Resource

An atlas of *Caenorhabditis elegans* chemoreceptor expression

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AUTHOR SUMMARY

Maps of gene expression patterns in the nervous system provide an important resource for neuron classification, for functional analysis and for developmental studies that ask how different neurons acquire their unique identities. By analyzing transgenic gfp reporter strains, we describe here the expression pattern of 244 putative chemosensory receptor-encoding genes, which constitute the largest gene family in *C.elegans*. We show that, as expected, chemoreceptor expression is enriched in chemosensory neurons but it is also expressed in a wide range of interneurons, motorneurons, as well as non-neuronal cells, suggesting that putative chemosensory receptors may not just sense environmental signals but also internal cues. We find that each chemoreceptor is expressed in a few neuron types, often just one, but each neuron type can express a large number of chemoreceptors. Interestingly, we uncovered that chemoreceptor expression is remarkably plastic, particularly in the context of the environmentally-induced dauer diapause stage. Taken together, this molecular atlas of chemosensory receptors provides an entry point for functional studies and offers a host of markers for studying neuronal patterning and plasticity.

ABSTRACT

One goal of modern day neuroscience is the establishment of molecular maps that assign unique features to individual neuron types. Such maps provide important starting points for neuron classification, for functional analysis and for developmental studies aimed at defining the molecular mechanisms of neuron identity acquisition and neuron identity diversification. In this resource paper, we describe a nervous system-wide map of the potential expression sites of 244 members of the largest gene family in the *C. elegans* genome, rhodopsin-like (class A) GPCR chemoreceptors, using classic *gfp* reporter gene technology. We cover representatives of all sequence families of chemoreceptors GPCRs, some of which were previously entirely uncharacterized. Most reporters are expressed in a very restricted number of cells, often just in single cells. We assign GPCR reporter expression to all but two of the 37 sensory neuron classes of the sex-shared, core nervous system. Some sensory neurons express a very small number of receptors, while others, particularly nociceptive neurons, co-express several dozen GPCR reporter genes. GPCR reporters are also expressed in a wide range of inter- and motorneurons, as well as non-neuronal cells, suggesting that GPCRs may constitute receptors not just for environmental signals, but also for internal cues. We observe only one notable, frequent association of coexpression patterns, namely in one nociceptive amphid (ASH) and two nociceptive phasmid sensory neurons (PHA, PHB). We identified GPCRs with sexually dimorphic expression and several GPCR reporters that are expressed in a left/right asymmetric manner. We identified a substantial degree of GPCR expression plasticity; particularly in the context of the environmentally-induced dauer diapause stage when one third of all tested GPCRs alter the cellular specificity of their expression within and outside the nervous system. Intriguingly, in a number of cases, the dauer-specific alterations of GPCR reporter expression in specific neuron classes are maintained during postdauer life and in some case new patterns are induced post-dauer, demonstrating that GPCR gene expression may serve as traits of life history. Taken together, our resource provides an entry point for functional studies and also offers a host of molecular markers for studying molecular patterning and plasticity of the nervous system.

INTRODUCTION

Molecular markers selectively expressed in individual neuron types represent invaluable tools to understand how cellular diversity in a nervous system is genetically encoded. Molecular markers that are constitutively and invariably expressed throughout the life of a specific neuron type provide static views of neuronal identity and hence provide entry points to study how invariable identity features are acquired during neuronal differentiation [1]. In contrast, some molecular features of a neuron display a remarkable plasticity in that their expression may be regulated by neuronal activity or in response to specific environmental cues. Such genes serve as markers to understand the nature of the gene regulatory programs that govern such dynamic features of a neuron. We reasoned that a significant expansion of the expression analysis of chemosensory G-protein-coupled receptors (GPCRs), initiated more than 20 years ago [2] using *gfp*-based reporter gene technology [3], may yield a significantly expanded resource of molecular markers that may label various aspects of neuronal identity and neuronal plasticity in the *C. elegans* nervous system.

Animal genomes encode five major classes of GPCRs, of which the rhodopsin class (or “class A”) is the largest class [4, 5](**Table 1**). Rhodopsin class GPCRs can be subdivided into phylogenetically deeply conserved neurotransmitter receptors (neuropeptides, acetylcholine, biogenic amines) as well as non-conserved, chemosensory-type GPCRs (from here on referred to as “csGPCRs”)(**Table 1**). The csGPCRs have independently expanded in distinct animal phyla where they serve to respond to diverse, physiologically relevant external and, supposedly, internal cues [4, 6, 7]. The genome of the nematode *C. elegans* encodes an exceptionally large battery of chemosensory-type csGPCRs composed of 1,341 protein-coding genes (**Table 2**)[2, 7, 8], a remarkable number given the small size of its nervous system (302 neurons constituting 118 anatomically defined neuron types)[9]. These csGPCRs have been subdivided by sequence into families and superfamilies, as summarized in **Table 2** [2, 7].

Wormbase contains expression data for 131 csGPCRs, however for only 76 of them the expression site has been defined with single cell resolution (**S1 Table**). The majority of these 76 reporters revealed expression in chemosensory neurons [2]. Functional studies have linked a small subset of these receptors to the sensation of specific environmental or

pheromonal cues [12-21], but in the absence of concerted de-orphanization efforts like those seen in other organisms [22, 23], the number of receptors with assigned ligands is still remarkably low.

Intriguingly, a subset of the previously characterized csGPCR genes were also expressed in non-sensory neurons [2, 24-28] suggesting that they may also function as receptors of internal ligands of unknown identity. Providing some hints to the identity of these ligands, one csGPCR subclass, encoded by the *srw* genes, displays sequence similarities to peptide receptors [11, 29]. The expression of csGPCRs in interneurons also prompted efforts to identify the function of some of these genes. Even though its ligand remains unknown, AIY-expressed *sra-11* was found to be involved in the associative learning paradigm, olfactory imprinting [30], while *sra-13* acts in the vulva to control vulval development, which is affected by food signals [26].

In spite of the relative paucity of known ligands, the previously published expression patterns of csGPCRs provided molecular indicators for a number of intriguing and generally very poorly understood nervous system features: (1) the expression pattern of the GPCR gene *str-2* revealed a left/right asymmetry in the two AWC olfactory neurons [31]; this lateralization phenomenon was later found to be required for olfactory discrimination [32] and spurred a host of studies aimed at revealing how this left/right asymmetry is developmentally programmed [33]. (2) The expression of several csGPCRs revealed a remarkable plasticity in response to changes in the environment. For example, expression of *srd-1* and *str-2* and *str-3* changes in ASI neurons in response to dauer pheromone [34], and expression of *srh-34* and *srh-234* in ADL is different in fed *versus* starved animals [35]. Using these dynamic reporter gene patterns, mechanisms controlling csGPCR plasticity have been elucidated [35, 36]. (3) The csGPCR genes *srd-1*, *srj-54* and *odr-10* have been found to be expressed in a sexually dimorphic manner in sex-shared sensory neurons, suggesting that sexual identity impinges on sensory perception [2, 37, 38].

In this resource paper, we examined the expression of 244 reporter transgenes that monitor expression of previously uncharacterized csGPCR genes (for simplicity, from here on referred to as “GPCRs”. Our explicit goal in this analysis was to (1) generate more neuronal identity markers, (2) test the hypothesis that many more sensory neurons may be lateralized, (3) identify more markers of neuronal plasticity, (4) identify more markers of sexual dimorphism and (5) examine the extent of expression in non-sensory and non-neuronal cells

(suggesting roles as receivers of internal signals). Based on the molecular classification of csGPCRs into defined families, we were also interested in determining whether the expression of specific subfamilies – particularly those whose expression has not previously examined – may reveal specific common themes (*i.e.,* patterns of co-expression or expression in specific cells) that may provide a hint to their function. We synthesize our findings with those of previous expression pattern analyses to carve out a number of general features of csGPCR expression patterns.

MATERIALS AND METHODS

Mutant Strains. Strains were maintained by standard methods [39]. Mutant alleles used in this study were: *pha-1(e2123)* [40], *him-5(e1490)* [41], *unc-43(n1186lf)* [42], *unc-43(n498gf)*[43] and *nsy-5(ky634)* [44].

Reporter and transgenic strain generation. GFP reporters were generated using a PCR fusion approach [45] and injected without being subcloned. Genomic fragments were fused to the GFP coding sequence, which was followed by the *unc-54* 3′ untranslated region. A list of primers for all constructs can be found in the Supplementary Methods. Amplicons were injected at 50ng/ml with the *pha-1* rescuing plasmid (pBX) as a co-injection marker (50ng/ml). Reporters were injected into a *pha-1(e2123)* or *pha-1(e2123);him-5(e1490)* mutant background strain [40], resulting in transgenic arrays with little mosaicism. For each construct 2 independent lines were scored. Reporter strains provided by the Vancouver Consortium were generated as described [46]. Further details and primer sequences used by the Vancouver Consortium can be found at http://www.gfpworm.org. A list of all reporter strains generated by us or provided by the Vancouver Consortium can be found in the Supplementary Methods.

Microscopy. Worms were anesthetized using 100mM sodium azide (NaN_3) and mounted on 5% agarose on glass slides. Images were acquired using an automated fluorescence microscope (Zeiss, AXIO Imager Z.2). Acquisition of several z-stack images (each ~1 mm thick) was performed with the ZEN 2 pro software. Representative images are shown following max-projection of Z-stacks using the maximum intensity projection type. Image reconstruction was performed using Fiji software [47].

Neuron identification. Neurons were identified either by labeling subsets of sensory neurons with DiD (Thermo Fisher Scientific) or by crossing reporter transgenes with landmark reporter strains in which known neuron types are labeled with a red fluorescent reporter. For dye filling, worms were washed with M9, incubated with DiD (1:500) in M9 for 1 hour at room temperature, washed 3 times with M9, and plated on agar plates coated with food for 1-3 hours before imaging. Red fluorescent reporter strains used for cell identification are: *otIs263[ceh-36p::TagRFP, rol-6(su1006)], vyIs51[str-2p::2xnls::TagRFP; ofm-1p::DsRed*][48], *otIs518[eat-4*^{Fosmid}*::sl2::mCherry::h2b]*[49], *otIs544[cho-1*^{Fosmid}*::sl2::mCherry::h2b*][50],

otIs564[unc-47^{Fosmid}::sl2::mCherry::h2b][51], *otIs612[flp-18p::NLG-1::GFP11, gpa-6p::NLG-1:::GFP1-10, flp-18p::mCherry, nlp-1p::mCherry], hdIs30[glr-1p::DsRed], otIs521[eat-4prom8::tagRFP; ttx-3::gfp]*.

Hierarchical clustering of neurons by GPCR reporter expression. Clustering was performed on binary expression data from 272 neuron-expressed GPCR reporters for which we had cell ID information. Expression data was from our own analysis and available data from wormbase.org [52]. Only positive neuronal cell ID information per GPCR reporter was included in the binary expression matrix with no distinction between the absence of expression and unknown expression per neuron. Data were clustered using the R pvclust package (https://cran.r-project.org/web/packages/pvclust/pvclust.pdf) [53] using the euclidean distance metric with average linkage, bootstrap 1000, and relative sample size ranging from a proportion of 0.5 to 1.4 of the original sample size. The relative proportion was incremented by 0.1 for each bootstrap resampling. Bootstrap Probability value (BP) and Approximately Unbiased p-values (AU) are derived from the multiscale-multistep bootstrap resampling. AU support values > 95 indicate well-supported clusters and should be considered when evaluating dendrogram cluster relationships. Alternative distance and linkage methods showed clustering of the PHA, PHB and ASH neurons in all cases (42 out of 84 cases had strong support with AU/BP >95).

Upstream intergenic distances and intron length calculations. GPCR upstream intergenic regions and intron lengths were extracted from *C. elegans* exon coordinates, version WS220 using a python script. Non-coding RNA exons were excluded from the intergenic distance calculations so that intergenic distances represent the nucleotide sequence distance between coding genes. The average intron length per gene was calculated by summing the intron sequence lengths for each gene and dividing by the total number of introns. Average intron lengths for genes with multiple isoforms were calculated for each isoform and then averaged, resulting in one average intron length per gene.

Generation of dauers and analysis of changes in expression. To analyze GPCR reporter gene expression in dauers, mixed populations of respective strains were allowed to exhaust food for 5-7 days at 20°C. Dauers were isolated from starved plates by treatment with 1% SDS for 30 min and imaged within 1-2 hours of isolation. The cellular identity of expression changes in dauers were confirmed with red landmark strains, as mentioned above.

RESULTS

Selection of csGPCRs for expression analysis and method of analysis

We chose to examine csGPCR expression patterns using *gfp*-based reporter gene technology, the standard tool of gene expression analysis in *C. elegans* [3, 54]. The obvious shortcoming of this technology is that reporter genes may not capture the full *cis*-regulatory content of the respective GPCR-encoding locus, but as we will describe in more detail below, most GPCR-encoding loci are compact with small intergenic regions and introns. We emphasize that our approach is not necessarily aimed at identifying the complete set of cells expressing a GPCR, but, following ample precedent, is rather aimed at identifying novel and informative patterns of expression, as incomplete as these patterns may be.

We utilized two sources of csGPCR reporters. A consortium at the University of British Columbia (Vancouver) has generated a valuable, large panel of reporters for 1886 genes in the *C. elegans* genome [46]. However, the site of expression of these reporters has not been determined with single cell resolution in the nervous system. We obtained 100 reporters from this collection that targeted GPCR loci and for every reporter that produced a stable pattern of expression, we undertook a detailed analysis of their sites of expression in the nervous system.

In addition to these 100 reporter genes, we generated 144 of our own reporter genes. We adhered to the following principles in the choice of genes and design of reporters: First, we aimed to cover all 23 classes of chemoreceptor genes defined by Thomas and Robertson [7](**Table 2**). Using phylogenetic trees assembled by Thomas and Robertson, we sampled each gene family evenly, generally avoiding the examination of close sequence paralogues, which we anticipated to reveal similar expression patterns.

Our own reporters mostly contain all 5' intergenic regions fused to *gfp* and contain at most 4 kb of sequence. The rationale behind this choice lies in the overall organization of GPCR loci (summarized in **S1 Fig**). 89% of the ~1,300 csGPCR loci contain 5' intergenic regions of less than 4kb. We chose all of our samples from this pool and the reporters generated by us capture the full intergenic region. The reporters from the Vancouver consortium contain about 3 kb of 5' intergenic region at most [46]. Furthermore, csGPCR loci tend to have small introns (average size 432 bp; almost half of them <200 bp; **S1 Fig**),

indicating that relatively little *cis*-regulatory information resides in these introns, which provided the basis for our focus on intergenic regions. For some genes with very short upstream intergenic regions (less than 500 bp) we included the first intron (if this was 300 bp or larger) in order to increase the regulatory space contained in the reporters. The coordinates for all reporter constructs can be found in the Supplementary Material.

Sites of expression within the nervous system were determined mainly for those reporters with most robust expression and was based on stereotyped cell position, cellular and process morphology and co-labeling with either DiD (which labels a subset of sensory neurons) or by crossing with landmark strains in which specific neuron types are labeled with a red fluorescent protein (see Material and Methods). All cell identification was initially done in young adult hermaphrodite animals. As we will describe in detail later, a number of these reporter strains were also subjected to analysis at different stages, under different conditions and in the two different sexes.

GPCRs are expressed in restricted patterns within and outside the nervous system

In our ensuing description of expression patterns of reporter genes, we summarize the expression observed with the previously described reporters, as well as the additional reporters analyzed by us. All of our expression analysis is summarized in a tabular form in **S1 Table.** Three overall features of the 375 csGPCR reporters are immediately apparent (**Fig 1**): first, 92% of analyzed reporters are expressed in the nervous system; second, expression is not restricted to the nervous system: 33% of the reporters are expressed both within and outside the nervous system and 8% are expressed exclusively in non-neuronal cells, and third, the vast majority of csGPCR reporters are expressed in very restricted number of cells (**Fig 1A,B**). Of the neuronally expressed reporters, 24% are expressed in single neuron pairs, 27% in 2 neuron pairs, 26% in 3-4 neuron pairs, 19% in 5-10 neuron pairs and the remaining 4% in more than 10 neuron pairs.

Expression outside the nervous system will be described in a later section. Within the nervous system, expression is most prominent in sensory neurons (**Fig 1C**). 84% of the reporters are expressed in amphid sensory neurons (which are made up of 12 pairs of neurons), 20% in phasmid sensory neurons (made up of 2 pairs of neurons, PHA and PHB), and 17% in other sensory neurons. We find that every sensory neuron, except for URY and

ADE neurons, expresses at least one GPCR (**Fig 1D; Table S2**). The number of GPCRs expressed in a given neuron shows a striking range. The ASI neuron expresses an impressive 99 GPCR reporters. After ASI, the nociceptive neurons ADL and ASH together with the phasmid neurons PHA and PHB are the sensory neurons with higher number of GPCRs, expressing 72, 51, 51 and 49 reporters respectively. Outside the amphid and phasmid neurons, the number of reporters expressed in sensory neurons dramatically drops, with all other sensory neurons expressing less than 10 GPCRs, in some cases only a single GPCR (**Fig 1; Table S2**). Of course, it needs to be kept in mind that we only consider expression of a fraction of the csGPCR loci and hence each of these total numbers is expected to increase by several fold once all csGPCR expression patterns are identified.

24% of the GPCR reporters for which we have information about neuron numbers are exclusively expressed in a single neuron class and in all these cases, the neuron class is a sensory neuron class (**Fig 2; Table S3**). In total, however, only nine sensory neurons express single-neuron specific GPCRs. The most striking one of them is the ADL nociceptive neuron, which expresses 23 single neuron-specific GPCR reporters (and an additional 49 GPCR reporters expressed in additional neurons). The ADL-expressed, single neuron-specific GPCRs do not fall into a specific GPCR subfamily but rather cover 7 distinct families. A small subset of the single neuron type specific GPCRs are expressed outside the nervous system as well (genes with asterisk in **Fig 2A**). This may indicate that these receptors do not detect external cues, but rather sense internal signals.

Notably, expression of the csGPCR reporter collection is clearly not restricted to sensory neurons. A striking 35% of the csGPCR reporters are expressed in inter- and motorneurons (**Fig 1, Fig 3; Table 3; S1 Table**). There is no unifying feature of the inter- or motorneurons that express GPCR reporters. They range from ventral cord motor neurons to head interneurons, and to command interneurons in the ventral cord. One interneuron, PVT, displays a very large number of expressed csGPCR reporters (57 different reporters); however, PVT expression is generally observed in an unusually large amount of reporter genes and may, like posterior gut expression, be a reporter gene artifact that relies on cryptic regulatory elements in the reporter.

97% of inter and/or motorneuron-expressed csGPCR reporters are also expressed in sensory neurons so only 3% of them show expression exclusively in inter or motorneurons. In light of the inter/motorneuron expression of csGPCR reporters, one can imagine that

csGPCR reporters that are expressed in sensory neurons may actually not function as receptors for external sensory cues, but may rather function as they likely do in inter/motorneurons, *i.e.* as receptors of internal signals.

We asked whether csGPCR expression profiles cluster by neuron type. To this end, we undertook unsupervised hierarchical clustering of expression profiles. The bootstrap value for most associations was very weak with two exceptions: csGPCR reporters are often coexpressed in the two tail phasmid neuron classes PHA and PHB (AU/BP>95) and expression in either or both of the phasmid neurons is associated with the expression in the head neuron ASH (AU/BP>95) (**Fig 4**). These associations are striking since all these 3 neuron classes are nociceptive neurons that respond to some similar cues and integrate sensory inputs from the head and tail [55, 56] and that directly innervate command interneurons involved in reversal behavior [9]. While GPCRs expressed in these neurons are likely involved in sensing nociceptive cues, it is notable that these co-expressed csGPCR came from a widely distinct sets of GPCR families (**Fig 4**).

Left/right asymmetric expression of csGPCR reporters

One major motivation for undertaking the csGPCR reporter analysis was to identify more lateralized neuron pairs in the nervous system. In vertebrates, there is a striking dearth of molecular correlates for widespread functional lateralization of the brain. In *C. elegans* the chance discovery of left/right asymmetric sensory receptor expression has opened up new vistas on lateralization of the *C. elegans* nervous system [58]. Specifically, the lateralized expression of several csGPCRs in the AWC olfactory neuron pair [31] and guanylyl cyclase receptors in the gustatory ASE neuron pair [59] revealed a common theme of lateralization providing means of sensory discrimination [32, 60, 61]. Since lateralization provides an elegant, straight-forward means for sensory discrimination, we speculated that such lateralization may be wide-spread in the nervous system and therefore took particular care in examining whether csGPCR reporters that we analyzed are expressed in a left/right asymmetric manner.

We indeed identified eight csGPCR reporters with left/right asymmetric gene expression in an otherwise bilaterally symmetric neuron pair. However, this laterality was only observed in the context of the AWC sensory neuron pair, which was previously known to

express several GPCRs in a left/right asymmetric manner [31, 62]. Using previously described sets of mutants, we found that the asymmetry of these GPCR reporters is controlled by the same calcium-dependent signaling pathway [33] that controls all other previously known asymmetric GPCRs in the AWC neurons (**Fig 5**). Of course, our limited analysis does not exclude the existence of left/right asymmetrically expressed GPCR genes in other neuron types, but it may not be as widespread as we initially hypothesized.

Sexually dimorphic expression of csGPCR reporters

Apart from brain lateralization, another domain of nervous system research displays a striking dearth of molecular markers. While the existence of sex-specific neurons is widely appreciated in the nervous system of most animals, including *C. elegans* [64], it is much less clear to what extent neurons that are shared by the two sexes of a given species display molecular differences. Recent anatomical work in *C. elegans* revealed intriguing synaptic wiring differences between sex-shared neurons in the two sexes [65], but even in *C. elegans* there is a dearth of dimorphic molecular markers of sex-shared neurons. Given the distinct priorities that males and hermaphrodites display toward food and mate searching [66] and given that a number of sex-shared sensory neurons are known to respond to different cues in a sex-specific manner [49, 67], we hypothesized that we may discover a multitude of sex-specifically expressed GPCRs. We indeed identified several GPCRs that are expressed in hermaphrodite-specific neurons (HSN, VC motor neurons) or in several male-specific neurons (**Fig 6**); however, we did not detect differences in GPCR expression in sex-shared neurons. We emphasize here, however, that we did not systematically analyze all 245 reporters that we analyzed in the hermaphrodite for differences in expression in the male, but rather focused on those GPCRs that show expression in 1-3 pairs of neurons in the hermaphrodites.

csGPCR reporter expression outside the nervous system

Moving outside the nervous system, we found expression of individual GPCRs in essentially all tissue types (**Fig 7** shows examples; summarized in **Table 4**). As we already mentioned above, the non-neuronal expression is often quite specific and there are only a few GPCRs that are expressed broadly in many different cell types (*e.g. srbc-58*, *srr-4*).

