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From Chanel to Dolce: Identification of neural substrates that mediate nematode attraction to perfume

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Abstract

The perfume industry reaches over 60 billion dollars in revenue annually, partially due to the numerous chemicals that allow for a cologne's highly attractive aroma. In addition, the preference of colognes by an individual and those around them can vary. Understanding how these perfumes are sensed, processed, and generate attractive preferences is still not understood. Using chemotaxis assays, we demonstrate strong attraction in the worm towards various oil-based colognes. We have begun to characterize the neural architecture that drives this behavior. We have identified multiple sensory genes, neurons and neurotransmitters mediating this attraction to human sensed colognes, like Chanel.

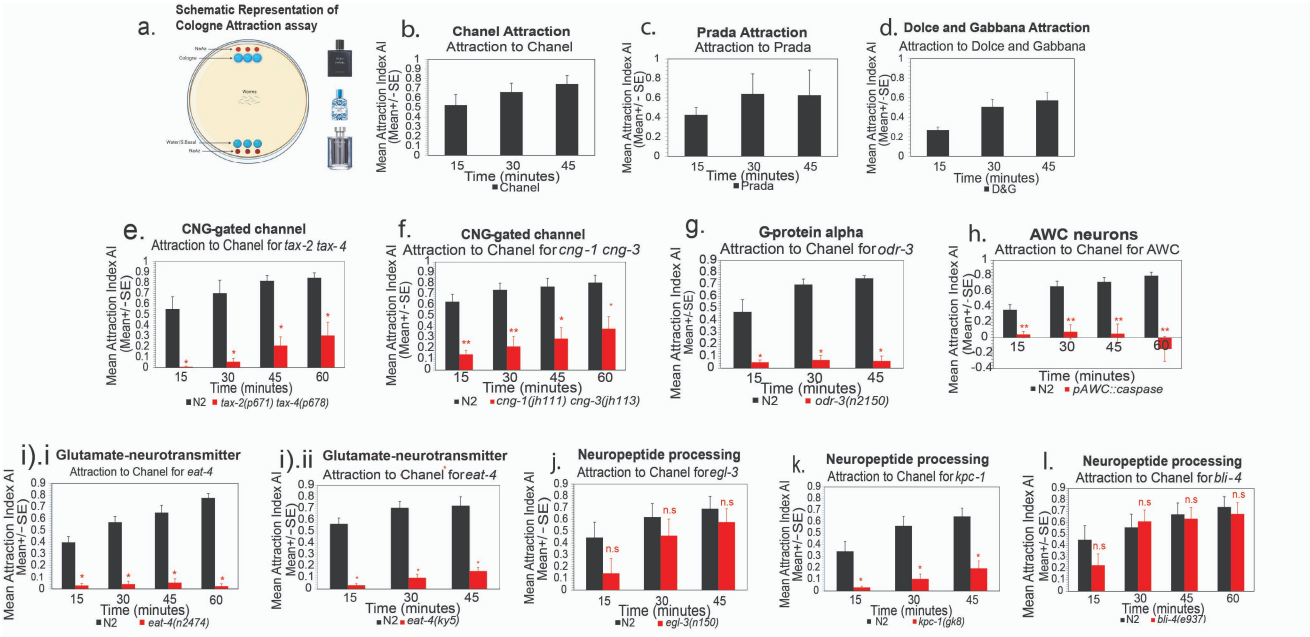

Figure 1. Worms are attracted to cologne and use select mechanisms to perform odor-guided behavior:

a) Schematic of behavioral assay for cologne attraction examination. Assay used for Chanel, Prada, and Dolce and Gabbana attraction assays. Assays ranging from 45 to 60 minutes in length.

b) Wild type animals were examined for attraction to Chanel, **c)** Prada, **d)** Dolce and Gabbana (D&G) colognes under identical conditions (0–45-minute assay) n=3-5 assays, conducted over 3-5 days.

e) CNG-gated ion channels, *tax-2(p671)* *tax-4(p678)* mutants are defective for Chanel attraction, 60-minute assay, n= 7 assays, conducted over 7 days.

f) CNG-gated ion channels, *cng-1(jh111)* *cng-3(jh113)* mutants are defective for Chanel attraction, 60-minute assay, n = 6 assays, conducted over 6 days.

g) G-protein alpha subunit mutant, *odr-3*. *odr-3(n2150)* mutants are defective for Chanel attraction, 45-minute assay, n = 3 assays, conducted over 3 days.

h) Sensory neurons, AWC, mediate olfactory behavior to Chanel. Worms lacking AWC sensory neurons through using AWC-specific caspase expression show defective attraction to Chanel, 60-minute assay, n = 7 assays, conducted over 7 days.

