ± 0.05	0.16 ± 0.05	-	10.59	
100723	CG4211	no on or off transient A	0.13 ± 0.09	0.19 ± 0.07	-	17.89	***
100729	CG7967	CG7967	0.25 ± 0.05	0.12 ± 0.06	-	0.90	
100735	CG10897	toutatis	0.06 ± 0.09	0.22 ± 0.04	-	NT	
100737	CG3351	mitochondrial ribosomal protein L11	0.07 ± 0.06	0.05 ± 0.04	-	12.59	
100745	CG32675	Transport and Golgi organization 5	0.16 ± 0.07	0.25 ± 0.06	-	NT	
100846	CG42543	multiplexin	0.25 ± 0.1	0.26 ± 0.10	-	NT	
100851	CG6765	CG6765	0.13 ± 0.07	0.21 ± 0.05	-	11.71	
100927	CG8795	CG8795	0.2 ± 0.14	0.29 ± 0.06	-	1.84	
100947	CG13933	CG13933	-0.19 ± 0.03	0.14 ± 0.02	-	34.29	***
100964	CG32834	CG32834	0.19 ± 0.09	0.22 ± 0.10	-	NT	
100969	CG13459	cp309	0.07 ± 0.06	0.05 ± 0.06	-	NT	
100998	CG1504	CG1504	0.22 ± 0.06	0.23 ± 0.08	-	NT	
101016	CG6976	Myosin 28B1	0.20 ± 0.03	0.16 ± 0.07	+	NT	
101047	CG32016	CG32016	0.14 ± 0.09	0.12 ± 0.08	-	20.15	***
101100	CG3234	timeless	0.26 ± 0.06	0.30 ± 0.07	-	6.56	

101125	CG9559	folded gastrulation	0.25 ± 0.10	0.19 ± 0.03	-	24.28	***
101156	CG31740	CG31740	0.22 ± 0.16	0.19 ± 0.06	+	NT	
101161	CG14617	CG14617	0.15 ± 0.02	0.13 ± 0.08	-	NT	
101166	CG12283	kekkon-1	0.16 ± 0.05	0.11 ± 0.05	-	19.56	***
101315	CG7636	mitochondrial ribosomal protein L2	0.12 ± 0.04	0.00 ± 0.08	+	NT	
101324	CG42251	CG42251	0.17 ± 0.06	0.17 ± 0.04	-	25.31	***
101327	CG12223	Dorsal switch protein 1	0.23 ± 0.06	0.13 ± 0.05	+	29.58	***
101347	CG31140	CG31140	0.04 ± 0.04	0.14 ± 0.06	-	32.09	***
101351	CG5818	mitochondrial ribosomal protein L4	0.02 ± 0.06	-0.01 ± 0.04	-	31.68	***
101352	CG5048	CG5048	0.19 ± 0.02	0.22 ± 0.04	-	10.83	
101372	CG42540	CG42540	0.24 ± 0.07	0.21 ± 0.02	+	NT	
101402	CG43388	Hyperkinetic	0.19 ± 0.06	0.22 ± 0.06	+	NT	
101423	CG14048	mitochondrial ribosomal protein L14	-0.03 ± 0.06	0.05 ± 0.02	-	30.46	***
101434	CG12809	nervous fingers 2	0.20 ± 0.08	0.27 ± 0.06	-	14.81	**
101443	CG14413	mitochondrial ribosomal protein S25	0.03 ± 0.02	0.11 ± 0.06	-	22.78	***
101449	CG1417	sluggish A	0.19 ± 0.06	0.25 ± 0.08	-	14.65	**
101459	CG8110	sunday driver	0.24 ± 0.02	0.21 ± 0.06	+	NT	
101477	CG17228	prospero	0.15 ± 0.07	0.10 ± 0.06	-	NT	
101503	CG32264	CG32264	0.13 ± 0.04	0.10 ± 0.08	-	NT	

101521	CG7238	septin interacting protein 1	0.11 ± 0.03	0.17 ± 0.06	-	20.84	***
101540	CG7499	Rh50	0.02 ± 0.11	0.18 ± 0.10	-	NT	
101547	CG10574	Inhibitor-2	0.18 ± 0.11	0.09 ± 0.06	+	NT	
101549	CG13608	mitochondrial ribosomal protein S24	0.07 ± 0.05	0.05 ± 0.07	+	NT	
101586	CG32373	CG32373	0.06 ± 0.08	0.10 ± 0.03	+	NT	
101628	CG15883	Odorant-binding protein 18a	0.20 ± 0.08	0.09 ± 0.16	-	11.90	
101670	CG4049	CG4049	0.24 ± 0.03	0.12 ± 0.04	-	17.25	***
101713	CGnone	N/A	0.15 ± 0.02	0.25 ± 0.05	+	35.78	***
101744	CG5065	CG5065	0.12 ± 0.08	0.02 ± 0.08	+	NT	
101758	CG1098	MLF1-adaptor molecule	0.12 ± 0.13	0.18 ± 0.07	-	14.87	**
101759	CG9533	rutabaga	-0.04 ± 0.05	0.09 ± 0.03	-	6.81	
101763	CG15862	cAMP-dependent protein kinase R2	0.23 ± 0.03	0.17 ± 0.04	+	NT	
101768	CG5226	CG5226	0.18 ± 0.06	0.25 ± 0.04	-	26.93	***
101779	CG6588	Fasciclin 1	0.11 ± 0.07	0.17 ± 0.05	+	12.31	
101811	CG15720	radish	0.02 ± 0.10	0.09 ± 0.04	+	12.34	***
101842	CG33960	Semaphorin-2b	0.16 ± 0.07	-0.04 ± 0.08	-	5.59	
101845	CG8985	Dromyosuppressin receptor 1	0.04 ± 0.05	0.07 ± 0.05	-	26.42	***
101874	CG8279	Phosphodiesterase 6	0.04 ± 0.14	0.24 ± 0.09	+	16.40	***
101885	CG8066	CG8066	0.19 ± 0.08	0.23 ± 0.04	+	NT	
101953	CG12071	CG12071	0.17 ± 0.06	0.20 ± 0.11	-	NT	

