

Mate-copying in *Drosophila*: a matter of taste or disgust?

Guillaume Lespagnol

May 24, 2019

Contents

1	Introduction	2
2	Material and Methods	5
2.1	Fly maintenance	5
2.2	Fly stains and crossings	5
2.3	General experimental procedures	6
2.3.1	Acceptance/Rejection experiment	7
2.3.2	Neuronal blockade experiment	8
2.4	Mate-copying score	9
2.5	Statistical analyses	9
2.6	Ethical statements	10
3	Results	10
3.1	A/R Experiment	10
3.2	Neuronal blockade experiment	11

(Danchin et al. 2018, p. 118).

Or several: Danchin et al. (e.g. 2018, p. 118) and Danchin et al. (but see 2018, p. 1789)

()

Or between brackets: (Danchin et al. 2018; but see Dagaëff et al. 2016, p. 1789).

1 Introduction

Sexual selection is at the origin of an intense struggle between conspecifics. In some species, it is by harm and winning is a matter of weight, strength or weapons (Clutton-Brock 1982; Anderson and Fedak 1985). In others it is by charms in a much more peaceful contest, and the breeders are chosen by the other sex. The mate-choice (i.e. intersexual selection) can lead to captivating and highly complex traits, such as courtships or songs in birds (**danchin_ecologie_2005**). Nevertheless, many species do not exhibit such traits and the choice is based on much more ambiguous and discreet signs. “The most difficult and important act of choice is the choice of a mate” (Fisher 1915), in context of mate-choice making a mistake can be very expensive since it impact individual’s offspring. To avoid mistakes, many species have acquired the capacity to learn from the observation of others and can therefore use social learning in numerous decision-making processes.

Social learning can take different form, as teaching or copying. The latter is simpler, and even exists in non-social invertebrates (Coolen et al. 2005; Laidre Mark E. 2010). Many different behaviours can be copied (Thornton Alex et al. 2010; Leeuwen et al. 2014). It’s particularly beneficial when individual learning is costly (time consuming or dangerous; also see (Webster M.M and Laland K.N 2008)) as in mate-choice. Therefore, copying the mate-choice of potentially older conspecifics can be a reliable choice for naive individuals to avoid unnecessary mistakes.

Mate-copying is a form of social learning in which the observation of a sexual interaction between conspecifics biases the subsequent mate-choice decision of the observer (Brown et al. 2011). It has been first demonstrated in fishes (Dugatkin Lee Alan and Godin Jean-guy J. 1992),

followed by observations in many vertebrates (Galef and White 1998; Yorzinski and Platt 2010) and recently in invertebrates (Mery et al. 2009; Fowler-Finn et al. 2015). Its benefits are double-sided, it allows naive individuals to avoid mistakes and make sure that their descendants will be preferred by conspecifics. Interestingly, in population with genetic preferences, mate-copying can override them (Dugatkin 1996; Witte and Ryan 1998). At larger scale, mate-copying can even shape preferences of entire populations and potentially lead to formation of local traditions. Such traditions transmitted vertically and horizontally for a trait-based preference and possibly for a long time can even lead to the appearance of animal culture (Brooks 1998; Danchin et al. 2018).

The existence of culture in non-human species has long been disputed (**laland_animals_2003**) but is increasingly accepted among scientists (Aplin et al. 2015; Whitehead 2017). The list of animals exhibiting a form of cultural tradition is growing constantly (Schaik et al. 2003; Thornton Alex et al. 2010; Whiten 2017), and one of the most recent may surprise many, *Drosophila melanogaster* (Danchin et al. 2018). Very few, if none, species have been studied as deeply and for whom knowledge in every scientific field (genetics, development, neuroscience...) is as extensive than *Drosophila Melanogaster*. Thus existence of mate-copying in this species represents a wonderful opportunity to understand the obscure neuronal root of an evolutive behavior broadly shared in the animal kingdom.

In *drosophila*, depending on if the stimulus is aversive or appetitive, different groups of neurons are involved (Busto et al. 2010; Vogt et al. 2014). Therefore, our first step was to test if mate-copying implies aversive or appetitive memory, by isolating different kinds of stimulus contained in copulation of conspecifics. We considered that a rejection represent an aversive stimulus and acceptance of copulation an appetitive stimulus for an observer female. So, we created two treatments by presenting a male rejected by a female ("Rejection" treatment) or a male accepted by a female ("Acceptance" treatment), for which we measured the inclination to copy.