I) Glutamate is required for attraction to Chanel. Examination of *eat-4* mutants**. i)** *eat-4(n2474)* mutants lacking glutamate signaling, and **ii)** *eat-4(ky5)* mutants were compared to wild type worms in the Chanel chemotaxis assay, 60- and 45-minute assays, respectively. *eat-4* mutants are defective for Chanel attraction, n= 3 and 5 assays, conducted over 3 and 5 days, respectively).

j-l) Neuropeptides are required for Chanel attraction. Neuropeptide processing single mutants, lacking *egl-3(n150)*, *kpc-1(gk8)* and *bli-4(e937)* were examined. *egl-3(n150)* mutants (normal response), *bli-4(e937)* mutants (normal response), *kpc-1(gk8)* mutants (reduced attraction observed), 45-, 45-and 60-minute assays, respectively, n = 5, 3 and 6 assays, conducted over 5, 3 and 6 days, respectively).

Black represents wild type columns; red represents mutant animals.

Mean ±SEM. ***p≤0.001, **p≤0.01, *p≤0.05; no asterisk (n.s) denotes no statistical difference. A Mann Whitney U Test was used to compare each genetic mutant or transgenic strain to wild type N2 worms tested on the same day in parallel. Number of assays per genotype tested are indicated as number of assays performed across a given number of days.

Description

Organisms across vertebrates and invertebrates can sense odors and generate appropriate decisions based on odor-guided behavior (Leon Noreña et al., 2025; Buck and Axel, 1991). Animals extensively use olfactory behavior to shape key behaviors during development, as well as during social interactions, sexual attraction, and defense-like behaviors (Mallick et al., 2024; Li and Liberles, 2015; Özlem Atmiş et al., 2025; Roberts et al., 2026). Human sensation of everyday smells that originate from attractive aromas, like colognes, are widely appreciated and used by millions of people. Despite this frequent use of colognes, and appreciation of their attraction, the understanding of olfactory pathways that shape behavior toward these types of colognes is not fully understood (Lenochova et al., 2012; Chróst et al., 2021). The molecular mechanisms that generate responses to different types of chemicals that may be perceived as variably attractive, or even repulsive in select cases are also not understood (Kurian et al., 2021; Ronnett and Moon, 2002).

The nematode, *C. elegans*, is capable of exquisite sensitivity to odorants that are perceived attractive, or repulsive, dependent on the nature of/or concentration of the odorant (Yoshida et al., 2012; Bargmann et al., 1993; Troemel et al., 1997; Chalasani et al., 2007). *C. elegans* are able to sense attractants ranging from single presented cues like diacetyl, benzaldehyde, and IAA (Sengupta et al., 1996; Troemel et al., 1997; Nutley et al., 2000; Bargmann et al., 1993). Through to more complex stimuli, like, bacterial food, coffee and other plant derived odors (Fryer et al., 2024; Vega et al., 2024). Various sensory molecules, neurons and neurotransmitters have been identified for these stimuli (Chalasani et al., 2007; Ramos et al., 2022; Yoshida et al., 2012). Despite these findings, understanding the sensory transduction molecules and circuits that require sensation of more complex stimuli, like colognes are not understood.

We sought to investigate how worms respond to oil-based colognes and begin identifying the neural circuitry involved in these responses. We show that *C. elegans* are attracted to Chanel, Prada, and Dolce and Gabbana. In the present study, we use a population chemotaxis assay that exposes *C. elegans* to different colognes, and we examine olfactory behavior to each cologne in worms to characterize the molecular machinery involved in odor-guided behavior to select colognes (Bargmann et al., 1993, Bargmann and Horvitz, 1991; Vega et al., 2024; Ramos et al., 2022). We examine genetic mutants and strains expressing neuron selective transgenes that remove neurons to begin to characterize the sensory transduction molecules, neurotransmitters and key neurons that mediate cologne attraction (Schiavo et al., 1992; Teo et al., 2022). We hope these studies provide a group of molecular substrates and key neural architecture to further investigate how worm olfactory circuits may be distinct but overlap dependent on the cologne presented and sensed by an individual. Furthermore, we hope our studies will begin to provide insight into how different types of odors sensed in humans, like colognes that are perceived as attractive may act through distinct but overlapping molecular pathways, neural circuits and neurotransmitter systems