101994	CG5869	CG5869	0.16 ± 0.06	0.21 ± 0.02	+	NT	
102024	CG13318	CG13318	0.21 ± 0.01	0.16 ± 0.07	-	31.50	***
102041	CG7649	Meltrin	0.07 ± 0.05	0.13 ± 0.06	-	25.09	***
102047	CG1079	Fire exit	0.02 ± 0.06	0.21 ± 0.07	-	9.25	
102073	CG17716	faint sausage	0.10 ± 0.12	0.15 ± 0.04	+	18.40	***
102078	CG9866	CG9866	0.15 ± 0.06	0.20 ± 0.11	-	NT	
102101	CG3218	female sterile (1) K10	0.00 ± 0.03	0.19 ± 0.02	-	NT	
102159	CG6354	Ribonuclear protein at 97D	0.19 ± 0.04	0.22 ± 0.04	+	NT	
102169	CG42683	CG42683	0.20 ± 0.08	0.22 ± 0.10	-	NT	
102187	CG1499	nyobe	0.06 ± 0.03	0.21 ± 0.09	-	25.96	***
102192	CG3915	Derailed 2	0.18 ± 0.01	0.22 ± 0.05	+	NT	
102196	CG17326	luna	-0.03 ± 0.13	0.14 ± 0.04	-	15.12	**
102202	CG14075	CG14075	0.11 ± 0.05	0.28 ± 0.02	-	20.84	***
102282	CG11019	CG11019	0.23 ± 0.04	0.23 ± 0.04	+	NT	
102293	CG43374	Cht6	0.17 ± 0.06	0.25 ± 0.07	+	NT	
102306	CG9273	Replication protein A2	0.08 ± 0.06	0.17 ± 0.05	+	17.45	***
102335	CG9350	CG9350	-0.01 ± 0.03	-0.02 ± 0.10	+	35.21	***
102362	CGnone	CGnone	0.12 ± 0.06	0.09 ± 0.07	+	27.00	***
102401	CG6730	Cyp4d21	0.19 ± 0.08	0.20 ± 0.06	-	NT	
102417	CG42613	CG42613	0.24 ± 0.04	0.28 ± 0.06	-	27.62	***
102443	CG5955	CG5955	0.17 ± 0.06	0.18 ± 0.06	-	23.09	***
102477	CG3082	lethal (2) k09913	0.19 ± 0.06	0.12 ± 0.06	+	31.00	***
102481	CG34384	CG34384	0.17 ± 0.05	0.19 ± 0.11	-	17.59	***
102525	CG42342	CG42342	0.07 ± 0.05	0.18 ± 0.09	-	18.15	***
102527	CG14025	Blastoderm-specific	0.18 ± 0.10	0.14 ± 0.05	+	28.56	***

		gene 25D					
102566	CG42687	CoRest	0.18 ± 0.01	0.21 ± 0.10	-	NT	
102597	CG34354	CG34354	0.04 ± 0.11	0.18 ± 0.04	+	22.87	***
102639	CG42555	tweek	-0.09 ± 0.04	0.06 ± 0.07	-	NT	
102698	CG10134	beat-Va	0.16 ± 0.04	0.26 ± 0.07	+	NT	
102707	CG42253	Na+-driven anion exchanger 1	0.12 ± 0.05	0.22 ± 0.08	-	9.09	
102709	CG13748	CG13748	0.20 ± 0.09	0.12 ± 0.17	-	6.78	
102755	CG12641	CG12641	-0.23 ± 0.09	0.26 ± 0.03	+	NT	
102771	CG18641	CG18641	0.17 ± 0.11	0.09 ± 0.07	-	11.37	
102793	CG14390	beat-Vc	-0.24 ± 0.08	0.05 ± 0.06	+	27.15	***
102795	CG31160	CG31160	0.20 ± 0.03	0.16 ± 0.03	+	30.09	***
102802	CG9486	CG9486	0.13 ± 0.05	0.19 ± 0.08	-	12.15	
102808	CG30197	CG30197	0.16 ± 0.09	0.03 ± 0.09	+	NT	
102823	CG42613	CG42613	0.14 ± 0.01	0.18 ± 0.13	-	11.62	
102892	CG5683	Adult enhancer factor 1	0.25 ± 0.02	0.23 ± 0.05	-	NT	
102916	CG32039	CG32039	0.17 ± 0.11	0.21 ± 0.05	-	15.93	***
103031	CG31997	CG31997	0.00 ± 0.03	0.20 ± 0.03	+	NT	
103140	CG3436	CG3436	0.21 ± 0.02	0.13 ± 0.07	+	16.62	***
103142	CG33181	CG33181	0.08 ± 0.07	0.10 ± 0.06	+	26.15	***
103146	CG12752	NTF2-related export protein 1	0.02 ± 0.03	0.18 ± 0.05	-	NT	
103201	CG6395	Cysteine string protein	0.17 ± 0.07	-0.03 ± 0.02	-	29.25	***
103222	CG12838	Tetraspanin 42Eo	0.15 ± 0.08	0.27 ± 0.10	-	NT	
103267	CG43375	CG43375	0.20 ± 0.03	0.06 ± 0.08	+	NT	
103296	CG13664	Cadherin 96Cb	0.05 ± 0.18	0.10 ± 0.05	-	NT	

103308	CG17834	CG17834	0.12 ± 0.14	0.12 ± 0.03	+	28.40	***
103351	CG11847	Caliban	0.20 ± 0.05	0.08 ± 0.01	-	NT	
103363	CG9262	Shaker cognate l	0.07 ± 0.08	0.17 ± 0.07	+	NT	
103373	CG2692	gooseberry-neuro	0.17 ± 0.08	0.22 ± 0.05	+	NT	
103378	CG11926	CG11926	0.02 ± 0.16	0.01 ± 0.10	-	NT	
103382	CG31543	HIF prolyl hydroxylase	0.25 ± 0.05	0.27 ± 0.07	-	NT	
103389	CG30429	CG30429	0.23 ± 0.17	0.22 ± 0.06	-	5.78	
103407	CG16993	inturned	0.16 ± 0.09	0.22 ± 0.05	+	NT	
103410	CG8789	wallenda	0.14 ± 0.04	0.19 ± 0.04	-	NT	
103414	CG9646	CG9646	0.14 ± 0.04	0.19 ± 0.08	-	NT	
103426	CG1107	auxillin	0.08 ± 0.13	0.06 ± 0.12	+	26.34	***
103449	CG42252	mind-meld	0.13 ± 0.02	0.23 ± 0.06	-	30.15	***
103485	CG8946	Sphingosine-1-phosphate lyase	0.22 ± 0.08	0.21 ± 0.07	+	NT	
103508	CG33936	CG33936	0.17 ± 0.04	0.12 ± 0.05	+	16.87	***
103533	CG34104	CG34104	0.08 ± 0.03	0.12 ± 0.05	+	32.15	***
103551	CG14447	Glutamate receptor binding protein	0.10 ± 0.05	0.23 ± 0.08	+	31.00	***
103557	CG6177	ldlCp-related protein	0.22 ± 0.09	0.19 ± 0.11	-	-1.35	
103566	CG15016	mitochondrial ribosomal protein S6	-0.02 ± 0.04	0.12 ± 0.02	-	24.59	***
103570	CG11194	Hairy/E(spl)-related with YRPW motif	0.12 ± 0.06	0.28 ± 0.07	-	11.25	
103597	CG3497	Suppressor of Hairless	0.19 ± 0.03	0.18 ± 0.04	-	-9.47	
103602	CG10639	CG10639	0.25 ± 0.11	0.13 ± 0.06	-	4.84	

