



## Special Issue: Biochemistry &amp; Animal Communication

## Innate and learned aspects of pheromone-mediated social behaviours



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## ARTICLE INFO

## Article history:

Received 31 March 2014  
 Initial acceptance 20 May 2014  
 Final acceptance 4 September 2014  
 Available online 3 October 2014  
 MS. number: 14-00269R

## Keywords:

associative learning  
 dopamine  
 innate behaviour  
 main olfactory epithelium  
 neural pathway  
 pheromones  
 reproductive behaviour  
 reward value  
 rodents  
 vomeronasal organ

All species perceive sensory stimuli from the environment through dedicated sensory modalities, and respond with appropriate behaviours designed to maximize fitness and reproductive success. In most mammalian species, information regarding sex, age and other species-specific social and reproductive characteristics is conveyed by pheromones, which are detected by the vomeronasal and olfactory systems. Traditionally, pheromone signals have been thought to possess intrinsic rewarding meanings and to trigger 'innate' hardwired social behavioural responses. In contrast, odorants are considered to possess mostly neutral reward value, but may induce approach or avoidance behaviours as a result of experience or through conditioning following pairing with stimuli that possess intrinsic rewarding properties. This review describes studies demonstrating that innate behavioural responses, with particular emphasis on reproductive responses mediated by pheromonal signals, are actually flexible and substantially influenced by past experience and associative learning. These attributes allow the animal to assign new motivational incentives to pheromones associated with social and reproductive behaviours, thus providing adaptive ability to cope with unique changes in internal and external environmental conditions. We argue that responses to pheromones are far more easily modified by experience than would be expected from hardwired innate responses, and that the behaviours they elicit are chiefly plastic and sensitive to modification throughout life by sensory-mediated emotional experience.

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*All behaviour is a reaction... to a certain extent, dependent on external stimulation...[and]... is spontaneous in so far as it is also dependent on internal causal factors, or motivational factors, responsible for the activation of an urge or drive.*

**Nikolaas Tinbergen (Tinbergen, 1969, p. 15)**

The behaviour of all living entities including insects (Dudareva & Pichersky, 2006), rodents (Davies & Krebs, 1997) and primates (Cartwright, 2000) is driven by sensory information that is acquired from the external environment. Such biotic and abiotic sensory cues, detected via specialized sensory mechanisms adapted to the unique niches of each species (Alcock, 2013; Lorenz, 1935), play a key role in behavioural decisions essential to the animal's reproductive success and survival (Davies & Krebs, 1997).

The interpretation of these stimuli to convey meaning that will guide the animals' behavioural decisions is largely dependent on that individual's internal state (Mannella, Gurney, & Baldassarre, 2013). According to the hydraulic model of Lorenz, a behaviour is associated with an action-specific energy (drive/motivation),

described as a reservoir containing a fluid that accumulates until the animal encounters a specific external sensory stimulus. When the animal perceives such a stimulus, given the right motivational (internal) state, the stored energy is released, leading to the execution of a fixed action (innate) behavioural pattern (Lorenz, 1950). Thus, a given stimulus may trigger a maximal reaction in one motivational state but may have no effect or even trigger an opposite reaction in another (Sullivan, Landers, Yeaman, & Wilson, 2000; Tinbergen, 1969).

One of the main internal factors affecting an animal's motivational state and subsequent innate behavioural decisions is its unique hormonal profile, which depends, among other factors, on its age, reproductive state and past experience (Hastings, O'Neill, & Maywood, 2007). In rats, *Rattus norvegicus*, as in other mammals, the maternal motivation of females to suckle newborn pups has been shown to be dependent on changes in the milieu of peripheral hormones including oestradiol, progesterone (Bridges, 1984) and prolactin (Bridges & Ronsheim, 1990). In nulliparous females, the latency to initiate pup-caring behaviour seems to correlate with oxytocin levels in the central nervous system. It has been suggested that oxytocin release in the brain might be part of an array of neuroendocrine events, mediated by the pup's odours, that together determine the initial aversion to pups observed in nulliparous females (Fahrbach, Morrell, & Pfaff, 1984). Furthermore, in rodents, male copulatory behaviour and motivational aspects of

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sexual behaviour are critically dependent on steroid hormones (testosterone) secreted in adulthood. Castration diminishes the motivation of males to investigate sexual partners and engage in copulatory behaviour (Harding & McGinnis, 2003; Harding & Velotta, 2011), and eliminates their preference for oestrous female odours over male odours (Paredes, Lopez, & Baum, 1998; Stern, 1970). It has been suggested that steroid hormones facilitate the responses of sensory neurons to conspecific stimuli (such as sexually relevant odours), so that a given external stimulus will be more likely to elicit a sexual response (Hull et al., 1999).

Another key factor affecting the reaction of an animal to a specific stimulus, and particularly the motivation to initiate innate behavioural responses, is its past learning experience. A neutral external stimulus can acquire a positive reward value once the animal learns that it predicts the occurrence of a rewarding event. As a result of this 'associative learning', the formerly neutral stimulus can induce the activation of reward-related circuits in the brain (Brischoux, Chakraborty, Brierley, & Ungless, 2009; Matsumoto & Hikosaka, 2009; Mirenovic & Schultz, 1996) and elicit an 'approach' behavioural response (Berridge, 2000).

Reproductive behaviours, including courtship, mating, pup nursing and aggression, are conventionally classified as hardwired, genetically programmed innate behaviours (Brouette-Lahlou, Godinot, & Vernet-Maury, 1999; Chamero et al., 2007; Choi et al., 2005; Roberts et al., 2010), which arise independently of the animal's experience and environment and are distinct from acquired (learned) behaviours (Lehrman, 1953). In most mammals these reproductive behaviours are largely regulated by chemosignals, referred to as pheromones. Pheromones are believed to carry intrinsic positive or negative reward values that mediate the innate emotional responses to these chemical signals.