Specific sites of non-neuronal expression include subsets of muscle cells, hypodermal cells, specialized epithelial cells, cells of the somatic gonad (distal tip cells), individual cells of the excretory system, glial cells and others (**Fig 7, Table 4**). There are no obvious, specific associations of non-neuronal expression with expression in a specific set of neuron types. Also, non-neuronally expressed GPCR receptors are not biased toward a single subfamily. GPCRs expressed in non-neuronal tissues that are exposed to the environment, e.g. epidermis, could be involved in sensing external cues but other non-neuronal cells will rather respond to internal signals. As a cautionary note, we can not presently exclude that non-neuronal expression may be the result of lack of repressor elements in the reporter constructs, but we note that in *C.elegans* there is presently little evidence for non-neuronal repressor mechanisms restricting gene expression to the nervous system (e.g. [68]).

Reporter gene analysis of entire csGPCR gene families

Do any of the patterns described above cluster with sequence similarity (*i.e*. family membership) of the receptors? As described above, specific features of csGPCR expression patterns do not correlate with family membership, but we wanted to pursue this issue further via a more comprehensive analysis of entire chemoreceptor gene families. As defined by sequence analysis [7], chemoreceptor gene families have very different sizes, ranging from a single gene per family (*srn* family) to 223 genes per family (*srh* family)(**Table 2**). We analyzed reporter gene expression patterns of all members of two small families to examine whether there are common themes in their expression patterns, their genomic location and *cis*-regulatory control regions. We also analyzed the expression of the one family, the *srn* family, which only has a single member, which is highly conserved in *Caenorhabditis* species, to assess whether it may show an unusual expression pattern. However, we find the *srn-1* reporter gene to be mainly expressed in amphid sensory neurons, like many other GPCRs (**Fig 8**).

The two small families for which we generated and analyzed reporter genes for all family members are the previously uncharacterized *srm* (6 members) and *srr* (9 members). Five out of the six *srm* family genes are syntenic to other family members (**Fig 8**). As these direct genomic adjacencies suggest local gene duplication, we could ask the question whether such local duplications also resulted in duplication of the 5' *cis*-regulatory control regions and to what extent such duplicated *cis*-regulatory control regions retained similar

expression profiles. We find that the adjacent *srm-1* and *srm-2* genes are expressed in a small set of mostly sensory neurons; some of these neurons are the same, others are different. The same theme applies to the adjacent *srm-4, srm-5* and *srm-6* genes. Their 5' upstream regions direct expression to distinct, but partially overlapping sets of neurons.

The *srr* gene family is composed of 9 members. Reporter genes for all members displayed expression in diverse sets of neuron types with no common theme emerging. Outside the nervous system, it is notable that half of the family members are expressed in distinct cell types of the pharynx (**Fig 8**), suggesting a role for these genes in sensing food.

Temporally regulated csGPCR reporter genes

We also sought to examine dynamic aspects of csGPCR expression. We focused on dynamics that relate to developmental timing and the response to harsh environmental conditions. To facilitate the identification of changes in expression, we focused our analysis on GPCRs that are robustly expressed in the adult in a small number of neurons (in most cases not more than 1-3 neuron pairs in the head and/or 1-2 neuron pairs in the tail). At the first larval stage we didn't detect any differences in expression in 79 out of 82 examined reporters. Due to the limitations of multicopy array based fluorescent reporters, moderate intensity changes within a cell type might be difficult to notice and could have been missed. Three reporter genes, *srh-11*, *sru-48,* and *sra-28,* show striking differences in first larval *versus* adult stages: All three reporter genes show expression in the ASK neuron at the L1 stage, but not at the adult stage (**Fig 9**). Additionally, *srh-11* is expressed brightly in the ASI neuron at the L1 stage but dimly at the adult stage (**Fig 9**). Furthermore, dim expression of *srh-11* and *sra-28* reporter genes in the tail phasmid PHB and PHA neurons respectively, is only observed at the L1 stage but not at the adult stage (**Fig 9**).

GPCR reporter gene expression changes in dauers

We found that a substantial number of GPCR reporter genes were dynamically expressed when animals enter the dauer stage, an environmentally controlled diapause arrest stage that is accompanied by substantial cell, tissue and behavioral remodeling [69, 70]. Initially again focusing on reporters that are expressed in a restricted number of neurons under well-fed conditions, we found that 16 out of 46 examined reporters show a diverse set

of changes in animals that were sent into the dauer stage via a standard starvation/crowding protocol (see Experimental Procedures). Many of the changes entail striking changes in the cellular specificity of GPCR reporter expression (**Fig 10, Table 5**). The vast majority of differences are observed in the nervous system, but some changes also occur outside the nervous system. Changes in GPCR reporter expression in the dauer stage have previously been described for two GPCR reporters [34](summarized with our novel patterns in **Table 5**), but the patterns we observe here are much broader and more complex. They can be summarized as follows:

(1) In most cases, there is stable and unchanged expression in several neuron classes in dauer and non-dauers, but upon dauer entry, expression is either turned on in additional neuron classes ("type I" regulation) or becomes undetectable in subsets of specific neuron classes ("type II" regulation) (**Table 5; Fig 10**). There are also combinations of both changes (type III regulation): In one particularly striking example, the *srh-71* reporter is expressed in some sensory neurons in both dauer and non-dauers, but undergoes a striking respecification in dauers. Reporter expression becomes undetectable in the lateral IL2, PHA and an additional pair of tail neurons in dauer, and instead is turned on in the AIZ and ASG neurons (and increases expression levels in ASI). This hints toward the re-routing of internal sensory information.

(2) In a number of cases reporter expression is strongly downregulated, becoming undetectable in all neurons in which the reporter is expressed (**Table 5; Fig 10**).

(3) The changes outside the nervous system concern three tissue types, muscle, the excretory cell and epithelial blast cells (**Fig 10)**. In two cases, expression of a specific csGPCR reporter is turned on in the dauer stage, while in another case expression becomes undetectable. These findings indicate that these tissue types now became receptive to signals in a dauer-specific manner, an unanticipated finding.

(4) The most recurrent set of changes in the expression of distinct reporters concern nociceptive neurons, namely the ASH, ADL and phasmid tail neurons. Of particular note is the PHA phasmid neuron, which shows the most consistent pattern of changes: 4 csGPCRs are turned off or strongly downregulated specifically in the dauer stage.

(5) The most unusual novel expression pattern observed in dauer stage animals concerns the PVP tail interneuron pair. We found that in dauers, expression of the *sri-9* reporter is turned

on in a left/right asymmetric manner, only in the PVPL neuron. The cellular identity of *sri-9* expression (as well as other expression changes) was corroborated by examining overlap of GPCR *gfp*-based reporters with *rfp*-based landmark strain (see Experimental Procedures).

Some csGPCRs serve as molecular markers of life history

Do reporter expression changes observed in dauers recover upon re-feeding to the pattern observed in control fed animals? Examining csGPCR reporter expression in well-fed adult animals that had passed through the dauer arrest stage during larval development, we found that the expression of 11 of the 18 reporters, which showed dauer-specific gene expression changes, recovers to that of the fed state, i.e. in these 11 cases, expression in the adult is independent on whether the animals had passed through the dauer stage or not.

For 7 csGPCR reporters we discovered intriguing, cell-type specific alterations in animals which have passed through the dauer stage (**Fig 11, Table 5**). We observed two types of changes:

(1) For 4 reporters (for *sri-9*, *sra-25*, *srh-71* and *sru-12*), we observed that expression which was induced in specific neuron types exclusively in dauers, retained this expression in postdauer animals: Dauer-induced expression of the *sri-9* reporter in PVPL, of the *sra-25* reporter in ADL, of the *sru-12* reporter in PVQ as well as of the *srh-71* reporter in AIZ and two ventral ganglion head motor neuron pairs is retained in post-dauer adults. In contrast, dauer-induced loss of *srh-71* expression in the lateral IL2 pair does not recover.

(2) In 4 cases (*sre-43*, *srh-71*, *sru-12*, *sra-25* reporters) we observed induction of expression in additional cell types exclusively in postdauer animals. *sru-12* reporter expression is specifically induced in the PLN neurons of postdauer animals, *sre-43* expression in dimly observed in the ASH neurons of postdauer animals, *sra-25* expression is dimly observed in the ASJ neurons in postdauer animals and *srh-71* reporter expression was induced in a non-neuronal pair, pharyngeal gland cells, in post-dauers.

In addition to these two categories, we found two instances, in which a sporadic and weak expression observed in animals that have not passed through the dauer stage will become highly penetrant and stable if they have passed through the dauer state (*sra-25* in BAG neurons, *sre-43* in ASJ, *srh-71* in ASI).

Note that all of the reporters for which we observe changes in postdauer recovery do recover their “fed patterns” in other neuron classes (these could be considered as internal

controls that argue against the changes in expression being a reporter gene artefact). Taken together, adult animals show neuron-type specific differences in the expression of GPCR reporters depending on whether they have passed through periods of distress. GPCR reporters therefore serve as reporters of life history traits.

L1 starvation recapitulates some but not all csGPCR reporter changes

We tested five of the 16 csGPCR reporters that displayed changes in the dauer stage for whether their expression also changes in another starvation-induced arrest stage, the starvation-induced L1 arrest stage. Comparing expression in 2 day-starved L1 (egg prep into M9 medium) to fed L1, we find that two reporters (*str-114* and *sra-25*) show the same changes as observed in dauer animals (**Fig 12**). In contrast, two reporters (*str-84* and *srg-32*) that change their expression in dauers, do not show changes in starved L1 vs. fed L1 (**Fig 12**). One reporter, *srh-15*, in addition to dauer-specific expression in ASK, is also expressed in ASI in starved L1. Hence, the response of GPCR expression to arrest conditions is diverse.

DISCUSSION

Together with previously published analyses, there are now reporter transgenes that monitor the expression of 373 of the ~1,300 chemosensory GPCR genes encoded in the *C. elegans* genome. One intrinsic limitation of reporter genes is that they do not necessarily capture the full complement of *cis*-regulatory control elements of a gene. However, given the compact nature of csGPCR loci, the inclusion of all 5' regions in most reporters and the small size of introns, the number of inaccuracies may be quite limited. Irrespective of whether the reporters are a reflection of the complete expression of a csGPCR, they nevertheless function as highly valuable molecular markers of cellular identity and plasticity. Meaning, reporter gene analysis decodes *cis*-regulatory information and provides read-out of regulatory states of specific cell types. The key conclusions of the expression patterns inferred from the reporter genes are as follows:

Restricted expression. Most csGPCRs show a very restricted expression in few cell types. Many GPCRs are expressed in single neuron classes. Those csGPCRs that express in multiple neuron types do not display a coherent set of coexpressing neurons, with one notable exception: the nociceptive ASH, PHA and PHB neurons display similar (but not identical) sets of csGPCR expression.

csGPCR coexpression within a neuron class. Some neurons display a remarkably large number of GPCRs. The ASI neuron displays the most csGPCR genes at 99, followed by many distinct types of nociceptive neurons. While csGPCRs have been found for all but two sensory neurons (URY and ADE), there is a striking disparity in the number of csGPCRs coexpressed in sensory neuron types. Amphid sensory neurons clearly coexpress the largest number of GPCRs, while other sensory neurons express many fewer csGPCRs. The nociceptive ADL stands out in the list of amphid neurons, as it is the neuron expressing the most single-neuron specific GPCR reporters.

Expression in sensory and non-sensory neuron classes. While expression of csGPCRs clearly predominates in sensory neurons, they are also expressed in inter- and motorneurons and in a diverse set of non-neuronal cells. In most cases, each GPCR is restrictively expressed, suggesting that many different cell types in an organism show very distinct and cell-type specific responses, likely to internal signals. The similarity of one GPCR family, the *srw* family, to peptide receptors of other animal species provides hints to the

nature of these ligands [11, 29]. The expression of many members of the *srr* family in pharyngeal tissues suggests another source of ligands; perhaps these receptors respond to cues from ingested bacteria. In vertebrates, chemosensory GPCRs are now also becoming increasingly appreciated as being expressed in non-neuronal cells [6].

Polymodality of sensory neurons. csGPCRs were detected in sensory neurons that are known to express distinct types of sensory receptors and engage in non-chemosensory behavior, *e.g.,* in gas-sensing neurons or different types of mechanosensory neurons. The expression of csGPCRs in these neuron classes may hint toward these neurons perceiving different sensory inputs, *i.e.,* they are likely polymodal. However, as discussed above, csGPCRs expressed in these neurons may not be involved in detecting external sensory cues, but measuring internal states.

Absence of gene family themes. The absence of any overarching expression theme within gene families is striking. We did not observe that the expression of family members clusters in specific neuron types or share any other specific expression features. Specifically: (a) left/right asymmetrically expressed csGPCRs in the AWC neurons do not fall into the same family; (b) csGPCR reporters that are differentially regulated in larval stages or in the dauer stage do not come from a single family; (c) GPCRs that share specific expression pattern themes (*e.g.,* coexpression in the nociceptive ASH, PHA and PHB neurons) do not derive from specific families; (d) non-sensory neuron-expressed or non-neuronal expressed GPCRs do not fall into a specific family. The only glimpse of perhaps some common function is observed in the small *srr* family (9 genes), half of which appear to be expressed in non-neuronal pharyngeal tissue. An important note of caution is that these conclusions are based only on reporter genes. However, the substantial sample size on which these conclusions are based lends some credence to these conclusions.

Combinatorial complexity. GPCRs generally act as homo- or heterodimers [71], thereby hugely increasing the amount of distinct sensory receptor complexes expressed in a cell. This combinatorial activity also makes prediction of function of a given GPCR very difficult in that a GPCR may have one function expressed in one cell (in combination with another GPCR), while it may have a very different function in another cell (in combination with yet another GPCR).

Left/right asymmetric csGPCR expression patterns. While we recovered novel

csGPCR genes expressed in a left/right asymmetric manner in the AWC neuron pair, we were surprised to find no other obvious left/right asymmetries in other sensory neuron pairs. Of course such asymmetries may still be found with currently not analyzed GPCR genes, but the number of AWC asymmetries recovered suggest that AWC neurons may be exceptional in their extent of lateralization.

The only other asymmetry that we found revealed itself not in a sensory, but an interneuron and only in an non-anticipated context. The *sri-9* reporter transgene becomes induced in dauer animals in PVPL, but not PVPR, and PVPL expression is retained in postdauer animals. Molecular asymmetries in PVP neurons have not previously been reported but can perhaps be inferred by the fact that PVPL and PVPR are innervated in a left/right asymmetric manner by unilateral neurons. Specifically, PVPL, but not PVPR, is innervated by the unilateral DVB neuron. Perhaps *sri-9* may play a role in this synaptic signaling context, but why this should be dauer-specific is unclear.

Plasticity of csGPCR expression. One notable feature of our analysis was the extent of plasticity that csGPCR reporters show in the context of the dauer stage. Dauer animals are thought to remodel most tissue types and significantly alter behavioral patterns. Changes in csGPCR expression and hence changes in the external and internal signal perception fit very well into the mold of organismal plasticity and illustrate the plasticity of many different tissue types (note, for example, the changes in csGPCR expression in muscle). We find it particularly intriguing that several csGPCRs represent markers of life history. Some of the changes in GPCR reporter gene expression in dauers is retained in postdauer animals and some csGPCR reporters turn on only in postdauer animals. Animal-wide expression transcriptomic analysis has previously identified large cohorts of transcripts that, like our csGPCR reporters, serve as marker of dauer life history, i.e. transcript changse in dauers and these transcript changes persisting in post-dauer animals [72]. However, due to the whole animal nature of this analysis, this previous study lacked cellular resolution. Our findings add a novel spatial component to these previous findings, since we find the life history traits to be strikingly neuron-type specific. The expression of the TRP channel gene *osm-9* has also previously been shown to be modulated during dauer and postdauer stages in a neuron class-specific manner; in this case, *osm-9* expression is downregulate in the ADL (but not AWA) chemosensory neurons and the repression is retained post-dauer, using RNAi-and chromatin-based mechanisms [73]. In all except one case that we report here, we observe

the opposite post-dauer effect; reporters that are turned on in dauers, persist in non-dauers. The mechanistic basis of this may hence be distinct from the *osm-9* case.

It is important to remember here that the life history trait observations are based on transcriptional reporter genes which, on the one hand, may not accurately reflect expression of the endogenous locus, but, on the other hand, clearly provide a definitive molecular "read out" of changes in the "regulatory state" of specific neuron types, depending on whether they have passed through the dauer stage or not. Moreover our transcriptional reporter also argue that the life history regulatory phenomenon must be transcriptional in nature. These GPCR reporters will therefore provide excellent starting points to analyze the molecular mechanisms controlling this plasticity.

Future uses of the csGPCR expression map. The csGPCR reporter atlas can be put to a number of future uses. The sites of expression of specific csGPCRs point to potential functions of the csGCPRs, guiding the future analysis of csGPCR knockout strains – many available by knockout consortia or easily constructable by CRISPR/Cas9 technology. For example, csGPCRs expressed in the polymodal nociceptive ASH, ADL and phasmid neurons may be mediating the response to a number of distinct sensory cues processed by these neurons [56, 74].

csGPCR expression patterns point to perhaps unexpected cellular sites of internal signal perception that warrant further investigation. For example, the excretory canal cell expresses at least six csGPCRs reporters (considering that we only examined reporters for ~20% of GPCR loci, this number may increase several fold). The relevance of this expression could be tested through the excretory cell-specific expression of dominant negative versions of G-protein downstream signaling components. Similarly, the cellular dynamics in csGPCR expression patterns point to specific cells undergoing changes that warrant future characterization. For example, the induction or suppression of csGPCR reporter expression during the dauer stage in specific sensory and interneurons that were not previously associated with dauer-specific functions may warrant a closer examination of other molecular and functional changes of these neurons during the dauer stage.

Because csGPCR reporter fusions also link precisely delineated sequences (used for reporter construction) to specific cellular sites of gene expression, patterns of coexpression of GPCRs can be used to extract *cis*-regulatory information, which in turn may point to *trans*-

acting factors involved in controlling GPCR gene expression. A proof of principle for this type of analysis has already been conducted, pointing to a critical function of, for example, a bHLH factor in controlling csGPCR expression in the ADL nociceptive neuron [28] and with now substantially more expression information available can be further extended to additional cell types.

Lastly, GFP reporter transgenes have generally served as invaluable starting points for genetic mutant screens in which the genetic control of specific biological processes can be investigated. The GPCR reporter collection provides a multitude of entry points. For example, the postdauer expression of multiple reporter genes can be used to screen for mutants in which these life history traits fail to be properly expressed. GFP reporter genes have also served as invaluable cellular identity markers and here again the csGPCR reporter collection can be used to assess how the identity of specific cell types is genetically controlled.

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Table 1: The five classes of GPCRs in animal genomes and their representation in *C.elegans*. Modified from [10].

Class [1]	**Subclass** [1]	**Gene number in *C. elegans***
Rhodopsin (Class A)	chemosensory	1,341 [a]
	peptidergic	153 [b]
	aminergic	16
	muscarinic (ACh)	3
Secretin (Class B)		3
Glutamate receptor (Class C)		7
Adhesion		5
Frizzled/Tas2		4

[1] Classification after [5].
[a] Will likely also contain peptide receptors (see text).
[b] Defined by sequence homology to known neuropeptide receptors [10].

Table 2: Overview of GPCR reporters and expression

Classification [a]		Gene counts		Reporters	Overview of expression		
Super-family	**Family**	**Old count [a]**	**New count [b]**	**Total # examined reporters [c]**	**Neurons only**	**Neurons + non-neuron**	**Non-neuron only**
Str	*srh*	218	223	43 (14)	24	16	3
	str	197 *	196 *	42 (16)	21	16	5
	sri	61	60	21 (7)	11	8	2
	srd	64	67	13 (6)	10	2	1
	srj	39	39	14 (1)	7	6	1
	srm	5	6	6 (-)	3	3	-
	srn	1	1	1 (-)	1	-	-
	all Str	585	591	140 (44)	77	51	12
Sra	*sre*	51	53	31 (20)	13	13	5
	sra	32	35	22 (11)	15	6	1
	srab	22	23	18 (6)	10	7	-
	srb	14	16	10 (4)	4	4	2
	all Sra	119	127	81 (41)	42	30	8
Srg	*srx*	98	105	20 (6)	12	7	1
	srt	61	67	16 (6)	13	2	1
	srg	59	61	23 (9)	15	7	1
	sru	41	40	12 (5)	6	6	-
	srv	30	30	12 (1)	10	2	-
	srxa	17	17	8 (4)	6	1	1
	all Srg	306	320	91 (31)	62	25	4
Solo	*srw*	99	115	11 (7)	8	1	2
Solo	*srz*	71	68	23 (1)	15	5	3
Solo	*srbc*	73	72	5 (2)	4	1	-
Solo	*srsx*	37	37	14 (4)	11	2	1
Solo	*srr*	10	9	9 (-)	4	5	1
Solo	*sro*	1	1	1 (1)	1	-	-
Totals:		1277	1341	375 (131)	224	120	31

Only sensory-type GPCRs are shown, other GPCR systems (hormone, neurotransmitter systems) are not. See text.
Numbers in parenthesis indicate previously described reporters extracted from Wormbase.
Footnotes:
[a] Based on Thomas and Robertson [7, 11], with the exception of *sro-1* which was published elsewhere [2]. Pseudogenes are excluded.
[b] New counts extracted from WS246 (some previous pseudogenes have become real genes and vice versa).
[c] Summarized in Table. S1
* Includes *odr-10*.