To investigate worm olfactory behavior to a variety of colognes, we examined wild type hermaphrodite worms for their chemotactic behavior to three different colognes. These colognes, Chanel (Bleu de Chanel), Prada Le Homme (Parfum) and Dolce and Gabbana were examined in a long-range chemotaxis assay in wild type N2 worms (Figure 1a-d, Bargmann et al., 1993, Vega et al., 2024). Wild type animals have been analyzed for attraction to an array of chemicals. In addition, the behavior towards an odor is often concentrated dependent (Bargmann et al., 1993, Bargmann and Horvitz, 1991; Harris et al., 2014; Yoshida et al., 2011, Ramos et al., 2022). In this study, wild-type worms were examined for chemotaxis to colognes at non-diluted forms from the original cologne bottles (Figure 1a-d, Schematic shown). Interestingly, wild-type animals were attracted to all colognes tested that we discuss in this study. These colognes stimulate odor-guided movement of worms towards each of the colognes by 30 minutes, and minimal numbers of worms at the control (Figure 1b-d). Each cologne generated significant positive attraction indexes between +0.5 and +0.9 (Figure 1 b-d). Wild type animals showed comparable index values across all colognes (Fig 1b-d). Suggesting, worms are attracted to different colognes across 45-minute exposure to each cologne tested. This provides a platform to investigate the molecular mechanisms and neural circuits that mediate cologne attraction. Our continued study focused on examining genetic mutants or transgenic strains in response to Chanel.

To investigate the sensory transduction molecules in cologne attraction, we examined mutants that lack distinct sensory expressed genes. Sensory encoding genes have been shown to mediate sensory responses from olfaction through to gustatory responses in *C. elegans* (Coburn and Bargmann, 1996; Tobin et al., 1997; Harris et al., 2014; Ramos et al., 2022). We present two sets of mutants that when examined show defective attraction to Chanel. CNG-gated-ion channel mutants lacking *tax-2* and *tax-4*-encoded cGMP-gated channels are required for Chanel attraction based on double mutants lacking both *tax-2* and *tax-4*(*tax-2*(*p671*) *tax-4*(*p678*)) showing strong defects to Chanel (Figure 1e). *tax*-encoded genes have been implicated in various sensory behaviors, including thermotaxis, gustation, olfaction and light sensation (Coburn and Bargmann, 1996; Harris et al., 2014; Ramos et al., 2022; Vega et al., 2024). In addition, we also tested CNG-gated channel mutants, encoded by *cng-1* and *cng-3* that have been shown to mediate thermotactic, olfactory behavior and plasticity behavior (Cho et al., 2005; O Halloran et al., 2017; He et al., 2016, Figure 1f). Interestingly, *cng-3* *cng-1* mutants were reduced although showing some attraction to Chanel. This suggests that CNG-gated channels encoded by *tax-2*/*4* and *cng-1*/*3* are required for attraction behavior to Chanel. We also investigated what additional sensory genes are required for cologne attraction. To do this, we examined mutants that lack key sensory transduction pathways for attraction and repulsion in *C. elegans*. Specifically, we focused on G-proteins expressed in key olfactory sensory neurons (Royaie et al., 1998; Vega et al., 2024; Harris et al., 2014). Upon examination of G-protein alpha mutants, mutants lacking *odr-3* (*odr-3*(*n1250*)) were defective for responses to Chanel (Figure 1g). Suggesting, *odr-3*-encoded G-proteins are required for Chanel attraction (Figure 1g). Based on our findings above, we sought to identify sensory neurons involved in cologne attraction. We examined transgenic strains that lack olfactory sensory neurons in the worm (Chalassani et al., 2007; Gray et al., 2005). Interestingly, strains lacking sensory neurons, AWC show defective attraction to Chanel, with AWC sensory neuron caspase expressing worms generating a severely defective attraction to Chanel (Beverly et al., 2011, Figure 1h). This suggests that AWC sensory neuron is one sensory neuron that plays a role in Chanel attraction (Figure 1h).

We sought to identify the methods of communication required for odor-dependent attraction to Chanel. We have identified two different forms of neurotransmission required for cologne attraction. We show that glutamate signaling is essential for Chanel attraction (Figure 1). This was determined through examination of *eat-4* mutants. *eat-4* encodes a vesicular glutamate transporter (VGLuT) that is essential for glutamate loading into small clear synaptic vesicles (Lee et al., 1999). *eat-4* mutants showed severe defects in attraction to Chanel (Lee et al., 1995, Figure 1i). We confirmed these defects in both independently generated mutant alleles of *eat-4*(*ky5*) and *eat-4*(*n2474*) mutants that both show strong defects to multiple colognes, including Chanel (Lee et al., 1999, Figure 1i(i and ii)). Both *eat-4* mutant alleles show severe defects in attraction to Chanel.