Then we investigated deeper neuronal mechanisms of mate-copying by searching which group of neurons is required for mate-copying. Indeed, the neuronal mechanisms of non-social learning is very well known in *Drosophila* (reviewed in Cognigni et al. (2018)). Regarding their

roles in the latter, two brain structures are particularly prone to be involved in mate-copying, the central complex and the mushroom body. The central complex, localized in the center of the insect brain plays a major role in decoding visual information. It receives visual inputs from the rest of the brain and controls vision-related behaviors, memory and learning (Guo et al. 2017). The mushroom body is an integrative center involved in learning, memory, decision-making and visual associative memory. Notably, specific groups of dopaminergic neurons localized in mushroom bodies are involved in the acquisition of aversive and appetitive visual memory (Liu et al. 2012; Vogt et al. 2014). On the contrary, despite a rich repertoire of well-studied social processes (Pasquaretta et al. 2016; Teseo et al. 2016; Dawson et al. 2018), neuronal mechanisms of social learning are still poorly understood. However, a recent study have found that dopamine is required in mate-copying (Monier et al. 2018). Dopamine is a neurotransmitter, that drive a variety of brain function among which the formation of appetitive and aversive memory (Riemensperger et al. 2005; Sitaraman et al. 2008; Alekseyenko et al. 2010; Berry et al. 2012; Yamamoto and Seto 2014). Dopamine is produced in dopaminergic neurons but we do not know which are involved in mate-copying. However, we do know some of the neurons required for non-social visual memory. Vogt et al. (2014) showed that neurons labeled by TH-GAL4 and Ddc-GAL4 transgene are essential in visual learning. Given that mate-copying involves visual learning, we expect these neurons to be required. Thanks to Liu et al., we know that UAS-GAL4 technology can be used to block specific sets of neurons (Liu et al. 2012). Precisely, by coupling UAS-GAL4 with the Shibire protein, it is possible to temporary silence specific groups of neurons and investigate in what processes they are essential. Our goal was to use a similar technique but concerning mate-copying. We used mutant flies expressing GAL4 in TH-labeled or Ddc-labeled neurons, that we have silenced to see if those neurons are required in mate-copying (for more details, see "Fly stains and crossings" section). We thus created two treatments: "Th" and "DDC" depending of the group of the neurons silenced, for which we calculated mate-copying scores. If one group is involved in mate-copying, the corresponding treatment will exhibit a mate-copying score similar to random choice, due to the incapacity of mutants to learn.

2 Material and Methods

2.1 Fly maintenance

We used the common Canton-S strain of *D.melanogaster* (wild-type, and UAS / Gal4 lines described above). Flies were raised and kept in 30 ml tubes containing standard corn flour-yeast-agar medium at $25^{\circ} \pm 1^{\circ}\text{C}$ and $56 \pm 4\%$ humidity with a 12:12H light:dark cycle. Humidity and temperature were controlled and adjusted continuously with two independent automatic humidifiers and one manual heater. Medium was cooked every 3 weeks and stored at 4°C until use. Flies were manipulated with a hand-made mouth aspirator made of a glass pipette, tubing and gauze.

Every morning, adult flies were removed from the breeding vials so that the newly emerged flies collected within the 6-8 hours were virgin. For Canton-S strain, 120 males and 120 females were used daily for breeding (20 tubes with 6 males and 6 females in each) and all other adults were euthanized in a freezer. For mutant strains, all adults were used for breeding.

Virgins were sexed without anesthesia, by gentle aspiration and then kept in unisex groups of 7 females or 14 males until experiments. Both demonstrator and observer flies were 3 or 4 days old. Males and females were used only once as females are reluctant to re-mate (Chapman et al. 2003) and reject males they just saw copulating (Loyau et al. 2012). After experiments, all flies were put in a food vial and cold-euthanized at the end of the day.

2.2 Fly stains and crossings

For the second experiment, we used two mutant genotypes, *Ddc-GAL4/w+;;UAS-Shits/+* and *w+/w-;;UAS-Shits/TH-GAL4*, obtained by crossing homozygous lines.

UAS-Shits is a transgene that contains an GAL4-specific enhancer, UAS (Upstream Activating Sequence) driving the production of Shibire protein in cells where GAL4 is present. Shibire is a thermosensitive protein that inhibits neuronal activity at restrictive temperature (30°C) by preventing vesicle recycling (Kitamoto 2001). *Ddc-GAL4* and *TH-GAL4* drive production of a transcriptional activator (GAL4) only in specific subsets of dopaminergic neurons. GAL4 activates the expression of genes downstream to UAS. *Ddc-GAL4* labels neurons involved in

appetitive olfactory memory: the blockade of these neurons by Shibire protein has been shown to impair the acquisition of such memory at restrictive temperature. TH-GAL4 labels neurons involved in aversive olfactory memory (Liu et al. 2012).

