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Chemical signals 'selected for' newborns in mammals

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Because of the powerful selective pressure for survival, neonatal mammals must rapidly locate and orally seize a nipple to gain the nutritional, energetic and protective advantages of milk. Thus, it is critical for females to facilitate the efforts of their offspring by presenting interface structures for milk transfer (the papilla mammae or nipple) that match the newborn receivers' psychology. Mammalian females have evolved nipples that exploit their neonates' most generally advanced sensory systems, viz. somesthesis and olfaction. Therefore, in addition to the production of odour cues derived from mammary and extramammary sources (saliva) and that reflect individual-specific conditions (diet, physiological stage, etc.), female nipples may have anatomical–physiological features that emit species-specific chemosignals. This mother-to-infant communication is briefly surveyed here based on studies in several species of lagomorphs, rodents and primates. In these species, the release of mammary chemostimuli ranging from individual-specific cues (i.e. arbitrary odorants) to species-specific signals (i.e. pheromones) is a general mechanism for eliciting neonatal arousal, motivation and attraction to the mother. Such chemostimuli provide guidance for localizing the nipple and elicit oral grasping of it. The behavioural activity of some of these chemostimuli does not appear to depend on learning, whereas others clearly depend on previous exposure and learning for their activity. In certain cases, unlearned mammary signals and arbitrary odour cues work in tandem, as the former can expedite the learning of the latter, which then take on a similar function to the unlearned signals. We review the degree of specialization of mammary semiochemical processes in mammalian mother-to-newborn communication from production and transmission by females to reception, integration and behaviour in newborns.

Mammals experience a powerful selective pressure during gestation, birth, lactation and weaning (e.g. Clutton-Brock, 1991), birth being the most noteworthy of these developmental passages. To respond adaptively to the natal transition, the fragile and 'inexperienced' newborns must swiftly reach a nipple to ingest the colostrum/milk and gain their biological and psychobiological benefits. Reciprocally, females must respond in a timely manner to their offspring, suckle them, produce/release milk and be focused on caring for the newborns and their immediate surroundings (e.g. nest maintenance, predator avoidance). Thus, synthesizing milk and suckling indicate a profusion of coevolved anatomical, physiological, (bio)chemical and behavioural traits, all of which respond to selective constraints that both females and newborns must optimally manage during the precarious natal transition and early development.

The rapidity of the transfer/acquisition of colostrum/milk is the antidote to neonatal metabolic exhaustion and exposure to bacterial infection. This process is clearly linked with neonatal viability in all mammalian species examined so far. For example, piglets, *Sus scrofa*, incur higher losses when colostrum intake is delayed or deficient (e.g. Decaluwé et al., 2014). Nonhuman primates and humans (in both historical societies and modern hunter-gatherers) endure high infant mortality, with globally 27% of their offspring dying in the first year and 47% failing to survive to puberty (Volk & Atkinson, 2013). Although causally unclear, this high infant mortality in humans is thought to be related in great part to the problematic initiation of suckling (Volk & Atkinson, 2013). Suckling ability is indeed inconstant among individual human infants, which leads to a variable delay in the transfer of colostrum (Dewey, Nommsen, Heinig, & Cohen, 2003). Under extreme conditions, such delays in colostrum intake can lead to actual threats to viability as emphasized in recent studies. For example, in modern rural Ghana, a 1 h delay in suckling after birth was shown to explain 22% of neonatal losses (Edmond et al., 2006). Conversely, the rapid intake of human milk mediates resistance to lethal gastrointestinal infection (Edmond, Kirkwood, Etego, Agyei, & Hurt, 2007).

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Accordingly, any anatomical–morphological, sensory, behavioural or cognitive methods by which females or newborns accelerate milk transfer and ingestion are advantageous to mother–progeny preservation and should have occurred at the species level throughout evolutionary history. Females must efficiently attract their offspring and induce them to suck their nipples, whereas newborns must be ready to detect, process and adequately react to the chemostimuli emitted by the mother. In this paper, we consider different systems of chemosignals in four species of mammals, wherein chemosignals coevolved to drive newborns to the mammae. We use the term 'selected for' but this does not imply a deliberate purpose. It refers to some degree of specialization of semiochemical processes at levels ranging from production and transmission by females to reception, integration and response by newborns. The term 'specialization' is used to denote phylogenetic canalization mechanisms which may be underlain by unique stimulus–response loops to regulate the interactions between lactating females and newborns in temporally specific ways.