103608	CG11164	CG11164	0.26 ± 0.08	0.25 ± 0.03	-	25.75	***
103631	CG9325	hu li tai shao	0.32 ± 0.04	0.25 ± 0.06	-	9.46	
103636	CG5919	CG5919	0.09 ± 0.09	0.11 ± 0.09	+	31.06	***
103656	CG5288	Galactokinase	0.07 ± 0.06	-0.01 ± 0.10	-	NT	
103703	CG4006	Akt1	0.20 ± 0.09	0.21 ± 0.04	+	10.20	**
103720	CG42341	cAMP-dependent protein kinase R1	-0.02 ± 0.05	0.15 ± 0.08	-	5.25	
103722	CG1789	CG1789	0.21 ± 0.00	0.11 ± 0.07	+	NT	
103734	CG11132	DMAP1	0.14 ± 0.05	0.24 ± 0.03	-	16.46	***
103756	CG1487	kurtz	0.12 ± 0.08	0.12 ± 0.06	+	14.06	***
103768	CG9611	flyers-cup	0.22 ± 0.11	0.24 ± 0.05	-	2.65	
103782	CG8849	mitochondrial ribosomal protein L24	0.13 ± 0.06	-0.02 ± 0.04	-	26.81	***
103783	CG11802	CG11802	0.22 ± 0.02	0.23 ± 0.03	+	NT	
103824	CG43223	CG43223	0.04 ± 0.07	0.08 ± 0.05	+	NT	
103830	CG9088	little imaginal discs	0.25 ± 0.06	0.12 ± 0.06	+	NT	
103831	CG5629	Phosphopantothenoylcysteine synthetase	0.22 ± 0.05	0.20 ± 0.06	-	19.68	***
103832	CG18005	beag	0.16 ± 0.05	0.13 ± 0.05	+	NT	
103844	CG34387	futsch	0.07 ± 0.08	0.04 ± 0.03	+	23.84	***
103916	CG32549	CG32549	0.17 ± 0.02	0.10 ± 0.11	+	NT	
103931	CG11516	Protein tyrosine phosphatase 99A	0.14 ± 0.07	-0.04 ± 0.24	-	20.96	***
103950	CG4743	CG4743	0.09 ± 0.09	0.18 ± 0.04	+	NT	
103958	CG17330	juvenile hormone acid	0.08 ± 0.07	0.18 ± 0.07	+	NT	

		methyltransferase					
103971	CG15465	CG15465	0.23 ± 0.04	0.22 ± 0.03	+	NT	
103973	CG5811	Neuropeptide Y receptor-like	0.07 ± 0.08	0.17 ± 0.04	+	25.03	***
104011	CG5412	CG5412	0.11 ± 0.05	0.15 ± 0.12	+	33.21	***
104022	CG11876	CG11876	0.10 ± 0.09	0.09 ± 0.03	-	NT	
104072	CG33528	Vesicular monoamine transporter	-0.01 ± 0.11	0.06 ± 0.11	+	16.90	***
104082	CG32647	CG32647	0.22 ± 0.08	0.09 ± 0.08	+	21.29	***
104143	CG12278	CG12278	0.16 ± 0.06	0.09 ± 0.05	-	NT	
104159	CG43140	polychaetoid	0.19 ± 0.14	0.08 ± 0.04	+	NT	
104166	CG6850	UDP-glucose-glycoprotein glucosyltransferase	0.23 ± 0.06	0.23 ± 0.04	-	NT	
104244	CG14074	CG14074	0.06 ± 0.10	0.28 ± 0.04	+	NT	
104252	CG6236	CG6236	0.18 ± 0.05	0.24 ± 0.10	-	14.00	**
104256	CG33145	CG33145	0.14 ± 0.10	0.11 ± 0.07	-	1.78	
104275	CG18766	CG18766	0.07 ± 0.05	0.16 ± 0.04	+	NT	
104278	CG9394	CG9394	0.21 ± 0.07	0.20 ± 0.06	+	13.93	***
104288	CG12758	serrano	0.20 ± 0.04	0.11 ± 0.08	+	22.21	***
104305	CG1124	CG1124	0.05 ± 0.02	0.06 ± 0.10	-	NT	
104389	CG42234	Dbx	0.17 ± 0.04	0.07 ± 0.10	-	17.21	***
104401	CG10327	TAR DNA-binding protein-43 homolog	0.06 ± 0.04	0.03 ± 0.02	+	NT	
104402	CG9650	CG9650	-0.01 ± 0.10	0.23 ± 0.05	-	13.06	***
104411	CG6657	vegetable	0.12 ± 0.07	-0.05 ± 0.02	+	23.15	***
104422	CG42344	bruchpilot	0.03 ± 0.07	0.04 ± 0.05	+	34.46	***

104443	CG11722	CG11722	0.17 ± 0.04	0.07 ± 0.05	+	21.18	***
104483	CG16740	Rhodopsin 2	0.17 ± 0.07	0.22 ± 0.07	-	11.71	
104486	CG6167	PICK1	0.19 ± 0.03	0.19 ± 0.04	-	30.40	***
104498	CG17912	CG17912	0.13 ± 0.05	0.12 ± 0.05	-	NT	
104502	CG8280	Elongation factor 1α48D	0.10 ± 0.05	0.16 ± 0.10	-	NT	
104549	CG8401	CG8401	0.11 ± 0.07	0.19 ± 0.08	+	28.31	***
104554	CG34342	CG34342	0.22 ± 0.06	0.20 ± 0.09	+	36.03	***
104560	CG15760	CG15760	0.22 ± 0.23	0.10 ± 0.09	-	27.15	***
104563	CG5954	lethal (3) malignant brain tumor	0.07 ± 0.11	0.21 ± 0.04	+	NT	
104582	CG4807	abrupt	0.18 ± 0.00	0.22 ± 0.04	-	10.31	**
104594	CG32390	cornetto	0.25 ± 0.13	0.28 ± 0.08	+	NT	
104656	CG1812	CG1812	0.03 ± 0.08	0.10 ± 0.12	+	NT	
104665	CG4620	unkempt	0.19 ± 0.08	0.15 ± 0.06	+	NT	
104671	CG4698	Wnt oncogene analog 4	0.03 ± 0.07	0.22 ± 0.12	+	11.49	***
104674	CG2092	scraps	0.15 ± 0.10	0.13 ± 0.05	+	24.87	***
104681	CG5529	BarH1	0.13 ± 0.12	0.18 ± 0.03	+	NT	
104688	CG3182	seizure	0.19 ± 0.02	0.21 ± 0.06	-	23.06	***
104745	CG8770	G protein β-subunit 76C	0.07 ± 0.07	0.08 ± 0.03	+	NT	
104750	CG8538	Aftiphilin	0.10 ± 0.07	0.19 ± 0.05	+	30.78	***
104802	CG30373	CG30373	0.15 ± 0.04	0.11 ± 0.05	-	29.84	***
104810	CG9641	CG9641	0.03 ± 0.10	0.10 ± 0.08	+	NT	
104874	CG34394	CG34394	0.07 ± 0.18	0.22 ± 0.06	-	NT	
104882	CG2101	mitochondrial ribosomal protein	0.02 ± 0.02	0.10 ± 0.10	+	NT	