As white recessive mutation *w⁻* impairs fly vision (Götz 1964), we used mutant females with one wild-type copy of the white gene for the experiments. To do so, we crossed *w⁺;;Shits* males with females from each Gal4 line. To obtain *w⁺;;Shits* strain from a *w⁻;;Shits* strain, we crossed males *w⁻;;Shits* with females *w⁺;;TM2/TM6b* over two generations and selected TM2 non TM6B flies only, with CO₂ anesthesia, and we then isolated homozygous *w⁺;;Shits* progeny.

TH-GAL4 and Ddc-GAL4 lines were provided by Guillaume Isabel in the same Canton-S background as the Wild-type strain.

2.3 General experimental procedures

Artificial male phenotypes were created by dusting virgin males with pink or green powder (Mery et al. 2009). Each vial of males was randomly assigned to a color. Before the experiment started, males were placed in a clean vial to remove the excess of dust for at least 20-30 min. Experiments took place in the same tube set-up and a similar but slightly modified speed-learning protocol than described in Dagaëff et al. (2016) (Figure 1, see also specific experiment section).

Demonstrator and observer flies were placed in two compartments of double plastic tubes, separated by a thin glass partition and closed by cotton plugs. All replicates were run in blocks of six trials with cardboard barriers between experimental set-ups, to prevent information exchange between the flies and disturbance from the surroundings.

During the demonstration, we always showed two different male phenotypes (color) to the observer females, with one favorite that copulated with the demonstrator female. If demonstrator females refused to copulate, the trial was discarded. Specifics of demonstrations for each experiment are described above (see specific experiment section).

Once the demonstrations were over, we started the mate-copying test by introducing a couple of colored virgin males (one of each color) in front of the observer female and we removed

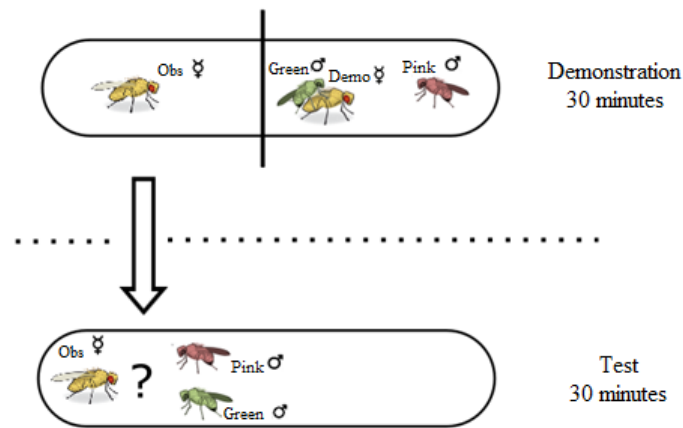


Figure 1: Légende ici.

the partition, allowing the female to freely choose between males for 30 min. The partition was put back in place when all three flies were in the same side of the tubes, to promote proximity between flies. During that time, we recorded the time of first courtship for each male, the time when copulation started and the color of the chosen male. The onset of the courtship was defined as the first wing-extension of a male (Figure 2).

2.3.1 Acceptance/Rejection experiment

During this first experiment, we tested whether mate-copying is achieved through aversive or appetitive memory. To do so, we split the negative and positive information given by the usual mate-copying demonstration. A classical demonstration, in which a demonstrator female chooses between two males, contains a rejection (negative information) of a male and an acceptance (positive information) of the other one. We thus created three demonstration treatments: (1) a control where a demonstrator female freely chooses between two males, (2) an “acceptance” treatment with one accepted male copulating with a demonstrator female, and (3) a rejection treatment with one male actively rejected by a female (Figure 3).

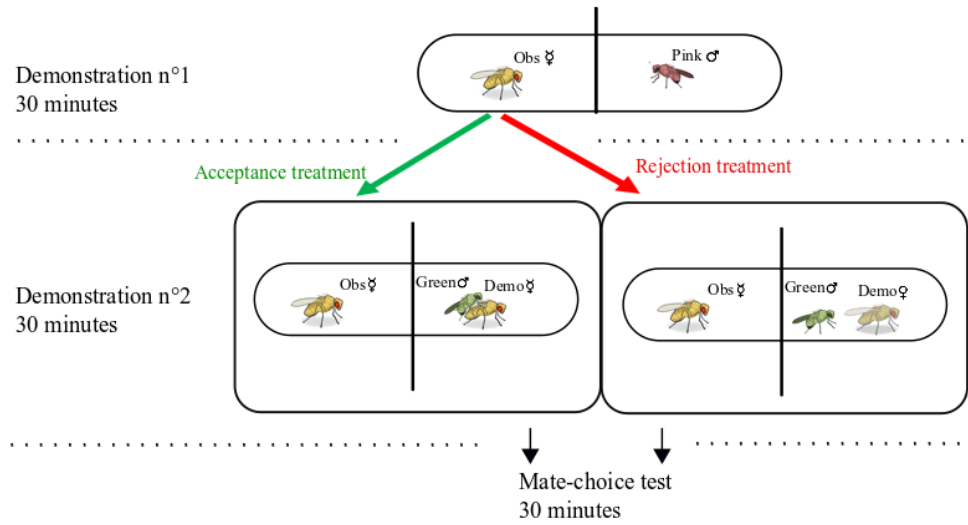


Figure 2: Légende ici.

