Current Biology *19*, 1654–1659, October 13, 2009 ©2009 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2009.08.017

Report

Social Facilitation of Long-Lasting Memory Retrieval in *Drosophila*

Marie-Ange Chabaud,[1,2,5] Guillaume Isabel,[1,5]
Laure Kaiser,[2,3,4] and Thomas Preat[1,*]
[1]Genes and Dynamics of Memory Systems, Neurobiology Unit,
Centre National de la Recherche Scientifique, École
Supérieure de Physique et de Chimie Industrielles,
10 rue Vauquelin, 75005 Paris, France
[2]Développement, Evolution, et Plasticité du Système Nerveux,
Centre National de la Recherche Scientifique, 1 Avenue de la
Terrasse, 91198 Gif-sur-Yvette Cedex, France
[3]Institut National de la Recherche Agronomique Centre de
Versailles-Grignon, UMR 1272, Physiologie de l'Insecte
Signalisation et Communication, Route de St Cyr, 78026
Versailles Cedex, France

Summary

Recent studies demonstrate that social interactions can have a profound influence on *Drosophila melanogaster* behavior [1–8] and cuticular pheromone patterns [8–10]. Olfactory memory performance has mostly been investigated in groups, and previous studies have reported that grouped flies do not interact with each other and behave in the same way as individual flies during short-term memory retrieval [11–13]. However, the influence of social effects on the two known forms of *Drosophila* long-lasting associative memory, anesthesia-resistant memory (ARM) and long-term memory (LTM), has never been reported. We show here that ARM is displayed by individual flies but is socially facilitated; flies trained for ARM interact within a group to improve their conditioned performance. In contrast, testing shows LTM improvement in individual flies rather than in a group. We show that the social facilitation of ARM during group testing is independent of the social context of training and does not involve nonspecific aggregation. Furthermore, we demonstrate that social interactions facilitate ARM retrieval. We also show that social interactions necessary for this facilitation are specifically generated by trained flies: when single flies trained for ARM are mixed with groups of naive flies, they display poor retrieval, whereas mixing with groups trained either for ARM or LTM enhances performance.

Results and Discussion

ARM Is Facilitated in Group Tests Independently of the Learning Context

We use an olfactory conditioning paradigm during which a first odor associated with electric shocks is followed by a second odor presented alone [11, 14]. Memory performance is normally measured on groups of flies in a T-maze, in which flies are allowed to choose between both odors for a given time [11]. Two forms of consolidated long-lasting memory can be obtained by repetition of learning trials: long-term memory (LTM) is formed after spaced conditioning, whereas massed conditioning leads only to the formation of anesthesia-resistant memory (ARM) [15, 16]. LTM is affected by partial protein-synthesis inhibition and thus depends on de novo protein synthesis, whereas ARM is insensitive to the same level of inhibition [15]. Two models have been proposed to explain the relationship between LTM and ARM. In the first, both forms of memory coexist after spaced conditioning [15, 17]. In the second model, ARM and LTM are exclusive, and only LTM is expressed after spaced conditioning [16]. For convenience, the memory formed after massed conditioning will be referred to as ARM, and the memory formed after spaced conditioning will be referred to as LTM, although the existence of the two models will be discussed when appropriate.

We studied the influence of group interactions on ARM by comparing individual and group performance during the test. Flies were massed trained in groups of 30–40 flies and tested either individually or in groups 24 hr or 48 hr after training. ARM scores of groups outstrip individual scores (Figure 1A; two-way ANOVA test, significant sociality factor, $p = 5.9\ 10^{-5}$) when flies were tested at both 24 hr and 48 hr (nonsignificant time factor: $p = 0.089$. Nonsignificant time × sociality interaction: $p = 0.86$). Fly interactions in a group therefore have a positive effect on ARM performance. Strikingly, at 48 hr individual ARM scores were not different from zero, whereas group scores remained high (Figure 1A; t test, $p > 0.20$).

In this first set of experiments, flies were massed trained in a group, and so it is plausible that the higher memory score displayed by flies tested in groups was due to a similar social setting during training and testing. We therefore searched for potential context effects occurring during massed conditioning by comparing individual and group training. The group enhancement of ARM performance occurred similarly after individual and group training, indicating that it is independent of the learning context and rather involves social interactions during the test (Figure 1B; two-way ANOVA, test context factor, $p = 0.0005$; learning context factor: $p = 0.25$; test × learning interaction, $p = 0.73$). Moreover, the social effect on ARM was not sex specific and did not rely on sexual interactions (Figure S1).