		S35					
104884	CG14211	MAPK Phosphatase 4	0.21 ± 0.06	0.20 ± 0.02	+	19.87	***
104913	CG14039	quick-to-court	0.24 ± 0.11	0.10 ± 0.11	-	7.93	
104920	CG13589	CG13589	0.19 ± 0.06	0.18 ± 0.07	+	21.18	***
104922	CG5093	Dorsocross3	0.03 ± 0.06	0.11 ± 0.05	+	NT	
104930	CG13130	CG13130	0.06 ± 0.06	0.15 ± 0.03	+	NT	
104946	CG4139	Karl	0.14 ± 0.09	0.10 ± 0.09	-	NT	
104975	CG1148	Osiris 2	0.20 ± 0.04	0.09 ± 0.09	-	24.18	***
104988	CG18659	CG18659	0.04 ± 0.06	0.15 ± 0.13	+	NT	
105052	CG18156	Mis12	0.07 ± 0.11	0.10 ± 0.03	+	NT	
105054	CG10719	brain tumor	0.05 ± 0.10	0.13 ± 0.09	+	NT	
105056	CG42784	CG42784	0.19 ± 0.03	0.20 ± 0.03	+	NT	
105064	CG3318	Dopamine N acetyltransferase	0.10 ± 0.15	0.20 ± 0.04	+	13.78	*
105066	CG4838	beaten path Ic	0.10 ± 0.17	0.05 ± 0.07	+	NT	
105073	CG11668	CG11668	0.12 ± 0.10	0.20 ± 0.05	+	NT	
105121	CG3845	NAT1	0.10 ± 0.04	0.08 ± 0.04	-	20.43	***
105132	CG8486	Piezo	0.22 ± 0.03	0.28 ± 0.04	-	3.53	
105148	CG1316	CG1316	0.19 ± 0.03	0.23 ± 0.11	-	-1.07	
105174	CG11897	CG11897	0.11 ± 0.01	0.10 ± 0.07	-	NT	
105179	CG10654	CG10654	0.07 ± 0.08	0.17 ± 0.07	+	21.28	***
105201	CG1130	scratch	0.17 ± 0.05	-0.06 ± 0.15	-	26.28	***
105271	CG13425	bancal	0.21 ± 0.07	0.26 ± 0.07	+	NT	
105284	CG1320	mitochondrial ribosomal protein L23	0.02 ± 0.03	0.10 ± 0.09	-	24.56	***
105293	CG31605	Basigin	0.08 ± 0.11	0.25 ± 0.02	+	NT	

105314	CG10382	wrapper	0.17 ± 0.06	0.15 ± 0.07	-	27.86	***
105362	CG4158	worniu	0.16 ± 0.04	0.08 ± 0.10	+	NT	
105371	CG17437	will die slowly	0.18 ± 0.07	0.21 ± 0.09	-	NT	
105412	CG42614	scribbled [???]	0.13 ± 0.08	0.24 ± 0.07	+	NT	
105421	CG15651	CG15651	0.05 ± 0.05	0.02 ± 0.03	+	22.21	***
105432	CG17907	Acetylcholine esterase	0.11 ± 0.07	0.19 ± 0.09	-	22.21	***
105477	CG32000	CG32000	0.07 ± 0.13	0.20 ± 0.03	+	NT	
105485	CG2835	G protein sα 60A	0.00 ± 0.11	-0.02 ± 0.07	+	13.87	*
105486	CG33197	CG33197	0.23 ± 0.07	0.24 ± 0.07	-	NT	
105489	CG3262	CG3262	0.26 ± 0.08	0.26 ± 0.04	+	14.00	**
105495	CG7437	mushroom-body expressed	0.14 ± 0.10	0.13 ± 0.04	+	7.34	
105534	CG9139	Rabex-5	0.20 ± 0.08	0.14 ± 0.03	-	1.43	
105536	CG43374	Cht6	0.07 ± 0.09	0.02 ± 0.06	-	NT	
105612	CG12598	Adenosine deaminase acting on RNA	0.01 ± 0.04	0.01 ± 0.06	+	NT	
105633	CG8036	CG8036	0.20 ± 0.04	0.23 ± 0.09	+	NT	
105662	CG7494	mitochondrial ribosomal protein L1	0.01 ± 0.01	0.00 ± 0.07	-	NT	
105667	CG1635	CG1635	0.14 ± 0.06	0.04 ± 0.08	+	31.18	***
105670	CG42233	CG42233	0.29 ± 0.07	0.28 ± 0.07	-	-2.76	
105676	CG3620	no receptor potential A	0.17 ± 0.05	0.13 ± 0.08	-	18.50	***
105693	CG5532	CG5532	0.21 ± 0.11	0.24 ± 0.09	+	NT	
105733	CG11984	CG11984	0.25 ± 0.11	0.19 ± 0.09	-	NT	

105740	CG9291	Elongin C	0.16 ± 0.08	0.28 ± 0.05	-	3.65	
105754	CG7535	GluClα	0.06 ± 0.10	0.07 ± 0.03	-	NT	
105803	CG7370	CG7370	0.07 ± 0.05	0.15 ± 0.05	+	NT	
105827	CG5463	CG5463	-0.05 ± 0.01	0.15 ± 0.05	-	9.06	
105832	CG4735	shutdown	0.15 ± 0.11	0.06 ± 0.03	-	NT	
105848	CG43223	CG43223	0.06 ± 0.14	0.21 ± 0.08	+	32.56	***
105852	CG8815	Sin3A	0.06 ± 0.06	0.08 ± 0.06	-	25.62	***
105858	CG18397	short spindle 3	-0.01 ± 0.06	0.17 ± 0.06	+	28.25	***
105881	CG9022	Oligosaccharyltransferase 48kD subunit	0.03 ± 0.04	0.07 ± 0.07	-	32.56	***
105883	CG1987	Rbp1-like	0.10 ± 0.10	0.22 ± 0.04	+	NT	
105901	CG6977	Cad87A	0.24 ± 0.02	0.11 ± 0.12	-	6.68	
105905	CG15704	CG15704	0.12 ± 0.07	0.23 ± 0.03	+	28.40	***
105906	CG14885	Guanylyl cyclase at 89Da	0.23 ± 0.02	0.26 ± 0.05	+	NT	
105931	CG13847	CG13847	0.19 ± 0.09	0.28 ± 0.03	+	NT	
105933	CG6005	CG6005	0.24 ± 0.02	0.19 ± 0.04	+	NT	
105944	CG9945	CG9945	0.17 ± 0.03	0.14 ± 0.08	+	NT	
105954	CG5215	Zinc-finger protein at 72D	0.20 ± 0.06	0.21 ± 0.05	-	NT	
105978	CG9854	hiiragi	0.17 ± 0.02	0.15 ± 0.04	+	26.62	***
105984	CG8183	Kinesin heavy chain 73	0.18 ± 0.12	0.07 ± 0.07	+	NT	
105987	CG31729	CG31729	0.11 ± 0.05	0.07 ± 0.02	-	18.62	***
106028	CG32120	senseless	0.23 ± 0.10	0.23 ± 0.11	-	25.34	***
106040	CG4952	dachshund	0.14 ± 0.05	0.23 ± 0.04	-	8.37	
106055	CG4045	CG4045	0.16 ± 0.08	0.22 ± 0.03	-	NT	
106063	CG11494	BTB-protein-VII	0.18 ± 0.06	0.05 ± 0.06	+	23.18	***