Male laboratory mice, *Mus musculus*, typically display strikingly different behaviours towards male and female conspecifics. Male intruders are usually viciously attacked, whereas female intruders are not attacked but instead are sexually mounted (Mackintosh, 1970; Scott & Fredericson, 1951). In an elegant set of behavioural assays it was demonstrated that these dimorphic behavioural responses are mediated mainly by pheromone signals secreted in urine and that they seem to be innate, requiring no prior learning (Connor, 1972). A sexually inexperienced (naïve) male that is isolated after weaning and introduced to a strange male will instigate an instinctive aggressive attack towards the intruder. When the naïve male is introduced to a male intruder swabbed with female urine (a major source of pheromones), it performs milder aggressive displays and attempts to mount it. However, when the male is introduced to a female swabbed with male urine, sexual behaviour towards the female is repressed and replaced with more forceful aggressive behaviour (Connor, 1972).

In contrast to the innate nature of pheromone action, numerous studies have demonstrated that the pheromone-mediated reproductive repertoire of behaviours is open to modifications through learning and past experience (Pfaus, Kippin, & Centeno, 2001). Modification through learning is evident both in goal-directed appetitive behaviours, in which the animal approaches and investigates the rewarding conspecific stimulus, and in consummatory aspects of reproductive behaviours (Argiolas & Melis, 2013).

This review focuses on the role of pheromone signals in regulation of the innate and learned aspects of reproductive responses. We discuss the integrative role of the main and the vomeronasal olfactory systems in mediating the innate and the learned rewarding properties of pheromonal signalling, as well as the neuroanatomical and the neurobiochemical basis underlying the rewarding effects of pheromones that shape reproductive behaviours.

## WHAT ARE PHEROMONES?

Pheromones are chemicals that have evolved as signals for communication between members of the same species (Wyatt, 2014). Chemical communication is ubiquitous across the animal kingdom, from insects (Wang & Anderson, 2010) through fish (Sorensen, Christensen, & Stacey, 1998) to mammals, including rodents and nonhuman primates (Stowers & Marton, 2005; Tirindelli, Dibattista, Pifferi, & Menini, 2009). In humans the existence of pheromonal communication is controversial (Doty, 2010), although several recent studies have demonstrated that human body secretions (Gelstein et al., 2011; Zhou & Chen, 2009) and two gender-specific human steroids, androstadienone and estratetraenol, might possess functional biological properties in conspecific communication (Grosser, Monti-Bloch, Jennings-White, & Berliner, 2000; Savic, Berglund, & Lindstrom, 2005; Zhou et al., 2014).

Pheromones are either single compounds or a combination of molecules in a precise ratio (Wyatt, 2014), which are emitted to the external environment by one individual (the releaser) and may elicit a variety of behavioural and endocrinological responses in another individual that detects them (Liberles, 2014). In mammals, specific pheromones convey information about the releaser, including its species, age, sex (Cheetham et al., 2007; He, Ma, Kim, Nakai, & Yu, 2008; Isogai et al., 2011; Leinders-Zufall et al., 2004; Meeks, Arnson, & Holy, 2010), reproductive/endocrine state, familiarity and social status (Ben-Shaul, Katz, Mooney, & Dulac, 2010; Bergan, Ben-Shaul, & Dulac, 2014; Hurst & Beynon, 2004). Pheromone molecules are released from a wide range of body secretions including urine (Beynon & Hurst, 2004), preputial gland secretions (Ponmanickam et al., 2013), tears (Gelstein et al., 2011; Haga et al., 2010), saliva (Talley, Laukaitis, & Karn, 2001) and mammary gland secretions (Charra et al., 2012; Schaal et al., 2009).

In most mammals, pheromonal cues and odorants are detected by two distinct nasal chemosensory structures, the main olfactory epithelium (MOE) and the vomeronasal organ (VNO) (Munger, Leinders-Zufall, & Zufall, 2009). In rodents, the MOE expresses about 1000 G-protein-coupled olfactory sensory receptors that are mostly devoted to detection of volatile odours such as natural odours and food signatures, as well as avoidance/fear-eliciting odours (for example, predator or spoiled food odour; Kobayakawa et al., 2007). The VNO expresses about 300 G-protein-coupled vomeronasal sensory receptors. These receptors, which detect both volatile and nonvolatile pheromones, play a critical role in identifying sex- and species-specific chemical cues and in mediating mating, territorial aggression, defensive responses to predators and associated endocrine changes (Chamero, Leinders-Zufall, & Zufall, 2012). Some vomeronasal sensory neurons have been found to harbour members of the formyl peptide receptor family, which seem to allow chemosignals associated with pathogen- and inflammation-related compounds to be detected (Liberles et al., 2009; Riviere, Challet, Fluegge, Spehr, & Rodriguez, 2009). Two additional known chemosensory structures in the nasal cavity of rodents are the Grüneberg ganglion neurons and the septal organ of Maserà (Giannetti, Saucier, & Astic, 1992; Grüneberg, 1973). Both are part of the MOE and are considered to be responsible for mediating specific olfactory behaviours, such as detection of alarm pheromones by the Grüneberg ganglion neurons (Brechtbuhl, Klaey, & Broillet, 2008; Table 1). The septal organ predominantly expresses a small subset of olfactory receptors that respond broadly to general odorants whose behavioural function is not yet understood (Ma et al., 2003).

Pheromonal cues are characterized by wide chemical and functional variability and are often classified according to two distinct criteria (Table 1). First, pheromonal ligands are classified by

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