2.3.2 Neuronal blockade experiment

This second experiment aimed at exploring the mechanisms underlying the results of the Acceptance/Rejection experiment by discovering one group of dopaminergic neurons involved in mate-copying.

The demonstration was similar to classical protocol (Figure 1), but we used *Ddc-GAL4/w+;;UAS-Shits/+* (treatment “Ddc”) and *w+/w-;;UAS-Shits/TH-GAL4* mutants (treatment “Gal4”) as observer females. The use of these mutants allowed us to have a temporal control on specific sets of neurons presumably involved in appetitive (Ddc) or aversive (TH) memory, thanks to the thermosensitive activation of Shibire. During the demonstration and 30 minutes before, observer mutant females were heated to a restrictive temperature of 33°C, thanks to a heating mat under the tube of these females. At 33°C, Shibire protein blocks the neurons in which it is expressed, and thus the acquisition of appetitive memory should be blocked in observer females of “Ddc” treatment, and the acquisition of aversive memory in “TH” females.

After all copulations ended, demonstrator males and females were removed. Observer females were then stored individually in clean tubes at 25°C for 3-4 hours to ensure that labelled neurons are no more blocked, then we proceeded to a classical test at 25°C.

2.4 Mate-copying score

As in previous studies (Danchin et al. 2018; Monier et al. 2018; Nöbel et al. 2018), a mate-copying score evaluated female's tendency to copy the choice of the demonstrator. A mate-copying score of 1 was assigned to females that copulated with the color preferred by demonstrator females and a score of 0 in the opposite case. For each treatment, a mate-copying index was calculated as the mean of mate-copying scores per treatment, a random choice indicated by a value of 0.5. All replicates where only one male courted the female before copulation were discarded because in these situations the female was not unambiguously in a position to make a choice between the two colors.

2.5 Statistical analyses

All statistical analyses were performed with the R software version 3.5.1 (R Core Team, 2018). For each treatment, the difference from a random choice was tested with a binomial test. Mate-copying scores were then analyzed in a generalized linear mixed model (GLMM, package lme4 (Bates et al. 2015)). Starting models contained the following fixed effects: treatment, normalized air pressure (air pressure in Toulouse-Blagnac weather station, at the time of the beginning of the experiment, minus mean air pressure), normalized air pressure variation within the six preceding hours and all interaction between these three variables, experimenter effect and its interaction with treatment. A random "block" effect was also introduced in the models to account for the non-independence of observer flies from the same block of 6 tubes-set up trained and tested in parallel. The significance of fixed effects was tested using Wald chi-square tests included in ANOVA function (car package, Fox and Weisberg (2018)). Model simplification was achieved by successive withdrawal of the non-significant terms in a backward selection approach, using P-values and starting with the highest-order interaction. The final model was chosen as the one with the lowest Akaike Information Criteria (AIC, Akaike, 1969). Comparisons between treatments were done using post-hoc X^2 tests.

2.6 Ethical statements

Behavioral observations of *D. melanogaster* required no ethical approval and complied with French laws regarding animal welfare. We kept the number of flies used in this study as small as possible. We handled flies by gentle aspiration without anesthesia to minimize damage and discomfort. After the experiments, individuals were euthanized in a freezer at -20°C.

3 Results

3.1 A/R Experiment

For this experiment, we tested 850 females among which 530 copulated during test, including 192 with double-courtship, 64 for each treatment. First we tested for female's color preference with binomial test but neither in the demonstration ($N = 850$, 426 females copulated with green males and 424 copulated with pink males; binomial test: $P = 0.973$) nor the test ($N = 530$, 270 copulated with green and 260 with pink males; binomial test: $P = 0.696$) was there any significant difference between the two colors.

For each treatment, the difference from random choice was tested with a binomial test, “acceptance” (where the observer female sees a copulation, $N = 64$, $P < 0.001$) and “control” ($N = 64$, $P = 0.03$) were both significantly different from random, but “rejection” treatment (where the observer female sees a male rejected without copulation, $N = 64$, $P = 0.382$) was not (Figure 4).