MATERNAL SIGNALLING AND THE NEWBORN RECEIVER'S PSYCHOLOGY

Female–neonate interactions pertaining to milk transfer are organized differently across the diverse life history traits of mammals (Eisenberg, 1981; Ewer, 1968; Gubernick & Klopfer, 1981). However, this behavioural multiplicity of mother–infant systems is characterized by common principles imposed by the constraints under which the biology and psychology of both the emitters and receivers evolved. The notion of receiver psychology means 'everything about the brain of the receiver animal that might affect its response to a signal' (Guilford & Dawkins, 1991, p. 2), or conversely, it might mean the mechanisms by which features of a signal exploit the ability of an animal to detect and discriminate stimuli (Miller & Bee, 2012). Within communication systems in which the parties are strongly asymmetrical in their immediate survivability, such as mammalian mothers and offspring, one may predict that the receiver's psychology of the more vulnerable party will prevail in shaping signalling modes (in the context of other selective forces, such as symbiotic acquisitions or predator and parasite avoidance). Accordingly, throughout evolution, newborns have imposed the perceptual/cognitive resources used by females to mediate the processes leading to the transfer of milk and associated commodities (maternal care) to their newborns.

Thus, although mammalian females can hypothetically exploit the whole range of neonatal perceptual systems, they can make use of only a subset of sensory modes to shape efficient infant-directed signals. Some species (e.g. prototherians, marsupials, most rodents, carnivores) deliver altricial neonates in which perception is restricted to somesthesis and chemoreception, whereas other species give birth to semiprecocial (e.g. primates) or precocial newborns (e.g. some rodents, ungulates, proboscidians, cetaceans) with an entire range of functional senses, including hearing and vision. Accordingly, touch, olfaction and taste constitute the minimal, common sensory basis of any mammalian neonatal receiver's psychology, and maternal signals must be tailored to it to be perceivable to the newborn. It is noteworthy that in neonates that are precocial (e.g. ungulates) or semiprecocial (e.g. primates), somesthesis and chemoreception may be rapidly embedded in multisensory processes sometimes to be completely replaced by hearing and vision (Schaal & Durand, 2012); none the less, such sensorially precocial neonates clearly appear influenced by chemostimuli immediately after birth (e.g. Morrow-Tesch & McGlone, 1990; Vince & Ward, 1984) and most likely remain so in later multimodal contexts.

The sensory appearance of postparturient females to their offspring is necessarily variable between species that give birth to either altricial newborns in a nest, semiprecocial newborns that are carried or precocial newborns that can follow on their own. However, it is mandatory to mammalian newborns of any type to make oral contact with the mother and interact with the interface structures of her body that canalize milk to their mouths. These structures are the papilla mammae, also called nipples or teats depending on species or usage. These specialized cutaneous interfaces are indeed pivotal in mammalian reproduction because, in addition to their obvious role as milk outlets, they induce the endocrine cascade that underlies nursing and maternal motivation (and, in certain cases, bonding), regulates adapted and protracted milk production, and in some species, inhibits ovarian activity which postpones conception of the next generation. The most efficient strategy for mammalian females to evolve detectable and graspable nipples/teats for their newborns is to shape the nipples/teats so that they are conspicuous, especially in tactile and olfactory terms. Thus, the coevolutionary adjustment between mammalian females and neonates has sculpted mammary structures that release milk concomitantly with attractive chemostimuli.

MULTICOMPONENT MAMMARY CHEMOSTIMULI

The most obvious and copious sources of mammary odorants are the colostrum and milk, whose odour properties depend in part on the female's lactational stage, physiological condition (body stores), dietary and aerial ecology (ingested versus inhaled odorants), stress level, and physical activity. Additional mammary substrates are secreted or excreted in much lower amounts by glands distributed in, on or beside the nipples. The entire range of elementary skin glands occurs on the nipples (also on the surrounding areolae in primates), including eccrine, apocrine and sebaceous glands (Koyama, Wu, Easwaran, Thopady, & Foley, 2013). In certain species, the mammary area is also endowed with anatomically differentiated glands that range from locally dense skin glands to visible structures involving several types of skin glands and accessories favouring scent dispersal and microbial activity (i.e. hair and warm, moist conditions). Such glandular differentiations are often considered as specializations evolved for communication (Adams, 1980; Albone, 1984). They are seen at least in the European rabbit, *Oryctolagus cuniculus* (the gland producing the mammary pheromone), sheep and antelopes (inguinal glands) and humans (Montgomery's glands). However, some of these mammary glandular specializations (e.g. Montgomery's glands) may have other functions, such as creating, by their lipid secretions, the airtight seal permitting suction, the relief of the friction stress of sucking and the protection of the skin/ductal entries from bacterial infection.

The film of substrates coating the nipples is never pure in terms of the origin of the components, and, depending on the species-specific behaviour, substrates from the mammary area become rapidly amalgamated with extramammary fluids. In most rodents and carnivores, postparturient females actively lick their nipple-lines to deposit amniotic and urogenital fluids, saliva and all types of secretions from multiple oral or facial (labial, salivary, lachrymal and Harderian) glands. In addition, nursing females often alternate grooming of their offspring and themselves, spreading odour traces that originate from the infant itself (excretions/secretions from oral, facial, anal or urogenital sources) along with their own saliva on their abdomen. Finally, suckling newborns inevitably spread amniotic fluid and saliva on the nipples during their first nursing episodes, and the nipples can subsequently become encrusted with mixed saliva, coagulated milk and other