106132	CG3891	Nuclear factor Y-box A	0.06 ± 0.15	0.15 ± 0.04	+	27.96	***
106174	CG12072	warts	0.15 ± 0.03	0.24 ± 0.13	-	10.28	
106185	CG10052	Retinal Homeobox	0.08 ± 0.08	0.12 ± 0.06	-	23.84	***
106192	CG5794	CG5794	0.21 ± 0.06	0.20 ± 0.08	-	31.00	***
106213	CG5690	Centrobin	0.18 ± 0.10	0.22 ± 0.09	-	NT	
106232	CG7978	Adenylyl cyclase 76E	0.12 ± 0.05	0.12 ± 0.07	-	11.12	
106241	CG1976	RhoGAP100F	0.08 ± 0.01	0.20 ± 0.09	-	22.93	***
106251	CG6422	CG6422	0.20 ± 0.05	0.23 ± 0.08	+	27.21	***
106268	CG18604	Salt-inducible kinase 3	0.02 ± 0.03	0.03 ± 0.04	-	21.18	***
106270	CG14998	ensconsin	-0.03 ± 0.14	0.18 ± 0.03	+	2.40	
106282	CG13272	CG13272	0.10 ± 0.09	0.23 ± 0.11	-	2.34	
106313	CG31670	earmuff	0.15 ± 0.06	0.15 ± 0.06	+	NT	
106319	CG18347	CG18347	0.02 ± 0.04	0.23 ± 0.05	+	NT	
106326	CG31005	qless	0.04 ± 0.04	0.17 ± 0.07	+	30.40	***
106331	CG15771	CG15771	0.20 ± 0.06	0.23 ± 0.01	+	6.95	
106337	CG14184	CG14184	0.14 ± 0.01	0.05 ± 0.09	+	NT	
106338	CG43225	axotactin	0.22 ± 0.03	0.20 ± 0.05	-	14.25	**
106344	CG7843	CG7843	0.07 ± 0.03	0.06 ± 0.02	-	20.06	***
106348	CG5674	CG5674	0.14 ± 0.10	0.16 ± 0.06	+	NT	
106358	CG34374	Rapgap1	0.25 ± 0.04	0.20 ± 0.07	-	20.59	***
106382	CG6187	RluA-2	0.21 ± 0.13	0.27 ± 0.12	-	-7.82	
106390	CG42396	wech	0.20 ± 0.03	0.25 ± 0.05	+	NT	
106405	CG31352	CG31352	0.09 ± 0.00	0.14 ± 0.13	-	13.31	*
106433	CG9343	Trithorax-like	0.13 ± 0.03	0.03 ± 0.03	+	39.28	***
106475	CG7903	CG7903	0.08 ± 0.06	-0.04 ± 0.02	+	21.40	***

106483	CG13760	CG13760	0.12 ± 0.11	0.16 ± 0.07	+	NT	
106484	CG15112	enabled	0.19 ± 0.02	0.10 ± 0.03	-	-0.82	
106492	CG7959	Big brother	0.17 ± 0.05	0.11 ± 0.07	-	11.21	
106500	CG5938	CG5938	0.23 ± 0.11	0.11 ± 0.07	+	22.81	***
106534	CG32532	CG32532	0.15 ± 0.05	0.11 ± 0.028	+	27.03	***
106629	CG4882	CG4882	-0.05 ± 0.12	0.03 ± 0.06	-	27.43	***
106632	CG6948	Clathrin light chain	-0.01 ± 0.14	0.06 ± 0.08	-	25.56	***
106644	CG10002	fork head	0.02 ± 0.01	0.18 ± 0.03	+	NT	
106652	CG31522	CG31522	0.25 ± 0.1	0.25 ± 0.12	-	NT	
106687	CG6181	CG6181	0.17 ± 0.1	0.25 ± 0.1	-	7.53	
106698	CG13384	CG13384	0.04 ± 0.02	0.12 ± 0.12	-	11.81	
106784	CG10366	CG10366	0.04 ± 0.13	0.08 ± 0.07	+	NT	
106785	CG4334	CG4334	0.25 ± 0.19	0.28 ± 0.10	-	NT	
106793	CG2859	TBP-associated factor 10	0.24 ± 0.11	0.28 ± 0.11	-	-13.91	*
106812	CG16858	viking	0.08 ± 0.06	0.05 ± 0.13	+	NT	
106820	CG15356	CG15356	0.14 ± 0.11	0.24 ± 0.07	+	NT	
106827	CG3717	bcn92	0.11 ± 0.07	0.18 ± 0.09	+	NT	
106842	CG9245	Phosphatidylinositol synthase	0.02 ± 0.07	0.01 ± 0.04	+	22.43	***
106890	CG14483	CG14483	0.02 ± 0.05	0.19 ± 0.05	-	NT	
106899	CG15237	CG15237	-0.05 ± 0.05	0.01 ± 0.02	+	19.71	***
106918	CG2685	CG2685	0.03 ± 0.15	0.14 ± 0.10	-	26.65	***
106919	CG7693	frayed	0.09 ± 0.05	0.05 ± 0.03	-	19.62	***
106928	CG7177	CG7177	0.03 ± 0.03	0.03 ± 0.06	+	36.68	***
106931	CG17221	CG17221	0.21 ± 0.12	0.23 ± 0.08	+	NT	
106961	CG8380	Dopamine transporter	0.11 ± 0.18	0.12 ± 0.05	-	8.25	

106984	CG30122	CG30122	0.22 ± 0.10	0.20 ± 0.12	-	2.84	
106987	CG13609	CG13609	0.04 ± 0.07	0.22 ± 0.04	-	NT	
107014	CG4109	Syntaxin 8	0.18 ± 0.08	0.27 ± 0.05	-	7.90	
107018	CG2811	CG2811	0.18 ± 0.11	0.15 ± 0.16	+	12.40	
107026	CG31739	CG31739	0.01 ± 0.07	0.05 ± 0.04	-	30.15	***
107039	CG13759	CG13759	0.11 ± 0.01	0.17 ± 0.11	-	27.96	***
107058	CG9652	Dopamine receptor	0.14 ± 0.07	0.08 ± 0.04	-	-7.94	
107064	CG3727	dreadlocks	0.26 ± 0.07	0.13 ± 0.05	-	26.68	***
107174	CG31706	CG31706	0.22 ± 0.03	0.11 ± 0.08	-	NT	
107204	CG8103	CG8103	0.20 ± 0.04	0.24 ± 0.08	-	NT	
107251	CG10949	CG10949	0.17 ± 0.04	0.24 ± 0.07	+	20.84	***
107307	CG34126	CG34126	0.21 ± 0.06	0.17 ± 0.09	-	NT	
107308	CG17642	mitochondrial ribosomal protein L48	0.02 ± 0.06	0.13 ± 0.05	-	23.09	***
107322	CG5864	AP-1σ	0.09 ± 0.09	0.22 ± 0.08	+	25.65	***
107335	CG10076	spire	0.21 ± 0.15	0.26 ± 0.06	-	4.59	
107343	CG11049	shaven	0.20 ± 0.13	0.23 ± 0.00	-	4.87	
107344	CG11579	armadillo	0.14 ± 0.05	0.09 ± 0.02	+	35.28	***
107351	CG11120	CG11120	0.25 ± 0.06	0.11 ± 0.02	-	NT	
107369	CG18768	Ankyrin 2	0.22 ± 0.10	0.26 ± 0.03	-	25.75	***
107390	CG4141	Pi3K92E	0.21 ± 0.05	0.23 ± 0.16	-	NT	
107408	CG5273	CG5273	0.02 ± 0.01	0.12 ± 0.08	+	27.12	***
107418	CG18445	oysgedart	0.17 ± 0.04	0.23 ± 0.02	-	2.40	
107473	CG33556	formin 3	0.22 ± 0.08	0.20 ± 0.07	-	NT	
107537	CG34123	CG34123	0.13 ± 0.02	0.16 ± 0.07	+	NT	
107539	CG32709	CG32709	0.15 ± 0.12	0.12 ± 0.03	+	NT	
107572	CG3157	γ-Tubulin at 23C	0.11 ± 0.17	0.10 ± 0.06	+	NT	