Table 3: Non-sensory neurons expressing GPCR reporter

		CLASS	REPORTER GENES
INTERNEURONS	Head	ADA	*srab-12*, ***sri-1***
		AIA	*sra-11, srab-4, (**srh-269**)*
		AIB	***srh-11***
		AIM	***srg-32***, ***srg-58***, ***srxa-14***
		AIN	***srg-14***, ***srh-277***
		AIY	*sra-11*, ***srab-3***, ***sri-1***, ***sri-12***, ***sri-36***, ***srx-14***, ***str-102***
		AUA	*sre-4*
		AVB	*sra-11*
		AVD	***srg-32***
		AVE	***srab-24***
		AVG	***srm-1***, *(**srsx-12**)*
		RIF	***sra-11***, ***srab-3***, *(**srh-266**)*
		RIG	***sre-4***
		RIH	*(**srm-5**)*, *(**srm-6**)*
		RIS	***srd-32***, ***srg-14***
		SAA	***srx-3***
	Midbody	BDU	***srab-8***, *srab-12*, ***sre-4***, ***sri-1***, ***sri-18***, ***srv-27***
		CAN	***srb-16***, ***srd-32***, ***srv-1***
		SDQ	*srab-12*
	Tail	DVA	***srd-32***, ***srx-113***
		DVC	*srab-4*
		LUA	*srab-12*
		PVP	*srab-12*
		PVQ	*sra-6*, ***sre-4***, ***srg-32***, ***srh-277***, ***sri-1***, *(**sru-17**)*, ***srv-32***, ***str-84***
		PVR	*sre-4*
		PVT	***sra-11***, ***sra-28***, *srab-4*, ***srb-7***, ***srb-16***, ***srbc-52***, ***srd-32***, *sre-11*, ***sre-22***, *sre-30*, ***sre-52***, ***srg-4***, ***srg-14***, ***srg-31***, ***srg-39***, ***srh-4***, ***srh-5***, ***srh-11***, ***srh-62***, ***srh-71***, ***srh-210***, ***srh-241***, ***srh-266***, ***sri-12***, ***sri-36***, ***sri-39***, ***sri-62***, ***srj-5***, ***srj-20***, ***srj-27***, ***srj-38***, ***srr-2***, ***srr-7***, ***srr-8***, ***srsx-12***, ***srsx-38***, ***sru-8***, ***sru-48***, ***srx-10***, ***srx-17***, ***srxa-7***, ***srz-13***, ***srz-27***, ***srz-54***, ***srz-102***, ***srz-104***, ***str-31***, ***str-52***, ***str-123***, ***str-143***, ***str-178***, ***str-217***, ***str-233***, ***str-236***, ***str-247***, ***str-249***, ***str-250***
MOTORNEURONS	Head	AVL	***srd-32***
		RID	***sra-14***, ***srab-3***, *srab-4*, ***sre-4***
		RMD	*(**sri-21**)*
		RMDD	***srr-3***
		RMDV	***srr-3***
		RME	*srab-4*, ***srg-14***
		RMG	*srab-12*
		SMD	***srx-3***
		SIA	*sro-1*
	Midbody	HSN	***sra-35***, ***srab-8***, ***srj-13***
	VNC	DA	***sra-36*** [DA8, DA9], ***srb-16*** [DA9], ***srd-4*** [DA9]
		DB	***srx-3***
		DD	***srsx-30***
		VA	*srab-4*, ***sra-36*** [VA11]
		VB	*srab-4*, ***srx-3***
		VC	*sra-11*, ***srb-16***
		VD	***srsx-30***
	Tail	PDA	***srx-3***

Bolded gene: newly identified in this paper**.** Non-bolded gene: previously identified. (Gene in parenthesis): ID based on position and morphology, not confirmed with neuron-specific reporter.

Table 4: Non-neuronal sites of GPCR reporter expression

TISSUE / CELL	REPORTER GENES
Coelomocytes	***srh-193***, ***srh-269***, ***srj-4***, ***str-250***
Excretory system[1]	*srab-14*, ***srm-3***, ***srr-4***, *srr-6*, ***srr-8***, *srv-1*, ***str-143***, ***str-148***
Glia	***srab-8***, ***srh-270***, ***srr-1***, ***srsx-30***, ***sru-2***, *sru-19*, *srw-29*, ***srw-145***, *str-47*
Gonad	*srbc-58*, ***srd-32***, *sre-24*, *srh-87*
Gut[2]	***srb-17***, ***srh-211***, ***srm-3***
Head mesodermal cell	***srb-16***, ***srd-32***, *srh-132*, ***srh-210***, ***srh-269***, ***srr-3***, ***srx-1***
Hypodermis	*sra-13*, *sra-39*, *srab-6*, *srab-13*, *srab-21*, *srbc-58*, *srd-39*, ***sre-7***, *sre-21*, *sre-22*, *sre-29*, *sre-53*, ***srh-76***, ***srr-4***, *sru-31*, *srw-108*, ***srw-118***, *srz-13*, *srz-94*, ***srz-99***, ***str-31***, *str-168*, ***str-250***
Muscle	*sra-2*, *sra-13*, ***srab-7***, ***srb-17***, *srbc-58*, ***srd-15***, ***srd-32***, ***sre-22***, *sre-29*, *srg-7*, ***srg-29***, ***srg-31***, ***srh-11***, ***srh-100***, *sri-19*, ***srr-3***, *srt-20*, ***sru-1***, ***srx-1***, *srx-41*, *srxa-2*, ***srz-94***, ***str-102***, *str-111*, ***str-114***
Pharynx	***sra-4***, *sra-10*, *sra-38*, *srb-6*, *srb-16*, *srbc-58*, *srd-15*, ***srd-32***, ***srg-29***, ***srg-31***, ***srg-39***, *srg-62*, ***srh-7***, ***srh-62***, ***srh-71***, *srh-92*, ***srh-100***, ***srh-142***, ***srh-201***, ***srh-210***, ***srh-269***, ***sri-5***, ***sri-36***, ***srj-4***, ***srj-5***, ***srj-13***, ***srj-38***, ***srm-1***, ***srm-3***, ***srr-1***, ***srr-2***, ***srr-3***, ***srr-4***, *srr-6*, ***srt-65***, ***sru-1***, *sru-31*, ***srv-17***, ***srx-10***, ***srz-54***, ***str-52***, ***str-85***, *str-108*, ***str-121***, ***str-123***, ***str-143***, ***str-236***, ***str-247***, ***str-250***
Rectal epithelium	*srbc-58*, ***srx-4***, ***str-31***, ***str-233***, ***str-250***
Seam cells	*sra-13*, ***srb-17***, *srbc-58*, *srd-39*, ***srh-130***, ***srh-266***, ***srj-20***, *srz-14*, ***str-31***, ***str-148***
Vulva	*sra-13*, ***srab-7***, *srab-13*, *srb-16*, ***srb-17***, *srbc-58*, *sre-56*, ***srh-11***, ***srh-130***, ***srh-210***, ***srh-270***, ***sri-5***, *sri-19*, ***srj-13***, ***srr-4***, ***srsx-12***, ***srx-1***, ***srx-4***, ***srz-102***, ***str-31***, ***str-52***, ***str-114***, ***str-247***, ***str-262***

Bolded gene: newly identified in this paper**.** Non-bolded gene: previously identified and retrieved from Wormbase.
See S1 Table for further details about specific sites of expression.
[1] The two str genes are in the excretory pore and duct cells, all others are in the excretory canal cell.
[2] Transcriptional gfp reporters often show posterior gut expression, which is considered an artifact. Only reporters showing bright expression throughout the gut are listed here. Previously described reporters with annotated gut expression in Wormbase are not included here.

Table 5: Changes in GPCR reporter expression in starvation-induced dauers, within and outside the nervous system. Reporter gene expression patterns were analyzed in starvation-induced dauers. Previously reported GPCR reporter changes are listed in the two bottom rows of the Table [34]. For the *srh-71* reporter, we also observe non-robust expression in a non-phasmid pair whose identity we have not determined.

Type of change	Reporter Gene	Reporter expression			Postdauer recovery		
		Constitutive expression in all stage (in dauer and non-dauer, fed L3 neurons and post-dauer)	**Cells only show expression in dauers**	**Constitutively expressed in fed animals only, i.e. downregulated specifically in dauers in respective cell**	**Recovers**	**Dauer pattern is retained post-dauer**	**Entirely new post-dauer expression**
dauer gains (type I)	***sri-9***	ADL	NSM (dim), OLL, AWC, AIM, AIZ, ADA, PDB, PVPL		NSM, OLL, AWC, AIM, AIZ, ADA turn off again	PVPL remains on, PDB occasionally on	none
	srh-15	ASH, PHA	ASK		recovers to fed condition	none	none
	str-114	ASH,ASI,PHA,head muscle	ASK, ASG		recovers to fed condition	none	none
	sra-25	ASH, ASI, BAG (dim)	ADL, PHB		PHB turn off again	ADL remains on, BAG becomes bright and stable	ASJ (dim)
	str-84	ASH, ASI,PHA,PHB,PVQ	Body wall muscle		recovers to fed condition	none	none
	srg-32	AVD, AIM,PVQ	Excretory cell		recovers to fed condition	none	none
dauer losses (type II)	***sre-43***	ADL, PHB (dim in dauers)		AWB, ASJ (variable), PHA	AWB, PHA turn on again	ASJ become stable	ASH (dim)
	srh-279	ADL		ADL down (but not off) in dauers	recovers to fed condition	none	none
	srz-67	ADL		ADL down (but not off) in dauers	recovers to fed condition	none	none
	srx-12			ADF, amphid sheath glia	recovers to fed condition	none	none
	sra-7			ASK down (but not off) in dauers. F and U rectal epithelial cells off	recovers to fed condition	none	none
both gains and losses (type III)	***srm-4***	ASH, PHB,ADL (dim)	ADL(bright), ALA	BAG	recovers to fed condition	none	none
	srx-4	ASK, ASI	ADL	B and Y rectal epithelial cells	recovers to fed condition	ADL expression partially remains	none
	srh-71	ASK, ASG,ASI (dim),IL2D/V	ASI (brighter), AIZ, two ventral ganglion MN pairs	IL2L/R, PHA	PHA expression comes back to fed state	ASI, AIZ, two ventral ganglion MN pairs remain on, IL2L/R remains off	pharyngeal gland cells (ventral g1)
	srsx-29	ADF	ASH	PHA	recovers to fed condition	none	none
	sru-12	ASI, ASH, ASJ,OLL,PHB	PVQ	IL2, PHA	IL2, PHA turn on again	PVQ remains on	PLN
Peckol et al. 2001	***srd-1***			ASI	recovers to fed condition	none	none
	str-2	ASI (dim)	ASI (brighter)	AWC	recovers to fed condition	none	none

FIGURE LEGENDS

Fig 1. Summary of GPCR reporter expression patterns.
(A) Overall tissue distribution of reporter expression patterns. Pie chart showing percentage of GPCR reporters expressed exclusively in neurons, in neurons and other cells types and exclusively in non-neuronal tissues. Numbers in parenthesis represent the absolute number of reporters in each category.
(B) Extent of reporter expression within the nervous system. Pie chart showing percentage of neuronal reporters expressed in 1 neuron pair, 2 pairs, 3-4 pairs, 5-10 pairs or more than 10 pairs. Numbers in parenthesis represent the absolute number of reporters in each category.
(C) Distribution of reporter gene expression within the nervous system. Pie charts showing percentage of GPCR reporters expressed in amphid neurons, phasmid neurons, other sensory neurons and inter- or motorneurons. Small pie charts on the upper right represent the percentage of reporters exclusively expressed in amphids, phasmids, other sensory neurons and inter- or motorneurons. Numbers in parenthesis show the absolute number of reporters in each category.
(D) Distribution within all sensory neurons. Worm schematics showing the absolute number of GPCR reporters found to be expressed in each sensory neuron type. PHC is a phasmid neuron by name only ("PH"). See **Table S2** for a list of GPCR gene names expressed in the sensory neurons shown here.

Fig 2. GPCR reporters expressed in single sensory neuron classes.
(A) Table showing all GPCR reporters expressed in a single neuron class. Genes in bold are newly identified in this paper. Genes in non-bold were previously described (data extracted from www.wormbase.org). ***** Reporter is also expressed in some non-neuronal tissue (for details see **S1 Table**). [1] N. Masoudi, S. Finkelstein and O. Hobert, in preparation.
(B) Representative examples of reporters expressed in a single neuron class identified in this study. Scale bars, 10μm.

Fig 3. GPCR reporters expressed in non-amphid/non-phasmid sensory neurons, interneurons and motorneurons.
Examples of GPCR reporters expressed in sensory neurons that are not amphids or phasmids (white font), interneurons (orange font) and motorneurons (blue font). Most examples represented here are from neurons classes that were not previously shown to express any sensory GPCR. Amphid neurons are shown in parenthesis. All scale bars,10μm, except *srsx-30* which is 30μm. See **Table 3** for a complete summary of GPCR reporters expressed in inter- and motorneurons.

Fig 4. The only coexpression association of GPCR reporters is in nociceptive neurons.
(A,B) Graphical representation of ASH, PHA and PHB co-expression. Green-filled square indicates expression. An asterisk denotes that the gene is exclusively expressed in the indicated neurons. Venn diagram was created with eulerAPE [57].
(C) Hierarchical clustering of neurons by GPCR reporter expression. Red lines show the well-supported ASH, PHA and PHB cluster (AU>95). AU: approximately unbiased p-value (percent), BP: Bootstrap Probability value (percent).
(D) Examples of reporter gene expression profiles in ASH/PHA/PHB. Scale bars, 10μm.

Fig 5. Lateralized GPCR reporter expression in the AWC neuron pair.
(A) Asymmetrically expressed GPCRs, indicated with arrowheads (top row), were all expressed in AWC as assessed by colocalization with the *ceh-36p::RFP* reporter (middle row). *str-130*, *srd-5*, *srx-1*, *srsx-5* and *srsx-37* reporters were expressed in AWC^{OFF} while *srt-7* was expressed in AWC^{ON} as assessed with the *str-2p::NLS::RFP* reporter which is an AWC^{ON} marker (bottom row). All pictures are dorso-ventral views unless otherwise indicated. *srt-13* and *srr-9* reporters were also found to be asymmetrically expressed in AWC, however since these reporters were dim and not very robust no further analysis was done. Scale bars, 10μm.
(B) AWC asymmetry. Previously known components of genetic pathways that control AWC asymmetries. Not all genes known to be involved are shown. Black and grey gene names indicate whether a gene is more active or more expressed (black) in one neuron compared with the other neuron. Scheme adapted from [63].
(C) Expression of the newly found AWC asymmetric GPCRs is regulated by previously described mechanisms. Representative pictures showing *srx-1* reporter expression (AWC^{OFF}) in different mutants of the previously described AWC asymmetry pathway. As expected, in *unc-43(n1186lf)* mutants, *srx-1* reporter is expressed in none of the AWC neurons (2 AWC^{ON} phenotype) while in *unc-43(n498gf)* and *nsy-5(ky634)* mutants *srx-1* is expressed in both AWC neurons (2 AWC^{OFF} phenotype). Scale bars, 10μm.
(D) Expression quantification of AWC asymmetric GPCR reporters in *unc-43(n1186lf)*, *unc-43(n498gf)* and *nsy-5(ky634)* mutants. Animals were scored as young adults and show the expected 2 AWC^{ON} or 2AWC^{OFF} phenotype. Between 20 and 40 animals were scored per genotype.

Fig 6. Expression of sex-specifically expressed GPCR reporters.
Examples of GPCR reporters expressed in hermaphrodite-specific (VCs, HSN) or male-specific neurons (CEMs, CP5, CP6, Rays). All scale bars,10μm, except *srb-16* which is 30μm.

Fig 7. Expression of non-neuronal GPCR reporters.
Examples of GPCR reporters expressed in different types of non-neuronal tissue. Scale bars, 10μm. See Table 4 for a complete summary of GPCR reporters expressed in non-neuronal tissues.

Fig 8. Reporter analysis of entire GPCR families.
Genomic loci, reporter scheme and gfp expression images for the *srm* **(A)**, *srr* **(B)** and *srn* **(C)** GPCR gene families. Only reporters expressed in the pharynx are shown for the *srr* family. Scale bars, 10μm.

Fig 9. Temporal regulation of GPCR reporters.
GFP images showing temporal expression changes (L1 versus young adult) of *srh-11*, *sru-48* and *sra-28* reporter genes. Neurons showing temporal changes in expression are outlined with red dotted lines. Scale bars, 10μm.

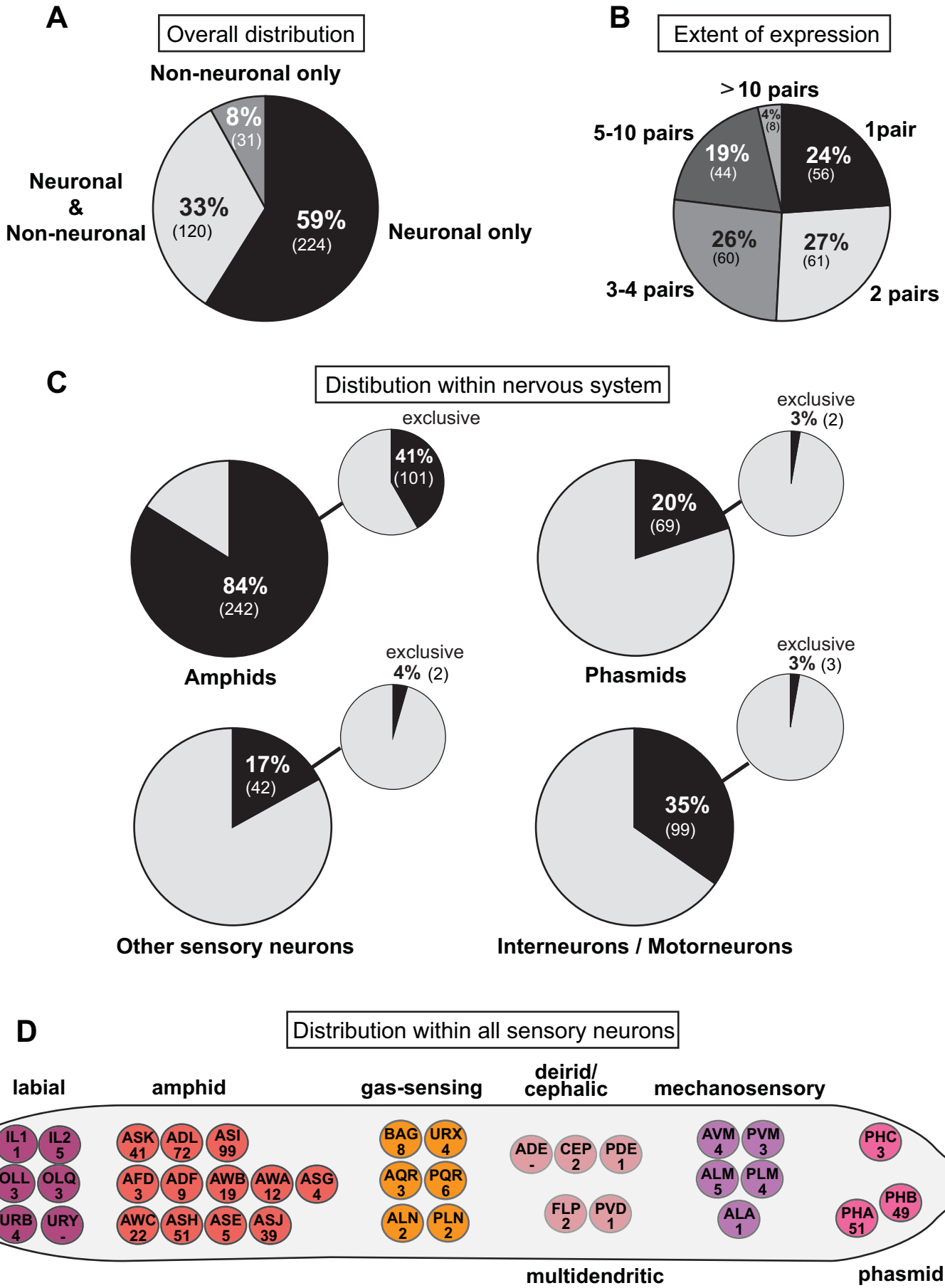
Fig 10. Examples of environment-induced changes in GPCR expression.
Examples of GPCR reporters that change expression in dauer. Designations of neuron types that change expression are highlighted in red. Asterisk indicates posterior gut autofluorescence. Insets for *srh-71*, *sre-43* and *srm-4* show enlarged and overexposed

images of cells that are too dim to be discernable in main panels. See Table 5 for a complete summary of GPCR expression changes in dauer. Scale bars, 10μm.

Fig 11. GPCR expression patterns as life history traits. Comparison of GPCR expression in 1-day old adult animals that either did pass through the dauer state (right panels) or did not (age-matched fed controls; left panels). Postdauer animals were in the dauer stage for 5-7 days. Designations of neuron types that retain dauer-specific expression or acquire postdauer-specific expression are highlighted in red. Inset for *sre-43* shows enlarged and overexposed images of cells that are too dim to be clearly discernable in the main panel. See Table 5 for a complete summary of GPCR expression changes in postdauer. Scale bars, 10μm.

Fig 12. GPCR reporter expression in starved L1 animals.
Examples of GPCR reporter expression in starved L1 worms. Eggs isolated by bleach treatment were allowed to hatch and were kept in M9 for 48 h. Designations of neuron types that change expression compared to fed L1 worms are highlighted in red. Scale bars, 10μm.

