Genetic and neuronal modulation of *D. melanogaster* female receptivity

Organizer: Peng Qionglin
Invited members: Su Xiangbin, Pan Yufeng
2018-9-28
How do we specify the topic?

- 199 items were found when searching keywords, *Drosophila receptivity*, in NCBI.

- The full texts of 136 articles were downloaded by Su Xiangbin.

- General topics, such as post-mating behavior, were drafted out after quickly read through those articles by Peng Qionglin.

- Prof. Pan Yufeng joined in the group.
How do we cooperate in a group?

The first discussion:

determining an appropriate topic and divide it into three small specific topics

- Part I  Overview, virgin female receptivity (Peng Qionglin)
- Part II  Sex-peptide (SP) signaling in post-mating switch (Su Xiangbin)
- Part III  Neuronal modulation of post-mating behaviors (Pan Yufeng)

The second discussion:

Combining three parts and rehearsing the journal report.
Genetic and neuronal modulation of *D. melanogaster* female receptivity
CONTENT

• Part I  Overview, virgin female receptivity
• Part II  Sex-peptide (SP) signaling in post-mating switch
• Part III  Neuronal modulation of post-mating behaviors
Courtship in *Drosophila melanogaster*

Discrete steps of male mating behavior:

1. Orientation towards and following the female
2. Touching abdomen with the foreleg
3. Wing extension and vibration
4. Licking of the female's genitalia
5. Attempted copulation
6. Copulation

Yamamoto, D. and M. Koganezawa (2013)
How does a female decide to copulate with a male?

-Two important male stimuli

Sex pheromones

Courtship songs

Yamamoto, D. and M. Koganezawa (2013)
How does a female decide to copulate with a male?

- Receptivity circuit inside female

Or67d mediates physiological responses to cVA

The responses to cVA were quantitatively indistinguishable in males and females.

Or67d functions in male and female mating behaviors

Or67d\textsuperscript{Gal4} mutant females display reduced receptivity

Or67d\textsuperscript{Gal4} mutant males display male-male courtship

How does a female decide to copulate with a male?

-Receptivity circuit inside female

Female receptivity phenotype of *icebox (ibx)* mutants caused by a mutation in the L1-type cell adhesion molecule *neuroglian (Nrg)*.
Genetic subdivision of *dsx* neurons

Different *dsx* genomic fragments

*dsx* fragment-GAL4 expression patterns

Zhou, C., et al. (2014)
dsx neurons and 41A01-GAL4 neurons are important for female receptivity

Zhou, C., et al. (2014)

Activation-Enhances female receptivity

Silencing-Decreases female receptivity

Silencing-Decreases female receptivity
pCd neurons are important for female receptivity

Silencing - Decreases female receptivity

Activation - Enhances female receptivity

Zhou, C., et al. (2014)
pC1 neurons are important for female receptivity

Silencing - Decreases female receptivity

Activation - Enhances female receptivity

Zhou, C., et al. (2014)
Calcium responses of female pC1 and pCd neurons to courtship song and cVA

Zhou, C., et al. (2014)
pCd and pC1 Neurons function in female receptivity

Zhou, C., et al. (2014)
How does a female decide to copulate with a male?

-Receptivity circuit inside female

**Abd-B are required for virgin female receptivity**

*Abd-B* plays a developmental role in forming the female receptivity circuit

*Abd-B* neurons is functionally required for virgin female receptivity

Abd-B, Abdominal-B homeobox (Hox) transcription factor

Silencing Abd-B neurons decreases pausing during courtship

Activating Abd-B neurons induces pausing

Abd-B neurons are required for virgin female receptivity

How does a female decide to copulate with a male?

- Receptivity circuit inside female

pain (painless) mutant females copulate earlier than wild-type females

Sakai, T., et al. (2009)

pain: a homolog of the mammalian TRPA1/ANKTM1
pain-GAL4 drives GFP reporter expression in the female brain

Sakai, T., et al. (2014)
Knockdown of *pain* expression in IPCs enhances female sexual receptivity

Sakai, T., et al. (2014)
Knockdown of *pain* expression in the MBs or EB do not affect female sexual receptivity

Sakai, T., et al. (2014)
How does a female decide to copulate with a male?