107574	CG8128	CG8128	0.21 ± 0.15	0.19 ± 0.09	+	NT	
107597	CG31092	Lipophorin receptor 2	0.23 ± 0.04	0.08 ± 0.00	+	27.15	***
107600	CG1902	CG1902	0.22 ± 0.10	0.20 ± 0.18	-	4.59	
107642	CG3861	knockdown	0.20 ± 0.10	0.07 ± 0.02	+	NT	
107656	CG4726	Major Facilitator Superfamily Transporter 3	0.16 ± 0.05	0.22 ± 0.06	+	10.40	
107658	CG7029	CG7029	0.24 ± 0.05	0.03 ± 0.05	-	NT	
107663	CG1147	neuropeptide F receptor	0.09 ± 0.17	0.06 ± 0.08	-	21.81	***
107715	CG4078	N/A	0.14 ± 0.07	0.01 ± 0.10	+	NT	
107716	CG1945	fat facets	0.15 ± 0.07	0.24 ± 0.01	-	NT	
107745	CG3204	Ras-associated protein 2-like	0.23 ± 0.07	0.19 ± 0.06	-	12.12	***
107767	CG7663	Cuticular protein 78Cb	0.15 ± 0.05	0.03 ± 0.03	-	NT	
107800	CG7224	CG7224	0.11 ± 0.08	0.14 ± 0.03	+	NT	
107811	CG9776	CG9776	0.13 ± 0.04	0.23 ± 0.02	+	NT	
107833	CG7675	CG7675	0.16 ± 0.19	0.19 ± 0.10	-	0.87	
107867	CG10147	CG10147	0.16 ± 0.04	0.21 ± 0.03	-	3.84	
107875	CG14511	CG14511	0.21 ± 0.04	0.20 ± 0.04	+	8.62	
107883	CG11280	tartan	0.14 ± 0.06	0.10 ± 0.05	-	12.09	
107885	CG15639	CG15639	0.22 ± 0.08	0.20 ± 0.03	+	31.87	***
107926	CG9896	CG9896	0.16 ± 0.17	0.26 ± 0.03	+	12.12	
107939	CG17742	CG17742	0.23 ± 0.07	0.20 ± 0.06	+	NT	
107945	CG7166	CG7166	0.17 ± 0.12	0.26 ± 0.05	-	10.65	
107967	CG32498	dunce	0.00 ± 0.09	0.11 ± 0.06	-	13.00	

107981	CG1308	CG1308	0.22 ± 0.09	0.24 ± 0.03	-	16.00	***
107987	CG1659	unc-119	0.25 ± 0.09	0.23 ± 0.06	-	10.93	
107992	CG7154	CG7154	0.15 ± 0.08	0.12 ± 0.07	+	21.62	***
108026	CG8730	drosha	0.20 ± 0.06	0.11 ± 0.06	-	NT	
108067	CG5186	scruin like at the midline	0.17 ± 0.08	0.26 ± 0.05	+	NT	
108069	CG6218	CG6218	0.21 ± 0.12	0.19 ± 0.08	-	-11.32	
108078	CG32103	CG32103	0.22 ± 0.06	0.19 ± 0.02	+	NT	
108084	CG6605	Bicaudal D	0.06 ± 0.10	0.07 ± 0.05	+	NT	
108086	CG6525	protein partner of snf	0.19 ± 0.08	0.12 ± 0.07	-	NT	
108108	CG17994	CG17994	0.20 ± 0.07	0.10 ± 0.11	-	NT	
108128	CG6827	Neurexin IV	0.16 ± 0.05	0.22 ± 0.06	+	NT	
108132	CG5237	CG5237	0.25 ± 0.12	0.17 ± 0.10	-	16.40	***
108150	CG4587	CG4587	0.15 ± 0.05	0.23 ± 0.04	+	NT	
108177	CG8524	NK7.1	0.15 ± 0.08	0.14 ± 0.18	-	NT	
108180	CG42788	CG42788	0.24 ± 0.08	0.08 ± 0.04	-	NT	
108193	CG10360	refractory to sigma P	0.19 ± 0.14	0.21 ± 0.09	-	3.37	
108196	CG10226	CG10226	0.01 ± 0.10	0.17 ± 0.04	+	NT	
108197	CG6739	CG6739	0.19 ± 0.03	0.23 ± 0.17	-	-0.41	
108235	CG30203	CG30203	0.12 ± 0.09	0.21 ± 0.09	+	7.50	
108246	CG8009	CG8009	0.13 ± 0.13	0.05 ± 0.08	-	NT	
108249	CG12254	Mediator complex subunit 25	0.19 ± 0.03	0.20 ± 0.07	+	23.21	***
108259	CG10603	mitochondrial ribosomal protein L13	-0.03 ± 0.04	-0.05 ± 0.04	-	12.86	

108287	CG32211	TBP-associated factor 6	0.19 ± 0.04	0.12 ± 0.02	+	NT	
108294	CG6718	calcium-independent phospholipase A2 VIA	0.17 ± 0.04	0.11 ± 0.04	-	20.78	***
108295	CG9134	CG9134	0.22 ± 0.05	0.24 ± 0.05	-	NT	
108312	CG7727	β amyloid protein precursor-like	0.13 ± 0.06	0.18 ± 0.03	-	14.75	**
108323	CG32250	CG32250	0.15 ± 0.07	0.06 ± 0.07	+	27.59	***
108332	CG3363	CG3363	0.19 ± 0.10	0.21 ± 0.18	+	NT	
108346	CG5316	CG5316	0.24 ± 0.08	0.13 ± 0.04	-	-0.69	
108351	CG9218	smooth	0.12 ± 0.06	0.13 ± 0.05	-	24.40	***
108358	CG6578	phantom	0.06 ± 0.06	0.23 ± 0.07	+	NT	
108361	CG1152	Glucose dehydrogenase	0.12 ± 0.11	0.12 ± 0.04	+	NT	
108371	CG42588	CG42588	0.13 ± 0.1	0.14 ± 0.04	+	NT	
108373	CG9613	Coenzyme Q biosynthesis protein 2	0.13 ± 0.03	0.14 ± 0.06	-	NT	
108375	CG6120	Tetraspanin 96F	0.24 ± 0.15	0.25 ± 0.05	+	23.00	***
108377	CG9688	mitochondrial ribosomal protein S18C	0.03 ± 0.02	0.02 ± 0.07	-	8.03	
108395	CG4574	Phospholipase C at 21C	0.16 ± 0.04	0.13 ± 0.04	+	NT	
108401	CG3738	Cyclin-dependent kinase subunit 30A	0.09 ± 0.03	0.28 ± 0.02	+	18.96	***

