Supplementary Material

Origins of aminergic regulation of behavior in complex insect social systems

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Data analysis and statistical methods

We compared the neuromodulation of biogenic amines (octopamine, OA; serotonin, 5-HT; and dopamine, DA) in solitary/presocial and eusocial insects using published data. Solitary and presocial species were combined in analyses because of the similarities in behaviors recorded. We created eight behavioral categories (activity, aggression, development, higher-order sensory integration, nutrition, reproduction, sensorimotor, and social functions; defined in Table S1) and five possible biogenic amine-behavioral category correlations (increase, decrease, modulation, none, and unknown).

For each species, we analyzed available published results and determined the type of biogenic amine-behavioral category correlation. We assigned a single value per species, biogenic amine, and functional category. *Increase* was assigned when increasing values of a given biogenic amine correlated with increasing values of a given behavioral category. *Decrease* was assigned when decreasing values of a given biogenic amine correlated with increasing values of a given behavioral category. *Modulation* was assigned when different doses correlated with different effects (for example, low levels of 5-HT in inside nest workers and high levels of 5-HT in outside nest workers) or if results in the literature were inconsistent. *None* was assigned when no significant relationship between the biogenic amine and the behavior was found. Empty cells in our figures indicate no information was available regarding biogenic amine function in a behavioral category for that species.

To represent evolutionary relationships among insects, we followed the phylogenies: Blattodea (Djernaes, et al., 2011, Coleoptera Misof, et al., 2014, Diptera Wiegmann, et al., 2011), Hemiptera (Song, et al., 2012, Wang, et al., 2014), Hymenoptera and Formicidae (Tree of Life: tol.org; Moreau and Bell, 2013, Schmidt, 2013), Lepidoptera (Regier, et al., 2013), Orthoptera (Song, et al., 2015); and (Misof, et al., 2014) for relationships among insect orders. The composite phylogenetic tree was constructed in Mesquite (Maddison & Maddison 2017). Images of insects were used with permission from PhyloPic (http://phylopic.org).

To compare effects of biogenic amines between solitary/presocial and eusocial insects, we built contingency tables for each biogenic amine and behavioral/functional category. We used the

Fisher exact test to determine whether social complexity (solitary/presocial versus eusocial) affected the function of biogenic amines.

Behavioral category	All insects	Solitary insects	Eusocial insects
Activity	Locomotion, escape response, circadian rhythms	n/a	n/a
Aggression	Defensive or agonistic actions, predation	n/a	Nestmate recognition
Development	Age-related physiological change	n/a	Age-related division of labor
Higher-order integration	Learning/memory, decision-making, emotion-like states, attention	n/a	n/a
Nutrition	Feeding behaviors, metabolism, sucrose responsiveness	n/a	Trophallaxis
Reproduction	Reproductive state, sex pheromone perception, female receptivity, oviposition	Parental care, mate selection	Colony foundation, reproductive division of labor
Sensorimotor functions	Sensory processing, reception, and response thresholds	n/a	n/a
Social functions	n/a	Parental care, mate selection	Trophallaxis, division of labor, collective action, brood care

Table S1: Behaviors comprising categories used for comparisons of solitary/presocial and eusocial insect aminergic control systems. n/a indicates no additional behaviors recorded in a given category.