- Receptivity circuit inside female

retn (retained/dead ringer) female behavior

RETN: A-T Rich Interaction Domain (ARID) transcription factor

*retn* is antagonistic to *fru<sup>M</sup>* in production of courtship and development of the moL

*fru<sup>M</sup>*-males gain courtship activity with reduced *retn* function

dsx controls sexual behavior

fru and dsx act as parts of a ‘switch’ system controlling sexual behavior

Insulin signaling regulates female sexual receptivity during starvation in *Drosophila*

Starvation regulates female sexual receptivity

Lebreton, S., et al. (2017)
*dilp* genes showed significantly reduced sexual receptivity after starvation

Lebreton, S., et al. (2017)
Mutations of single dilps differentially affect female receptivity

Lebreton, S., et al. (2017)
Disrupting the insulin signaling in specific neuronal circuitries inhibits the effect of starvation on sexual receptivity

Lebreton, S., et al. (2017)
SUMMARY

• Whether virgin females accept males depends on multiple facts, courtship song, cVA, sensory neurons, CNS, transcription factors and so on.

• The mind of females would change after copulation, so called post-mating switch.
References


References


CONTENT

• Part I  Overview, virgin female receptivity
• Part II  Sex-peptide (SP) signaling in post-mating switch
• Part III  Neuronal modulation of post-mating behaviors
Overview:

From: MF wolfneer. 2002. The gifts that keep on giving physiological functions and evolutionary dynamics of male seminal proteins in Drosophila.

Mating behavior:

A. Orientation of the male towards the female.
B. Love song of the male.
C. The male licks the genitalia of the female.
D. Attempted copulation.
E. Copulation.
F. A rejection response by the female.

Female Post-mating behavior in *drosophila*:

1. Stimulate female egg production and ovulation.
2. Reduce their receptivity to mating.
4. A mated female has a short lifespan.
The function of sperm and seminal fluid proteins:

<table>
<thead>
<tr>
<th>sperm</th>
<th>seminal fluid proteins</th>
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<tr>
<td>Fertilization</td>
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<td>Increase egg production rate</td>
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<td>Store sperm to maintain the state of intersection</td>
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<tr>
<td>Sperm competition</td>
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<tr>
<td>Increase egg production rate</td>
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<td>Reduce female lifespan</td>
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<td>Reduce their receptivity to mating</td>
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<tr>
<td>Mediate sperm storage</td>
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</tbody>
</table>
Accessory glands proteins:

**Acps**: accessory gland proteins

Fig. The “evolutionary EST screen” that identified Acp genes.

From: MF Wolfner. 2002. The gifts that keep on giving physiological functions and evolutionary dynamics of male seminal proteins in Drosophila.
Sites of synthesis of seminal fluid proteins:

Accessory glands proteins:

Table 1
Sites of synthesis of seminal fluid proteins

<table>
<thead>
<tr>
<th>Site of synthesis</th>
<th>Nature of secreted substances</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accessory gland main cells</td>
<td>An estimated 83 accessory gland proteins, many with unknown functions. Acps include peptides, prohormones, glycoproteins, enzymes (putative proteases, protease inhibitors, lipases) and antibacterial peptides</td>
<td>[29,34,36,89,91,100,107,117]</td>
</tr>
<tr>
<td>Accessory gland secondary cells</td>
<td>Filaments of unknown constituents</td>
<td>[5,83]</td>
</tr>
<tr>
<td>Ejaculatory duct</td>
<td>Dup 99B (peptide)</td>
<td>[90]</td>
</tr>
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<td></td>
<td>Esterase-6 (enzyme)</td>
<td>[44,71]</td>
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<td></td>
<td>Glucose dehydrogenase (enzyme)</td>
<td>[17,18]</td>
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<td></td>
<td>Andropin (peptide)</td>
<td>[66,89]</td>
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<td>Drosomycin (peptide)</td>
<td>[39]</td>
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<td>Ejaculatory bulb</td>
<td>PEB-me (protein)</td>
<td>[63,67]</td>
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<td>cis-Vaccenyl acetate (lipid)</td>
<td>[14,16]</td>
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<tr>
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<td>Esterase-6 (enzyme)</td>
<td>[99,105]</td>
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<tr>
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<td>Drosomycin (peptide)</td>
<td>[39]</td>
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</table>

Egg-laying: Acp70A（sex peptide）、Acp26Aa、Dup99B.