108406	CG30498	boca	0.13 ± 0.07	0.08 ± 0.10	+	37.06	***
108409	CG1072	Arrowhead	0.22 ± 0.09	0.23 ± 0.03	+	17.75	***
108414	CG4758	Translocation protein 1	0.22 ± 0.14	0.13 ± 0.08	-	1.40	
108433	CG6713	Nitric oxide synthase	0.24 ± 0.04	0.18 ± 0.10	+	NT	
108444	CG8155	CG8155	-0.07 ± 0.05	0.03 ± 0.07	+	13.40	*
108450	CG32743	no-on-and-no-off transient C	0.24 ± 0.06	0.14 ± 0.05	+	13.43	***
108455	CG4316	Stubble	0.24 ± 0.01	0.14 ± 0.10	-	NT	
108481	CG42260	CG42260	0.16 ± 0.11	0.14 ± 0.04	+	NT	
108483	CG9065	CG9065	0.13 ± 0.07	0.12 ± 0.06	-	6.96	
108494	CG16779	CG16779	0.25 ± 0.10	0.25 ± 0.08	+	9.40	
108508	CG12467	CG12467	0.25 ± 0.05	0.25 ± 0.11	+	NT	
108560	CG5884	par-6	-0.01 ± 0.05	0.05 ± 0.03	-	8.43	
108586	CG5688	Grip163	0.23 ± 0.04	0.20 ± 0.06	-	NT	
108598	CG4082	Minichromosome maintenance 5	0.20 ± 0.13	0.17 ± 0.10	-	NT	
108604	CG15629	CG15629	0.15 ± 0.03	0.15 ± 0.09	+	-4.66	
108607	CG4036	CG4036	0.20 ± 0.06	0.23 ± 0.05	+	NT	
108608	CG10023	Focal Adhesion Kinase	0.26 ± 0.04	0.31 ± 0.09	-	19.65	***
108650	CG6095	CG6095	0.21 ± 0.03	0.15 ± 0.03	+	NT	
108729	CG1963	pterin-4a-carbinolamine dehydratase	0.11 ± 0.05	0.19 ± 0.08	-	28.40	***
108753	CG33639	CG33639	0.11 ± 0.03	0.16 ± 0.07	+	NT	
108797	CG7145	delta-1-Pyrroline-5-	0.15 ± 0.09	0.11 ± 0.04	-	NT	

		carboxylate dehydrogenase 1					
108839	CG5380	CG5380	0.13 ± 0.05	0.04 ± 0.09	-	NT	
108876	CG4931	specifically Rac1-associated protein 1	0.19 ± 0.05	0.21 ± 0.03	-	NT	
108879	CG10118	pale	0.04 ± 0.07	-0.09 ± 0.10	-	NT	
108903	CG2277	CG2277	0.15 ± 0.08	0.19 ± 0.08	-	NT	
108907	CG7250	Toll-6	0.25 ± 0.02	0.17 ± 0.06	-	NT	
108929	CG8632	CG8632	0.10 ± 0.10	0.06 ± 0.05	+	24.59	***
108959	CG14721	CG14721	0.09 ± 0.02	0.20 ± 0.03	-	24.68	***
108993	CG8597	lark	0.15 ± 0.07	0.26 ± 0.09	-	10.15	
108997	CG12954	mitochondrial ribosomal protein L41	0.06 ± 0.06	0.10 ± 0.05	-	8.18	
109084	CG6998	cut up	0.11 ± 0.05	0.08 ± 0.09	-	-1.72	
109111	CG11100	Mesoderm-expressed 2	0.20 ± 0.16	0.14 ± 0.06	+	30.71	***
109193	CGnone	CGnone	0.25 ± 0.03	0.22 ± 0.04	+	11.14	***
109243	CG18773	Lcp65Ab2	0.20 ± 0.08	0.09 ± 0.08	+	NT	
109334	CG18661	CG18661	0.21 ± 0.09	0.21 ± 0.11	+	5.59	
109410	CG5729	Dgp-1	0.18 ± 0.03	0.22 ± 0.11	-	11.62	
109413	CG15609	Eps15 homology domain containing protein-binding protein 1	0.21 ± 0.04	0.07 ± 0.06	-	13.12	
109436	CG2910	spenito	0.19 ± 0.03	0.18 ± 0.04	-	28.78	***
109443	CG7168	CG7168	0.06 ± 0.06	0.05 ± 0.03	+	21.90	***
109479	CG30015	CG30015	0.15 ± 0.04	0.20 ± 0.03	+	18.37	***

109506	CG17065	CG17065	0.15 ± 0.09	0.17 ± 0.06	+	25.59	***
109516	CG34402	CG34402	0.25 ± 0.18	0.04 ± 0.17	-	-0.79	
109594	CG8177	CG8177	0.14 ± 0.05	0.22 ± 0.09	+	19.34	***
109606	CG17336	Ligand-gated chloride channel homolog 3	0.14 ± 0.08	0.19 ± 0.04	+	26.03	***
109613	CG13927	gamma-glutamyl carboxylase	0.24 ± 0.09	0.15 ± 0.18	-	-1.16	
109622	CG14411	CG14411	0.11 ± 0.02	0.12 ± 0.04	-	14.62	**
109629	CG6512	CG6512	0.07 ± 0.02	0.03 ± 0.06	+	NT	
109637	CG8318	Neurofibromin 1	-0.01 ± 0.08	0.07 ± 0.09	-	22.21	***
109654	CG32672	Autophagy-specific gene 8a	0.12 ± 0.03	0.02 ± 0.10	+	24.06	***
109659	CG4913	ENL/AF9-related	0.22 ± 0.06	0.27 ± 0.06	-	-2.63	
109662	CG5904	mitochondrial ribosomal protein S31	0.00 ± 0.05	0.03 ± 0.04	-	28.28	***
109673	CG30426	eggless	0.12 ± 0.07	0.12 ± 0.06	+	NT	
109699	CG18676	tipE homolog 3	0.20 ± 0.04	0.05 ± 0.05	+	NT	
109732	CG13475	HGTX	0.25 ± 0.05	0.17 ± 0.02	-	19.00	***
109739	CG43065	bruno-2	0.25 ± 0.13	0.00 ± 0.32	-	-3.69	
109742	CG17023	Dead box protein 80	0.23 ± 0.07	0.11 ± 0.12	-	10.40	
109767	CG10732	CG10732	0.11 ± 0.10	0.24 ± 0.06	+	22.15	***
109768	CG31451	CG31451	0.15 ± 0.04	0.2 ± 0.1	-	-0.16	
109770	CG7781	CG7781	0.22 ± 0.17	0.21 ± 0.06	-	-0.82	
109793	CG4314	scarlet	0.16 ± 0.11	0.26 ± 0.10	-	NT	
109806	CG13287	CG13287	0.20 ± 0.07	-0.03 ± 0.18	-	16.43	***
109819	CG3279	CG3279	0.22 ± 0.06	0.18 ± 0.08	-	NT	