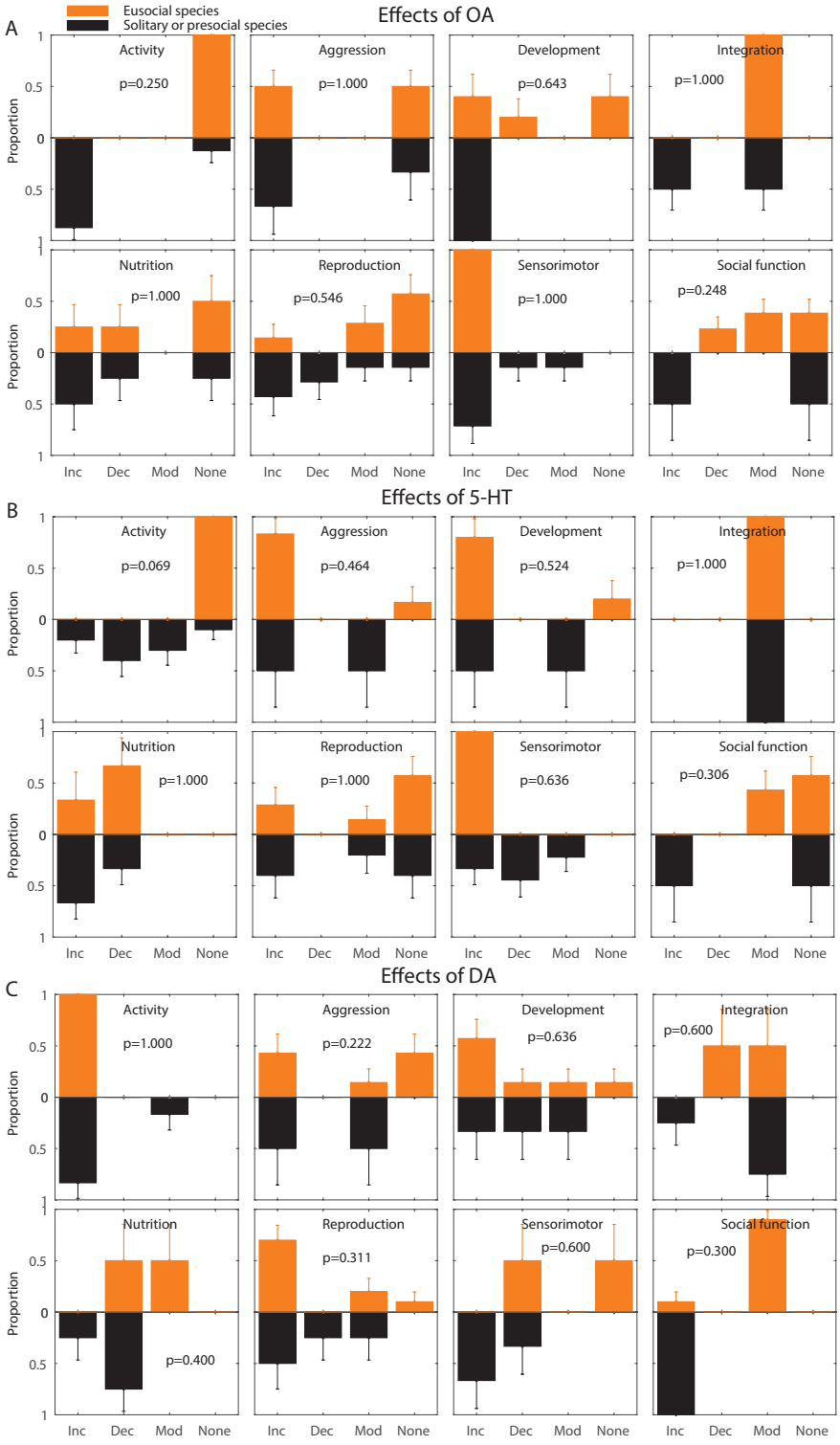

Figure S1: Distribution of effects of the biogenic amines in solitary/presocial and eusocial insects by behavioral category. **A.** Octopamine (OA); **B.** Serotonin (5-HT); **C.** Dopamine (DA).

Histogram coding: Orange (eusocial species); black (solitary and presocial species) Inc: increase; Dec: decrease; Mod: modulation; None: no effect. p-values calculated using a Fisher test on absolute numbers.

OCTOPAMINE

Species	Activity	Aggression	Development	Integration	Nutrition	Reproduction	Sensorimotor function	Social function
Hodotermopsis sjostedti		Ishikawa, et al., 2016						Ishikawa, et al., 2016
Leucophaea maderae	Page, 1987				Cohen, et al., 2002			
Periplaneta americana	Goldstein and Camhi, 1991			Goldstein and Camhi, 1991			Goldstein and Camhi, 1991	
Reticulitermes flavipes								
Zootermopsis nevadensis								
Nicrophorus orbicollis								Panaitof, et al., 2016
Tribolium castaneum	Nishi, et al., 2010							
Tribolium freemani			Hirashima, et al., 1999					
Aedesal bopictus								
Anopheles gambiae						Fuchs, et al., 2014		
Calliphora erythrocephala			Nässel and Laxmyr, 1983					
Drosophila melanogaster	Sadaf, et al., 2015, Saraswati, et al., 2004, Yellman, et al., 1997	Hoyer, et al., 2008, Zhou, et al., 2008		Burke, et al., 2012, Müller, 1997, Schwaerzel, et al., 2003	Luo, et al., 2014	Certel, et al., 2010, Lee, et al., 2003		
Neobellieria bullata								
Phormia regina					Long and Murdock, 1983			
Teleopsis dalmanni		Bubak, et al., 2014						
Lygus hesperus						Brent, et al., 2016		
Pyrrhocoris apterus						Chvalova, et al., 2014		
Rhodnius prolixus								
Myzus persicae								
Acromyrmex echinatior								Smith, et al., 2013
Apis mellifera	Burrell and Smith, 1995	Burrell and Smith, 1995, Robinson, et al., 1999	Harris and Woodring, 1995, Schulz, et al., 2002a, Schulz and	Barron, et al., 2007, Burrell and Smith, 1995, Chen, et al., 2008, Hammer and	Braun and Bicker, 1992, Scheiner, et al., 2002		Kloppenburg and Erber, 1995, Mercer and Menzel, 1982, Robinson, et al., 1999,	Barron, et al., 2007, Schulz, et al., 2002a, Schulz and Robinson, 2001