We also examined the role of neuropeptides for cologne attraction, we examined three different enzyme mutants that lack pro-protein convertases that are essential for processing most neuropeptides in the worm (Kass et al., 2000; Husson et al., 2006; Figure 1j-l). Neuropeptide processing mutants show defects in body touch, nose touch, heat avoidance and odorant induced escape behaviors (Kass et al., 2001; Nkambeu et al., 2019; Harris et al., 2021). *egl-3*, *kpc-1* and *bli-4* are key genes that encode *C. elegans* processing enzymes for neuropeptides. Therefore, we examined each mutant lacking *egl-3*, *kpc-1* and *bli-4* encoded gene function (Figure 1j-l). *egl-3*(*n150*) mutants were overall normal for Chanel attraction (Figure 1j). *bli-4*(*e937*) mutants showed normal attraction (Figure 1l, Thacker et al., 1995). *kpc-1*(*gk8*) mutants were significantly defective during the first 15 to 30 minutes of the assay (Figure 1k, Salzberg et al., 2014). This study suggests that glutamate and neuropeptide signaling are both important for attraction to Chanel. Taken together, we have shown worms are highly attracted to multiple colognes and have identified multiple *cng*-encoding genes, a G-protein-alpha subunit, a key sensory neuron and multiple neurotransmitter types to be involved in cologne attraction.

Methods

Wild type and all mutant worms were grown under standard *C. elegans* protocols containing NGM agar and *E. coli* OP50 food source (*E.coli* OP50 strain-purchased from CGC, Minnesota, Brenner et al., 1974).

Chemotaxis Assay. Chemotaxis assay plates are NGM (Nematode Growth Media) prepared 2 days before each assay. Approximately 50 wild type young adult worms were tested in each chemotaxis assay. Briefly, NGM plates used for the assay were left at room temperature on the day of the behavioral assay. Wild type worms are washed 3 times in S. basal solution (As described in Bargmann et al., 1993; Bargmann and Horvitz, 1991; Troemel et al., 1997). The remaining worm pellet was added through pipetting to the center of the NGM assay plate as seen in figure 1a. In select assays, worm populations were transferred through worm picking from an on-food plate to a non-food plate and left for 30 seconds and then transferred to a drop of S. basal placed in the center of the chemotaxis plate. Once the worm pellet had dried (3-5 minutes), 3 drops of cologne, 2 microliters per drop were added at one side of the chemotaxis plate (as shown in Figure 1, schematic diagram, a small amount of cologne was added to a new microcentrifuge tube on the day of the assay) (Vega et al., 2024). A control sample of water was added to the opposite side of the assay plate. Small drops of sodium azide (1 microliter at 0.5M) were used to paralyze worms either at the Cologne source or control source (1 microliter). Worms that are in the center of the plate at the beginning will be left to analyze their chemotaxis over multiple times (15, 30, 45 and 60 minutes after worms were added to assay plate), which will either be analyzed for attraction, repulsion, or no biased to

the cologne odor. To determine any chemotactic attraction or avoidance, index's were generated based on calculating distribution of worms across NGM agar assay plates at 15, 30, 45 and in select cases 60 minutes after cologne addition (see Figure 1a-l). To determine attraction index throughout the assay with wild type and all genetic mutants (Bargmann et al., 1993). Total number (#) of worms at odor source (paralyzed at cologne)-total number (#) of worms paralyzed at control sample on opposite side of the assay plate/total number (#) worms on the whole chemotaxis assay plate counted at the beginning of the assay (i.e. includes all worms at attractant, control and worms that did not make either point source). Attraction Index values range from 0 to +1.0, 0 being no attraction and increasing positive number representing stronger attraction (Bargmann et al., 1993 and Wormbook.org).

All mutants were compared to wild type animals tested in parallel on the same day. Mean+/-SE was determined per experiment, and a *Mann Whitney U Test* was performed for examination of significant differences between wild type and mutant genotypes across the time points (15, 30 45, 60-minutes), tested on same day. Across all mutants tested in this study, the number of assays per genotype tested are indicated as the number of assays (n) performed across a given number of days (See Figure legend).

Reagents

N2 wild type, BR5514 *tax-2(p671) tax-4(p678)*, KJ5560 *cng-1(jh111) cng-3(jh113)*, MT6308 *eat-4(ky5)*, MT6318 *eat-4(n2474)*, CX2205 *odr-3(n2150)*, MT150 *egl-3(n150)*, VC48 *kpc-1(gk8)*, CB937 *bli-4(e937)*, PY7502 oyIs85 [*ceh-36p::TU#813+ceh-36p::TU#814+srtx-1p::GFP+unc-122p::DsRed*]. *E.coli* OP50 bacteria strain.

Colognes purchased/used in present study: Bleu de Chanel, Prada La Homme, Dolce and Gabbana. Nordstrom store. Bleu de Chanel (Eau De Parfum) product additionally purchased from Amazon (size 3.4 Oz).

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