We then searched for a similar social effect on LTM performance. No positive group effect was induced after spaced conditioning; performance was higher in individual flies than in groups (Figure 1C; two-way ANOVA test, significant sociality factor, $p = 0.029$; nonsignificant time factor, $p = 0.079$; nonsignificant time × sociality interaction, $p = 0.24$). Because the time factor was marginal, we analyzed 24 hr and 48 hr testing times seperately, and it appeared that the difference between scores of individual and group flies was marginal at 24 hr and significant at 48 hr (t test, 24 hr: $p = 0.052$. 48 hr: $p = 0.043$). Thus, social interactions increased memory retrieval after massed but not after spaced conditioning, supporting the view that

---

*Correspondence: thomas.preat@espci.fr

[4]Present address: Institut de Recherche pour la Développement, UR 072, Laboratoire Evolution, Génomes, et Spéciation, UPR 9034, Centre National de la Recherche Scientifique, 1 Avenue de la Terrasse, 91198 Gif-sur-Yvette Cedex, France

[5]These authors contributed equally to the work.

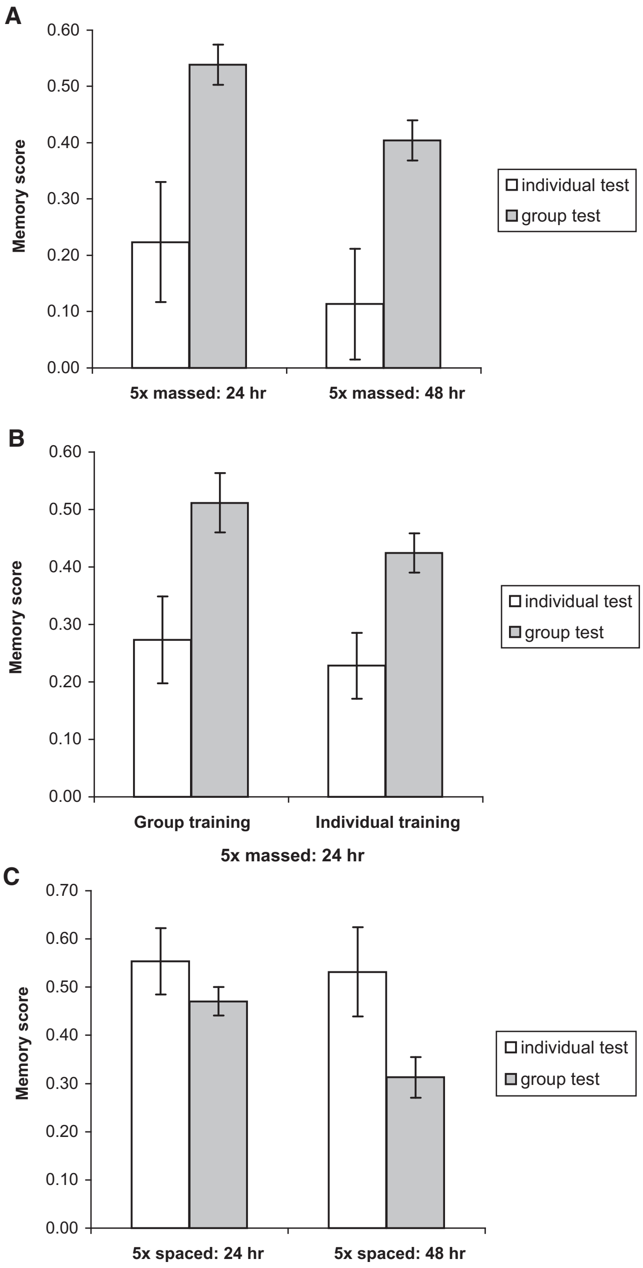

Figure 1. ARM Is Socially Facilitated in Group Tests Independently of the Learning Context

(A) Twenty-four hour and 48 hr olfactory memory induced by the massed conditioning protocol (ARM) of groups of flies, tested as individuals (n = 120) or in groups (n = 10–15). ARM scores of groups outstrip the level of individual scores ($p = 5.9\ 10^{-5}$).

(B) Twenty-four hour ARM scores, measured in individual flies (n = 120 individuals) or in groups of flies (n = 10). Flies were either trained in groups (left) or trained individually (right). The group enhancement of ARM performance occurred similarly after individual or group training (p = 0.0005).

(C) Twenty-four hour and 48 hr olfactory memory induced by the spaced conditioning protocol (LTM) of groups of flies, tested as individuals (n = 100–120) or in groups (n = 10–18). Performance after spaced conditioning was higher in individual flies than in groups (p = 0.029). In all panels, data correspond to the mean ± SEM of the memory score.