Receptivity: Acp70A、Dup99B.

Sperm storage: Acp36DE.

Sex-peptide controls female post-mating behavior in *Drosophila*. 
Structure and function analysis in Sex peptide:

Fig. Structure–function relationship in Sex-peptide.
Several receptors may interact with SP. SP receptor very likely interacts with the carboxy-terminal part of SP known to be essential for eliciting the post-mating responses. The prolines indicated in red are hydroxylated and may interact with pattern recognition receptors (PRR) and thus induce antimicrobial peptide synthesis. The amino-terminal part of SP is essential for inducing the synthesis of juvenile hormone (JH) and for binding to sperm.


Fig. Female post-mating responses analyzed by using RNA interference:

Fig. Effect of SP on female receptivity:

Fig a and b. Effect of SP on oviposition and ovulation:
Molecular mechanisms of sex peptides and sex peptide receptors in post-mating response:


2. Sex peptide receptor mediates the post-mating switch in Drosophila reproductive behaviour.

3. SPR acts in nervous system.
Sex peptide regulates the gradual release of sperm in female drosophila:


Fig. Sex-Peptide Lacking the N-Terminal End Cannot Bind to Sperm.

Fig. SP Containing a Modified Trypsin Cleavage Site Binds to Sperm Permanently and Cannot Be Cleaved.
Conclusions:

In sum, the PMR of D. melanogaster females can be divided into two phases: the short-term PMR and the long-term PMR, respectively. The short-term PMR are induced immediately after mating mainly by free SP, the long-term PMR, lasting about one week, by the C-terminal SP fragment cleaved from SP bound to the sperm tail. Both responses likely elicit the PMR by binding of SP to specific sites in the central and peripheral nervous systems.
Molecular mechanisms of sex peptides in post-mating responses:


2. Sex peptide receptor mediates the post-mating switch in Drosophila reproductive behaviour.

3. SPR acts in nervous system.
SPR is required for the post-mating switch induced by SP.

Fig a. Protocol for behavioural experiments in b–e. b, Receptivity of virgin females. c, Number of eggs laid per female

From: Nilay Yapici. 2008. A receptor that mediates the postmating switch in drosophila reproductive behavior.
From: Nilay Yapici. 2008. A receptor that mediates the postmating switch in drosophila reproductive behavior.

Fig d, Re-mating frequency. e, Ovipositor extrusions per minute during a ten-min courtship assay with a naive wild-type male.
Sex Peptide Receptor is required for the release of stored sperm by mated Drosophila melanogaster females

Frank W. Avila*, Alexandra L. Mattei*, and Mariana F. Wolfner
Department of Molecular Biology and Genetics, Cornell University, Ithaca, NY, USA
Fig. SPR is required to mediate SP’s effect on sperm release from storage.

From: Nilay Yapici. 2008. A receptor that mediates the postmating switch in drosophila reproductive behavior.
Molecular mechanisms of sex peptides in post-mating responses


2. Sex peptide receptor mediates the post-mating switch in Drosophila reproductive behaviour.

3. SPR acts in nervous system.
SPR is expressed in the female reproductive organs and nervous system.

Fig. SPR is expressed in the female reproductive organs and nervous system.

From: Nilay Yapici. 2008. A receptor that mediates the postmating switch in drosophila reproductive behavior.
SPR acts in fru neurons.