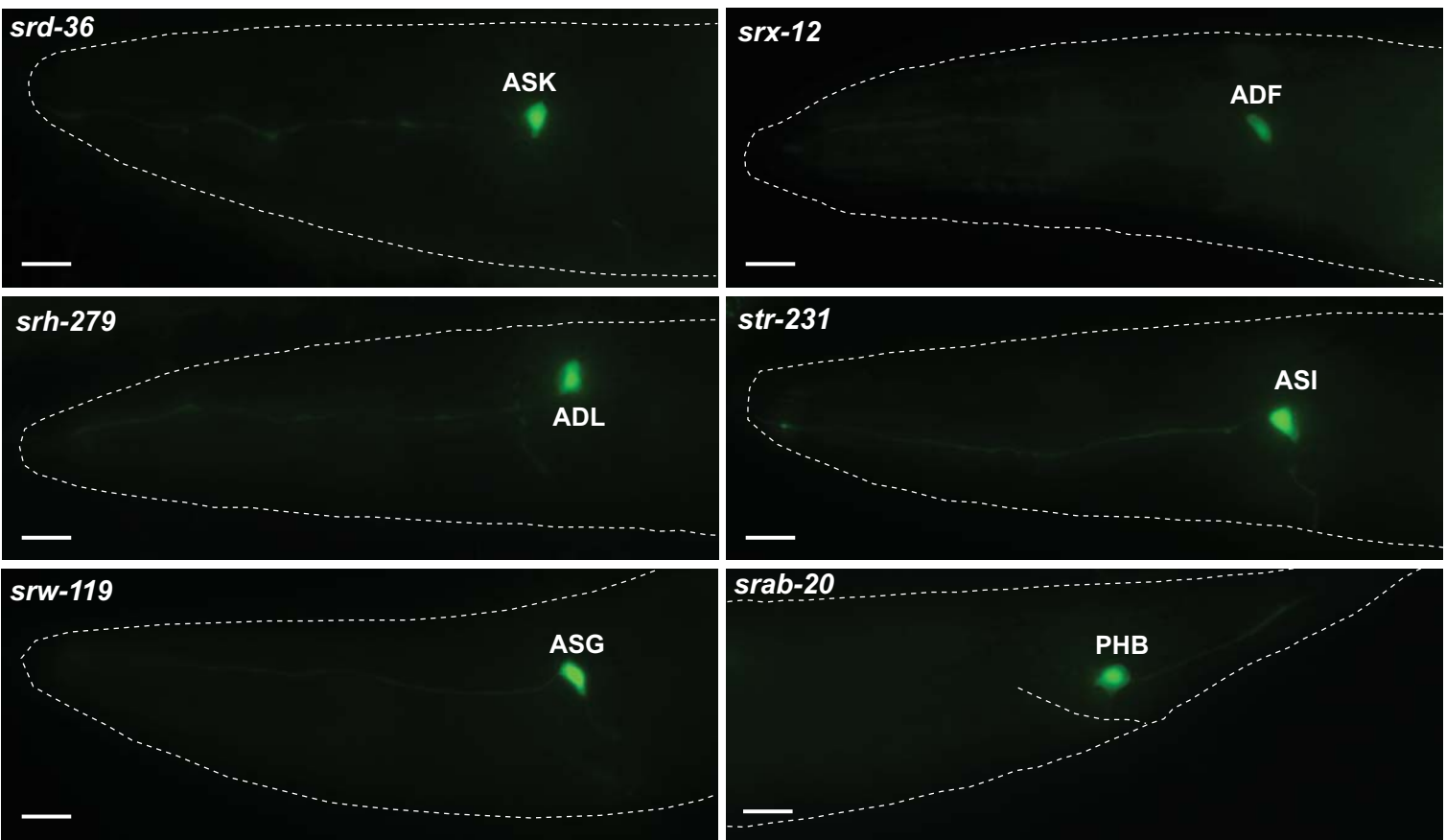
Figure 1

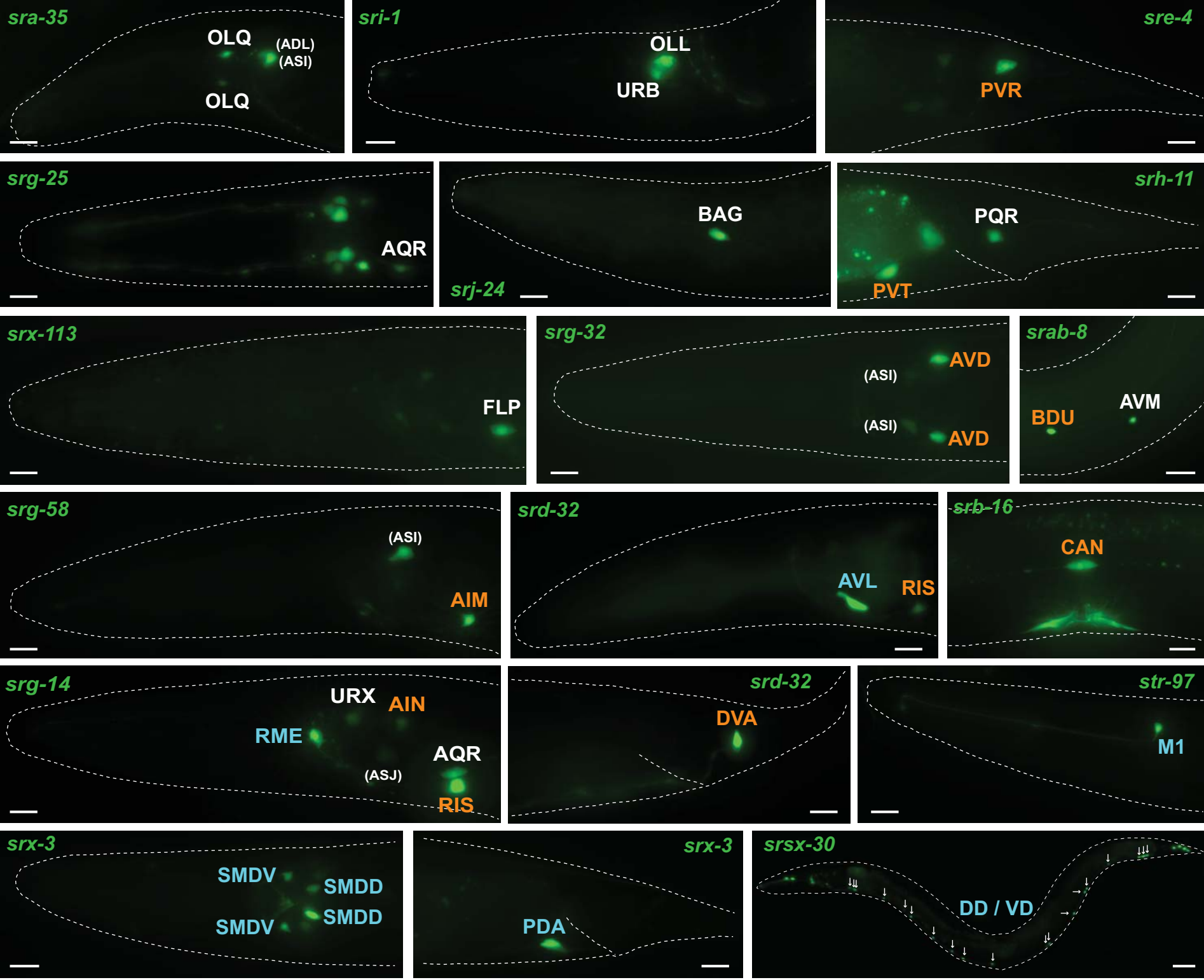

A
Overall distribution
Non-neuronal only
8%
(31)
Neuronal
&
Non-neuronal
33%
(120)
59%
(224)
Neuronal only
B
Extent of expression
>10 pairs
4%
(8)
5-10 pairs
19%
(44)
1pair
24%
(56)
26%
(60)
27%
(61)
3-4 pairs
2 pairs
C
Distibution within nervous system
exclusive
41%
(101)
84%
(242)
Amphids
exclusive
3% (2)
20%
(69)
Phasmids
exclusive
4% (2)
17%
(42)
Other sensory neurons
exclusive
3% (3)
35%
(99)
Interneurons / Motorneurons
D
Distribution within all sensory neurons
labial
amphid
gas-sensing
deirid/
cephalic
mechanosensory
IL1 1
IL2 5
OLL 3
OLQ 3
URB 4
URY -
ASK 41
ADL 72
ASI 99
AFD 3
ADF 9
AWB 19
AWA 12
ASG 4
AWC 22
ASH 51
ASE 5
ASJ 39
BAG 8
URX 4
AQR 3
PQR 6
ALN 2
PLN 2
ADE -
CEP 2
PDE 1
FLP 2
PVD 1
AVM 4
PVM 3
ALM 5
PLM 4
ALA 1
PHC 3
PHB 49
PHA 51
multidendritic
phasmid

A

ASK	*sra-7*, sra-9,* ***srb-5****, srbc-64, srbc-66,* ***srd-36****, srg-2, srg-8,* ***srw-108****,
ADL	***sre-21****, srh-25, srh-132*,* ***srh-193****,* ***srh-199****,* ***srh-279****, srh-281,* ***sri-9****,* ***sri-28****,* ***sri-45*[1]****,* ***sri-50[1]****, sri-51, sru-4,* ***srv-3****,* ***srv-4****,* ***srw-138****,* ***srz-4****, srz-6,* ***srz-28****,* ***srz-61*[1]****,* ***srz-67****,* ***srz-99****,* ***srz-103***
ASI	***sra-17****, srd-1, srg-47,* ***srj-23****, str-3****,* ***str-231***
AWA	*odr-10*
AWB	*srab-1, str-1, str-44, str-163*, str-220*
ASG	***srw-119***
ADF	***srx-12***
ASH	*srv-11*
PHB	***srab-20****,* ***srx-110***

B





Sensory neurons Interneurons Motorneurons

Figure 3

Figure 4

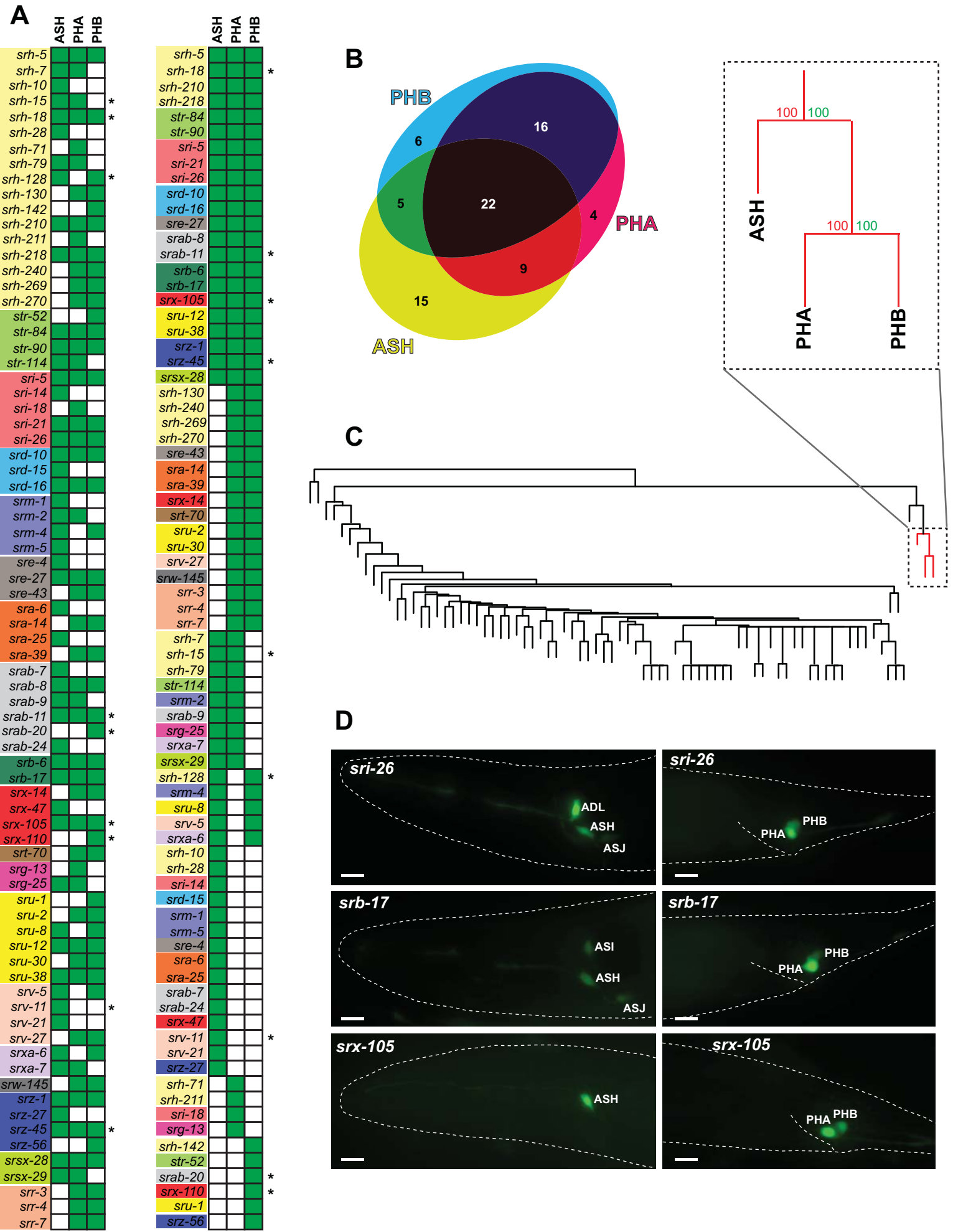
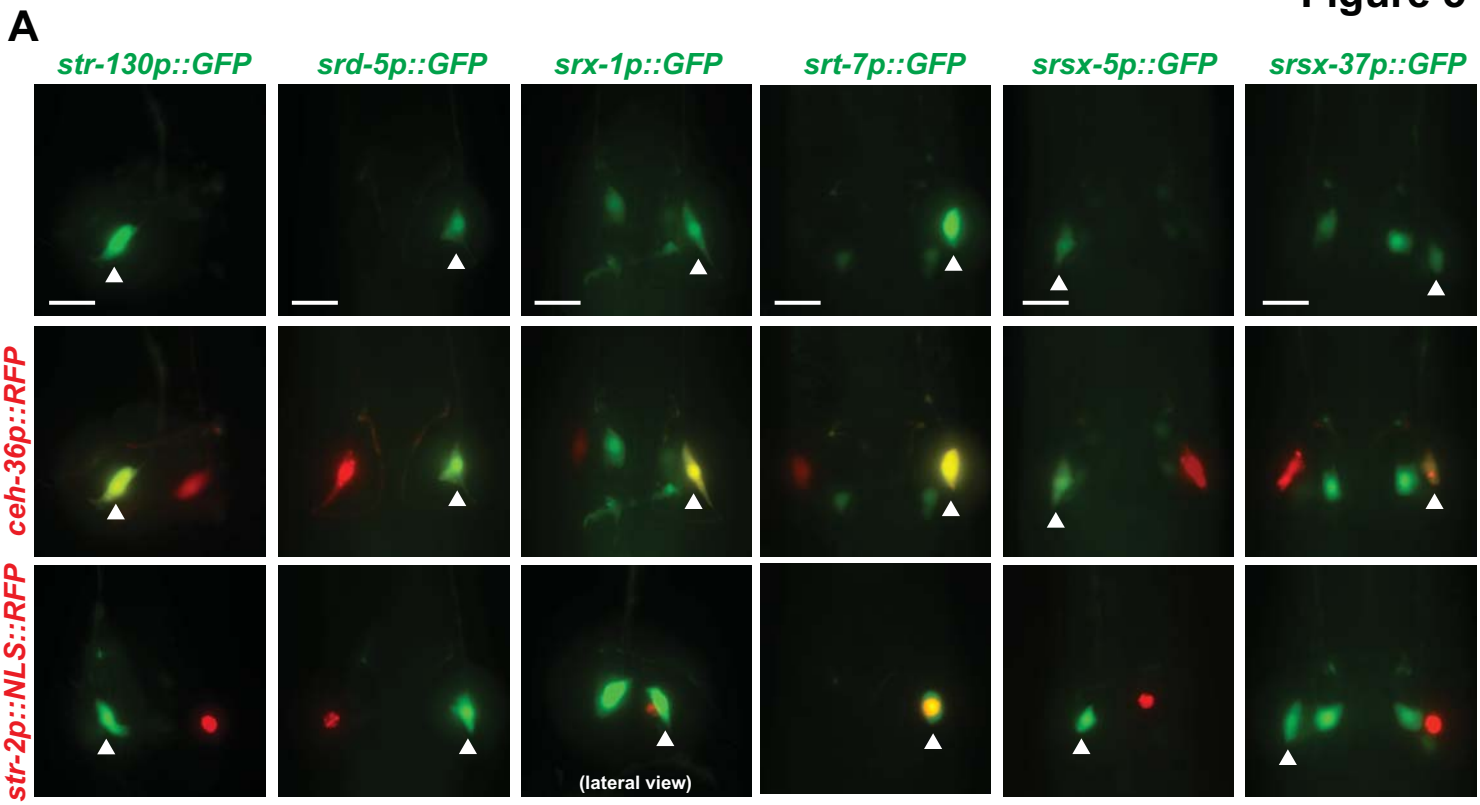
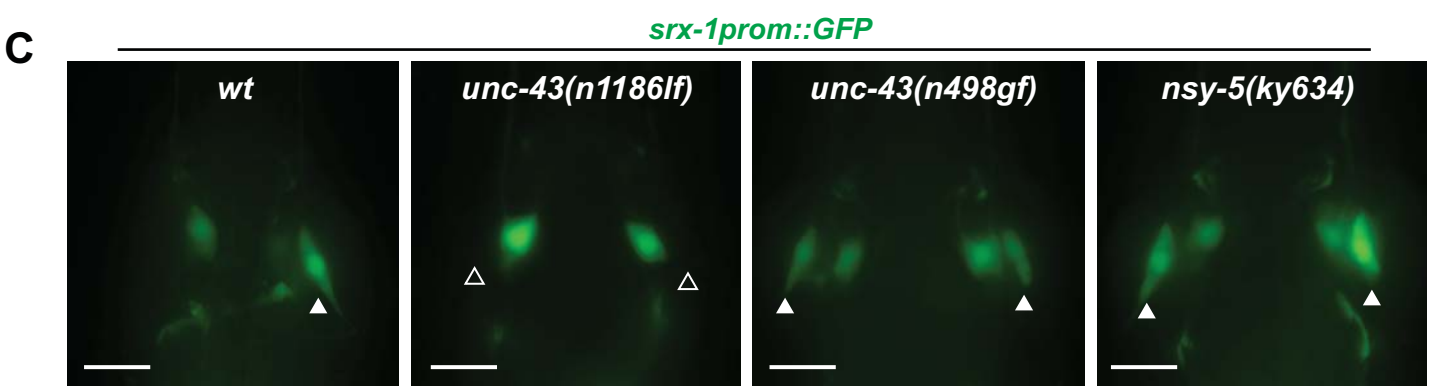
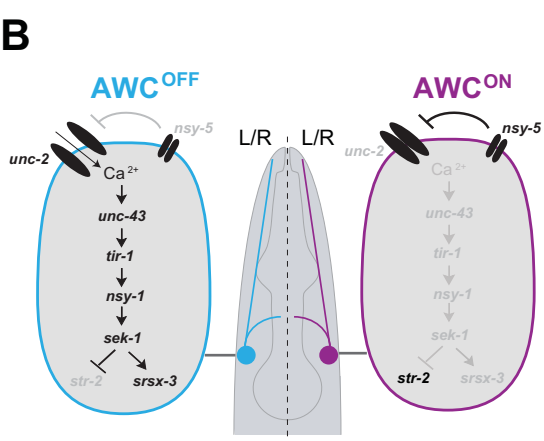