LTM but not ARM is present after spaced conditioning [16]. Alternatively, if the memory obtained after spaced conditioning is composed of both LTM and ARM, as is often proposed [15, 17], it could mean that the behavioral expression of LTM is predominant over that of ARM because it is retrieved more efficiently. After making these initial observations, we scrutinized the behavioral mechanisms underlying the social improvement of ARM.

The Positive Group Effect on ARM Is Due to Social Facilitation of ARM Retrieval, Not to Aggregation

The social effect that takes place during ARM retrieval could be explained by three main hypotheses. In the first, the social phenomenon would not be directly related to memory, and during the test, flies trained with massed conditioning would simply tend to aggregate in the tube where flies are most abundant. In the second hypothesis, the social phenomenon would involve communication about odor quality linked to conditioning: during the test, flies trained with massed conditioning would send signal(s) telling their neighbors that they should either avoid the conditioned odor or orient to the unconditioned odor (the perception of this signal could be restricted or not to flies trained with massed conditioning). In the third hypothesis, social interactions would facilitate memory retrieval.

To discriminate between these hypotheses, we tested the performance of single flies conditioned with the massed protocol to avoid one odor and mixed them with groups conditioned with the same protocol to avoid the opposite odor. If social interactions were linked to nonspecific aggregation or odor-specific communication, we would expect a decreased score for individual massed-trained flies when they are mixed with a group trained for the opposite odor (as compared to massed-trained flies tested alone). However, if social interactions facilitate ARM retrieval, these single flies should have high scores, similar to those of their mixed groups (but specific for their respective odor).

Interestingly, individual massed-trained flies tested among a group of massed-trained flies conditioned to the opposite odor recalled their own conditioned odor better than when they were tested individually; they showed a score superior to massed-trained flies tested individually and similar to that of massed-trained flies tested in a group (Figure 2A; one-way ANOVA test, p = 0.003). The fact that group interactions increase the ARM performance of single flies even if the group is trained for the opposite odor indicates that social interactions act on ARM retrieval and do not involve aggregation. This conclusion was strengthened by the observation that the performance of groups of massed-trained flies was not affected during the test by the presence of groups trained for the opposite odor with either the spaced (Figure 2B) or the massed (Figure 2C) protocol.

Only Flies with ARM Are Influenced by Social Interactions during Memory Retrieval

If groups of flies trained with the massed protocol facilitate ARM retrieval, they should have no influence on flies that have no ARM. To challenge this hypothesis, we used two groups of flies, naive wild-type flies and massed-trained *radish* (*rsh*) mutants that are deficient for ARM [15]. When mixed with a group of massed-trained flies, naive flies displayed a score not different from zero (Figure 3A; t test, p = 0.55), showing that the group effect produced by massed-trained flies requires the presence of memory. Similarly, *rsh* flies trained for ARM and mixed with a group of wild-type flies trained for the same odor displayed a low score similar to that of control *rsh* flies (Figure 3B; t test, p = 0.55). The performance of *rsh*