Fig: SPR acts in fru neurons. a, b, c, Receptivity (a), egg-laying (b) and re-mating (c) assays for females of the indicated genotype, mated with wild-type males

From: Nilay Yapici. 2008. A receptor that mediates the postmating switch in drosophila reproductive behavior.
Conclusions:
References:


References:


CONTENT

• Part I  Overview, virgin female receptivity
• Part II  Sex-peptide (SP) signaling in post-mating switch
• Part III  Neuronal modulation of post-mating behaviors
Neuronal modulation of post-mating behaviors in *D. melanogaster* females

Pan Yufeng

2018-9-28
How do I find related papers?

500+ papers: read titles and journal names;

38 papers: read abstract or more;

22 papers: this presentation.
What happens to female during mating?

- Transfer of sperm
- Transfer of seminal fluids including sex-peptide (SP)
- Transfer of male-specific pheromones (e.g. cVA)
- Physical contact/stimulation
What happens to female during mating?

- Transfer of sperm
- Transfer of seminal fluids including sex-peptide (SP)
- Transfer of male-specific pheromones (e.g. cVA)
- Physical contact/stimulation
- Fertilization
- SP-induced post-mating behaviors
- Reduce female attractiveness;
- Unknown
Question 1: how do mated females behave differently?

- Mated females consume more amino acids
Fig 4. A post-mating signal elevates amino acid consumption during the dark phase. (A) The experimental scheme for the CAFE assays. Each L phase is shown by a white box and each D phase by a gray box. (B and C) Amino acid consumption during L (orange bars) and D (blue bars) phases was quantified using no-choice CAFE assays with the following strains: virgin CS females and CS females mated with CS or $SP^0/\Delta^{130}$ males (B;
A Molecular and Cellular Context-Dependent Role for Ir76b in Detection of Amino Acid Taste

Graphical Abstract

Authors
Anindya Ganguly, Lisa Pang, Vi-Khoi Duong, Angelina Lee, Hanni Schoniger, Erika Varady, Anupama Dahanukar

Correspondence
anupama.dahanukar@ucr.edu

In Brief
Ganguly et al. demonstrate that Ir76b mediates cellular and behavioral responses to amino acids that underlie post-mating yeast and amino acid feeding preferences of Drosophila females. Ir20a, possibly one among many factors, plays a role in changing Ir76b activity from an ungated salt receptor to an amino-acid-gated receptor.
Another study shows that mating has no influence on amino acids consumption.
Question 1: how do mated females behave differently?

- Mated females consume more amino acids
- Mated females are more aggressive
Sperm and sex peptide stimulate aggression in female Drosophila

Eleanor Bath, Samuel Bowden, Carla Peters, Anjali Reddy, Joseph A. Tobias, Evan Easton-Calabria, Nathalie Seddon, Stephen F. Goodwin & Stuart Wigby
Figure 1. Two proposed pathways for mating-induced female aggression
This is all the data this paper has.
Mentions in news, blogs & Google+

News articles (17)

Butting heads: sex enranges female fruit flies
Breitbart News Network

Butting heads: sex enranges female fruit flies
Yahoo! News

Sex enranges female fruit flies – Reports
Uncova

Frisky Female Fruit Flies Become More Aggressive Towards Each Other After Sex
Science Newsline

Butting heads: sex enranges female fruit flies
Yahoo! News

Butting heads: sex enranges female fruit flies (AFP)
Yahoo! News

Make love, then war: Study shows sex enranges female fruit flies
The Malay Mail Online

Frisky female fruit flies become more aggressive towards each other after sex
Phys.org
Question 1: how do mated females behave differently?

- Mated females consume more amino acids
- Mated females are more aggressive
- Mated females have increased locomotion activity
Drosophila male sex peptide inhibits siesta sleep and promotes locomotor activity in the post-mated female

R. Elwyn Isaac¹,* , Chenxi Li¹, Amy E. Leedale¹ and Alan D. Shirras²

(filled circle, virgin female; open square, mated female; filled triangle, male)
open bar, virgin;
hatched bar, mated to SP0 male;
dotted bar, mated to wt male.
Question 1: how do mated females behave differently?

