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Acp70A regulates *Drosophila* pheromones through juvenile hormone induction

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ABSTRACT

Mated *Drosophila melanogaster* females show a decrease in mating receptivity, enhanced ovogenesis, egg-laying and activation of juvenile hormone (JH) production. Components in the male seminal fluid, especially the sex peptide ACP70A stimulate these responses in females. Here we demonstrate that ACP70A is involved in the down-regulation of female sex pheromones and hydrocarbon (CHC) production. *Drosophila* G10 females which express *Acp70A* under the control of the vitellogenin gene *yp1*, produced fewer pheromones and CHCs. There was a dose-dependent relationship between the number of *yp1-Acp70A* alleles and the reduction of these compounds. Similarly, a decrease in CHCs and diene pheromones was observed in *da* > *Acp70A* flies that ubiquitously overexpress *Acp70A*. Quantitative-PCR experiments showed that the expression of *Acp70A* in G10 females was the same as in control males and 5 times lower than in *da* > *Acp70A* females.

Three to four days after injection with 4.8 pmol ACP70A, females from two different strains, exhibited a significant decrease in CHC and pheromone levels. Similar phenotypes were observed in ACP70A injected flies whose ACP70A receptor expression was knocked-down by RNAi and in flies which overexpress ACP70A N-terminal domain. These results suggest that the action of ACP70A on CHCs could be a consequence of JH activation. Female flies exposed to a JH analog had reduced amounts of pheromones, whereas genetic ablation of the corpora allata or knock-down of the JH receptor Met, resulted in higher amounts of both CHCs and pheromonal dienes.

Mating had negligible effects on CHC levels, however pheromone amounts were slightly reduced 3 and 4 days post copulation. The physiological significance of ACP70A on female pheromone synthesis is discussed.

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1. Introduction

In *Drosophila melanogaster*, mating is largely dependent on sex pheromones, although visual and auditory signals are also involved (Antony and Jallon, 1982). Sex pheromones are long-chain cuticular hydrocarbons (CHCs) that act by contact or at short distances. CHCs are sexually dimorphic: on males, the predominant hydrocarbons have 23 or 25 carbon chains and one double bond. The most abundant are 7-tricosene (7-T; C23:1) and 7-pentacosene (7-P; C25:1) (Antony and Jallon, 1982; Jallon, 1984; Antony et al., 1985). Virgin females have high levels of CHCs with 27- and 29-carbon chains and two double bonds. The 7,11-heptacosadiene (7,11-HD; C27:2) and the nonacosadiene (7,11-ND; C29:2), account for about forty percent of the total CHCs in most females (Antony et al., 1985; Jallon and David, 1987). 7-T has been found to inhibit male courtship and to stimulate mating in females (Jallon, 1984; Grillet et al., 2006), whereas the 7,11-dienes enhance male preference (Antony et al., 1985; Billeter et al., 2009). Some minor compounds, such as 7-P and 7-heptacosene (7-H, 27:1) were also shown to stimulate male courtship (Antony et al., 1985; Ferveur and Sureau, 1996).

In most insects, mating elicits a behavioral and physiological switch in females, triggered by components in the male ejaculate, which are transmitted, along with sperm, into females (Avila et al., 2011). These post-mating responses have been extensively studied in *Drosophila* and include increased ovogenesis (Soller et al., 1999), ovulation (Heifetz et al., 2000) and decreased sexual receptivity (Wolfner, 1997). These changes are triggered by a complex set of more than a hundred of proteins and peptides (Findlay et al., 2008). Among these, the accessory gland proteins (ACPs), especially ACP70A (also named sex peptide), play a major role (Chen et al., 1988; Chapman et al., 2003; Liu and Kubli, 2003). This 36-amino-acid peptide passes from the reproductive tract into the

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 1  2  3  4  5  6  7  8  9  10 11 12 13 14 15 16 17 18 19 20 21 22
ATGAAAACTCTAGCTCTATTCTTGGTTCTCGTTTGCGTACTCGGCTTGGTCCAGGCCTGGGAATGG
 M  K  T  L  A  L  F  L  V  L  V  C  V  L  G  L  V  Q  A  W  E  W

 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44
CCGTGGAATAGGAAGCCTACAAAGTTTCCAATTCCAAGCCCCAATCCTCGTGATAAGTGGTGCCGT
 P  W  N  R  K  P  T  K  F  P  I  P  S  P  N  P  R  D  K  W  C  R

 45 46 47 48 49 50 51 52 53 54 55
CTTAATTTGGGGCCCGCCTGGGGTGGAAGATGTTAA
 L  N  L  G  P  A  W  G  G  R  C  *
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Fig. 1. Nucleotide and peptide sequences of Canton-S Acp70A. The N-terminal part of Acp70A used in transgenic flies is shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article)