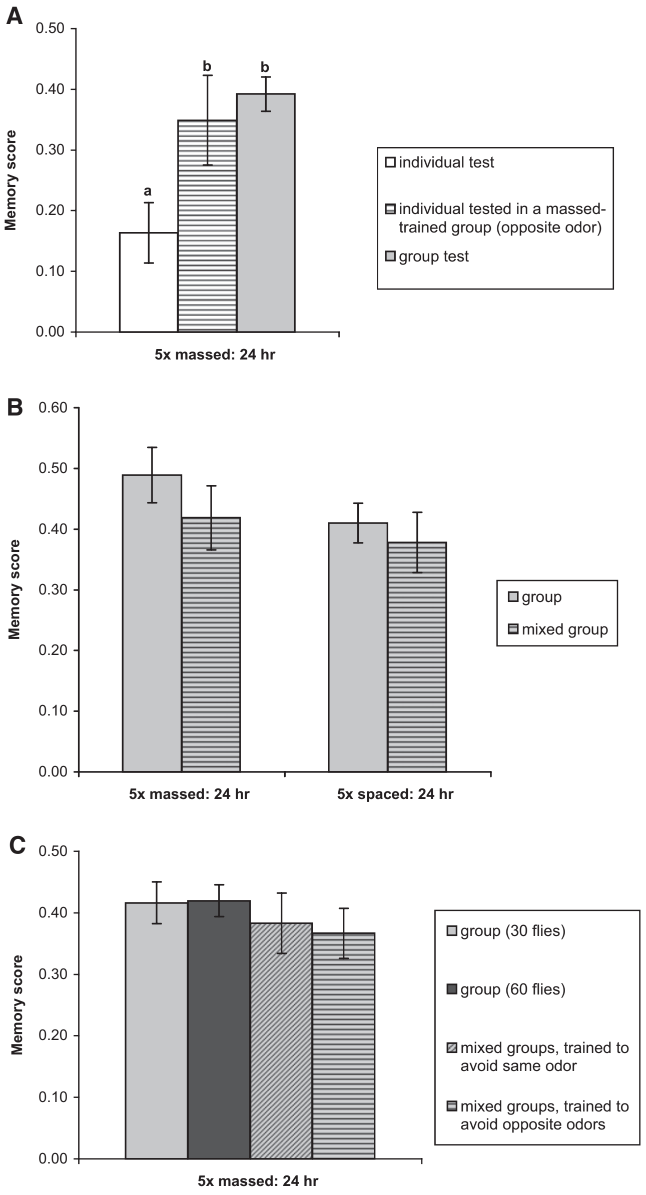

Figure 2. The Positive Group Effect on ARM Is Due to Social Facilitation of Memory Retrieval

(A) Observed 24 hr ARM scores measured in individual flies (n = 192 individuals), in individual flies tested among groups of massed-trained flies conditioned to avoid the opposite odor (n = 192 individuals), and in groups of flies (n = 32). Data represent the mean ± SEM of the memory score. One-way ANOVA followed by Tukey statistic: lowercase letters indicate significant differences at $p < 0.05$. Groups of massed-trained flies in which individual flies were introduced had scores of 0.43 ± 0.02, similar to those of control groups (t test with Dunn-Sidak correction, p = 0.20, n = 96).

(B) Observed 24 hr ARM and LTM scores when both groups were mixed at testing (n = 13 mixed groups) are compared with scores of nonmixed groups of massed-trained (n = 16 groups) and spaced-trained (n = 11 groups) flies. Scores of massed- and spaced-trained flies were not influenced by the mixing (t test; p = 0.34 for ARM and p = 0.61 for LTM).

(C) Observed 24 hr ARM scores when both groups of massed-trained flies were conditioned to avoid opposite odors and mixed at testing (n = 16) are compared with scores of mixed groups of massed-trained flies conditioned to avoid the same odor (n = 16) and with scores of groups of 30 and groups of 60 massed-trained flies (n = 12). Scores of massed-trained flies were not influenced by mixing with flies trained for the opposite odor (one-way ANOVA test, p = 0.76). For all panels, data represent the mean ± SEM of the memory score.

flies was therefore not enhanced by social interactions with trained wild-type flies. Only flies that display ARM are positively influenced by massed-trained flies during the memory test. These results are in agreement with the view that social interactions enhance ARM performance by facilitating memory retrieval.

The Social Facilitation of ARM Retrieval Requires Interactions with Trained Flies

Which types of interactions are at the origin of the social facilitation of ARM retrieval? In particular, are these interactions specific to flies trained with the massed conditioning protocol, or does the simple fact of being in a group facilitate ARM retrieval? We first investigated this issue by testing single massed-trained flies mixed during the test with groups of naive flies. Groups of naive flies did not facilitate ARM retrieval; individual massed-trained flies mixed with naive groups showed a poor performance, similar to that of massed-trained flies tested individually, and both showed significantly lower scores than massed-trained flies tested in groups (Figure 4A; one-way ANOVA test, p = 0.003).

In a second step, we mixed single massed-trained flies with groups of massed-trained flies or of spaced-trained flies conditioned for the same odor. Interestingly single massed-trained flies mixed with either massed- or spaced-trained flies showed a score significantly higher than that of massed-trained flies tested individually, and similar to the score of massed-trained flies tested in groups (Figures 4B and 4C; one-way ANOVA test, respectively p = 0.022 and p = 0.008 for the mixing in a massed-trained group and in a spaced-trained group).

These results show that the simple fact of being in a group is not enough to produce social facilitation of ARM retrieval and that specific interactions with trained flies are necessary. The social interactions at the origin of this enhanced memory retrieval are not specific to massed-trained flies; they are also observed with spaced-trained groups. This could be due to the fact that ARM is present after both massed and spaced conditioning [15, 17]. Alternatively, only LTM might be present after spaced conditioning [16], but groups of both massed- and spaced-trained flies might share a common feature that is perceived by massed-trained flies in the test situation. For example, in the presence of the conditioned odor, both trained groups might produce an alarm molecule that facilitates ARM retrieval by enhancing attention or motivation. LTM-trained flies may perceive the alarm but experience no visible effect on their performance, possibly because their memory retrieval is already very efficient.