To test for the significance of mate copying among treatments, we built a global model including the effects of experimenter, treatment, normalized air pressure (actual air pressure minus global mean of air pressure), normalized air pressure variation (for the last six hours) and the interaction between air pressure and variation of air pressure. The selected model included the effect of treatment, air pressure, variation of air pressure and the interaction between air pressure and its variation. Only the treatment had a significant effect on mate-copying (GLMM, χ^2 : $N = 192$, $\chi^2 = 10.447$, $p = 0.005$), air pressure (GLMM, χ^2 : $N = 192$, $\chi^2 = 0.572$, $p = 0.449$) and variation of air pressure (GLMM χ^2 : $N = 192$, $\chi^2 = 1.831$, $p = 0.176$) were non-

significant. The interaction between air pressure and variation of air pressure was close to be significant (GLMM χ^2 : $N = 192$, $\chi^2 = 2.946$, $p = 0.086$), as we could have expected in regard of the results of Dagaëff et al. (2016). No significant difference has been found between “control” and “acceptance” treatments ($\chi^2 = 1.76$, $P = 0.18$; Fig4), but both are different from “rejection” treatment (acceptance - rejection: $\chi^2 = 11.62$, $P < 0.005$; control - rejection: $\chi^2 = 4.52$, $P = 0.033$; Fig4).

3.2 Neuronal blockade experiment

For this second experiment, we tested 336 females, among which 208 copulated, including 88 with double courtship. Female’s color preference was tested with a binomial test, but we found no preference between the two colors in demonstrations ($N = 336$, 151 females copulated with green males and 185 copulated with pink males; binomial test: $p < 0.072$) and tests ($N = 208$, 107 copulated with green and 101 with pink males; binomial test: $p < 0.729$). As for the previous experiment, we first tested difference from random choice for each treatment with a binomial test: females from “Ddc” treatment exhibited a mate-copying score different from random ($N = 39$, $p < 0.024$) while “TH” did not ($N = 49$, $p < 0.568$)(Fig 5). To test for the effect of treatment on mate-copying efficiency, we built a global model, including the effects of experimenter, treatment, normalized air pressure (actual air pressure minus global mean of air pressure), normalized air pressure variation (for the last six hours) and the interaction between air pressure and variation of air pressure. The selected model included the effect of treatment, air pressure, variation of air pressure and the interaction between air pressure and its variation. Again, only the treatment had a significant effect on mate-copying (GLMM, χ^2 : $N = 88$, $\chi^2 = 4.245$, $p = 0.0394$), while effect of air pressure, variation of air pressure and interaction between air pressure and air pressure variation were non-significant (GLMM, χ^2 : $N = 88$, $\chi^2 = 0.619$, 0.259 and 2.176 respectively, $p = 0.4315$, 0.611 and 0.14 respectively)(Fig 4). Voir Figure (3).

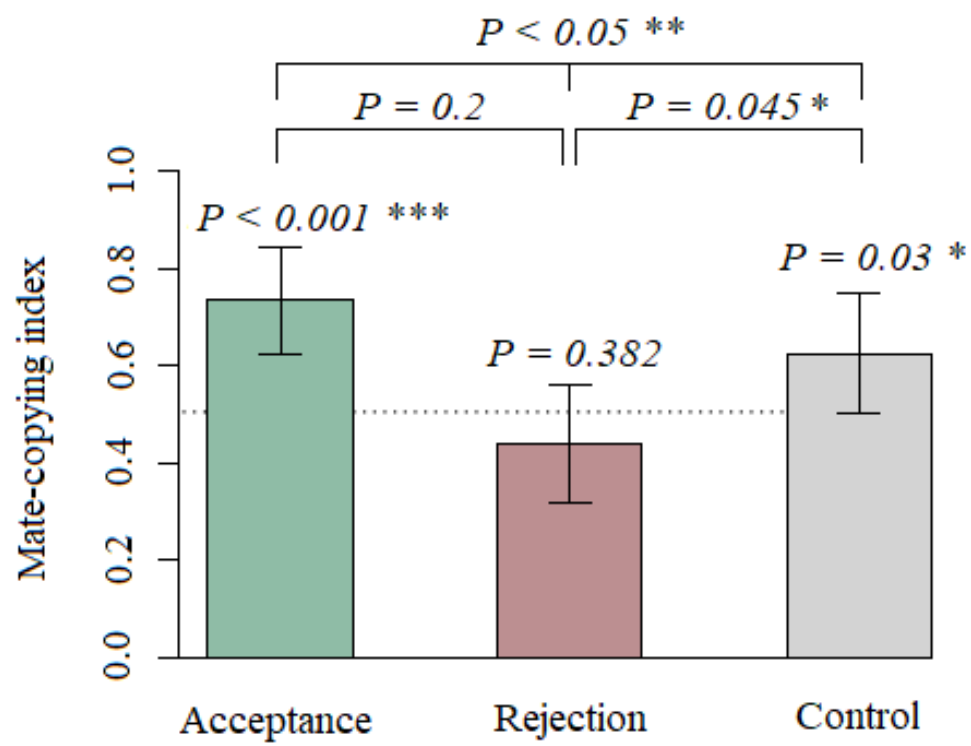


Figure 3: Légende ici.