			Robinson, 2001, Schulz, et al., 2002b	Menzel, 1995, Menzel, et al., 1999, Mercer and Menzel, 1982			Scheiner, et al., 2002	
Bombus terrestris		Bloch, et al., 2000				Bloch, et al., 2000		Bloch, et al., 2000
Camponotus fellah								Boulay, et al., 2000
Camponotus mus								
Diacamma sp.								
Formica japonica		Aonuma and Watanabe, 2012b	Aonuma and Watanabe, 2012a		Wada-Katsumata, et al., 2011	Aonuma and Watanabe, 2012a		Wada-Katsumata et al., 2011)
Formica polyctena		Szczuka, et al., 2013	Wnuk, et al., 2010					Wnuk, et al., 2010
Formica rufa								
Harpegthos saltator		Penick, et al., 2014				Penick, et al., 2014		Penick, et al., 2014
Pheidole dentata			Seid and Traniello, 2005					Seid and Traniello, 2005, Sandridge et al., unpublished
Pheidole morrisi								(Sandridge et al., unpublished)
Polistes chinensis								
Oecophylla smaragdina		Kamhi, et al., 2015						Kamhi, et al., 2015
Polyrhachis moesta		Koyama, et al., 2015			Koyama, et al., 2015			Koyama, et al., 2015
Solenopsis invicta		Vander Meer, et al., 2008				Boulay, et al., 2001	Vander Meer, et al., 2008	
Streblogthus peetersi			Cuvillier-Hot and Lenoir, 2006			Cuvillier-Hot and Lenoir, 2006		Cuvillier-Hot and Lenoir, 2006
Veromessor pergandei						Muscedere, et al., 2015		Muscedere, et al., 2015
Vollenhovia nipponica		Ohkawara and Aonuma, 2016				Ohkawara & Aonuma, 2016)		
Xylocopa appendiculata								
Agrotis ipsilon	Barrozo, et al., 2010						Barrozo, et al., 2010	
Bombyx mori			Hirashima, et al., 1999			Pophof, 2002	Pophof, 2002	
Caloptilia fraxinella							Lemmen and Evenden, 2015	
Galleria mellonella L						Abdoun, et al., 1995		
Helicoverpa zea								
Mamestra brassicae							Grosmaitre, et al., 2001	

Manduca sexta	Claassen and Kammer, 1986			Claassen and Kammer, 1986			Dolzer, et al., 2001	
Trichoplusia ni					Linn and Roelofs, 1986		Linn and Roelofs, 1986	
Gryllus bimaculatus	Adamo, et al., 1995	Rillich, et al., 2011, Rillich and Stevenson, 2011, 2015, Stevenson, et al., 2005, Stevenson and Rillich, 2017, Stevenson and Schildberger, 2013		Mizunami, et al., 2009, Unoki, et al., 2005		Abdoun, et al., 1995, Sakai, et al., 2017		
Locusta migratoria				Bacon, et al., 1995				Ma, et al., 2015
Schistocerca americana	Morris, et al., 1999, Orchard, et al., 1993, Sombati and Hoyle, 1984b			Sombati and Hoyle, 1984a				

SEROTONIN

	Activity	**Aggression**	**Development**	**Integration**	**Nutrition**	**Reproduction**	**Sensorimotor function**	**Social function**
Hodotermopsis sjostedti								
Leucophaea maderae	Page, 1987				Cohen, 2001			
Periplaneta americana	Goldstein and Camhi, 1991			Goldstein and Camhi, 1991			Goldstein and Camhi, 1991	
Reticulitermes flavipes					Nuss, et al., 2010			
Zootermopsis nevadensis								
Nicrophorus orbicollis						Panaitof, et al., 2016		Panaitof, et al., 2016
Tribolium castaneum	Nishi, et al., 2010							
Tribolium freemani								
Aedes albopictus								
Anopheles gambiae	Fuchs, et al., 2014							
Calliphora erythrocephala			Nässel and Laxmyr, 1983					
Drosophila melanogaster	Neckameyer, et al., 2007, Yellman, et al., 1997, Yuan, et al.,	Alekseyenko, et al., 2014, Alekseyenko, et al., 2010,	Neckameyer and Bhatt, 2012	Sitaraman, et al., 2008, Vargas, et al., 2010	Neckameyer, et al., 2007, Vargas, et al., 2010 Neckameyer,		Neckameyer, et al., 2007	

