Decoding ants’ olfactory system sheds light on the evolution of social communication

Patrizia d’Ettorre\textsuperscript{a,b,1}, Nina Deisig\textsuperscript{c}, and Jean-Christophe Sandoz\textsuperscript{d}

Chemical communication is the primordial and possibly most efficient way of transmitting messages between living units (1). It has reached its apex in the “superorganisms” (2), for example in colonies of eusocial insects, such as honey bees (3). Colony survival and reproductive success rely on the chemical communication channel to maintain an advanced social organization characterized by high levels of cooperation and low levels of conflicts (1, 4, 5). Eusocial bees and ants are model organisms for understanding social chemical communication; hence, recent research has focused on the identification of chemoreceptors (6). A new study by Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals.

Chemoreceptors can be differentiated into olfactory receptors (ORs), gustatory receptors, and ionotropic receptors, as well as several other receptor classes (8). ORs are transmembrane proteins representing the interface between animals and their olfactory environment for detecting food sources or, in a social context, nestmates or sexual partners. They are expressed in olfactory receptor neurons (ORNs) in the insect antenna; after binding odors, information is transferred to the brain, eventually inducing behavioral responses. It has long been believed that perception of “general” odors (food and flower scent) is separated from that of “social” odors (e.g., pheromones), and that these are detected by different ORs. Recent research contradicts such strict partition: even highly specialized ORNs (sex pheromone ORNs) may respond to ordinary odors (9). In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).

Are CHCs exclusively detected by ORs of the 9-exon subfamily? With an elegant approach, Slone et al. (7) uses the ant Harpegnathos saltator to investigate the molecular mechanisms underlying chemoreception of socially relevant semiochemicals. In ants, colonymate recognition relies on cuticular hydrocarbons (CHCs), which also inform about caste and reproductive status (1, 10). Being primarily a barrier against desiccation and pathogens, CHCs have been co-opted to serve as a multicomponent cue/signal (11), first in solitary species for reproduction behavior (e.g., species recognition), then in social species, where they serve at least two functions (signature mixtures and pheromones) at different levels (individual, within colony, between colonies). However, ambiguity remains about the mechanisms by which chemoreceptors regulate social behavior. Recent data indicate that ORs underwent a huge expansion in ants; based on their sequence, OR genes were classified in different subfamilies, with the 9-exon OR subfamily thought responsible for CHC-detection (12).
On the evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).

Consequences for Neuro-Ethological Models of Insect Social Communication

The evolution of cooperation (and of altruism) is a persisting conundrum for evolutionary biologists and scientists in general: How can a Darwinian selfish unit (e.g., an individual organism) forego its own reproduction for “the good of the society”? Social insects provide an answer, deep-rooted in more than a century of kin-selection theory-inspired theoretical and empirical work (17, 18). A sensory system allowing detection of kinship (originally equal to colony membership) (5) would be a key preadaptation facilitating the emergence of sociality by preventing altruistic acts toward unrelated individuals. In social insects, CHCs play a crucial role in colony-sociality by preventing altruistic acts toward unrelated individuals. In one scenario, ants would evolve neural responses in the pheromone coding part of the antennal lobe in Agrotis moths (9).
the T6 subsystem. Proving that information from both subsystems is indeed relevant for nestmate discrimination will require using lesion/neural block approaches. Transgenic methods and the possibility to use genome-editing tools (CRISPR/Cas9) could prove decisive to this goal. We believe that Slone et al.’s (7) work will stimulate proponents of the “dedicated subsystem theory” to come forward with compelling new data, bringing the field closer to a deep understanding of the neuro-ethology of social communication.

Acknowledgments
We thank the CNRS. The authors are supported by the French National Research Agency through Project PheroMod ANR-14-CE18-003 (to P.d. and N.D.) and the Bee-o-CHOC Project (J.C.S.).