4 Discussion

So far, mate-copying studies in *Drosophila melanogaster* were based on the acceptance or rejection of different phenotypes by a demonstrator. Here we showed that the acceptance, not the rejection, of a single male is sufficient to induce mate-copying in females. When a female witnessed an acceptance of male followed by a copulation, she exhibited mate-copying. In the other case, when observer female witnessed only a rejection of the male, her subsequent choices was similar to random. In both cases, only a part of the information was available for the female; but it seems that negative information is not used, since mate-copying score are not significantly different between control and rejection. Although several studies have already demonstrated mate-copying without copulation between demonstrators in fish, they are hardly comparable to our study. As it was not about copulation but time spent close to the favorite male (Dugatkin Lee Alan and Godin Jean-guy J. 1992; Galef and White 1998). Notably, a study on lekking birds (*Tetrao tetrix*) showed that females exhibited mate-copying only when the males were able to copulate with demonstrator females. But again, mate-copying was not a matter of biased copulation but of biased attraction to preferred males. In our study, both demonstration and test involved copulation and so it leave little doubt about results. The fact that mate-copying relies on acceptance and positive information rather than rejection and negative information is pertinent in regard of evolution. Females can reject copulation for several individual-specific reasons and so acceptance is much more informative. For example, in flies a female can reject a male if she recently mated (Chapman et al. 2003). In this case, the reason for rejection is pointless for other females and uninformative about the male quality, which is potentially excellent. Whereas for acceptance, the quality of the male is more likely to play a role in it. However, we used non-virgin demonstrator females in rejection experiment, and males can smell that the female has recently mated (**jallon_few_1984**). Even though we made sure the male courted the female, it is possible that his behaviors differs and that the female observer sees it. In these conditions, its inclination to copy the choice of demonstrator may be impacted, leading to the observed results. This point demand further investigation.

We found that TH-labeled neurons are required in mate-copying, while Ddc neurons are not. When heated to a restrictive temperature, Ddc-GAL4 females copied the choice of the

demonstrator despite the fact that Ddc neurons was silenced; while in the same context, the choice of TH-GAL4 females were similar to random. Except the results of Monier et al. (2018), no study have investigated the neuronal basis of mate-copying. But studies that have studied non-social (direct) learning and the formation of appetitive and aversive memory had antagonistic results; TH was responsible of aversive memory and Ddc of appetitive memory. In the light of such results and given that we found mate-copying is based on appetitive memory, we expected Ddc-neurons to be required in mate-copying, but we were wrong. TH neurons are required in formation of aversive non-social memory and appetitive social memory. Thus, groups of neurons involved in direct associative learning (non-social) are different from those involved in social learning. However, similar results have been found very recently in rats. Carrillo et al. (2019) et al showed that a specific groups of neurons (in area 24 of Anterior cingulate cortex) responded when a rat experienced pain (laser) and when witnessing pain of conspecifics (represented by squeaking) but not to a fear-conditioned sound. Rat exhibited typical distress behavior when they witnessed other pain or fear-conditioned sound (freezing). But when neurons of area 24 were silenced, only the socially triggered freezing was reduced. This study shows that even for an identical behavior, the groups of neurons involved are different, depending if it involves direct or indirect (social) stimuli. However, stimuli and behaviors are different, and mechanisms observed are potentially specific to context. But pain and other's pain both involved ACC, it could be interesting to do same for mate-copying. Finally, if certain sort of memory overlap (visual or olfactory), other didn't (direct indirect) not depending of the kind of the stimuli but of? It shows the highly pronounced similarity in mechanism between insect and mammals but also underlies complexity of brain. In light of such results, it seems that social and non social learning are based on different group of neurons. Meanwhile, learning based on cues of different kind (olfactory, visual...) involves overlapping group of neurons. This findings is interesting in regard of evolution, group of different neurons respond to a stimuli depending he concern self or other. There is several explication, it's adaptive of being able to differentiate if stimuli on self or other, or evolved later in evolution. Information is of totally different nature, concerning self or others, a good step is to study it in highly socialized species. In human and primates, mirror neurons and amygdala are responsible for social cognition and behavior, dedicated structure. In

non social insect, different but overlapping group of neurons lead social or non social cognition and learning. Interesting to study it in intermediate developed brain to understand how it evolved through complexification of brain. Also, given that mechanisms of social cognition are similar in drosophila and human, it could be a good starting point to get better understanding of autism in human. Study that look at evolutionary process with a mechanistic approach have been underdone for so long ->