• Mated females consume more amino acids
• Mated females are more aggressive
• Mated females have increased locomotion activity
• Mated females have increased starvation resistance
SHORT TAKE

Mating increases starvation resistance and decreases oxidative stress resistance in *Drosophila melanogaster* females

Brandy Rush,1 Sarah Sandver,1 Jessica Bruer,1 Robin Roche,2 Michael Wells2 and Jadwiga Giebiltowicz1

2002; Kubli, 2003). Mated females show reduced sexual receptivity and a substantial increase in egg production. Mating also

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**Fig. 1** Age-dependent profiles of starvation resistance in virgin and mated Canton-S females reared on molasses/cornmeal medium containing 7% yeast. Bars represent mean (± SEM) survival time, which was significantly longer for mated than for virgin females at every age tested (t-test: P < 0.01

---

**Percent survival**

- **Virgin**
- **Mated**
Increased starvation resistance in mated females may depend on selective accumulation of lipids.
In the first replication, there were 19 virgin and 26 mated females and the mated females lived an average of approximately 6 days longer.

Rather than a “cost of mating,” there appears to be a “cost of virginity” to female *D. melanogaster* in the wild.
Question 1: how do mated females behave differently?

- Mated females consume more amino acids
- Mated females are more aggressive
- Mated females have increased locomotion activity
- Mated females have increased starvation resistance
- Mated females lay eggs and reject males
Sex-peptide is the molecular basis of the sperm effect in *Drosophila melanogaster*

Huanfa Liu and Eric Kubli*

Zoological Institute, University of Zurich-Ircher, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Edited by Wendell Roelofs, Cornell University, Geneva, NY, and approved May 21, 2003 (received for review March 25, 2003)
Dispatches

Sexual Behavior: How Sex Peptide Flips the Postmating Switch of Female Flies
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
Figure 1. *fru*\(^{\text{GAL4}}\) neurons mediate female reproductive behaviours.
A receptor that mediates the post-mating switch in *Drosophila* reproductive behaviour

Nilay Yapici, Young-Joon Kim, Carlos Ribeiro & Barry J. Dickson

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**Figure 4** | **SPR acts in fru neurons.** **a, b, c.** Receptivity (a), egg-laying (b) and re-mating (c) assays for females of the indicated genotype, mated with wild-type males and assayed according to the protocol of Fig. 1a. For the RNAi rescue groups, the recombinant *fru* gene was expressed by a heat-induced UAS-SPR transgene. The RNAi and rescue groups are denoted by different symbols and the genotype combinations are indicated above columns.
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
- Subsets of ascending VNC neurons;
The *egghead* gene involved in glycosphingolipid biosynthesis provides an essential component to the SP response.
Clonal analysis of VNC Ap neuronal projections to the central brain.

egh expression in VNC neurons (tshGAL4) rescues mutant phenotype.
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
- Subsets of ascending VNC neurons;
- *fru* and *ppk*-positive sensory neurons in the genital tract;
Control of the Postmating Behavioral Switch in *Drosophila* Females by Internal Sensory Neurons

Chung-hui Yang,¹,³ Sebastian Rumpf,¹,³ Yang Xiang,¹ Michael D. Gordon,² Wei Song,¹ Lily Y. Jan,¹ and Yuh-Nung Jan¹,*

ppk-GAL4 Labels SP-Responsive Neurons
ppk-GAL4 and fru-GAL4 Expression Overlap in Sensory Neurons on the Female Reproductive Tract
SPR Acts in *ppk*+ *fru*+ Sensory Neurons
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
- Subsets of ascending VNC neurons;
- *fru* and *ppk*-positive sensory neurons in the genital tract;
- *dsx* neurons are involved (several sub-types, **including** *ppk*-positive sensory neurons, octopaminergic neurons, SAG neurons and Mip neurons);
Control of sexual differentiation and behavior by the doublesex gene in *Drosophila melanogaster*

Elizabeth J Rideout¹,³,⁴, Anthony J Dornan¹,⁴, Megan C Neville¹,²,⁴, Suzanne Eadie¹ & Stephen F Goodwin¹,²
Neural Circuitry Underlying *Drosophila* Female Postmating Behavioral Responses


...type and fitness before sanctioning mating [1]. An unresponsive female exhibits rejection behaviors such as kicking and ovipositor extrusion [1, 6–8]. A receptive female will facilitate copula...