By investigating memory performance in different social situations of training and testing, we have shown that the memory performance of a group does not always reflect individual performance. Previous studies did not report differences in short-term memory performance between flies tested individually and those tested in groups, in either aversive or appetitive olfactory memory [12, 13]. We have demonstrated that long-lasting aversive memory performances displayed by groups can outstrip performances of individuals: ARM performance tested individually is lower than performance tested in groups. This effect is strong; the conditioned response of odor avoidance was no longer expressed in individuals at 48 hr but was still clearly detected in groups.

Drosophila is known to be aggregative [1, 2]. One could therefore imagine that massed-trained flies have a weak individual memory and aggregate during the test, either passively

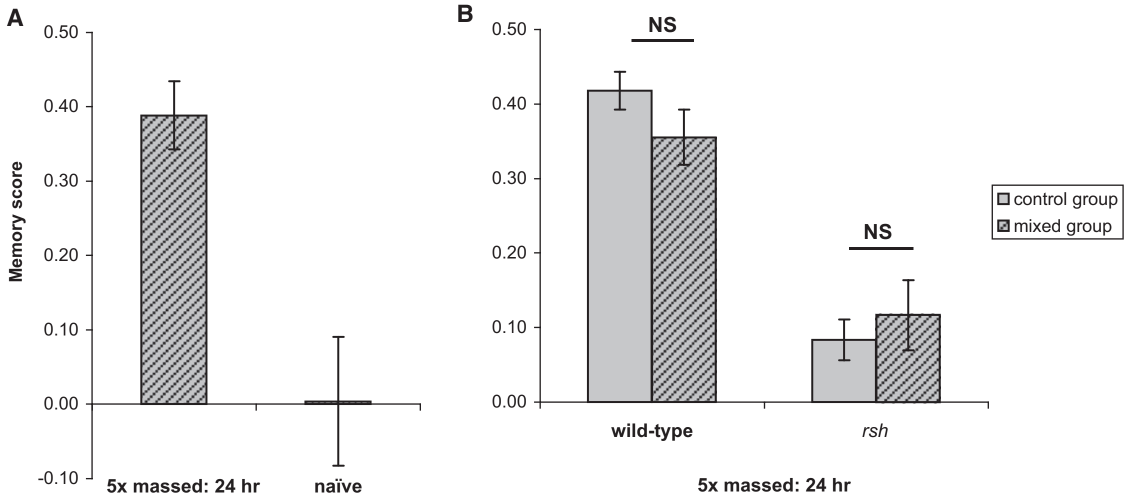

Figure 3. Naive Wild-Type Flies and *radish* (*rsh*) Mutants with Deficient ARM Are Not Influenced by Flies Trained with Massed Conditioning

(A) Observed 24 hr memory scores of massed-trained flies and naive flies when both groups were mixed at testing (n = 12 mixed groups). Naive flies displayed a score not different from zero (p = 0.55).

(B) Observed 24 hr ARM scores for wild-type and *rsh* flies when both groups were mixed at testing (n = 13 mixed groups) are compared to ARM scores of wild-type groups and *rsh* groups alone (n = 13). The performance of *rsh* flies was not enhanced by social interactions with massed-trained wild-type flies (p = 0.55). In all panels, data represent the mean ± SEM of the memory score. NS indicates a nonsignificant difference.

or by communicating signals specific to the conditioned or unconditioned odor. On the contrary, our results indicate that the social effect during the test is due to facilitation of memory retrieval. The poor ARM performance of individuals does not reflect poor learning or memory loss but rather reflects a memory-retrieval deficit that occurs in solitary flies and that can be compensated by social interactions within a group. Although the molecular and cellular mechanisms at play in this process remain to be determined, an attractive hypothesis is that, during memory retrieval, trained flies produce stress signals that alarm their mates and enhance their mates' attention or motivation to respond. Stressed flies have been shown to release repellant odorants that include CO_2 [18], and it will be important to test whether this particular signal plays a role in mediating social facilitation of ARM. Any putative alarm molecule secreted by trained flies during the test (i.e., in the presence of the conditioned odor) would represent a signal about the existence of a dangerous environment without specifying the nature of the danger. In that context, it will be interesting to investigate whether the social effect is only observed after aversive conditioning and not after appetitive conditioning.

Social information sharing, used by a wide range of species, is an advantageous solution in which animals adapt their behavior to the environment by extracting knowledge from neighbors [19–24]. This phenomenon is not restricted to vertebrates or colonial insects; for instance, the wood cricket uses social information to adapt its predator-avoidance behavior [21]. The ease with which influences of the social environment on behavior can be quantified, and the variety of powerful genetic tools available, make *Drosophila* an ideal model for future studies of sociality, learning, and memory [24].