-> conclusion

References

- Alekseyenko, Olga V., Carol Lee, and Edward A. Kravitz (May 2010). “Targeted Manipulation of Serotonergic Neurotransmission Affects the Escalation of Aggression in Adult Male *Drosophila melanogaster*”. In: *PLOS ONE* 5.5, e10806.
- Anderson, Sheila S. and Michael A. Fedak (Aug. 1985). “Grey seal males: energetic and behavioural links between size and sexual success”. In: *Animal Behaviour* 33.3, pp. 829–838.
- Aplin, Lucy M. et al. (Feb. 2015). “Experimentally induced innovations lead to persistent culture via conformity in wild birds”. In: *Nature* 518.7540, pp. 538–541.
- Bates, Douglas et al. (Oct. 2015). “Fitting Linear Mixed-Effects Models Using lme4”. In: *Journal of Statistical Software* 67.1, pp. 1–48.
- Berry, Jacob A. et al. (May 2012). “Dopamine Is Required for Learning and Forgetting in *Drosophila*”. In: *Neuron* 74.3, pp. 530–542.
- Brooks, Robert (Feb. 1998). “The importance of mate copying and cultural inheritance of mating preferences”. In: *Trends in Ecology & Evolution* 13.2, pp. 45–46.
- Brown, Culum, Kevin Laland, and Jens Krause (June 2011). *Fish Cognition and Behavior*. John Wiley & Sons.
- Busto, Germain U., Isaac Cervantes-Sandoval, and Ronald L. Davis (Dec. 2010). “Olfactory learning in *Drosophila*”. In: *Physiology (Bethesda, Md.)* 25.6, pp. 338–346.
- Carrillo, Maria et al. (Apr. 2019). “Emotional Mirror Neurons in the Rat’s Anterior Cingulate Cortex”. In: *Current Biology* 29.8, 1301–1312.e6.
- Chapman, Tracey et al. (Aug. 2003). “The sex peptide of *Drosophila melanogaster*: female post-mating responses analyzed by using RNA interference”. In: *Proceedings of the National Academy of Sciences of the United States of America* 100.17, pp. 9923–9928.
- Clutton-Brock, T. H. (Jan. 1982). “The Functions of Antlers”. In: *Behaviour* 79.2-4, pp. 108–124.
- Cognigni, Paola, Johannes Felsenberg, and Scott Waddell (2018). “Do the right thing: neural network mechanisms of memory formation, expression and update in *Drosophila*”. In: *Current Opinion in Neurobiology* 49, pp. 51–58.

- Coolen, Isabelle, Olivier Dangles, and Jérôme Casas (Nov. 2005). “Social Learning in Noncolonial Insects?” In: *Current Biology* 15.21, pp. 1931–1935.
- Dagaëff, Anne-Cécile et al. (Nov. 2016). “Drosophila mate copying correlates with atmospheric pressure in a speed learning situation”. In: *Animal Behaviour* 121, pp. 163–174.
- Danchin, Etienne et al. (Nov. 2018). “Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions”. In: *Science* 362.6418, pp. 1025–1030.
- Dawson, Erika et al. (Sept. 2018). “Social environment mediates cancer progression in Drosophila”. In: *Nature Communications* 9, p. 3574.
- Dugatkin Lee Alan and Godin Jean-guy J. (Aug. 1992). “Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*)”. In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 249.1325, pp. 179–184.
- Dugatkin, L A (Apr. 1996). “Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*.” In: *Proceedings of the National Academy of Sciences of the United States of America* 93.7, pp. 2770–2773.
- Fisher, R. A. (Oct. 1915). “The evolution of sexual preference”. In: *The Eugenics Review* 7.3, pp. 184–192.
- Fowler-Finn, Kasey D. et al. (Dec. 2015). “The complexities of female mate choice and male polymorphisms: Elucidating the role of genetics, age, and mate-choice copying”. In: *Current Zoology* 61.6, pp. 1015–1035.
- Fox, John and Sanford Weisberg (Sept. 2018). *An R Companion to Applied Regression*. SAGE Publications.
- Galef Benett G., JR and David J. White (Mar. 1998). “Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*”. In: *Animal Behaviour* 55.3, pp. 545–552.
- Götz, Karl Geokg (June 1964). “Optomotorische Untersuchung des visuellen systems einiger Augenmutanten der Fruchtfliege *Drosophila*”. In: *Kybernetik* 2.2, pp. 77–92.
- Guo, Aike et al. (Dec. 2017). “Vision, Memory, and Cognition in *Drosophila*”. In: *Reference Module in Neuroscience and Biobehavioral Psychology*.