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**A**

Percent receptive

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<td>(66)</td>
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<td>(46)</td>
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**B**

Ovipositor extrusion/min

<table>
<thead>
<tr>
<th></th>
<th>UAS-mSP/+;UAS-mSP/+</th>
<th>d sxGal4/+</th>
<th>d sxGal4,elav-Gal80/+</th>
<th>UAS-mSP/+;d sxGal4/UAS-mSP</th>
<th>UAS-mSP/+;d sxGal4,elav-Gal80/UAS-mSP</th>
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<tr>
<td>mated</td>
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<td>(38)</td>
<td>(41)</td>
<td>(22)</td>
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**A**

Percentage remaining

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**B**

Ovipositor extrusion/min

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<td>virgin</td>
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**A**

**B**

**virgin**

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dsx, fru and ppk sensory neurons in the reproductive tract
$dsx$ neurons in Abg involved in post-mating behaviors
Question 2: what’s the neural basis for post-mating behaviors

- **fru**GAL4 neurons are involved;
- Subsets of ascending VNC neurons;
- **fru** and **ppk**-positive sensory neurons in the genital tract;
- **dsx** neurons are involved (several sub-types, including **ppk**-positive sensory neurons, **octopaminergic neurons**, SAG neurons and Mip neurons);
Sexually Dimorphic Octopaminergic Neurons Modulate Female Postmating Behaviors in *Drosophila*

Carolina Rezával, Tetsuya Nojima, Megan C. Neville, Andrew C. Lin, and Stephen F. Goodwin

We first evaluated the effects of depleting OA on female behavior by testing a null mutation in the gene that encodes

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**Figure Legend**

**A**
- Copulation (%)
- 31°C vs. 22°C
- **p < 0.01**

**B**
- Ovipositor extrusion
- 31°C vs. 22°C
- **p < 0.01**

**C**
- Egg laying
- 31°C vs. 22°C
- **p < 0.0001**

**D**
- Remating (%)
- M vs. ♀
- *p < 0.05*

**E**
- Ovipositor extrusion
- M vs. ♀
- **p < 0.01**

**F**
- Courtship index
- M vs. ♀
- *p < 0.05*

**G**
- Egg laying
- M vs. ♀
- **p < 0.0001**

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*Tdc2+ Neurons Are Involved in Post-mating Behaviors*
Sexually Dimorphic Tdc2/dsx+ Abg neurons involved post-mating behaviors
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
- Subsets of ascending VNC neurons;
- *fru* and *ppk*-positive sensory neurons in the genital tract;
- *dsx* neurons are involved (several sub-types, including *ppk*-positive sensory neurons, octopaminergic neurons, SAG neurons and Mip neurons);
Identification of VT lines that induce post-mating behaviors when driving UAS-kir2.1
SAG neurons
SAG neurons are downstream of *ppk*, *fru* and/or *dsx* sensory neurons in the reproductive tract.
SAG neurons are *dsx*-positive, but *fru*-negative
Question 2: what’s the neural basis for post-mating behaviors

- *fruGAL4* neurons are involved;
- Subsets of ascending VNC neurons;
- *fru* and *ppk*-positive sensory neurons in the genital tract;
- *dsx* neurons are involved (several sub-types, including *ppk*-positive sensory neurons, octopaminergic neurons, SAG neurons and *Mip neurons*);
Female-specific myoinhibitory peptide neurons regulate mating receptivity in *Drosophila melanogaster*.

Mip-neurons are involved in post-mating behaviors.
dsx-positive Mip neurons are involved in receptivity
Mip neurons may position within the SPSN and SAG signaling axis.
References


References