Figure 5







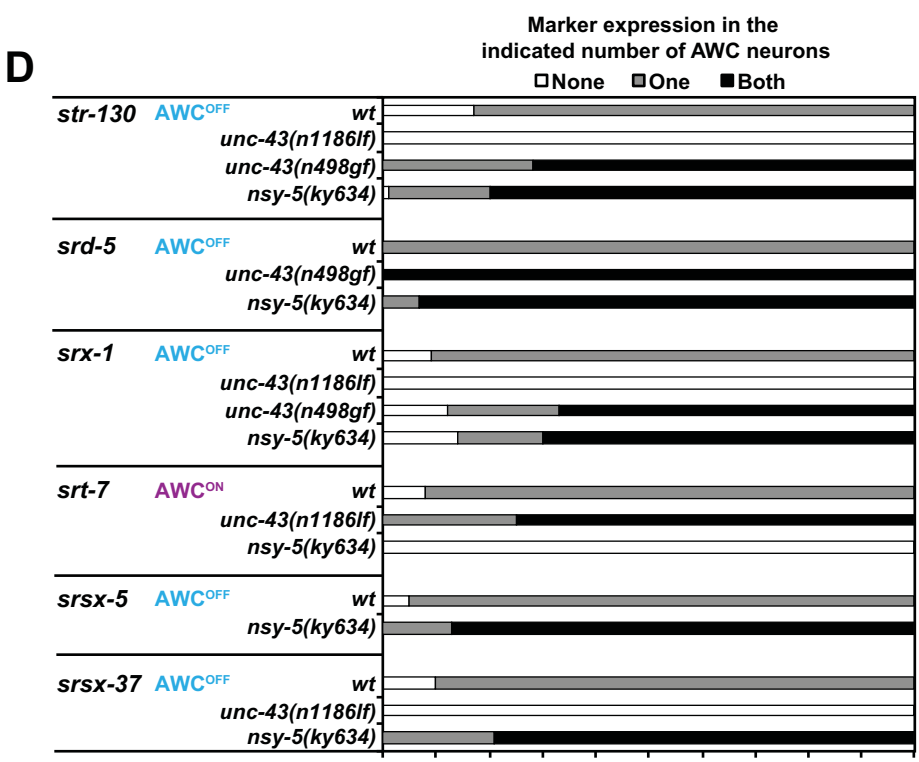


Figure 6

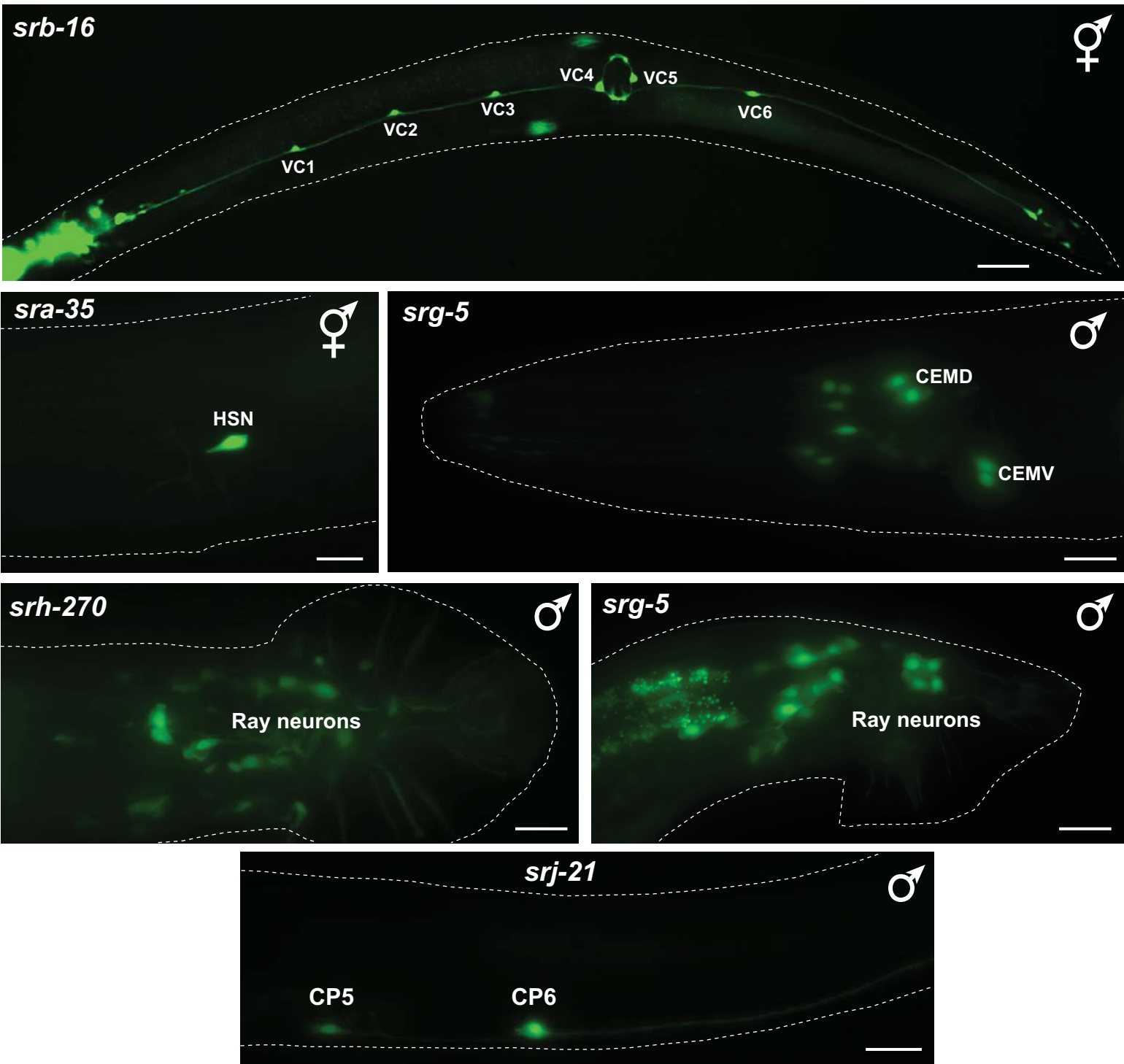
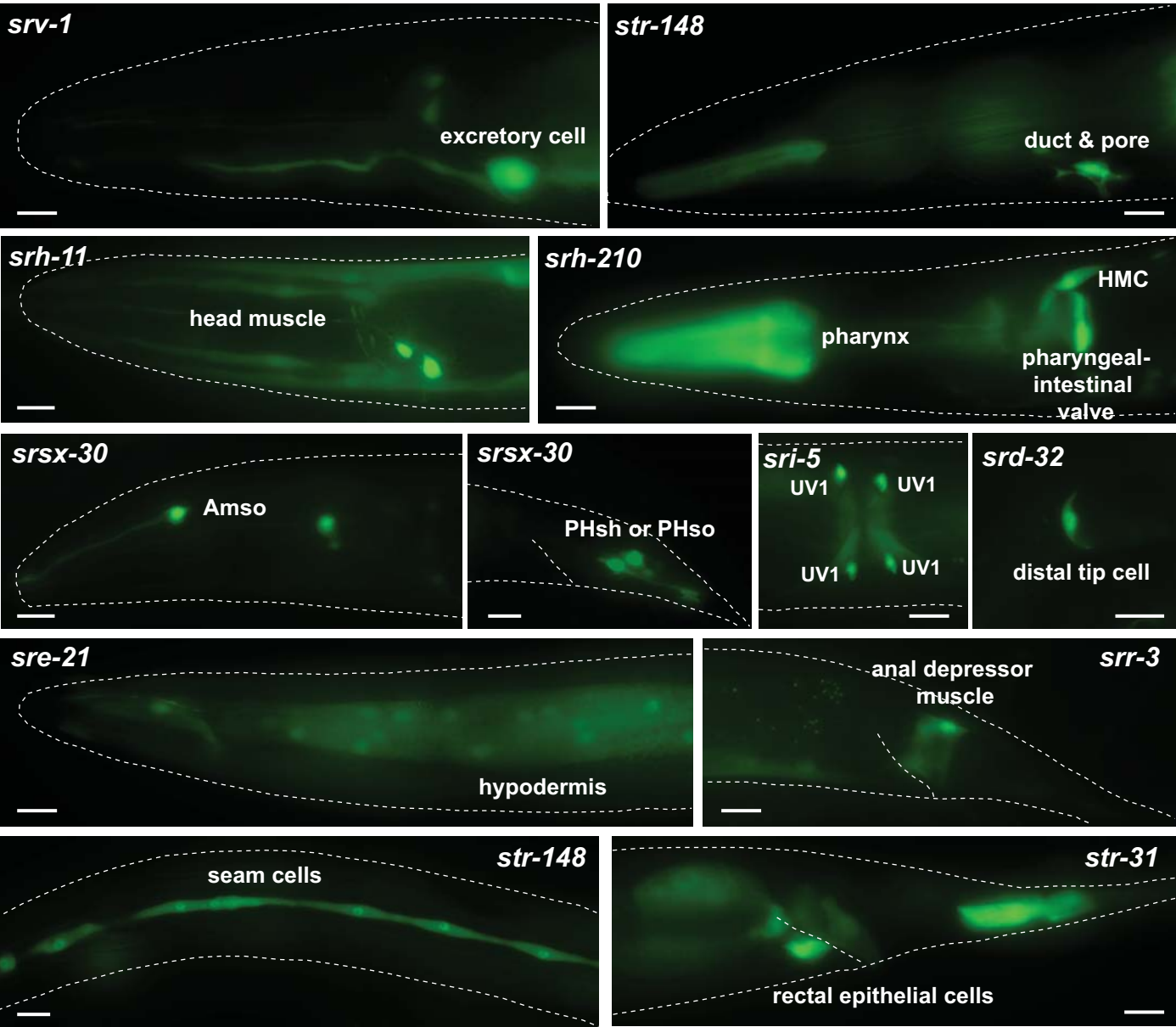

srb-16
VC1
VC2
VC3
VC4
VC5
VC6
sra-35
HSN
srg-5
CEMD
CEMV
srh-270
Ray neurons
srg-5
Ray neurons
srj-21
CP5
CP6

Figure 7


srv-1
excretory cell
str-148
duct & pore
srh-11
head muscle
srh-210
HMC
pharynx
pharyngeal-
intestinal
valve
srsx-30
Amso
srsx-30
PHsh or PHso
sri-5
UV1
UV1
UV1
UV1
srd-32
distal tip cell
sre-21
hypodermis
srr-3
anal depressor
muscle
str-148
seam cells
str-31
rectal epithelial cells

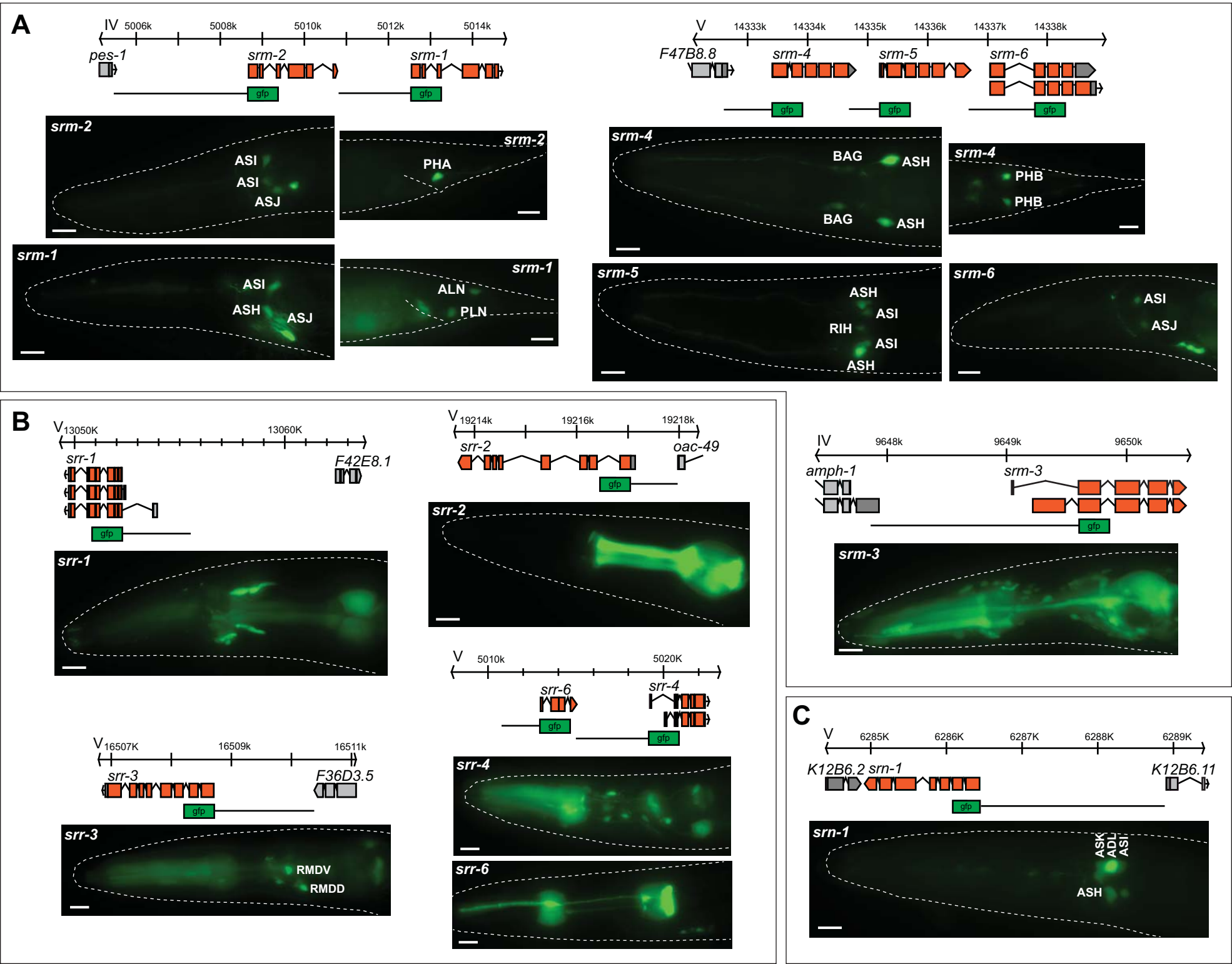

A
IV 5006k 5008k 5010k 5012k 5014k
pes-1
srm-2
srm-1
gfp
srm-2
ASI
ASI
ASJ
srm-2
PHA
srm-1
ASI
ASH
ASJ
srm-1
ALN
PLN
V 14333k 14334k 14335k 14336k 14337k 14338k
F47B8.8
srm-4
srm-5
srm-6
srm-4
BAG
ASH
BAG
ASH
srm-4
PHB
PHB
srm-5
ASH
ASI
RIH
ASI
ASH
srm-6
ASI
ASJ
B
V 13050K 13060K
srr-1
F42E8.1
srr-1
V 19214k 19216k 19218k
srr-2
oac-49
srr-2
V 5010k 5020K
srr-6
srr-4
srr-4
srr-6
V 16507K 16509k 16511k
srr-3
F36D3.5
srr-3
RMDV
RMDD
IV 9648k 9649k 9650k
amph-1
srm-3
srm-3
C
V 6285K 6286K 6287K 6288K 6289K
K12B6.2 srn-1
K12B6.11
srn-1
ASK
ADL
ASI
ASH

Figure 9

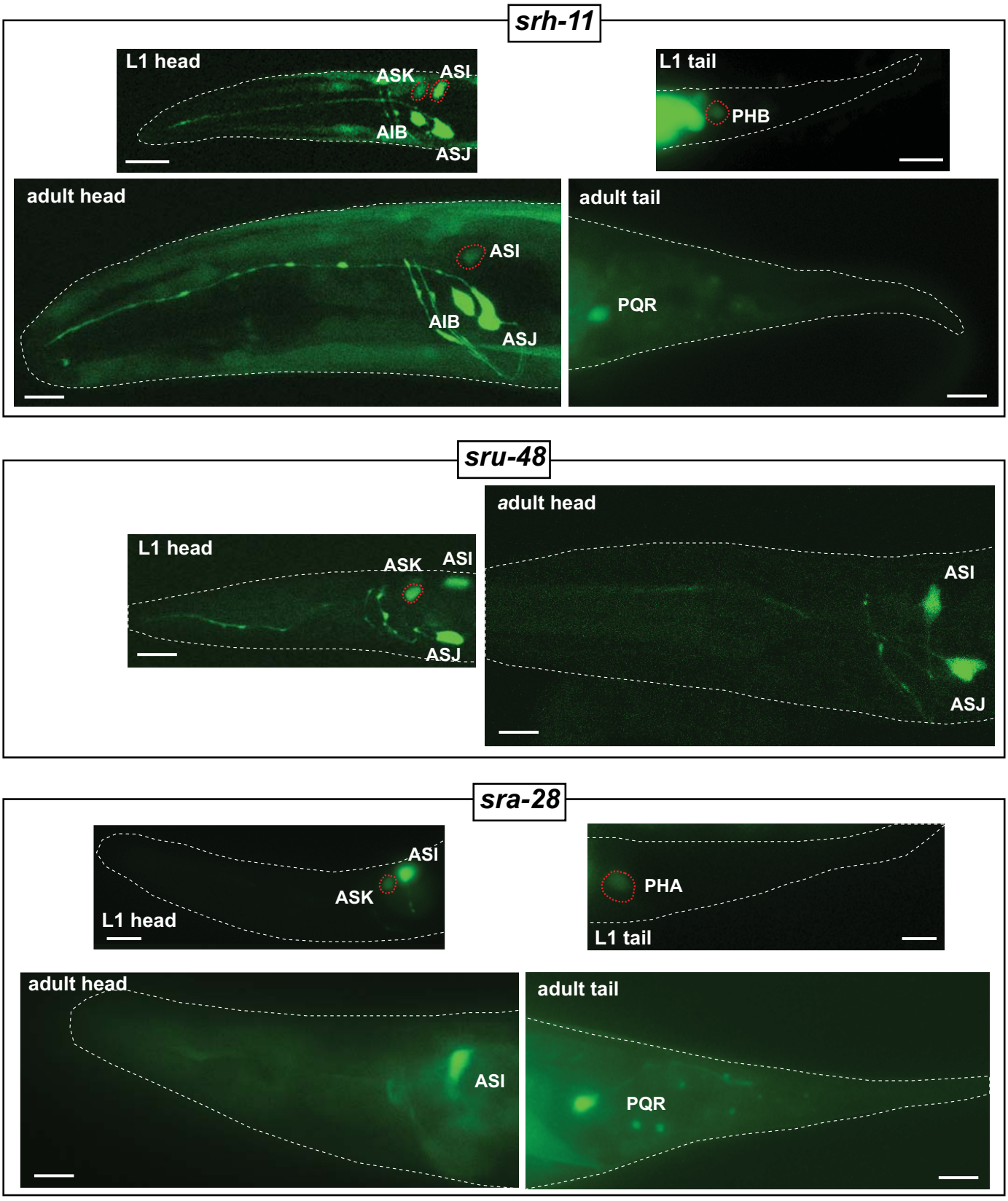
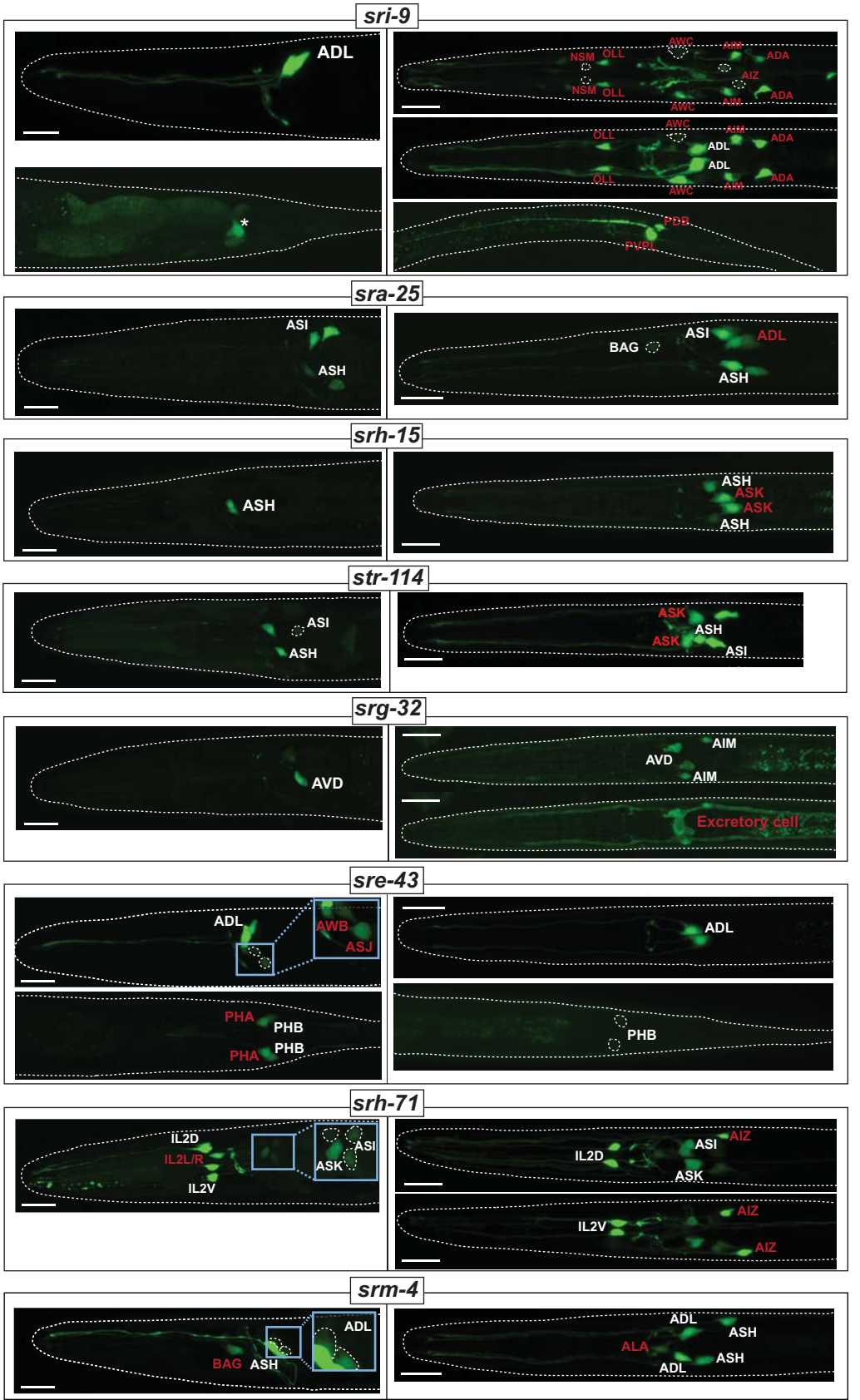

srh-11
L1 head
ASK
ASI
AIB
ASJ
L1 tail
PHB
adult head
ASI
AIB
ASJ
adult tail
PQR
sru-48
L1 head
ASK
ASI
ASJ
adult head
ASI
ASJ
sra-28
ASI
ASK
L1 head
PHA
L1 tail
adult head
ASI
adult tail
PQR

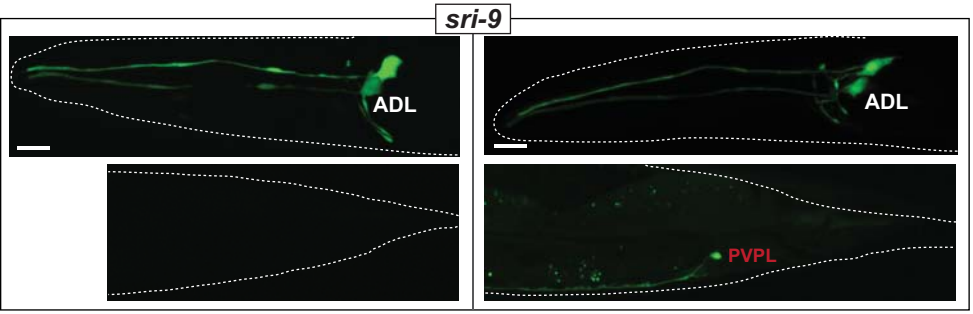
Figure 10


L3/L4 larvae
Dauers
sri-9
ADL
*
AWC
AIM
ADA
NSM
OLL
AIZ
ADL
PDB
PVPL
sra-25
ASI
ASH
BAG
ADL
srh-15
ASH
ASK
str-114
ASI
ASH
ASK
srg-32
AVD
AIM
Excretory cell
sre-43
ADL
AWB
ASJ
PHA
PHB
srh-71
IL2D
IL2L/R
IL2V
ASI
ASK
AIZ
srm-4
BAG
ALA