Experimental Procedures

Conditioning Procedure

Drosophila melanogaster wild-type strain Canton-Special (CS) and *radish* (*rsh*) mutant flies were raised at 18°C and 60% humidity in a 12:12 hr light: dark cycle. Flies were trained with classical olfactory aversive conditioning protocols as described [14] except that for repeated (massed or spaced) conditioning, five cycles were used instead of ten. These experimental conditions promote stronger ARM performance (Figure S2) than that previously reported [14, 15]. Conditioning was performed on samples of 30–40 flies aged between 2 and 3 days. In the case of individually trained *Drosophila*, flies were gathered into groups of 35 flies directly after training.

Memory Test

Memory tests were performed at 25°C and 80% relative humidity under dim red light.

For group memory tests, flies were tested in the T-maze apparatus for 3 min. A mean group memory score and its standard error were then calculated from ten to 18 groups. A memory score represents the normalized probability of a correct choice. For individual memory tests, single flies were collected without anesthesia from groups just before the test and introduced alone into the T-maze [11] to choose between octanol or methylcyclohexanol odor over a 3 min period. At the end of the test period, the presence of the fly in one odor compartment or the other was recorded. To compare the memory scores of individuals and groups, we first pooled 12 consecutive individual results (six flies conditioned with each odor) to calculate a memory score similar in essence to that of a group score [12, 14]. A mean individual memory score and its standard error were then calculated from eight to 16 pools.

In the case of tests with mixed groups, we needed to differentiate between two populations of flies. To do this, we marked flies of one of the two groups by clipping the tips of their wings under brief CO_2 anesthesia 24 hr before training. We checked that flies with clipped wings displayed normal scores after massed and spaced conditioning. Mixed groups each consisted of 30 flies either trained for ARM and LTM with opposite odors (Figure 2B) or both trained for ARM with opposite odors (Figure 2C); groups were mixed just before testing. In the experiment with mixed groups of naive or *rsh* flies and CS massed-trained flies (Figure 3), approximately 12 naive or *rsh* flies were mixed with the group of about 30 massed-trained flies just after conditioning. Control groups consisted of 30 *rsh* or CS massed-trained flies. In experiments testing single massed-trained flies mixed in groups of about 30 flies (naive, massed-trained, or spaced-trained flies) (Figure 4), we marked single flies and introduced them into groups just before testing. We calculated scores of these single flies as for single flies tested alone.

Statistical Analyses

Mean scores were compared via two-tailed t tests in the case of two groups (Figures 2A, 2B, 3B, and 4B; see also Figure S2) or one-way ANOVA in the case of several groups. This was followed by the post-hoc Tukey-Kramer test if results were significant (Figures 2 and 4). Mean scores of Figures 1 and 2C and Figure S1 were analyzed by two-way ANOVA including calculation of the interaction between both considered factors (GLM procedure of the software "R"); subsequently, the post-hoc Tukey-Kramer test was used for assessing significance in the same factor among more than two groups (Figure S1). The individual 48 hr ARM score of Figure 1A and the scores of naive flies (Figures 3A and 4A) were tested for significance with a t test for single mean against zero [25]. For all statistical analyses, we used the significance level alpha = 0.05, except when we used data in two comparisons, where the significance level alpha = 0.025 was used, after application of the Dunn-Sidak correction [25].