	2006, Yuan, et al., 2005	Johnson, et al., 2009			et al., 2007			
Neobellieria bullata	Dacks, et al., 2003				Dacks, et al., 2003			
Phormia regina					Haselton, et al., 2009, Long and Murdock, 1983			
Teleopsis dalmanni		Bubak, et al., 2014, Bubak, et al., 2016						
Lygus hesperus						Brent, et al., 2016		
Pyrrhocoris apterus						Chvalova, et al., 2014		
Rhodnius prolixus					Orchard, 2006			
Myzus persicae					Kaufmann, et al., 2004			
Acromyrmex echinatior								Smith, et al., 2013
Apis mellifera			Harris and Woodring, 1992	Blenau and Erber, 1998, Chen, et al., 2008, Mercer and Menzel, 1982	French, et al., 2014		Mercer and Menzel, 1982	
Bombus terrestris						Bloch, et al., 2000		
Camponotus fellah					Boulay, et al., 2000			Boulay, et al., 2000
Camponotus mus					Falibene, et al., 2012			
Diacamma sp.								
Formica japonica		Aonuma and Watanabe, 2012b	Aonuma and Watanabe, 2012b			Aonuma and Watanabe, 2012a		
Formica polyctena		Szczuka, et al., 2013						
Formica rufa		Kostowski, et al., 1975						
Harpegnathos saltator		Hoyer, et al., 2005, Penick, et al., 2014	Penick, et al., 2014			Hoyer, et al., 2005, Penick, et al., 2014		Penick, et al., 2014
Pheidole dentata	Giraldo, et al., 2016b		Giraldo, et al., 2016a, Seid and Traniello, 2005	Giraldo, et al., 2016b			Giraldo, et al., 2016b, Muscedere, et al., 2012	Giraldo, et al., 2016b, Muscedere, et al., 2012, Seid and Traniello, 2005; Sandridge et al., unpublished data
Pheidole morrisi								(Sandridge et al., unpublished data)
Polistes chinensis						Sasaki, et al., 2009		

Oecophylla smaragdina		Kamhi, et al., 2015						
Polyrhachis moesta								
Solenopsis invicta						Boulay, et al., 2001		
Streblognathus peetersi			Cuvillier-Hot and Lenoir, 2006			Cuvillier-Hot and Lenoir, 2006		Cuvillier-Hot and Lenoir, 2006
Veromessor pergandei		Muscedere, et al., 2015						
Vollenhovia nipponica		Ohkawara and Aonuma, 2016				Ohkawara and Aonuma, 2016		
Xylocopa appendiculata								
Agrotis ipsilon	Barrozo, et al., 2010					Barrozo, et al., 2010	Barrozo, et al., 2010	
Bombyx mori							Hill, et al., 2003	
Caloptilia fraxinella							Lemmen and Evenden, 2016	
Galleria mellonella L								
Helicoverpa zea					Cohen, et al., 1988			
Mamestra brassicae							Grosmaitre, et al., 2001	
Manduca sexta	Claassen and Kammer, 1986			Claassen and Kammer, 1986		Kloppenburg, et al., 1999	Dolzer, et al., 2001, Kloppenburg, et al., 1999, Kloppenburg and Mercer, 2008	
Trichoplusia ni	Linn and Roelofs, 1986					Linn and Roelofs, 1986	Linn and Roelofs, 1986	
Gryllus bimaculatus	Dyakonova, et al., 1999			Dyakonova, et al., 1999			Dyakonova, et al., 1999	
Locusta migratoria					Kaufmann, et al., 2004			
Schistocerca americana								
Schistocerca gregaria					Baines and Tyrer, 1989			Anstey, et al., 2009

DOPAMINE

	Activity	**Aggression**	**Development**	**Integration**	**Nutrition**	**Reproduction**	**Sensorimotor function**	**Social function**