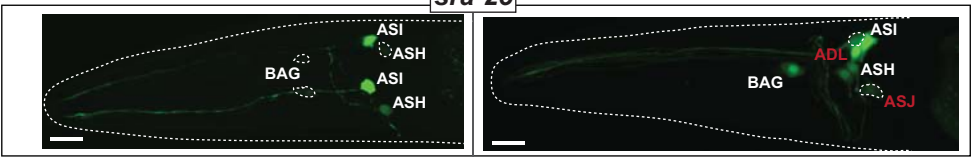
Adult fed controls

Postdauer adults

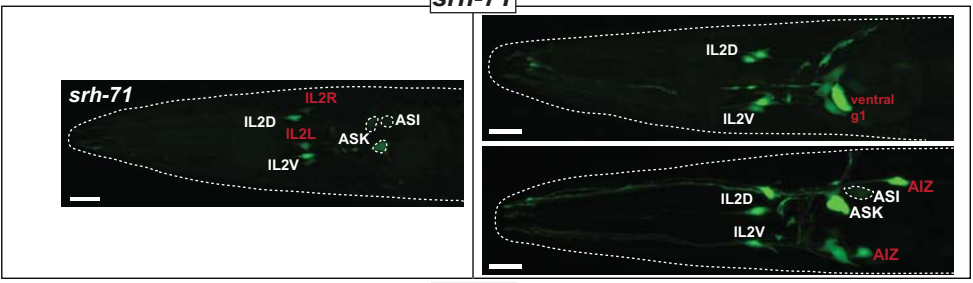
sri-9



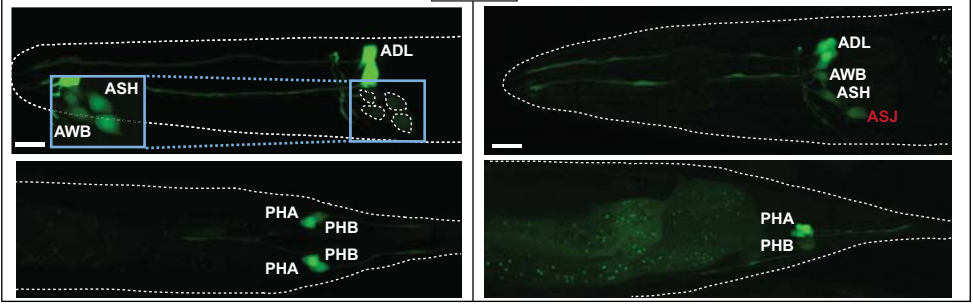
sra-25



srh-71



sre-43



sru-12

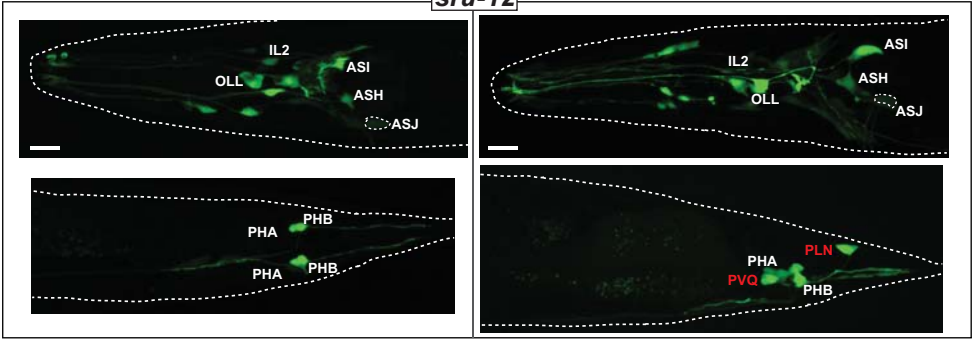
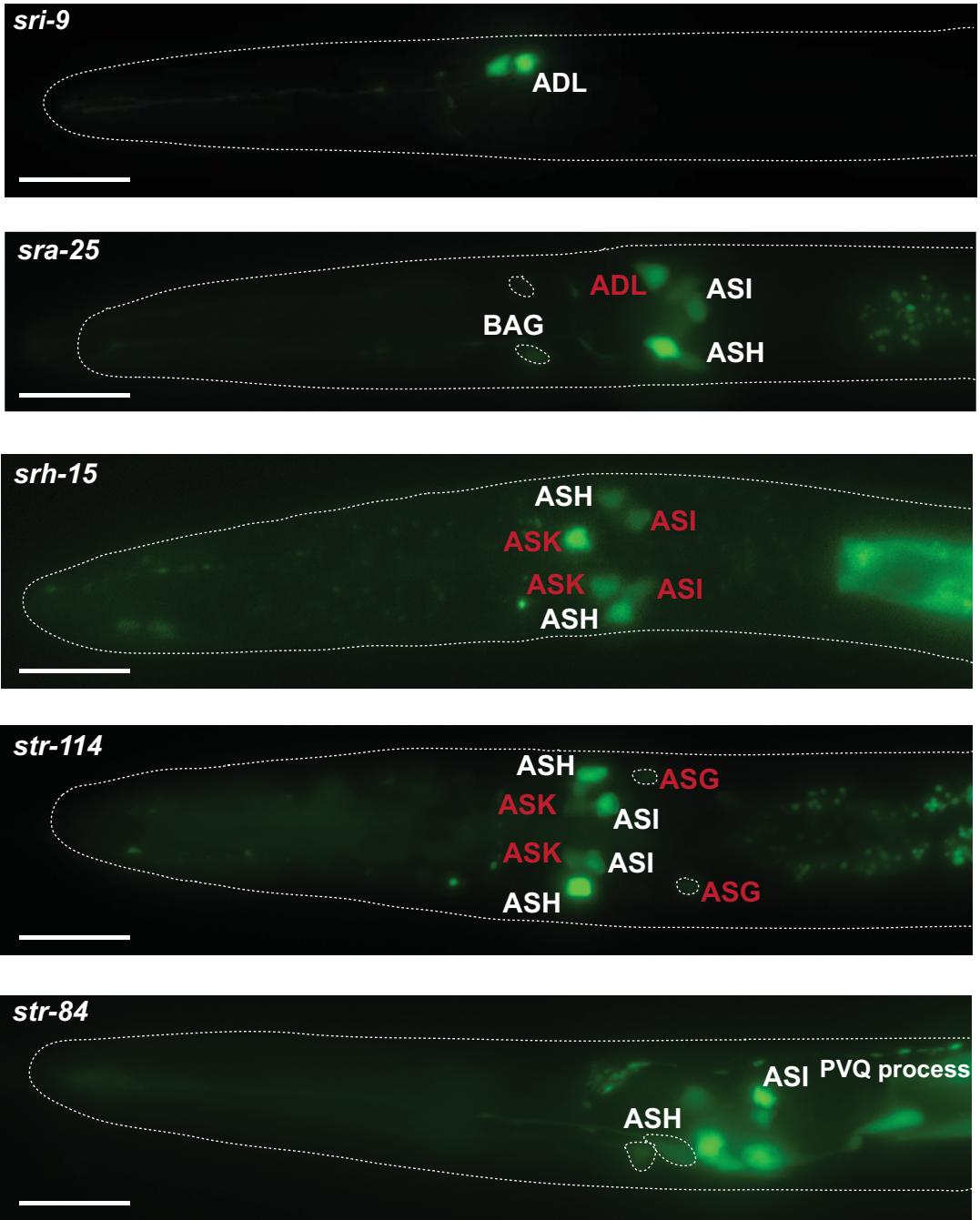
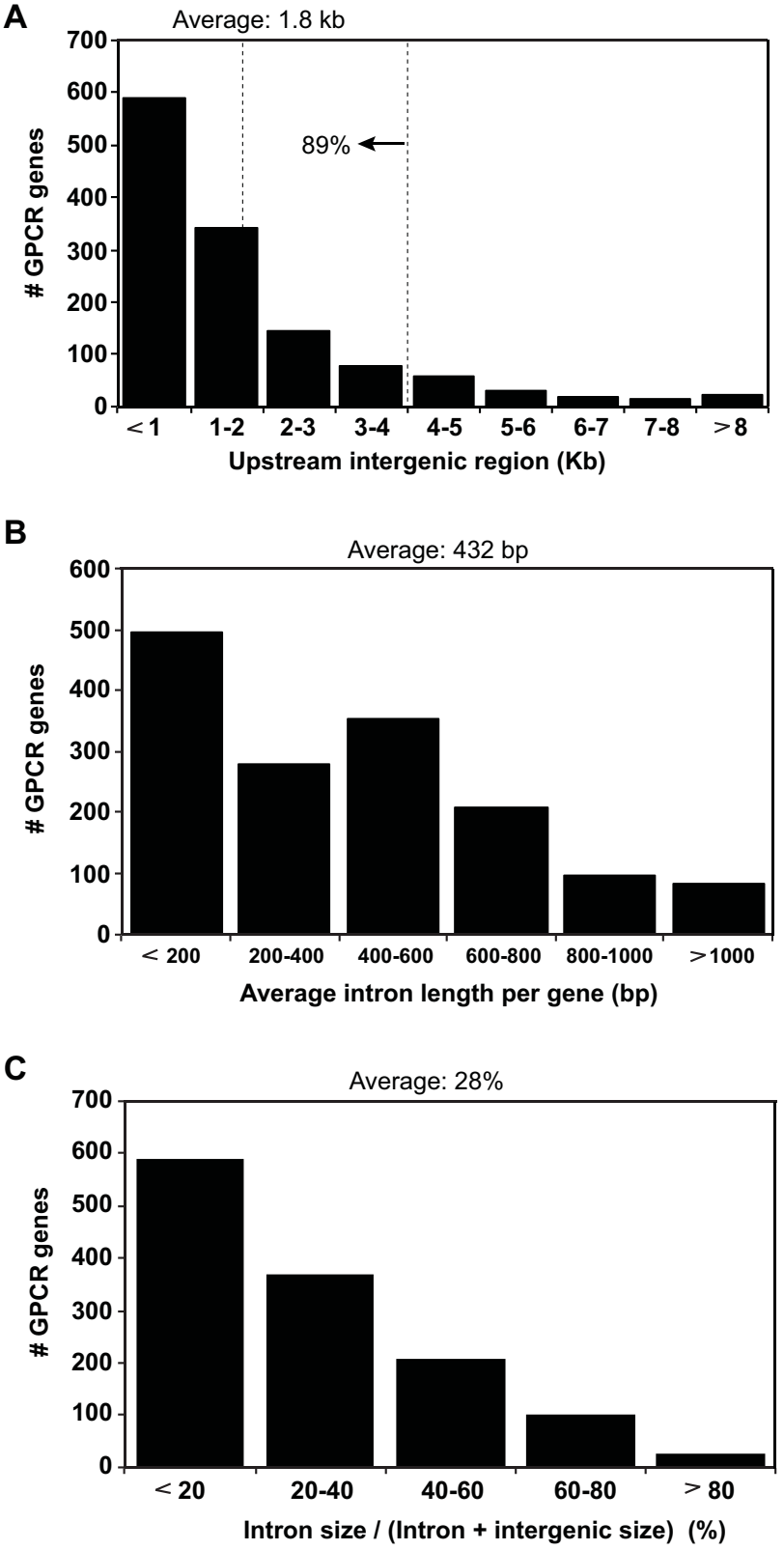


Figure 12


sri-9
ADL
sra-25
ADL
ASI
BAG
ASH
srh-15
ASH
ASI
ASK
ASK
ASI
ASH
str-114
ASH
ASG
ASK
ASI
ASK
ASI
ASH
ASG
str-84
ASI
PVQ process
ASH



S1 Fig. csGPCR gene locus analysis.
(A) Histogram of upstream intergenic region distances of all *C. elegans* cs GPCR genes. The average size of the 5' intergenic region (= distance to next gene) is 1.8kb. 89% of all loci have a 5' intergenic region of smaller than 4kb.
(B) Histogram of average combined intron length (bp) per GPCR gene.
(C) The intergenic region of the majority of GPCR is substantially larger than the combined intronic region.

Table S1: Masterlist of all examined GPCR reporters

Gene	Source	Expression
sra-1	WormBase	SPD, SPV (males only)
sra-2	BC13750	Few dim head neurons, muscle
sra-4	BC11958	2 head neuron pairs (dim, crappy), pharynx
sra-6	WormBase	ASIf, ASH, SPDm, SPVm, PVQ, ALM, PLM, AVM, PVM
sra-7	WormBase	ASK, unidentifed cells in tail
sra-9	WormBase	ASK
sra-10	WormBase	URX, ALA, some sensory neurons, interneurons, pharyngeal neurons and muscle / tail neurons, intestine
sra-11	BC15147	URX, AVB, RIF, AIY, 1 pair in ventral ganglion, 1 pharyngeal neuron, PVT (in Wormbase another sra-11 reporter is annotated as also being expressed in AIA and VC)
sra-13	BC13517	ADL, ASI, ASJ (in Wormbase another sra-11 reporter is annotated as being expressed in AWC, AWA, hypodermis, body wall muscle, vulval muscle, seam cells)
sra-14	BC14819	ADL, ASJ, 1 pair anterior to AWB, RID, PHA, PHB, 1 pair a bit posterior to PHB, 1 more neuron in the tail, ray expression in males
sra-17	BC13708	ASI (in Wormbase another sra-17 reporter is annotated as being expressed in AWA and several other unidentified neurons)
sra-20	WormBase	head neurons
sra-21	WormBase	head neurons
sra-22	WormBase	amphid neurons
sra-23	BC13491	ASI, AWB, 2 single midline neurons - one dorsal (on top of ASKs) and one ventral (anterior to ASJ), PQR
sra-25	BC13401	ASI, ASH, BAG (dim)
sra-28	BC14650	ASI, PQR, other dim pairs, sometimes PVT
sra-29	WormBase	amphids, intestine
sra-36	BC11976	ASI, some worms show dim expression in a couple more head neuron pairs, DA8, DA9, VA11
sra-35	BC14646	OLQ, ADL, ASI, HSN
sra-38	WormBase	pharynx, head neurons, unidentifed cells in head
sra-39	WormBase	ASJ, ADL, PHA, PHB, intestine, hypodermis
srab-1	WormBase	AWB
srab-3	BC14730	ASK, RID, AIY, RIF, 1 pair in ventral ganglion
srab-4	WormBase	pm6, AWB, RID, AIA, AFD, PVT, NSM, I4, I2, DVC, RME, VA, VB
srab-6	BC14733	Hypodermis
srab-7	BC14732	ASK, ASH, ASI (dim & not so consistent), (AWA dim), vulva muscle?, anal depressor muscle
srab-8	BC14734	ASK, ASI, ASH, ASJ, one pair posterior to AWB (some space in btw), PHA, PHB, one pair just posterior to PHB (sometimes dimmer), HSN, AVM, BDU, Amso, ray expression in males
srab-9	BC12175	ASH, ASJ, (AWA), 1 more head neuron pair, sometimes PHA
srab-10	BC14736	Few dim head neurons, hypodermis
srab-11	BC14832	ASH, PHA, PHB
srab-12	WormBase	BDU, ADA, PVP, PVD, PHC, LUA, IL2, IL1, CEP, SDQL, RMG, (ventral cord neuron)
srab-13	BC14738	ASK, ASJ, AWA, vulval cells, sometimes hypodermis
srab-14	WormBase	excretory cell, head neurons, amphids, mechanosensory neurons, pharyngeal neurons, tail neurons, phasmids, ASE
srab-16	WormBase	AWC, AWB
srab-20	BC12045	PHB (in Wormbase another srab-20 reporter is annotated as PHA-expressed)
srab-21	WormBase	Larva: hypodermis, nervous system, neurons along body
srab-23	BC14744	dim crappy expression in a few head neurons
srab-24	BC14746	ASI, ASH, AVE, AWB (variable)
srab-25	BC15054	No expression
srb-3	WormBase	amphid neurons, phasmid neurons, intestine
srb-5	BC12285	ASK
srb-6	WormBase	ADL, ADFf, ASH, PHA, PHB, pharynx
srb-7	BC11985	Few dim head neurons, gut, PVT - crappy
srb-8	WormBase	rectal gland cells, intestine
srb-10	BC14816	2 head neuron pairs? (crappy expression)
srb-12	WormBase	unidentifed cells in head, intestine
srb-13	BC14700	Several head neurons (variable)
srb-16	BC14820	Several head neurons, I1 or I2 pharyngeal neurons, head mesodermal cell?, pharynx, vulva, CAN, VC, DA9, 1 neuron pair in the tail, PVT, another cell in PAG?
srb-17	OH14364 / OH14365	ASI, ASH, ASJ, PHA, PHB, strong gut expression, seam cells, vulva, head muscle
srbc-7	OH14971 / OH14972	ASJ, unidentified neuron pair, occasionally ASH
srbc-52	BC16010	Crappy and variable exp in few head neurons, PVT
srbc-58	BC16165	Bright expression in many tissues (neurons, pharynx, muscle, hypodermis, vulva, gonad, seam cells)
srbc-64	WormBase	ASK
srbc-66	WormBase	ASK
srd-1	WormBase	ASI (expression undetectable in dauer), ADFmale, R8male?, R9male?
srd-4	OH13857 / OH13858	BAG, DA9, another motorneuron next to DA9, one neuron pair in tail
srd-5	OH13859 / OH13860	Asymmetric expression in AWC OFF, dim ASI
srd-10	OH13861 / OH13862	ASH, another neuronal pair localized between AWB and ADL, AQR variable, PHA, PHB
srd-11	OH13863 / OH13864	AWB, 1 more pair located between AWB and ASI
srd-15	BC15142	ADF, ASI (dim), ASH (dim), gut, pharynx (dim), muscle (dim)
srd-16	WormBase	ASI, ASH, PHA, PHB
srd-17	WormBase	AWC
srd-23	WormBase	AWB, ASK
srd-32	OH14368	ADL (dim), AVL, RIS, head mesodermal cell, pharynx (dim), pharyngeal-intestinal valve (dim), anal depressor muscle, stomatointestinal muscle, PVT, DVA, distal tip cell, CAN
srd-33	WormBase	ASE and other head neurons
srd-36	BC15860	ASK
srd-39	WormBase	hypodermis, seam cells, intestine
sre-1	WormBase	ADL, ASJ faint
sre-4	BC14726	URB, ASH, RID, RIG, AUA, (AWC), 2 more head neuron pairs, PVR, PVQ, another tail neuron pair, BDU
sre-6	WormBase	nerve ring, tail neurons, intestine
sre-7	BC14822	Few head neuron pairs, hypodermis
sre-11	WormBase	head neurons, PVT, intestine
sre-12	WormBase	head neurons, intestine
sre-16	WormBase	head neurons, intestine
sre-18	WormBase	amphids, tail neurons
sre-21	BC14644	ADL, hypodermis
sre-22	BC14656	URB, another head neuron pair, 1 tail neuron pair, hypodermis, muscle, sometimes PVT
sre-23	WormBase	head neurons, neurons along body, tail neurons, unidentifed cells in head, unidentified cells in tail
sre-24	WormBase	head neuron, intestine, rectal gland cells, spermatheca
sre-25	BC15863	1 head neuron pair? (Expression quite dim and crappy)
sre-26	WormBase	head neurons, intestine
sre-27	BC14827	ADL, ASH (variable), ASJ (variable), another head neuron pair, PHA, PHB
sre-28	WormBase	unidentifed cells in head, intestine
sre-29	WormBase	body wall muscle, hypodermis, head neurons, intestine
sre-30	BC14699	Several head neurons (dim), sometimes PVT
sre-31	WormBase	amphids, phasmids, intestine
sre-32	BC14727	Couple of neurons in head and tail (sick strain, very low penetrance)
sre-37	WormBase	CEPD (only in L1 and L2)
sre-42	WormBase	nervous system, intestine
sre-43	BC14724	ADL, AWB (dimmer), ASJ, PHA, PHB
sre-44	BC14825	ADL, sometimes other dim pairs
sre-45	WormBase	head neurons, tail neurons
sre-47	WormBase	unidentifed cells in head
sre-49	WormBase	intestine
sre-51	WormBase	1-2 pairs of head neurons
sre-52	BC11973	1-3 head neuron pairs (quite dim and variable), PVT
sre-53	WormBase	unidentifed cells in head, intestine, hypodermis
sre-56	WormBase	vulval muscle, unidentified cells in head
srg-2	WormBase	ASK
srg-4	OH14238	ASK, ASI (dim), in few worms one neuron in the ventral ganglion, PVT
srg-5	BC12021	IL2, OLQ (dimmer), MALE: CEMs and Ray neurons
srg-7	WormBase	intestine, body wall muscle, amphids, phasmids, unidentifed cells in head
srg-8	WormBase	ASK, intestine, rectal gland cells
srg-9	BC11822	ASK, ASI, one neuron pair anterior to ASK, a couple more neurons - quite mosaic and variable
srg-13	WormBase	PHA, neurons along body
srg-14	OH14329 / OH14240	AQR, PQR, ASJ (dim), RMEL/R, (URX), AIN, RIS, sometimes PVT, one extra pair in male tail.
srg-25	OH14360 / OH14361	AQR, PQR, PHA, ADL, ASH, (AVH or AVJ), (AFD)
srg-29	OH14241 / OH14242	ASI, other neuronal expression (variable & not distinct), a lot of GFP background (pharynx, head muscle…)
srg-30	WormBase	ASE and other head neurons
srg-31	OH14243	ASI, ASJ, aprox 3 more pairs in head, (PLM), (PLN), (ALN), sometimes AVM & PVM, sometimes PVT, sometimes pharynx, anal depressor muscle.
srg-32	OH14244 / OH14245	AVD, AIM, PVQ
srg-33	BC15144	ASI, sometimes one neuronal pair in the anterior ganglion (much dimmer and less consistent), uterus
srg-36	WormBase	ASI, weak or inconsistent expression in few other neurons
srg-37	WormBase	ASI, weak or inconsistent expression in few other neurons
srg-39	OH14246 / OH14247	ASI, sometimes a neuron pair in the ventral ganglion next to ASJ, pharynx (dim), posterior gut, PVT, dim crap background
srg-41	WormBase	ASK, ASI, tail neurons
srg-47	WormBase	ASI
srg-58	OH14248 / OH14249	ASI, AIM
srg-62	BC15866	pharynx
srg-64	OH15128 / OH15129	Few head neurons (quite variable and crappy)
srg-66	OH14250	ASI, sometimes dim expression one of the phasmids
srh-4	OH13833 / OH13834	ADL, PVT sometimes
srh-5	OH13835 / OH13836	ADL, ASH, PHA and PHB (phasmids crappy), PVT sometimes
srh-7	OH13837 / OH13838	ASH, BAG (dimmer), PHA (variable), gut, pharynx (dim), sometimes you see other dim neurons in the head.
srh-10	WormBase	ASJ, ASH
srh-11	BC10848	ASJ, AIB, head muscle, vulval cells?, PQR, PVT, ray expression in males
srh-15	BC15959	ASH, PHA
srh-18	WormBase	ASH, PHA, PHB
srh-25	WormBase	ADL
srh-28	BC16177	ASJ, ASH
srh-62	OH14289 / OH14290	ASK, ASI, ASJ, 2-3 more neuron pairs, OLL (dim), phasmids?, sometimes PVT, pharynx - a bit mosaic and variable
srh-68	WormBase	ADL, several neurons
srh-71	OH14267 / OH14268	IL2, ASK, ASI (dim), ASG, one pair above ASJ, pharynx, sometimes PVT, PHA and one other non-phasmid pair, ray expression in males
srh-74	OH14958 / OH14959	ADL, ASH
srh-76	OH14291 / OH14292	1 head neuron pair, hypodermis - dim and variable
srh-79	BC15143	ADL, ASH, PHA
srh-87	WormBase	spermatheca
srh-92	WormBase	pharynx
srh-100	OH14293 / OH14294	ASI, ASJ, 1 pair in ventral ganglion, other dim crap in the background (pharynx, muscle, neurons). Variable and crappy. Sometimes you see neurons in VNC.