- Kitamoto, T. (May 2001). “Conditional modification of behavior in *Drosophila* by targeted expression of a temperature-sensitive shibire allele in defined neurons”. In: *Journal of Neurobiology* 47.2, pp. 81–92.
- Laidre Mark E. (May 2010). “How rugged individualists enable one another to find food and shelter: field experiments with tropical hermit crabs”. In: *Proceedings of the Royal Society B: Biological Sciences* 277.1686, pp. 1361–1369.
- Leeuwen, Edwin J. C. van, Katherine A. Cronin, and Daniel B. M. Haun (Nov. 2014). “A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*)”. In: *Animal Cognition* 17.6, pp. 1421–1425.
- Liu, Chang et al. (Aug. 2012). “A subset of dopamine neurons signals reward for odour memory in *Drosophila*”. In: *Nature* 488.7412, pp. 512–516.
- Loyau, Adeline et al. (Oct. 2012). “When not to copy: Female fruit flies use sophisticated public information to avoid mated males”. In: *Scientific reports* 2, p. 768.
- Mery, Frédéric et al. (May 2009). “Public versus personal information for mate copying in an invertebrate”. In: *Current biology: CB* 19.9, pp. 730–734.
- Monier, Magdalena et al. (2018). “Dopamine and Serotonin Are Both Required for Mate-Copying in *Drosophila melanogaster*”. In: *Frontiers in Behavioral Neuroscience* 12, p. 334.
- Nöbel, Sabine, Etienne Danchin, and Guillaume Isabel (Sept. 2018). “Mate-copying for a costly variant in *Drosophila melanogaster* females”. In: *Behavioral Ecology* 29.5, pp. 1150–1156.
- Pasquaretta, Cristian et al. (Mar. 2016). “How social network structure affects decision-making in *Drosophila melanogaster*”. In: *Proceedings of the Royal Society of London B: Biological Sciences* 283.
- Riemensperger, Thomas et al. (Nov. 2005). “Punishment Prediction by Dopaminergic Neurons in *Drosophila*”. In: *Current Biology* 15.21, pp. 1953–1960.
- Schaik, Carel P. van et al. (Jan. 2003). “Orangutan cultures and the evolution of material culture”. In: *Science (New York, N.Y.)* 299.5603, pp. 102–105.
- Sitaraman, Divya et al. (Apr. 2008). “Serotonin is necessary for place memory in *Drosophila*”. In: *Proceedings of the National Academy of Sciences* 105.14, pp. 5579–5584.

- Teseo, Serafino, Liisa Veerus, and Frédéric Mery (June 2016). “Fighting experience affects fruit fly behavior in a mating context”. In: *The Science of Nature* 103.
- Thornton Alex, Samson Jamie, and Clutton-Brock Tim (Dec. 2010). “Multi-generational persistence of traditions in neighbouring meerkat groups”. In: *Proceedings of the Royal Society B: Biological Sciences* 277.1700, pp. 3623–3629.
- Vogt, Katrin et al. (Aug. 2014). “Shared mushroom body circuits underlie visual and olfactory memories in *Drosophila*”. In: *eLife* 3. Ed. by Mani Ramaswami, e02395.
- Webster M.M and Laland K.N (Dec. 2008). “Social learning strategies and predation risk: minnows copy only when using private information would be costly”. In: *Proceedings of the Royal Society B: Biological Sciences* 275.1653, pp. 2869–2876.
- Whitehead, Hal (July 2017). “Gene–culture coevolution in whales and dolphins”. In: *Proceedings of the National Academy of Sciences* 114.30, pp. 7814–7821.
- Whiten, Andrew (July 2017). “Culture extends the scope of evolutionary biology in the great apes”. In: *Proceedings of the National Academy of Sciences* 114.30, pp. 7790–7797.
- Witte, Klaudia and Michael J. Ryan (Jan. 1998). “Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*”. In: *Behavioral Ecology* 9.5, pp. 534–539.
- Yamamoto, Shinya and Elaine S. Seto (2014). “Dopamine Dynamics and Signaling in *Drosophila*: An Overview of Genes, Drugs and Behavioral Paradigms”. In: *Experimental Animals* 63.2, pp. 107–119.
- Yorzinski, Jessica L. and Michael L. Platt (Feb. 2010). “Same-Sex Gaze Attraction Influences Mate-Choice Copying in Humans”. In: *PLoS ONE* 5.2.