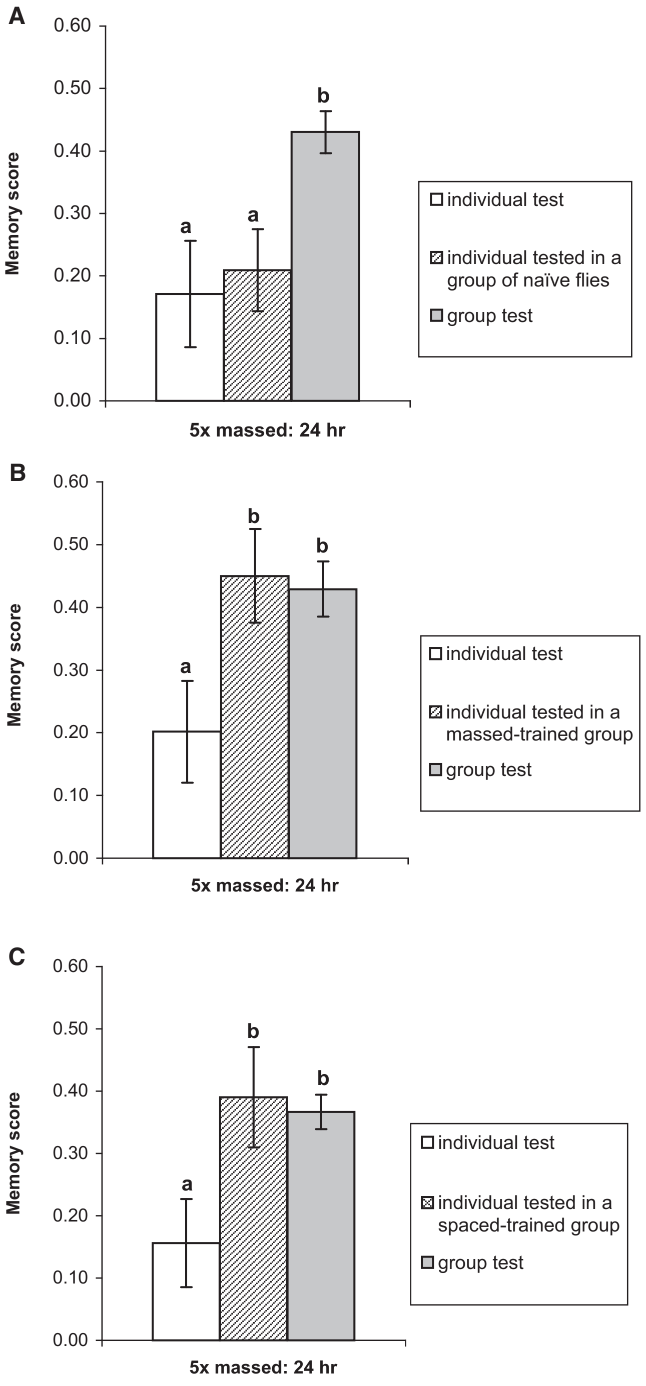

Figure 4. The Social Facilitation of ARM Retrieval Requires Interactions with Trained Flies

(A) Observed 24 hr ARM scores, measured in individual flies (n = 96 individuals), in individual flies tested among groups of naive flies (n = 96 individuals), or in groups of flies (n = 16). Groups of naive flies did not facilitate ARM retrieval. We verified that groups of naive flies had a score not different from zero when a massed-trained fly was introduced (score = −0.004 ± 0.020; t test, p = 0.85, n = 64).

(B) Observed 24 hr ARM scores, measured in individual flies (n = 120 individuals), in individual flies tested among groups of massed-trained flies conditioned to avoid the same odor (n = 120 individuals), and in groups of flies (n = 20). Groups of massed-trained flies facilitated ARM retrieval. Groups of massed-trained flies in which single massed-trained flies were introduced had normal scores (ARM score = 0.37 ± 0.02, not different from the control group score; t test with Dunn-Sidak correction, p = 0.21, n = 60).

(C) Observed 24 hr ARM scores, measured in individual flies (n = 144 individuals), in individual flies tested when mixed with groups of spaced-trained flies (n = 144 individuals), or in groups of flies (n = 28). Groups of spaced-trained flies facilitated ARM retrieval. We checked that groups of spaced-trained flies in which single massed-trained flies were introduced had scores that would normally be expected after spaced conditioning (LTM score = 0.39 ± 0.02, n = 84). Data represent the mean ± SEM of the memory score. One-way ANOVA followed by Tukey statistic: lowercase letters indicate significant differences at $p < 0.05$.

Supplemental Data

Supplemental Data include two figures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01589-9.

Acknowledgments

We thank Yadin Dudai and members of our laboratory for helpful discussions. We thank Antoine Branca for help with "R." We thank Valérie Goguel and Niki Scaplehorn for their valuable comments on the manuscript. This work was supported by the Agence Nationale pour la Recherche, the Fondation Bettencourt-Schueller, and the Fondation pour la Recherche Médicale (to T.P.). M.-A.C. was supported by a grant from the Université Paris 13, Ecole Doctorale Vivant et Sociétés (Ministry of Research). G.I. was supported by the Fondation pour la Recherche Médicale.