srh-127	OH14305 / OH14306	ADL, ASJ, at least 1 pharyngeal neuron, PHC
srh-128	BC15868	ASH, PHB - (mosaic and variable)
srh-130	OH14307 / OH14308	ADL, (FLP), one more head neuron pair, ALM, PHA, PHB, sometimes seam cells and some vulval cells
srh-132	WormBase	ADL, head mesodermal cell
srh-139	WormBase	ADL, several neurons
srh-142	OH14295 / OH14296	ASK, ASI, ADF, ASE, PHB, pharynx
srh-147	WormBase	intestine
srh-182	WormBase	head neurons (NOT ASE)
srh-186	WormBase	ADL
srh-193	OH14297 / OH14298	ADL, sometimes coelomocytes
srh-199	OH14299 / OH14300	ADL
srh-201	OH14301 / OH14302	ASI, ASJ, 1 tail neuron pair (projects anteriorly all the way to the nerve ring), pharynx, green crap in the background - crappy
srh-210	OH14313	pharynx, pharyngeal-intestinal valve, head mesodermal cell, vulva, ASH, few head and RVG neurons (not distinct expression), PVT sometimes, phasmids (variable), male rays
srh-211	OH14315 / OH14316	ADL, ASI, AWB, ASH, PHA, sometimes bright gut
srh-218	OH14317 / OH14318	ADL and ASH, PHA, PHB, sometimes you see other cells in the head (a bit variable)
srh-220	WormBase	ADL
srh-234	WormBase	ADL
srh-240	OH14319 / OH14320	ASJ, ASI (dim), PHA, PHB, maybe other DiD filling cells - crappy in general
srh-241	OH14321 / OH14322	ASK, ASI, gut, PVT sometimes
srh-266	OH14269 / OH14270	ADL, 1 neuron pair in RVG projecting anteriorly that could be RIFs (much dimmer than ADL), sometimes PVT and dim seam cells.
srh-269	OH14323 / OH14324	PHA (rarely also others in tail, PHB?), ASK, 2-3 more pairs in head (incl. AIA?), head mesodermal cell (?), pharynx (pharyngeal gland cells and muscles), ceolomocytes
srh-270	OH14337 / OH14338	ADL, other head neurons in anterior and ventral ganglion (much dimmer), PHA, PHB, vulva, anterior sheath/socket cells (Amsh/Amso?), males - expression in rays
srh-277	OH14303 / OH14304	AIN (dim), a couple more neuron pairs , PVQ
srh-279	BC15870	ADL
srh-281	WormBase	ADL
sri-1	OH13839 / OH13840	PVQ, OLL, URB, AIY, ADA, BDU
sri-5	OH13841 / OH13842	ASH, ASK, 1 bright neuron pair just posterior to ASI, 1 neuron pair at the level of ASH just posterior to the nerve ring, maybe other neurons? (a bit variable), VNC (dim), PHB, sometimes dim PHA, vulva muscle and uv1 cells, pharynx - In general very bright.
sri-9	OH13843 / OH13844	ADL
sri-12	OH13845 / OH13846	ADL, URX, AIY, PQR, PVT
sri-14	WormBase	AWC, ASH
sri-18	OH13847 / OH13848	ADL, ASJ, sometimes you see a couple more much dimmer head neurons (ASI, midline neuron in front of ASK), BDU, PHA, I1 pharyngeal neurons (dim)
sri-19	WormBase	1 pair head neurons, body wall muscle, vulval muscle
sri-21	OH13849 / OH13850	ASH, another neuronal pair that looks like an inter/motorneuron (could be RMDL/R??), 2 big cells around the RVG that are not neurons,PHA, PHB
sri-24	BC16070	Few head neurons (expression dim and not very consistent)
sri-25	WormBase	intestine
sri-26	OH14366 / OH14367	ADL, ASH, ASJ, ASK (dimmer), PHA, PHB
sri-27	WormBase	intestine
sri-28	BC16142	ADL (very dim)
sri-33	WormBase	amphid neurons
sri-34	WormBase	amphid neurons, intestine (larva)
sri-36	OH13851 / OH13852	ASI, ASK (dim), 1 neuron pair in ventral ganglion, AIY, pharynx, pharyngeal-intestinal valve, PVT
sri-39	OH13853 / OH13854	ASK, ASI, 1 bright sensory pair in front of ASK, sometimes ASJ, a couple more dim pairs, sometives PVT
sri-45	OH14964 / OH14965	ADL, unidentified cells
sri-50	OH14953	ADL
sri-51	WormBase	ADL
sri-62	OH13855	ADL, sometimes you can see a couple more dim pairs in the head (below ADL and in the ventral ganglion), gut, sometimes PVT
srj-4	OH14222	one pair in front of ASK, ASI (dim), ASJ (dim), pharynx (dim), strong expression in coelomocytes
srj-5	OH14223 / OH14224	ASI, ASK (dimmer and more variable), pharynx (dim), PVT
srj-13	OH14975 / OH14976	ASI, pharynx, VNC neurons (dim), HSN, vulva muscle, posterior gut, 1 neuron pair in the ventral ganglion, GFP crap in the background
srj-20	OH14225	ASI, sometimes another dim pair, seam cells (in older animals not visible), PVT
srj-21	OH14339 / OH14340	(AWA), (AWC), 3 more neuron pairs (variable), males: CP5, CP6
srj-22	OH14226	(AWA), (AWC), males: CP5, CP6
srj-23	OH14970	ASI, Intestine
srj-24	BC15290	BAG, ASI (much dimmer)
srj-25	OH14227	ASI, 1 pair in ventral ganglion - a bit crappy
srj-27	OH14228 / OH14229	2 head neuron pairs (maybe more), PVT, male rays
srj-38	OH14230 / OH14231	pharynx, several dim neurons (sensory and not-sensory), ASI (a bit more prominent), sometimes dim VNC, PVT, 3 male specific cells in the posterior VNC, male rays
srj-44	OH15130 / OH15131	A couple of head neurons (dim)
srj-53	OH15132 / OH15133	(ASI) a bit variable
srj-57	WormBase	intestine
srm-1	OH14760	Several head sensory neurons (ASI, ASH, ASJ...), one neuron pair in ventral ganglion, AVG, ALN, PLN, pharynx
srm-2	OH14761	ASI, ASH, ASJ, a couple more neuron pairs (posterior to ASH and ASJ), PHA
srm-3	OH14762	Relatively broad expression: neuronal and non-neuronal (pharynx, gut, excretory cell)
srm-4	OH14763	ASH, ADL (dim), BAG, PHB
srm-5	OH14764	ASH, ASI, (RIH)
srm-6	OH14765	ASJ, ASI, 3 inter/motorneurons from RVG, gut
srn-1	OH15134 / OH15135	ASK, ADL, ASI, ASH, (RIH), 2 more head neuron pairs
sro-1	WormBase	ADL, SIA
srr-1	OH15136 / OH15137	glia, pharynx, male rays
srr-2	OH14766	strong pharyngeal expression (isthmus and terminal bulb), posterior gut, PVT sometimes
srr-3	OH14767	RMDV, RMDD, sometimes other dim neurons, pharynx (sometimes I2 neurons), pharyngeal-intestinal valve, head mesodermal cell, anal depressor muscle, phasmids (dim)
srr-4	OH14768	Expressed brightly and broadly: pharynx, excretory cell, hypodermis, vulva, several head neurons, phasmids
srr-6	BC15141	neurons in RVG, strong pharyngeal expression, sometimes excretory cell
srr-7	OH14770	ASK, ASI, at least one more sensory neuron pair in lateral ganglion, IL2s, PVT, phasmids (dim, not very consistent)
srr-8	OH14771	ASI (dim), a couple more head neuronal pairs, PVT, excretory cell
srr-9	OH14772	ASI (dim), 1 neuron pair anterior to ASK (could be non-sensory), asymmetrically expressed in AWC?? (crappy)
srr-10	OH14773	head neurons, tail neurons - crappy and variable
srsx-3	WormBase	AWB, AWC OFF
srsx-5	OH14774	Asymmetric expression in AWC OFF, ASK, ASI
srsx-6	OH15138 / OH15139	2 head neuron pairs
srsx-9	BC15567	1 head neuron pair (very dim)
srsx-12	OH14232 / OH14233	Some head neurons (variable), PVT, (AVG), vulva muscle
srsx-17	WormBase	nervous system
srsx-18	WormBase	linker cell
srsx-27	OH14341 / OH14342	ASI, sometimes you see a second pair
srsx-28	OH14234 / OH14235	ASH, ASI (dim), ADF, a subset of cholinergic VNC neurons, PHA, PHB
srsx-29	BC16140	ADF, PHA, sometimes really dim ASH
srsx-30	BC15999	ASI (dim), BAG, (I4), 3 more head neuron pairs, DD, VD, Amso, PHsh or Phso
srsx-34	WormBase	head neurons (NOT ASE)
srsx-37	OH14370 / OH14371	ADL, Asymmetric expression in AWC OFF
srsx-38	OH14235 / OH14236	ASK (dim), ASI, 2-3 more pairs (dim), pharyngeal neurons?, PVT
srt-7	BC14751	AWA, asymmetric expression in AWC ON
srt-8	BC14750	ASI, sometimes an inter/motorneuron in the ventral ganglion - variable
srt-13	BC15789	Asymmetric expression in AWC OFF (dim and variable)
srt-20	BC14755	ASI, ASJ, sometimes a couple more head neurons, body wall muscle
srt-26	WormBase	AWC ON
srt-27	BC14839	ASG, ASI (dim)
srt-28	WormBase	AWC ON
srt-29	WormBase	AWC ON, intestine
srt-36	BC14840	ASI, sometimes a couple other dim head neurons - dim and variable
srt-38	BC14842	ASI (really dim), in most worms you don't see much
srt-45	WormBase	AWC OFF
srt-47	WormBase	AWC OFF
srt-63	WormBase	more than 10 neurons (not ASE)
srt-65	BC15345	ADL, ASI (dim), some pharyneal cells close to the tip of the nose
srt-68	BC15006	ADF, ASI (dim), URX, sometimes 1 inter/motorneurons in the ventral ganglion or RVG
srt-70	BC14836	ADF, PHB, sometimes dim PHA
sru-1	OH13877 / OH13878	OLQ, ASK, PHB, pharynx (dim), head muscle (dim)?
sru-2	OH13879 / OH13880	Few head neurons (variable) - up to three pairs around metacourpus, sometimes sheat/socket cells in the head, PHA, PHB
sru-4	WormBase	ADL
sru-8	OH13881 / OH13882	ASK, ASI, ASH, 1 very bright pair in front of ASK, I neuronal pair in ventral ganglion, PHB, PVT - variable
sru-12	OH13883 / OH13884	ASI, ASH, ASJ, IL2, OLL, PHA, PHB
sru-17	BC11911	ADL and ASI (both relatively dim), some pharyngeal neurons, other dim cells (could be neurons), inter/motorneuron from RVG, (PVQ), cells close to the tip of the nose (support cells?)
sru-19	WormBase	amphid neurons, Amso
sru-27	WormBase	Less than 10 neurons (not ASE)
sru-30	OH13885 / OH13886	ASI, ASJ, PHA, PHB
sru-31	WormBase	head neurons, pharynx, intestine, hypodermis
sru-38	WormBase	AWB, ASH, phasmids, intestine
sru-48	OH13887 / OH13888	ASI, ASJ, PVT, gut
srv-1	BC14593	ASI, ASG, CAN, excretory cell, gut
srv-3	OH14750	ADL
srv-4	BC15938	ADL (very dim)
srv-5	OH14751	ASK, AWB, ASH, ASJ, 1 more sensory neuron pair (close to AWB), PHB - a bit variable
srv-8	OH14752	ASK, another sensory neuron pair, another pair that could be inter/motorneuron, (PHC)
srv-11	WormBase	ASH
srv-12	OH14753 / OH14754	ADL and ASJ
srv-17	OH14755	ASI (pretty dim), pharynx (dim), dim GFP crap in the background
srv-21	OH15140 / OH15141	ASH, ASJ, one pair just on top of AWB
srv-27	OH14756	ASK, URB (quite dim), 1-2 more head neuron pairs, ALM, BDU, (PDE), PHA, PHB
srv-32	OH14757	BAG, AFD, PVQ
srv-34	OH14758 / OH14759	ASK, AWA, one neuron in RVG, dim crap in the background
srw-29	WormBase	neuronal sheath cell
srw-85	WormBase	less than 10 neurons (not ASE)
srw-103	WormBase	amphid neurons
srw-108	BC15940	ASK, head hypodermis
srw-112	WormBase	head neurons
srw-118	WormBase	hypodermis
srw-119	OH14973 / OH14974	ASG
srw-138	BC16107	ADL (dim)
srw-139	WormBase	Less than 10 neurons (not ASE)
srw-140	WormBase	male sensory rays
srw-145	OH14362 / OH14363	3 head sensory neuron pairs, PHA, PHB, glia

srx-1	OH13865 / OH13866	Asymmetric expression in AWC OFF, ADL, 2 more dim pairs, head mesodermal cell, vulval muscle, anal depressor muscle
srx-3	OH13867 / OH13868	SMDV, SMDD, SAAV, (SAAD), (AVH/AVJ), DB, VB, PDA
srx-4	OH13869 / OH13870	ASK, ASI, vulval cells, B and Y rectal epithelial cells
srx-9	WormBase	Larva: intestine, head neurons, tail neurons
srx-10	OH13871 / OH13872	ASI, posterior gut, pharynx, PVT, dim neuronal crap in the background.
srx-12	BC16112	ADF, amphid sheath glia
srx-14	BC16051	AWB, ASK (dimmer), ASI (dimmer), AIY, PHA, PHB
srx-17	OH13873 / OH13874	ASI, 1 pair of inter/motorneurons in ventral ganglion, sometimes other neurons - variable, PVT
srx-22	OH13875 / OH13876	(I2), ASI (dim), 1 pair in between ASK and AWB (dim)
srx-41	WormBase	head neurons, tail neurons, head muscles, posterior intestine
srx-44	OH14968 / OH14969	ADL, ASI
srx-45	WormBase	linker cell
srx-47	WormBase	AWA, ASH, unidentifed cells in tail, posterior intestine
srx-76	WormBase	ASE and other head neurons (less than 10)
srx-102	BC15798	Few head neurons (variable)
srx-105	BC15802	ASH, PHA, PHB
srx-108	BC15804	2 head neuron pairs (many animals don't show expression)
srx-110	BC16049	PHB
srx-113	BC15808	FLP, 4 more head neuron pairs, PLM, DVA
srx-114	WormBase	head neurons, phasmid neurons
srxa-1	BC14896	AWB, ADF
srxa-2	WormBase	Larva: body wall muscle
srxa-5	WormBase	pharyngeal neuron, head neuron
srxa-6	BC14847	ASI (dim), sometimes ASH (vey dim and less consistent), PHB
srxa-7	BC14770	ASI, ASH, PHA, bright PVT
srxa-8	WormBase	amphid neurons
srxa-14	BC14775	ADL, AIM, hypodermis, gut
srxa-15	WormBase	amphid neurons, phasmid neurons, intestine
srz-1	BC14844	ASH, ASI, PHA (quite dim), PHB, posterior gut - A bit variable
srz-4	OH15142 / OH15143	ADL
srz-6	WormBase	ADL
srz-13	BC14760	Few head neurons, PVT, hypodermis (variable)
srz-14	BC14758	Seam cells, 2 tail neurons? (not very consistent)
srz-16	BC16016	ADL (relatively dim), sometimes also dim ASI
srz-24	OH14954 / OH14955	ADL, ASI, sometimes ASK
srz-27	BC14767	ASH, ASI, AWB (dimmer and less consistent), sometimes you see other neurons in the head (variable), PVT
srz-28	BC14768	ADL (extreme mosaicism)
srz-32	OH14962 / OH14963	ADL, ASH
srz-42	BC14757	Several neurons in head and tail (crappy)
srz-45	BC14765	ASH, PHA, PHB
srz-54	OH14265 / OH14266	ASI, sometimes a pair of inter/motorneurons from the ventral ganglion, dim crap in the head and tail, pharynx, gut, PVT
srz-56	OH14838 / OH14839	ADL, PHB? (the positional information is a bit confusing, sometimes it looks like PHA)
srz-61	OH14966 / OH14967	ADL, unidentified cells
srz-66	OH14956 / OH14957	ADL, sometimes another unidentified neuron pair
srz-67	BC16202	ADL
srz-74	BC16019	Few animals show crappy exp in 1-4 head neurons (not a good line).
srz-94	BC16116	Hypodermis, muscle
srz-99	BC14764	ADL, sometimes hypodermis, very mosaic
srz-102	OH14343 / OH14344	ADL, sometimes you see another dim cell, PVT, vulva
srz-103	BC14845	ADL
srz-104	OH14840 / OH14841	ADL, sometimes PVT
str-1	WormBase	AWB
str-2	WormBase	AWC ON, ASI faint
str-3	WormBase	ASI
str-31	OH14271 / OH14272	Rectal epithelial cells, head and tail hypodermis, vulva, seam cells, PVT. There is some neuronal exp but it's variable and crappy
str-33	WormBase	head neurons, ALM, PLM
str-44	WormBase	AWB
str-47	WormBase	rectal gland cells, nose sheath cells
str-52	OH14273 / OH14274	ASI, other dim pairs in the head, pharynx, sometimes PVT, sometimes vulva, PHB, other neurons in tail, tail epidermis - in general expression variable and not very distict
str-84	OH14378 / OH14379	ASI, ASH, 1 neuron pair around the RVG (seems a bit more dorsal though - projects ventrally), PHA, PHB, PVQ
str-85	OH14376 / OH14377	few head neurons pairs, pharynx
str-90	BC13455	ADL, sometimes ASH, sometimes dim ASI, sometimes another dim pair, 1 midline neuron in btw ASJs, PHA, PHB
str-94	OH14275 / OH14276	rectal valve cells? Crappy
str-97	OH14372 / OH14373	M1, ASI (dim)
str-102	OH14374 / OH14375	ASI, ASJ, AIY, DVA or DVB, anal depressor muscle
str-108	WormBase	intestine, pharynx, nervous system
str-111	WormBase	body wall muscle, head neurons, tail neurons
str-112	WormBase	head neurons?
str-114	OH14380 / OH14381	ASH, ASI, PHA, vulval muscle, (head muscle)
str-115	WormBase	intestine
str-121	OH14277 / OH14278	pharynx, several head neurons (not distinct at all), dim GFP in the background
str-123	OH14388 / OH14389	1 pharyngeal neuron, ASI, 1 pair in front of ASK, 1 pair on top of ASJ, 1 pair in ventral ganglion, pharynx, sometimes PVT, other dim crap in the background - overall a bit variable
str-125	OH14390 / OH14391	Few head neuron pairs (at least some are interneurons - AIY-like), quite crappy and variable
str-129	OH14392 / OH14393	Few head neurons, crappy and variable
str-130	OH14394 / OH14395	Assymmetric expression in AWC OFF, a couple of dim neuron pairs
str-143	OH14396 / OH14397	head neurons, pharynx, gut, PVT, sometimes VNC, duct cell, pore cell - Broad not very distinct expression, a bit variable
str-148	OH14398 / OH14399	Seam cells, duct cell, pore cell, in animals that don't show bright seam cell expression I see a couple of head neurons.
str-158	WormBase	intestine
str-163	WormBase	AWB, intestine
str-168	WormBase	Larva: hypodermis
str-178	OH14279 / OH14280	ADL, PVT, sometimes other dim experssion in the background
str-199	WormBase	AWC
str-220	WormBase	AWB
str-231	OH14281 / OH14282	ASI
str-233	OH14283 / OH14284	BAG, few head neurons ,sometimes PVT, 2 big cells close to the nose, rectal epithelial cells
str-236	OH14400 / OH14401	ASI, one pair below ASI, one pair in ventral ganglion, pharynx, posterior gut, PVT, a bit variable and crappy
str-247	OH14285 / OH14286	ASI, one neuron pair in ventral ganglion, anterior pharynx, posterior gut, vulva muscle, PVT, some other cells in the anterior head
str-249	OH14402 / OH14403	A few head neurons, PVT, variable and crappy
str-250	OH14386 / OH14387	ASI, other head neurons and non-neuronal cells, REC and tail hypodermis, PVT, dim pharynx, sometimes ceolomocytes, dim VNC. In general expression not very crisp.
str-253	OH14369 / OH14385	Few head neurons, dim variable and crappy
str-261	OH14287 / OH14288	ASK, AWA
str-262	OH14384	Few head neurons?, vulval muscle, variable and crappy
odr-10	WormBase	AWA