109822	CG5104	CG5104	0.11 ± 0.11	-0.06 ± 0.2	+	NT	
109828	CG8301	CG8301	0.14 ± 0.04	0.17 ± 0.07	+	NT	
109849	CG42599	PFTAIRE-interacting factor 1A	0.17 ± 0.05	0.25 ± 0.06	+	8.65	
109858	CG9819	Calcineurin A at 14F	0.15 ± 0.01	-0.01 ± 0.01	+	22.75	***
109871	CG12581	CG12581	0.07 ± 0.03	0.19 ± 0.01	+	NT	
109880	CG18582	mushroom bodies tiny	0.23 ± 0.04	0.13 ± 0.08	+	NT	
109881	CG10697	Dopa decarboxylase	0.06 ± 0.06	0.13 ± 0.04	-	37.15	***
109882	CG32226	Peroxin 23	0.24 ± 0.14	0.25 ± 0.09	+	NT	
109949	CG8433	Ext2	0.09 ± 0.04	0.15 ± 0.08	+	NT	
109974	Cgnone	N/A	0.20 ± 0.04	0.15 ± 0.07	+	25.00	***
109975	CG32425	CG32425	0.04 ± 0.09	0.18 ± 0.06	-	NT	
109993	Cgnone	N/A	0.16 ± 0.05	0.06 ± 0.06	+	NT	
110014	CG4099	Scavenger receptor class C, type I	0.12 ± 0.17	0.04 ± 0.07	+	NT	
110051	CG30329	Vacuolar H+ ATPase subunit 100-3	0.18 ± 0.03	0.1 ± 0.08	+	NT	
110053	CG14110	CG14110	0.20 ± 0.09	-0.01 ± 0.06	+	18.53	***
110058	CG16700	CG16700	0.09 ± 0.04	0.08 ± 0.03	+	NT	
110059	CG13140	dpr19	0.16 ± 0.12	0.11 ± 0.06	+	NT	
110075	CG13965	CG13965	0.09 ± 0.05	0.22 ± 0.06	-	NT	
110076	CG17161	grapes	0.08 ± 0.02	0.27 ± 0.01	+	NT	
110077	CG3427	Epac	0.17 ± 0.05	0.19 ± 0.06	+	13.06	
110175	CG3069	TBP-associated	0.21 ± 0.04	0.13 ± 0.05	+	NT	

		factor 10b					
110178	CG1271	CG1271	0.08 ± 0.12	0.20 ± 0.04	+	NT	
110184	CG7766	CG7766	0.22 ± 0.03	0.25 ± 0.09	-	NT	
110193	CG43227	milton	0.23 ± 0.05	0.06 ± 0.01	+	NT	
110196	CG10585	CG10585	0.18 ± 0.06	0.19 ± 0.08	-	NT	
110204	CG3938	Cyclin E	0.24 ± 0.05	0.25 ± 0.09	+	13.28	*
110212	CG8288	mitochondrial ribosomal protein L3	0.11 ± 0.07	0.02 ± 0.05	-	16.00	***
110213	CG32555	RhoGAPp190	0.18 ± 0.04	0.19 ± 0.10	-	NT	
110228	CG4720	Protein kinase at 92B	0.09 ± 0.02	0.29 ± 0.01	+	17.06	***
110235	CG7940	Actin-related protein 5	0.21 ± 0.23	0.06 ± 0.10	-	17.28	***
110240	CG6607	CG6607	0.15 ± 0.05	0.21 ± 0.14	-	12.21	
110246	CG6327	CG6327	0.25 ± 0.12	0.26 ± 0.15	-	1.68	
110252	CG31371	CG31371	0.06 ± 0.07	0.13 ± 0.07	+	33.21	***
110265	CG10440	CG10440	0.24 ± 0.06	0.27 ± 0.05	-	22.53	***
110274	CG8585	Ih channel	0.12 ± 0.15	-0.06 ± 0.09	+	31.62	***
110290	CG1451	APC-like	0.11 ± 0.05	0.25 ± 0.06	+	21.43	***
110345	CG7015	Upstream of N-ras	0.20 ± 0.11	0.06 ± 0.06	-	13.12	
110346	CG4030	CG4030	0.06 ± 0.09	0.16 ± 0.07	+	NT	
110415	CG4832	centrosomin	0.20 ± 0.09	0.09 ± 0.17	+	NT	
110432	CG6863	Tolkin	0.20 ± 0.05	0.15 ± 0.04	+	31.37	***
110456	CG4495	CG4495	0.25 ± 0.1	0.26 ± 0.08	-	5.37	
110494	CG33950	terribly reduced optic lobes	0.18 ± 0.04	0.19 ± 0.14	-	NT	
110495	CG32244	Neurotrophin 1	0.25 ± 0.02	0.09 ± 0.07	-	10.87	

110512	CG3630	CG3630	0.11 ± 0.09	0.12 ± 0.07	+	NT	
110518	CG32062	Ataxin-2 binding protein 1	-0.01 ± 0.03	0.10 ± 0.04	+	34.81	***
110552	CG2204	G protein oα 47A	0.04 ± 0.16	0.16 ± 0.12	+	19.69	***
110578	CG4611	CG4611	0.07 ± 0.10	0.28 ± 0.07	+	NT	
110594	CG2819	PvuII-PstI homology 13	0.18 ± 0.11	0.19 ± 0.01	-	NT	
110606	CG3985	Synapsin	0.19 ± 0.06	0.09 ± 0.05	+	NT	
110616	CG3016	CG3016	0.16 ± 0.04	0.05 ± 0.14	-	NT	
110636	CG34401	CG34401	0.21 ± 0.07	0.20 ± 0.06	-	20.40	***
110663	CG17370	Signal peptide peptidase-like	0.18 ± 0.02	0.12 ± 0.05	+	NT	
110664	CG6582	Aac11	0.21 ± 0.04	0.17 ± 0.06	+	29.93	***
110665	CG4679	CG4679	-0.05 ± 0.08	-0.01 ± 0.02	-	13.84	*
110686	CG42555	tweek	0.19 ± 0.06	0.12 ± 0.05	+	NT	
110692	CG6428	CG6428	0.14 ± 0.15	0.24 ± 0.05	-	2.43	
110696	CG5300	Klp31E	0.19 ± 0.01	0.18 ± 0.12	+	29.56	***
110708	CG8422	Diuretic hormone 44 receptor 1	0.07 ± 0.21	0.1 ± 0.06	-	-5.01	
110717	CG10392	super sex combs	0.04 ± 0.06	0.07 ± 0.01	-	15.68	***
110737	CG12125	CG12125	0.24 ± 0.09	0.12 ± 0.02	+	NT	
110774	CG15218	Cyclin K	0.18 ± 0.09	0.13 ± 0.05	+	NT	
110786	CG3530	CG3530	0.24 ± 0.05	0.14 ± 0.02	+	7.37	
110805	CG7020	DISCO Interacting Protein 2	0.10 ± 0.08	0.28 ± 0.06	-	NT	