Received: June 18, 2008
Revised: August 1, 2009
Accepted: August 3, 2009
Published online: September 24, 2009

References

1. Lefranc, A., Jeune, B., Thomas-Orillard, M., and Danchin, E. (2001). Non-independence of individuals in a population of *Drosophila melanogaster*: Effects of spatial distribution and dispersal. C. R. Acad. Sci. III *324*, 219–227.
2. Tinette, S., Zhang, L., and Robichon, A. (2004). Cooperation between *Drosophila* flies in searching behavior. Genes Brain Behav. *3*, 39–50.
3. Ganguly-Fitzgerald, I., Donlea, J., and Shaw, P.J. (2006). Waking experience affects sleep need in *Drosophila.* Science *313*, 1775–1781.
4. Yurkovic, A., Wang, O., Basu, A.C., and Kravitz, E.A. (2006). Learning and memory associated with aggression in *Drosophila melanogaster.* Proc. Natl. Acad. Sci. USA *103*, 17519–17524.
5. Levine, J.D., Funes, P., Dowse, H.B., and Hall, J.C. (2002). Resetting the circadian clock by social experience in *Drosophila melanogaster.* Science *298*, 2010–2012.
6. Fujii, S., Krishnan, P., Hardin, P., and Amrein, H. (2007). Nocturnal male sex drive in *Drosophila.* Curr. Biol. *17*, 244–251.
7. Mery, F., Varela, S.A.M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I., and Wagner, R.H. (2009). Public versus personal information for mate copying in an invertebrate. Curr. Biol. *19*, 730–734.
8. Krupp, J.J., Kent, C., Billeter, J.C., Azanchi, R., So, A.K.C., Schonfeld, J.A., Smith, B.P., Lucas, C., and Levine, J.D. (2008). Social experience modifies pheromone expression and mating behaviour in male *Drosophila melanogaster.* Curr. Biol. *18*, 1373–1383.
9. Kent, C., Azanchi, R., Smith, B., Formosa, A., and Levine, J.D. (2008). Social context influences chemical communication in *D. melanogaster* males. Curr. Biol. *18*, 1384–1389.

10. Ritchie, M.G. (2008). Behavioural genetics: The social fly. Curr. Biol. *18*, R862–R864.
11. Tully, T., and Quinn, W.G. (1985). Classical conditioning and retention in normal and mutant *Drosophila melanogaster.* J. Comp. Physiol. [A] *157*, 263–277.
12. Phelan, L.L., Rodd, Z., Byers, D., and Rosellini, R.A. (1998). Odor passive avoidance learning in individual *Drosophila melanogaster*: Parametric investigations of unconditioned stimulus intensity and inter-trial-interval. Learn. Motiv. *29*, 83–101.
13. Tempel, B.L., Bonini, N., Dawson, D.R., and Quinn, W.G. (1983). Reward learning in normal and mutant *Drosophila.* Proc. Natl. Acad. Sci. *80*, 1482–1486.
14. Pascual, A., and Preat, T. (2001). Localization of long-term memory within the *Drosophila* mushroom body. Science *294*, 1115–1117.
15. Tully, T., Preat, T., Boynton, S.C., and Del Vecchio, M. (1994). Genetic dissection of consolidated memory in *Drosophila.* Cell *79*, 35–47.
16. Isabel, G., Pascual, A., and Preat, T. (2004). Exclusive consolidated memory phases in *Drosophila.* Science *304*, 1024–1027.
17. Dubnau, J., and Tully, T. (1998). Gene discovery in *Drosophila*: New insights for learning and memory. Annu. Rev. Neurosci. *21*, 407–444.
18. Suh, G.S.B., Wong, A.M., Hergarden, A.C., Wang, J.W., Simon, A.F., Benzer, S., Axel, R., and Anderson, D.J. (2004). A single population of olfactory sensory neurons mediates an innate avoidance behaviour in *Drosophila.* Nature *431*, 854–859.
19. Sumpter, D.J. (2006). The principles of collective animal behaviour. Philos. Trans. R. Soc. Lond. B Biol. Sci. *361*, 5–22.
20. Leadbeater, E., and Chittka, L. (2007). Social learning in insects—From miniature brains to consensus building. Curr. Biol. *17*, R703–R713.
21. Coolen, I., Dangles, O., and Casas, J. (2005). Social learning in noncolonial insects? Curr. Biol. *15*, 1931–1935.
22. Galef, B.G., and Laland, K.N. (2005). Social learning in animals: Empirical studies and theoretical models. Bioscience *55*, 489–499.
23. Langridge, E.A., Franks, N.R., and Sendova-Franks, A.B. (2004). Improvement in collective performance with experience in ants. Behav. Ecol. Sociobiol. *56*, 523–529.
24. Leadbeater, E. (2009). Social learning: What do *Drosophila* have to offer? Curr. Biol. *19*, R378–R380.
25. Zar, Z.H. (1999). Biostatistical Analysis, Fourth Edition (Upper Saddle River, NJ: Prentice Hall).