Poster at International Society for Chemical Ecology meeting, Tours, France 2010

UNIVERSITY OF OXFORD

Pheromones are not (quite) what you think

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What are the distinguishing characteristics of **pheromones** and **signature mixtures***?

Surprisingly, it seems it's not the innateness of responses to pheromones nor the specificity of pheromone receptor proteins, though these are common to many (most?) pheromones. Instead, the distinguishing characteristics of signature mixtures (SMs)* are the combination of a requirement for learning and the variability of the cues learnt (Figure, below) (Wyatt 2010).

Confusing the two ideas has, for example, caused a minority of researchers to deny that mammals have pheromones. In contrast to a species-wide pheromone, there is no single SM to find as, I suggest, SMs are a 'receiver-side' phenomenon and it is the differences in SMs which allow animals to distinguish each other . Mammals, social insects, and other animals have both pheromones and SMs.

Many of the presumed differences between pheromones and signature mixtures (SMs) are not supported when examined in detail (Wyatt 2010). For example, though male moth response to female sex pheromone shows highly specialized receptors for pheromone and dedicated brain areas specific for pheromone processing, other non-sex pheromone processing in insects may be by less specific receptors, without dedicated glomeruli in the brain. Narrowly tuned specialized receptors and dedicated glomeruli are not a prerequisite for a pheromone (e.g. honeybee alarm pheromone, Wang et al. 2008).

* Signature mixtures: 'variable subsets of molecules of an animal's chemical profile which are learnt by other animals, allowing them to distinguish individuals or colonies'.
[Derived from Wyatt's (2005) 'signature odor' and Johnston's 'mosaic signal' (*sensu* 2003 and 2005)].

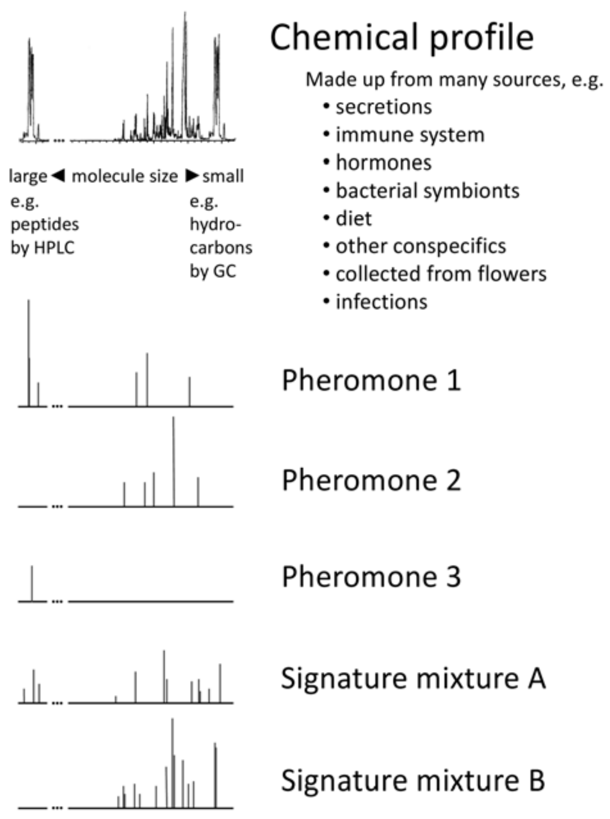

Fig from Wyatt (2010). Layout inspired by Fig. 1 of Schaal (2008).

◀ Pheromones occur in a background of molecules which make up the **chemical profile** consisting of all the molecules extractable from an individual. The chemical profile (top) is an imaginary trace from an imaginary column (at one end is HPLC with large proteins, at other end is GC with small volatile molecules). The profile could have come from any kind of animal, invertebrate or vertebrate. Pheromones and SMs can be molecules of any size depending on species and/or habitat.

The **pheromones** could include sex pheromones or ones related to life stage or caste. The pheromones would be the same in all individuals of the same type in a species, dominant male, worker ant forager, etc; that is, they are anonymous, common across the species.

The **signature mixtures** (A and B) are subsets of variable molecules from the chemical profile that are learnt for distinguishing individuals or colonies. Signature mixtures (SMs) may be a 'receiver-side' concept. Different receivers might learn different SMs of the same individual. For example, a male might learn a different SM of their mate from the SM of the same female learnt by her offspring. Hypothetically the male might learn different SMs for the same female in different contexts, say immune-system associated molecules in one context and more diet influenced molecules in another.

All signature mixtures, and almost all pheromones, whatever the size of molecules, are detected by olfaction (as defined by receptor families and glomerular processing), in mammals by the main olfactory system or vomeronasal system or both. The processing of all signature mixtures, and most pheromones, is combinatorial across a number of glomeruli, even for some sex pheromones which appear to have 'labeled lines'. A small minority of pheromones act directly on target tissues (allohormone pheromones) or are detected by non-glomerular chemoreceptors such as taste.

Conclusions. Distinguishing between signature mixtures and pheromones could help our understanding. For example, a male mouse's urine contains a complex mixture of his individual profile plus pheromones with primer effects on females, including the Bruce effect (contact with an unfamiliar male blocks the pregnancy (Brennan 2009)). When a female mates, she learns the individual SM of her male mate in her accessory olfactory lobe – a memory which prevents his pheromones from eliciting the pregnancy block. Thus there are two distinct kinds of chemical information, a male testosterone-dependent pheromone(s) (the same for all males), and each male's different individual SM (including his urinary odour type and peptides related to the MHC).

Karlson and Lüscher ended their 1959 paper introducing 'pheromones' by throwing the definition open for discussion. In a similar spirit I would welcome comments and suggestions for improving the ideas presented here. I am also updating *Pheromones and animal behaviour* for its second edition, due 2011.

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