

Joris M. Koene · Andries ter Maat

The distinction between pheromones and allohormones

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Many interactions between individuals are mediated by substances that are often referred to as semiochemicals. Over the years, several terms have become established that distinguish between the different types of interactions that involve semiochemicals between and within species. We agree with Ruther and Steidle (2002) that a standardised terminology is essential and facilitates the communication between different disciplines. Therefore, in a previous issue of this journal, we proposed the term allohormones for substances that are transferred from one individual to another free-living member of the same species and that induce a direct physiological response, bypassing sensory organs (Koene and Ter Maat 2001). In this issue, Ruther and Steidle (2002) question the utility of the term allohormone. With this reply, we respond to their criticism and clarify why we think it is important to distinguish allohormones from pheromones.

Chemically mediated interactions between individuals can be classified as interspecific or intraspecific. Interspecific chemicals, for which Bethe (1932) initially proposed the term alloiohormones¹, are now clearly defined and separated in several categories: depending on who benefits from them and/or who produces them they are labelled as allomones, kairomones, synomones, or apneumones (Brown et al. 1970; Nordlund and Lewis 1976; Dicke and Sabelis 1988).

¹Note that according to spelling rules *alloio-* (Gk. *alloios*, of another sort or kind, different) cannot be used as a prefix. The combining form *allo-*, which is often used in English (e.g. allopatric), originates from the Greek word for other, *allos*.

J.M. Koene (✉)
Department of Evolutionary Biology,
Westfälische Wilhelms-Universität,
Hüfferstrasse 1, 48149 Münster, Germany
E-mail: jkoene@uni-muenster.de

A. ter Maat
Faculty of Biology, Vrije Universiteit, De Boelelaan 1087,
1081 HV Amsterdam, The Netherlands

Chemicals used in the interactions between individuals of the same species, in our opinion, are not as clearly defined; nearly all are referred to as pheromones. In particular, some of the intraspecific substances that have been discovered in recent years are not satisfactorily described by this term. Karlson and Lüscher (1959) already hinted at this problem when they defined the term pheromone. They indicated that, in the future, it might be necessary to refine their definition. The possible solution that they suggested was to make a distinction between pheromones acting via the senses, and “telemones” acting via the blood system. The definition of allohormones that we proposed (Koene and Ter Maat 2001) is very similar to their definition of “telemones”. The major differences being that these substances were then still hypothetical and, as it turns out, do not necessarily enter via the digestive system as Karlson and Lüscher presumed at that time. Finally, they are not necessarily blood-borne.

Ruther and Steidle (2002) argue that our definition of an allohormone meets that of a primer pheromone. To support this, they mention the text book example of the queen pheromone of the honey bee *Apis mellifera*, which consists of several components (queen mandibular gland complex; Slessor et al. 1988). At least one of these components is transferred orally between individuals through trophallaxis. However, whether the transferred substance acts via taste receptors or acts internally remains to be determined (Winston and Slessor 1998). If the gustatory sense is involved we would classify this substance as a primer pheromone; if the substance acts internally we would classify it as a primer allohormone. By giving several examples (see Koene and Ter Maat 2001) we hoped to illustrate that allohormones can have a primer as well as a releaser function, just like pheromones. The examples of induction of oviposition in the fruit fly (*Drosophila funebris*; Baumann 1974a, 1974b) and inhibition of remating in the house fly (*Musca domestica*; Riemann et al. 1967; Leopold et al. 1971a, 1971b) represent primer allohormones that alter the physiology and cause their effect via the CNS. The

examples of the increased sperm storage in the garden snail (*Helix aspersa*: Koene and Chase 1998; Rogers and Chase 2001; Landolfi et al. 2001) and induced sperm transport in the assassin bug (*Rodnius prolixus*: Davey 1958) represent releaser allohormones that result in an immediate (though covert) response.

To conclude, like pheromones, allohormones can have a primer or releaser function. The difference between pheromones and allohormones is based on the way in which these intraspecific substances function: pheromones act via the senses, while allohormones circumvent the senses. Given the large number of allohormones that are already known, we think this is a legitimate and useful distinction.

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