Table S2: List of all identified sensory neurons with GPCR expression

Cell	ADF	ADL	AFD	ALA	ALM	ALN	AQR	ASE	ASG	ASH	ASI	ASJ	ASK	AVM	AWA	AWB	AWC	BAG	CEP	FLP	IL1	IL2	OLL	OLQ	PDE	PHA	PHB	PHC	PLM	PLN	PQR	PVD	PVM	URB	URX
# GPCR	9	72	4	1	5	2	9	5	4	51	99	39	41	4	12	19	22	8	2	2	1	5	3	1	1	51	49	1	4	2	6	1	3	4	4
Genes	srb-6	**sra-13**	srab-4	sra-10	sra-6	**(srg-31)**	**srd-10**	srab-14	srh-71	sra-6	sra-6	**sra-13**	sra-7	sra-6	sra-13	**sra-23**	sra-13	**sre-25**	srab-12	**(srh-130)**	srab-12	srab-12	**srh-62**	**sra-35**	(srv-27)	srab-12	**sra-14**	**sra-14**	srab-12	sra-6	**(srg-31)**	**sra-23**	srab-12	sra-6	**sre-4**	sra-10
	srd-15	**sra-14**	**(srg-25)**		srab-14	**srm-1**	**srg-14**	srd-33	**srh-27**	**srab-7**	**sra-13**	**sra-14**	sra-9	**srab-8**	sra-17	srab-1	srab-16	**srd-5**		**(srh-113**		**srg-5**	**sri-1**	**sre-5**		sra-39	**srab-8**	**srab-8**		**srh-127**	**(srg-31)**	**srm-1**			srab-14	**sre-22**	**(srg-14)**
	srh-142	**sre-35**	**srv-32**		**srh-120**		**srg-25**	srg-30	**srv-1**	**srab-7**	sra-17	sra-39	**srab-3**	srab-14	**(srab-7)**	srab-4	**srd-5**	srd-17				**srh-71**	**sru-12**	**sru-1**		srb-6	**srab-9**	**srab-11**	**(srg-31)**					**srg-11**	**sri-1**	**sri-12**
	sra-28	sra-39			**srv-27**			**srh-142**	**sre-119**	**srab-8**	**sra-23**	**srab-7**	**srab-8**	**srg-31**	srab-9	srab-16	srd-17	**srj-24**				**srr-7**				**srab-11**	**srab-20**						**srg-25**		**sri-1**	**sre-27**	**srt-68**
	sra-29	srb-6			str-33			sre-76		**srab-9**	**sra-25**	**srab-9**	**srab-8**		**srab-13**	srab-24	srd-4	**srm-4**				**sru-12**				srb-6	**srb-6**						**srh-11**				
	srt-68	**srd-32**								**srab-11**	**sra-28**	**srab-13**	**srab-7**	**srab-8**	**srab-13**	srd-11	srd-11	(**srj-21**)								srb-6	srb-6						**sri-12**				
	srt-70	sre-1								srab-24	**sre-35**	**srb-17**	**srb-5**		**srb-5**	srd-23	(**srj-22**)	**srt-7**								**srb-17**	**srb-17**										
	sru-12	**sre-21**								srb-6	**sru-36**	**srbc-7**	srbc-64		**sru-34**	**srh-211**	**srt-7**	srax-3								**srd-10**	**srd-10**										
	srua-1	**sre-27**								**srb-17**	**srab-7**	sre-1	srbc-66		sre-47	sru-1	**srax-5**									srd-16	srd-16										
		sre-43								**srd-10**	**srab-8**	**sre-27**	srd-21		**str-261**	sru-38	**srax-37**									**sre-27**	**sre-27**										
		sre-44								**srd-15**	srab-24	**sre-43**	**srd-36**		odr-10	**srv-5**	**srt-7**									**sre-43**	**sre-43**										
		srg-25								srd-16	**srb-17**	**srg-14**	srg-2			**srv-14**	srt-26									srg-13	srh-5										
		srh-4								**sre-4**	srd-1	**srg-31**	**srg-4**			**srua-1**	srt-28									**srg-25**	srh-18										
		srh-5								**sre-27**	**srd-5**	srh-10	srg-8			**srv-27**	srt-29									srh-5	**srh-128**										
		srh-25								**srg-25**	**srd-15**	**srh-11**	**srg-9**			srr-1	srt-29									srh-7	**srh-130**										
		srh-68								**srh-5**	srd-16	**srh-28**	srg-41			str-44	srt-45									**srh-15**	**srh-142**										
		srh-76								**srh-7**	**sre-4**	**srh-62**	**srh-62**			str-163	srt-47									srh-38	**srh-210**										
		srh-79								srh-10	**srg-9**	**srh-100**	**srh-71**			str-220	**sru-1**									**srh-71**	**srh-218**										
		srh-127								**srh-15**	**srg-29**	**srh-127**	**srh-142**				str-2									srh-79	**srh-240**										
		srh-130								srh-18	**srg-31**	**srh-201**	**srh-241**				**str-130**									**srh-130**	**srh-269**										
		srh-132								**srh-28**	**srg-33**	**srh-240**	**srh-269**				str-199									**srh-210**	**srh-270**										
		srh-139								**srh-79**	srg-36	**sri-18**	**sri-5**													**srh-211**	**sri-5**										
		srh-186								**srh-128**	srg-37	**sri-26**	**sri-26**													**srh-218**	**sri-21**										
		srh-193								**srh-210**	**srg-39**	**sri-39**	**sri-36**													**srh-240**	**sri-26**										
		srh-199								**srh-218**	srg-41	**srj-4**	**sri-39**													**srh-269**	**srm-4**										
		srh-211								**sri-5**	srg-47	**srm-1**	**srj-5**													**srh-270**	**srr-3**										
		srh-218								srl-14	**srg-58**	**srm-2**	**srm-1**													**sri-5**	**sri-4**										
		srh-220								**sri-21**	**srg-66**	**srm-6**	**srr-7**													**sri-18**	**srr-7**										
		srh-234								**sri-26**	**srh-62**	**sri-20**	**sru-5**													**sri-21**	**srua-28**										
		srh-266								**srm-1**	**srh-71**	**sru-12**	**srua-38**													**sri-26**	**srt-70**										
		srh-270								**srm-2**	**srh-100**	**sru-30**	**sru-1**													**srm-2**	**sru-1**										
		srh-279								**srm-4**	**srh-142**	**sru-48**	**sru-8**													**sru-1**	**sru-2**										
		srh-281								**srm-5**	**srh-201**	**sru-5**	**sru-5**													**sru-2**	**sru-8**										
		sri-9								**srua-28**	**srh-211**	**sru-12**	**sru-8**													**sru-8**	**sru-12**										
		sri-12								**srua-29**	**srh-240**	**sru-21**	**sru-27**													**sru-27**	**sru-30**										
		sri-18								**sru-8**	**srh-241**	**sru-34**	**sru-34**													**sru-34**	**sru-38**										
		sri-26								**sru-12**	**sri-18**	**sru-44**	**srua-108**													**sru-108**	**srv-5**										
		sri-28								sru-38	**sri-36**	**srz-24**	**sru-4**													**sru-4**	**srv-27**										
		sri-45								**sru-5**	**sri-39**	**str-102**	**sru-14**													**sru-14**	**srw-145**										
		sri-50								srv-11	**srj-4**		**sru-26**													**sru-26**	**srw-148**										
		srl-51								**srv-21**	**srj-5**		**str-261**													srv-38	**srx-105**										
		srl-62								srx-47	**srj-13**															**srv-27**	**srx-110**										
		srm-1								**srx-105**	**srj-20**															**srw-145**	**srx-6**										
		srq-1								**srsa-6**	**srj-23**															**srw-14**	**srz-1**										
		srsx-37								**srsa-7**	**srj-24**															**srx-105**	**srz-45**										
		srt-65								srx-1	**srj-25**															**srsa-7**	**srz-56**										
		srv-4								**srz-27**	**srj-38**															**srr-1**	**str-52**										
		sru-17								**srz-45**	**(srj-53)**															**srz-45**	**str-84**										
		srv-3								**str-84**	**srm-1**															**str-84**	**str-90**										
		srv-4								**str-90**	**srm-2**															**str-90**	**str-114**										
		srv-12								**str-114**	**srm-5**															**str-114**											
		srw-138									srm-6																										
		sru-1									srm-1																										
		sru-44									srr-7																										
		sru-14									srr-8																										
		srz-4									srr-9																										
		srz-5									srsa-5																										
		sru-16									srsa-27																										
		sru-24									srsa-28																										
		sru-28									srsa-30																										
		sru-32									srsa-38																										
		sru-56									srt-8																										
		srz-61									srt-20																										
		srz-66									srt-27																										
		srz-67									srt-36																										
		srz-99									srt-38																										
		srx-102									srt-65																										
		srz-103									srt-68																										
		srx-104									sru-8																										
		str-90									sru-12																										
		str-178									sru-17																										
		str-217									sru-30																										
											sru-48																										
											srv-1																										
											srv-17																										
											srv-4																										
											srx-10																										
											srx-17																										
											srx-22																										
											srxa-6																										
											srxa-7																										
											srz-1																										
											srz-15																										
											srz-27																										
											srz-54																										
											str-2																										
											str-3																										
											str-52																										
											str-84																										
											str-90																										
											str-97																										
											str-102																										
											str-114																										
											str-123																										
											str-231																										
											str-236																										
											str-247																										
											str-250																										

Gene in bold: newly identified in this paper
Gene in non-bold: previously identified
(Gene in parenthesis): ID based on position and morphology, not confirmed with neuron-specific reporter

Table S3: Primers

Primer sequences for the reporters generated by the Vancouver consortium (BC strains) can be found at http://www.gfpworm.org

Gene	Strain	Primer A*	Primer B
srb-17	OH14364 / OH14365	cagaagaaatggacacaactgactt	ttggattgttaagagcaagatggaa
srbc-7	OH14971 / OH14972	gtggttgcaagtcggaccc	gccttcttgagaagaggacat
srd-4	OH13857 / OH13858	cattatcgcataactgaaatatctgg	ctttgtacatttttgatatttttac
srd-5	OH13859 / OH13860	tgaactttctacatgtattatgc	tatttttggaatgagggaattataac
srd-10	OH13861 / OH13862	gtaccttactttaacttattgtttc	gttgaatttggtctgtgagctg
srd-11	OH13863 / OH13864	acattattgataatcatacaatggg	gatagagtccagcatttttcaag
srd-32	OH14368	tgttccacaaaaattcgaaagagc	cttcaaacggcaaatgatgacact
srg-4	OH14238	tgtatcagtcacttctgtcatcagg	tgcattggctcattttatgctc
srg-14	OH14329 / OH14240	aggacctcaaggtgttgatgg	tctgaagaaagtacggtgccc
srg-25	OH14360 / OH14361	agtgagctggcgcaggtttg	caatcaatatgaatagaagacaaaagta
srg-29	OH14241 / OH14242	ttcgttgttgtacccagacgg	agaaactggtgtctgatacaagg
srg-31	OH14243	ccggatttgcagaataccaagc	agtgatgagaaggcttgacagc
srg-32	OH14244 / OH14245	caatttatcgcactgatctctgaag	ttgaggggcgcgaagagtaac
srg-39	OH14246 / OH14247	gttgcttcaaacacataggctcc	aacagagtgatcaagaagaaccac
srg-58	OH14248 / OH14249	ggacacaggctcatgatgttatg	acattgaggaagtggagttgctc
srg-64	OH15128 / OH15129	tgggtcatttctgcaacacgtag	gtcgttgagctgagcgtcac
srg-66	OH14250	tcaactgtaatggttgtttcccac	gtccagcttgacgtcttccag
srh-4	OH13833 / OH13834	gataattgaaacgaagtatttgaaac	taatttttttttggggattttgg
srh-5	OH13835 / OH13836	ggttgtttgatatttttctaa	gtttttgactcaatgtgagg
srh-7	OH13837 / OH13838	gaacaggaaattttggaagcg	gattttattaaaccaagtattaaaagttaa
srh-62	OH14289 / OH14290	gtcaccattgtggttttggagc	caggtctgctttcaacaacagg
srh-71	OH14267 / OH14268	gggttcgaattggagacagacg	ggcggagaagtctctagacat
srh-74	OH14958 / OH14959	gcacaacattgaatgcaccagc	aaaaacaccctggctatgttggg
srh-76	OH14291 / OH14292	acagatgagccagaaccaatgg	gagtctgctttgtgccgacat
srh-100	OH14293 / OH14294	agggaattccagtgctttcac	agatgtaggagaaggcaagtg
srh-127	OH14305 / OH14306	tgaacacttgttttttcagtacaac	ttatttgaaaatttggtaggtgagg
srh-130	OH14307 / OH14308	tgtcctggtgtgatttcgatattcc	taataagaaaatttaggcttagg
srh-142	OH14295 / OH14296	ctgatcgctgggcatttgaag	cccgaaaatatgaagtggcac
srh-193	OH14297 / OH14298	agattaccgccgtttaggctg	tgagtcattccggaggaggc
srh-199	OH14299 / OH14300	cagtagtttgaaccgccataacg	atccggtatacatgtatagttcat
srh-201	OH14301 / OH14302	cggaatctgatttgccgaaatcaac	aaactgccgcgaacatcatcc
srh-210	OH14313	gtcatggttataaaagctagatc	ttgattattgcaagaatgtttattttaag
srh-211	OH14315 / OH14316	agtttggtagtttttatccgctg	ttgttgctcaatgtgaatgatcgg
srh-218	OH14317 / OH14318	gctagcatttcttgtatggattc	atcgttaaacataaaatatcagcaa
srh-240	OH14319 / OH14320	ctctgcaaatgtcccactttattcg	ctgacaaagtgcacaattaattcgc
srh-241	OH14321 / OH14322	gcagttattcattttctgaaaacc	attgatttgaaaatttttgattaaaag
srh-266	OH14269 / OH14270	ccaacagtaattgttaattttctgc	tttgtggtgaaatgttgaatcaatc
srh-269	OH14323 / OH14324	ccagttatccattggtctaaatttg	gttgagattaaaagtttaaaacaaa
srh-270	OH14337 / OH14338	ggaagtaatgtttgagggttgtg	tttcagaaatgtgaagctagactaa
srh-277	OH14303 / OH14304	gttgcacagccggttatgcg	ttgtggcgacggcgacca
sri-1	OH13839 / OH13840	gaaaattgcattatattaatgttgttcaag	catttttagtatgctaaactc
sri-5	OH13841 / OH13842	ccattctgaaattgaaaaatttgaac	gctggaaaagctgaaaaaatg
sri-9	OH13843 / OH13844	ttctgagctgtaatttggaaaactg	gtttttgaagccttgaaataaaccg
sri-12	OH13845 / OH13846	tttcgagttctaggagctcaaaaag	gctgaaaaattggaattttcactg
sri-18	OH13847 / OH13848	tattttaatgttttcaaaactctctg	tacgtgattgaaaaatggagctg
sri-21	OH13849 / OH13850	agaatgcgtacaattttgccg	acatatgtgaaaaaaaggcattgg
sri-26	OH14366 / OH14367	aggacatccattgccactatttg	gacttttcaaataaaaatattcttgc
sri-36	OH13851 / OH13852	gatttttagtgtgacccgttatg	gggtggtgaagtttatcgtcat
sri-39	OH13853 / OH13854	actttttgctgctgctacgtc	tcaactgacatgtcacttgatttg
sri-45	OH14964 / OH14965	gacttgacaatttggccagc	tgaagtcacattgaaactcattgc
sri-50	OH14953	ccaaaagggcatcgagaattgg	aaggaacaagatatatgaaagct
sri-62	OH13855	gtagttccttaattgtttgacgtg	catttgagtgatttcatttgggg
srj-4	OH14222	tgtcagtgacgagtagatcatgg	gagtccaaaaatgcgtgaatcc
srj-5	OH14223 / OH14224	gcttttccgttgatcgacccc	aatgccaaaaattagtggcatattc
srj-13	OH14975 / OH14976	gaaagaacacgtgaaatgagcaac	tctatgtgcccagcgaattagc
srj-20	OH14225	accttcagcagttttacacgac	tagtgcgcccagttaacaaac
srj-21	OH14339 / OH14340	tgtcggaattcaacacgtcgg	tgaggacagtagttttctattatactc
srj-22	OH14226	gaatgaagtattgcgcccagtc	tgtcggaattcaacacgtcgg
srj-23	OH14970	agaaggcgatgagagcgacc	tggagaccaagtgaatgatcgg
srj-25	OH14227	tgggaacaatacagctcaagtg	agcttgtgcgcatttttacagtg
srj-27	OH14228 / OH14229	gtaacgagcacaaatcacgcc	aaatgaacatgctccgccgac
srj-38	OH14230 / OH14231	agagccacatgagtttccgttg	ggcgtaggatgaggaagaagc
srj-44	OH15130 / OH15131	aagcaacctacgaatcatggag	ttcaccaagaaagttagggcac
srj-53	OH15132 / OH15133	tctaaagaaaactgaataggactgg	attcgtcgagcatcactcgtg
srm-1	OH14760	gtaattatccattgggaattgtcgg	atctgaaatatttaaaggtatttgatagat
srm-2	OH14761	gttcttgatagaatagccttctgag	ttctggaattttggatacgagttta
srm-3	OH14762	caagtcagccatttctttctgg	ctgtgaaaaaaatatattctttctaataaa
srm-4	OH14763	tgtttctaatttttcttgaaacatc	tgggtgttatggattattggtatga
srm-5	OH14764	aacttctgaagttcggtcatttgc	agttcaataatgtgagtctgcaaac
srm-6	OH14765	ggtaatcaaaactgaatcgaagc	ctgaaattaaatgttgttatgattccttttt
srn-1	OH15134 / OH15135	tggcctacggaagctctcg	agccattttatttctggaaacaaga
srr-1	OH15136 / OH15137	tcatacatacacacatagtagaggg	cgcttcaaccatcggggtttc
srr-2	OH14766	gcgcatttttggcgtaaaaagagg	tgttgaaaaatttgaaaatttttcagcacga
srr-3	OH14767	caccgattactgttttgaaagctg	ctttttctattcgaatttacaaagttttcc
srr-4	OH14768	agttcttgtagaacaaggaattcag	tccgttcatgaacaactttgactca
srr-7	OH14770	gttgatatacatttggaaagcgtag	acatagtaacgagcacaaatcacgc
srr-8	OH14771	catggcgaataagaaaaatgacg	accaggaagatccacgacaaa
srr-9	OH14772	gggcacgtttgatttaaatgatctc	caatttatcgagttctgaaatgaaa
srr-10	OH14773	ccactggatccgacattttgtag	tccaaaactttttaaaatcaagtcaa
srsx-5	OH14774	gcccgattgcaatgatttctcg	cacaatgcacattgcaaataagc
srsx-6	OH15138 / OH15139	cacatgtcttgcatatacacaaacg	ccagcgtgccgtacatttttc
srsx-12	OH14232 / OH14233	aggtcaagcacattggcgatg	ttattaacggactcgacgctc

srsx-27	OH14341 / OH14342	ctcatttgattcaaacttatgcagg	tttgagcagaaatgaaacagtttg
srsx-28	OH14234 / OH14235	gcagctcgacgaatgacagttg	tctccttcgaaacgtagtcaaac
srsx-37	OH14370 / OH14371	aaatatgagaagctgctggaac	cttctcaaaaagctgataccataaca
srsx-38	OH14235 / OH14236	tcaacaagcttccgatccacc	agagactccattgtttgggtgtc
sru-1	OH13877 / OH13878	aagggaattatcaaactgatacttc	gtattgtatcagggagtccagac
sru-2	OH13879 / OH13880	aagatcctgcagtgagttgatc	cggaacgattagagatatttcaggc
sru-8	OH13881 / OH13882	cgagaatgaattcgccaataatgc	gtaaattttcgatggcacagg
sru-12	OH13883 / OH13884	gaaagcaggagacaattattgtg	cgttgatctccttgaattgatac
sru-30	OH13885 / OH13886	caaggagttcgaaaatgttctg	tttgcggggaataaggtgacc
sru-48	OH13887 / OH13888	cgtccgctccagttgaaatgac	ttcccaaaagttgattgagccg
srv-3	OH14750	cggccataattttgaaagttcacgg	ttttggaggagaaagttgagcaaat
srv-5	OH14751	aacaaactctgtgtatgcgtaaacg	aatctgaaataatattgaatagaaa
srv-8	OH14752	gaagtcgagataataacaaatcatg	ctggaaaactgaaattatcctgatc
srv-12	OH14753 / OH14754	tagtactttgctttgaagagatctc	tttagactttcaagttggaattctt
srv-17	OH14755	tatgcgtctgtgctctcttctaag	agactttgtgttaacatcatcgtcg
srv-21	OH15140 / OH15141	taagtgggatacaataagaacaacg	ttctgaaaatctacttttaatgtaa
srv-27	OH14756	aaccacgcatatagaatatccctgg	ctgaaataatttgttttaatttttg
srv-32	OH14757	gcaacatgtaagctataaagactac	ctagaaatattttagaaaagttgat
srv-34	OH14758 / OH14759	aaacacgacgttatgctgaatgaag	atctgatttagattttagcacaaaag
srw-119	OH14973 / OH14974	gtggatttatgcgatcaggtttcg	gatgtttccagaaaggtgaagc
srw-145	OH14362 / OH14363	tcatttttttgcagctgaaatttgg	tttttgtattagttttaagtgcagtgag
srx-1	OH13865 / OH13866	gagaccagatgcgagatgaatg	agttcaatcatctggtacaaggc
srx-3	OH13867 / OH13868	caagcgcattgatttaatttagatg	tgactgcttcagagaaactccc
srx-4	OH13869 / OH13870	acctgaaaattcttgttctctgg	gaattccatcatgttctgctgg
srx-10	OH13871 / OH13872	cttgcacggaaaaggcccgac	cttggagagtgatgattatagcg
srx-17	OH13873 / OH13874	gaaagctttgtaaattccgaagg	catccttcgaggggccccaac
srx-22	OH13875 / OH13876	cggtgtttgtgatagcacggtag	tatggctctcgcccatatctg
srx-44	OH14968 / OH14969	tctaataactccaactgaacccc	aatccagtttcgtgacgcttcg
srz-4	OH15142 / OH15143	tcgtcgtcaatcgttggcatac	ccgcaccaattcctccaatcac
srz-24	OH14954 / OH14955	gtgttcgaagaaggaaatcccc	tgactcgagttgctcatctctg
srz-32	OH14962 / OH14963	agctcagaagcatagtcctatgc	cgtggtgaactccatgagagac
srz-54	OH14265 / OH14266	caacagcgattcaccaatccc	gtgagccaacatggaattcgg
srz-56	OH14838 / OH14839	gccaatttgccgatgtgccg	agctcgtagaattcatgagagc
srz-61	OH14966 / OH14967	cgagaaaaacagcggagaatagg	ccactgatctgaaactgattttcc
srz-66	OH14956 / OH14957	agtgtagctcgtgcttcagag	tatggcttgcttgcgttatgg
srz-102	OH14343 / OH14344	tagaatgcaaccataagctc	ggtgatatatacaaatatgaggttgc
srz-104	OH14840 / OH14841	caaacttcaacagttcgacccc	tgcttggaaaataagcgaaatcc
str-31	OH14271 / OH14272	tgcttcacaggaaacggtctg	tatctcacgaaaaaactacttcggaac
str-52	OH14273 / OH14274	ttcggtaaaattcacaatagagg	gaaattgtagtagctgatagttatg
str-84	OH14378 / OH14379	cgttatagttcgatagtttttctgtca	tgttgaaagtttaactgaaaatttgaaact
str-85	OH14376 / OH14377	tgtcgtcacttcgcgattgag	ccattttgcacttatcctatagaacg
str-94	OH14275 / OH14276	cgtgaaacagtggacatttcttc	aattcgcatctgaaagaatcaaaaa
str-97	OH14372 / OH14373	ggtggttccaatatcaaatcag	caatggtatatgcttgagtaaacat
str-102	OH14374 / OH14375	gaatgaggaactgatttaggccc	actgagaatgttaaaaagggaagt
str-114	OH14380 / OH14381	gaattgacaaagggtttgcagac	ctgaaaacaaagcgctcatattttaa
str-121	OH14277 / OH14278	gttagagctggatcttttatggg	ctgaaaatttcggaaattgactatg
str-123	OH14388 / OH14389	aaaaatcccaatcaaatatgaatgc	cgttgctaacaaatgatgtgcattc
str-125	OH14390 / OH14391	gaggagagaaagctggagatcg	ctggaaagtataagtatgttgagta
str-129	OH14392 / OH14393	aggacaagacaaagatatgatctcg	tacctgaggaccggaaatgaaattt
str-130	OH14394 / OH14395	tcgcagaataacttttgtttaaccg	tttccatcgtaatgtgtttcggtta
str-143	OH14396 / OH14397	gaatccctactacgtcatttcattg	gaagttatatcataatgaataaattccg
str-148	OH14398 / OH14399	caccagagaaaggagacaggc	tttcgtggaaaattggagtgaaatg
str-178	OH14279 / OH14280	tattctcttttcaactggccgac	ttttgaatagtgtttcagtgtctga
str-231	OH14281 / OH14282	gatacatcgtttcatcatgatac	ggcgactcaataatgggccgt
str-233	OH14283 / OH14284	cgttcaatgatgcgaataaattc	ttcatccgttggcgacattat
str-236	OH14400 / OH14401	aggatgctacaattaggggacg	tgaattaataattctagaagtaatagtttc
str-247	OH14285 / OH14286	gtgaagtgacttccttaattgac	tttcacaccgtttttttttgcgtc
str-249	OH14402 / OH14403	aaatactttaaacaggagttcagcg	tattttattttaggaactgttagaaaaaat
str-250	OH14386 / OH14387	gcttagccgctccaataaactaac	gttgccttgatatttgtgaaaacaa
str-253	OH14369 / OH14385	agccaaactttgctcgacatctg	gtcaattttgagttttctagacttttctag
str-261	OH14287 / OH14288	accattgtttgtcggcagctc	tttttctttgctttgaaaaaaaatt
str-262	OH14384	gagcgaaaagctcataattacacg	attttgaaacaaaacttccttcaacc