Hodotermopsis sjostedti								
Leucophaea maderae	Page, 1987				Allen, et al., 2011			
Periplaneta americana	Weisel-Eichler and Libersat, 2002			Goldstein and Camhi, 1991			Goldstein and Camhi, 1991, Weisel-Eichler and Libersat, 2002	
Reticulitermes flavipes								
Zootermopsis nevadensis			Yaguchi, et al., 2016					Yaguchi, et al., 2016
Nicrophorus orbicollis								Panaitof, et al., 2016
Tribolium castaneum	Miyatake, et al., 2008, Nishi, et al., 2010							
Tribolium freemani								
Aedes albopictus					Fukumitsu, et al., 2012	Fukumitsu et al., 2012)		
Anopheles gambiae	Fuchs, et al., 2014							
Calliphora erythrocephala			Nässel and Laxmyr, 1983					
Drosophila melanogaster	Alekseyenko, et al., 2010, Draper, et al., 2007, Yellman, et al., 1997	Alekseyenko, et al., 2013	Neckameyer and Bhatt, 2012	Aso, et al., 2010, Claridge-Chang, et al., 2009, Cohn, et al., 2015, Kim, et al., 2007, Liu, et al., 2012, Schwaerzel, et al., 2003, Selcho, et al., 2009, Van Swinderen and Andretic, 2011, Zhang, et al., 2007		Neckameyer, 1998a, b	Van Swinderen and Andretic, 2011	
Neobellieria bullata								
Phormia regina					Long and Murdock, 1983			
Teleopsis dalmanni								
Lygus hesperus						Brent, et al., 2016		
Pyrrhocoris apterus						Chvalova, et al., 2014		
Rhodnius prolixus								
Myzus persicae								
Acromyrmex echinatior								Smith, et al., 2013
Apis mellifera	Beggs, et al., 2007, Bozic and Woodring, 1998		Harano, et al., 2007, Harris and Woodring, 1992	Blenau and Erber, 1998, Chen, et al., 2008, Mercer and	Scheiner, et al., 2002	Harano, et al., 2008, Harris and Woodring, 1995	Mercer and Menzel, 1982, Scheiner, et al., 2002	Bozic and Woodring, 1998, Wagener-Hulme, et al., 1999

				Menzel, 1982				
Bombus terrestris				Perry, et al., 2016		Bloch, et al., 2000		
Camponotus fellah								
Camponotus mus								
Diacamma sp.		Okada, et al., 2015, Shimoji, et al., 2017				Okada, et al., 2015		Okada, et al., 2015
Formica japonica		Aonuma and Watanabe, 2012b, Wada-Katsumata, et al., 2011	Aonuma and Watanabe, 2012a		Wada-Katsumata, et al., 2011	Aonuma and Watanabe, 2012a		Wada-Katsumata, et al., 2011
Formica polyctena		Szczuka, et al., 2013	Wnuk, et al., 2010					Wnuk, et al., 2010
Formica rufa								
Harpegnathos saltator		Hoyer, et al., 2005, Penick, et al., 2014	Penick, et al., 2014			Hoyer, et al., 2005, Penick, et al., 2014		Penick, et al., 2014
Pheidole dentata			Seid and Traniello, 2005					Giraldo, et al., 2016b, Muscedere, et al., 2013, Seid and Traniello, 2005; Sandridge et al., unpublished
Pheidole morrisi								(Sandridge et al., unpublished)
Polistes chinensis						Sasaki and Harano, 2007		
Oecophylla smaragdina		Kamhi, et al., 2015						
Polyrhachis moesta								
Solenopsis invicta		Vander Meer, et al., 2008				Boulay, et al., 2001	Vander Meer, et al., 2008	
Streblognathus peetersi			Cuvillier-Hot and Lenoir, 2006			Cuvillier-Hot and Lenoir, 2006		Cuvillier-Hot and Lenoir, 2006
Veromessor pergandei						Muscedere, et al., 2015		Muscedere, et al., 2015
Vollenhovia nipponica		Ohkawara and Aonuma, 2016				Ohkawara & Aonuma, 2016)		
Xylocopa appendiculata	Sasaki and Nagao, 2013							
Agrotis ipsilon								
Bombyx mori			Hirashima, et al., 1999, Noguchi and Hayakawa, 2001					
Caloptilia fraxinella							Lemmen and Evenden, 2016	

Galleria mellonella L								
Helicoverpa zea								
Mamestra brassicae								
Manduca sexta	Claassen and Kammer, 1986			Claassen and Kammer, 1986				
Trichoplusia ni								
Gryllus bimaculatus		Rillich and Stevenson, 2014		Mizunami, et al., 2009, Unoki, et al., 2005				
Locusta migratoria								
Schistocerca americana								
Schistocerca gregaria					Baines and Tyrer, 1989			

Table S2: References to studies documenting biogenic amine functions for behaviors in eight categories.

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