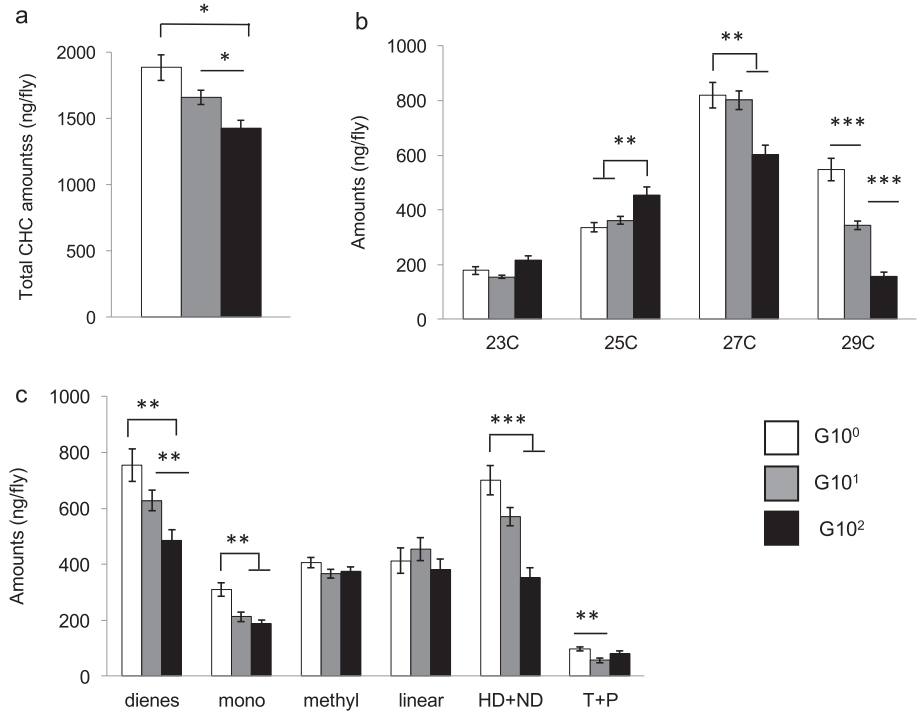

Fig. 2. Hydrocarbon amounts extracted from female flies derived from the G10 line and carrying 0 (white bars),1 (grey bars) or 2 (black bars) *Acp70A* alleles ($G10^0$, $G10^1$, $G10^2$, respectively). a: total hydrocarbon amounts (C23 to C29); b: amounts of hydrocarbons of different lengths; c: amounts of hydrocarbons of different classes. Each bar represents mean ± SEM ($n = 10$). *, ** and *** above bars indicate significant differences (one-way ANOVA, $P = 0.05$, 0.01 and 0.001, respectively) between means. HD: 7,11-heptacosadiene; ND: 7,11-nonacosadiene; T: 7-tricosene; P: 7-pentacosene; dienes: alkadienes; mono: alkenes; methyl: 2-methyl-alkanes; linear: linear alkanes.

Table 1
Analysis of differences between the CHC profiles of females issued from the G10 line: *P{Acp70A$^{g\ Yp1\ hs}$}/P{Acp70A$^{g\ Yp1\ hs}$}*, ($G10^2$); *P{Acp70A$^{g\ Yp1\ hs}$}/+* ($G10^1$) and +/+ ($G10^0$). CHC identities are given in the first column. Statistical analysis was performed using a one-way ANOVA followed by Tukey's multiple comparison post-hoc test. Values in bold indicate significant CHC variations with Acp70A dose. The last three columns give the mean quantities (±SEM) of CHCs (ng/fly) produced by ten 5-day old females at 25 °C.

CHC	*F*	P_{0-1}	P_{0-2}	P_{1-2}	$G10^0$	$G10^1$	$G10^2$
Total CHCs	10.45	**<.01**	0.55	0.07	1884.6 ± 97.2	1660.6 ± 54.8	1427.5 ± 58.1
9-T	1.24	0.52	0.91	0.30	6.9 ± 1.6	3.7 ± 1.9	12.7 ± 4.3
7-T	6.10	**0.02**	0.99	**0.01**	41.1 ± 3.5	19.0 ± 2.9	42.0 ± 8.0
23:0	4.61	0.96	**0.03**	**0.05**	121.1 ± 9.1	123.6 ± 3.3	148.0 ± 7.1
7,11-PD	14.15	0.99	**<.0001**	**<.0001**	32.9 ± 3.5	33.7 ± 3.8	104.3 ± 18.1
Me-24	28.00	**0.05**	**<.0001**	**<.0001**	33.0 ± 3.1	42.0 ± 2.9	86.1 ± 8.3
9-P	0.27	0.96	0.89	0.75	70.2 ± 5.9	68.3 ± 4.3	75.5 ± 5.1
7-P	4.53	**0.04**	**0.04**	1.00	55.7 ± 4.9	37.7 ± 6.1	37.3 ± 3.4
25:0	3.18	0.10	0.99	0.09	134.5 ± 9.4	172.2 ± 13.9	133.1 ± 13.6
7,11-HD	1.70	0.93	0.21	0.36	360.1 ± 28.7	347.2 ± 22.2	296.4 ± 26.0
Me-26	3.48	0.58	0.26	**0.04**	237.4 ± 14.3	255.7 ± 12.7	208.2 ± 11.4
9-H	17.20	1.00	**<.0001**	**<.0001**	49.4 ± 4.2	49.2 ± 5.3	16.1 ± 4.3
7-H	32.79	**0.002**	**<.0001**	**<.0001**	55.4 ± 5.3	32.5 ± 4.6	7.3 ± 2.1
27:0	2.59	0.99	0.16	0.13	105.2 ± 17.0	108.1 ± 14.6	64.1 ± 14.2
7,11-ND	56.46	**<.0001**	**<.0001**	**<.0001**	340.2 ± 28.6	223.7 ± 11.7	55.6 ± 11.5
Me-28	38.83	**<.0001**	**<.0001**	0.98	129.1 ± 9.3	61.2 ± 2.3	63.0 ± 4.8
9-N	3.28	0.10	0.009	0.01	0.9 ± 0.9	1.2 ± 1.0	8.5 ± 2.4
7-N	4.70	0.93	0.002	**<.0001**	1.8 ± 1.3	0.5 ± 0.3	10.3 ± 2.0
29:0	0.39	0.99	0.71	0.75	51.6 ± 18.5	50.0 ± 13.8	34.2 ± 13.2

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