



Chemo sense

EDITORIAL

Evolution of Flying Noses

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Comparing the relative complexity of the olfactory systems of birds shows that a well-developed sense of smell is more common in birds than generally believed. In this issue, Van Buskirk and Nevitt review several hypotheses for the evolution of olfactory ability in birds. Variation in relative olfactory bulb size between species leads to the hypothesis that olfactory ability is limited to ancestral avian groups, or alternatively, that olfaction tends to be correlated with ecological factors such as nesting strategy, habitat or diet. Contrary to both these hypotheses, Van Buskirk and Nevitt find that olfactory ability is broadly distributed throughout the modern birds, and is neither limited to more ancestral taxa nor restricted to select groups. They provide new insights about the evolution of

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Evolutionary Arguments for Olfactory Behavior in Modern Birds

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Introduction

Although most birds can smell (Bang and Wenzel 1985), our understanding of avian olfactory ability is hampered by the widespread assumption that they cannot (Balthazart 2001). With large eyes and reduced olfactory bulbs, one might reasonably conclude that smell is of little use to these highly visual animals. Yet anatomical differences in the size and complexity of avian olfactory systems suggest not only that most birds have a well developed sense of smell, but that selection pressures on olfactory ability have varied considerably among species (Cobb 1960b; Bang 1965, 1966, 1971; Bang and Cobb 1968; Bang and Wenzel 1985). While anatomical data are available for a broad range of species, our ability to identify ecological and evolutionary patterns in olfactory ability is limited by a lack of behavioral and physiological studies exploring the sense of smell in birds. Exceptions are the tube-nosed seabirds (Procellariiformes) (for

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Odour increases tolerance of pain

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behavioral traits in their work on the Procellariiformes: an unexpected association between nesting habitat and behavioral response to dimethyl sulfide, an ancient marine odorant associated with primary productivity. This relationship has implications for the evolution of foraging strategies for this group.

Now imagine a machine that can identify the smell of something and then direct itself toward - or away from - the source of the odour. To achieve this goal, the device must be able to recognize odours instantaneously and then respond appropriately. It must then decide if the recognized smell is increasing, diminishing or not changing intensity. A new patented algorithm by E-Nose Pty Ltd achieves these goals of artificial olfaction, using the algorithm and an e-nose carried by, and directing the movements of moving vehicles. It will find application in search and rescue, location of buried or obscured objects such as landmines or bodies, and many kinds of biological and environmental research. Future issues will describe progress in the research and development of these "Flying E-Noses" ■

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review see Warham 1996; Nevitt 2000; Nevitt and Bonadonna 2005), turkey vultures (*Cathartes aura*) (Stager 1964; Houston 1988), kiwis (*Apteryx sp.*) (Sales 2005), and homing pigeons (*Columba livia domestica*) (Papi 1989, 1990, 1991; Waldvogel 1989; Benvenuti et al. 1992; Papi and Wallraff 1992; Wallraff 2001, 2005) (for review see Roper 1999). However, an increasing number of behavioral studies of other species suggests that olfactory abilities are more broadly distributed and specialized than we generally assume (Bang and Wenzel 1985; Petit et al. 2002; Hagelin et al. 2003; Roper 2003; Mennerat et al. 2005).

Despite the lack of research in this area, several hypotheses have been proposed for the evolution of avian olfactory ability in birds. One phylogenetic pattern that emerged from early anatomical comparisons is the tendency for more ancestral groups, such as Procellariiformes (petrels and albatrosses) and Apterygiformes (kiwis), to have proportionally larger olfactory bulbs than more recently evolved groups such as Passeriformes (perching birds) (Wenzel 1971). Relative olfactory bulb size among bird orders has also been correlated to ecological factors such as their association with water, type of nesting strategy, or diet (Cobb 1960b; Bang 1971). Subsequent studies which were more careful to control for the effects of body and brain size suggested instead that a larger relative bulb size was associated with nocturnal or crepuscular activity patterns (Healy and Guilford 1990).

However, there are additional problems to consider with these analyses. First, there is no clear physiological mechanism linking relative olfactory bulb size with the ability to detect odor per se, thus calling into question whether bulb size is a true index of olfactory ability (Roper 1999). Second, despite an increasing number of molecular and morphological investigations of avian subgroups, phylogenetic relationships among higher-level avian taxa remain unclear (Cracraft et al. 2004). Without a generally accepted phylogeny of the modern birds (Neornithes), we cannot infer an evolutionary history of olfactory ability within this diverse group.

The purpose of this mini-review is thus two-fold. We will first provide a brief overview of

olfaction in birds, and then suggest a promising approach that avoids some of the pitfalls described above. Though uncertainty in the modern bird phylogeny makes it difficult to study the evolution of olfaction, we have found that a comparative approach can be successfully applied to subgroups with better-developed phylogenies, leading to new insights about the evolution of behavioral traits. We will use our investigation of foraging behavior among the procellariiforms (tube-nosed seabirds) as an example of this approach.

Avian Olfactory Anatomy

The olfactory anatomy of birds is well characterized, thanks to an elegant series of comparative anatomical studies of the peripheral olfactory structures (Bang 1971; Wenzel 1971; Bang and Wenzel 1985) and bulbs in 21 orders of birds (Cobb 1960a, 1960b; Bang and Cobb 1968). Peripheral olfactory structures typically include a set of two external nares (nostrils) and a series of epithelium-lined intranasal chambers (conchae) in the maxilla (upper beak). The third nasal chamber is lined with olfactory epithelium supported on a sheet of cartilage that can be highly convoluted in some species to form spiral-shaped olfactory tubercles. As in mammals, reptiles and fishes, the olfactory epithelium gives rise to the olfactory nerves that project to paired olfactory bulbs in the brain (Bang 1971). Variation in both the relative size of olfactory bulbs and the degree of folding of the tubercles has fueled discussion about whether these features can predict the relative olfactory abilities of the major orders of birds. Some species show a high degree of folding or scrolling of the tubercles within the third nasal conchae, a feature that provides increased surface area for the olfactory epithelium. Bang (1965), for example, noted a positive relationship between this surface area and relative olfactory bulb size. Species with a large relative olfactory bulb size and highly scrolled olfactory tubercles include several groups that are known to hunt by smell, including the Procellariiformes (tube-nosed seabirds), the Cathartidae (new world vultures), and Apterygiformes (kiwis).

One group of birds with unusual anatomical specializations is the waterbirds, an

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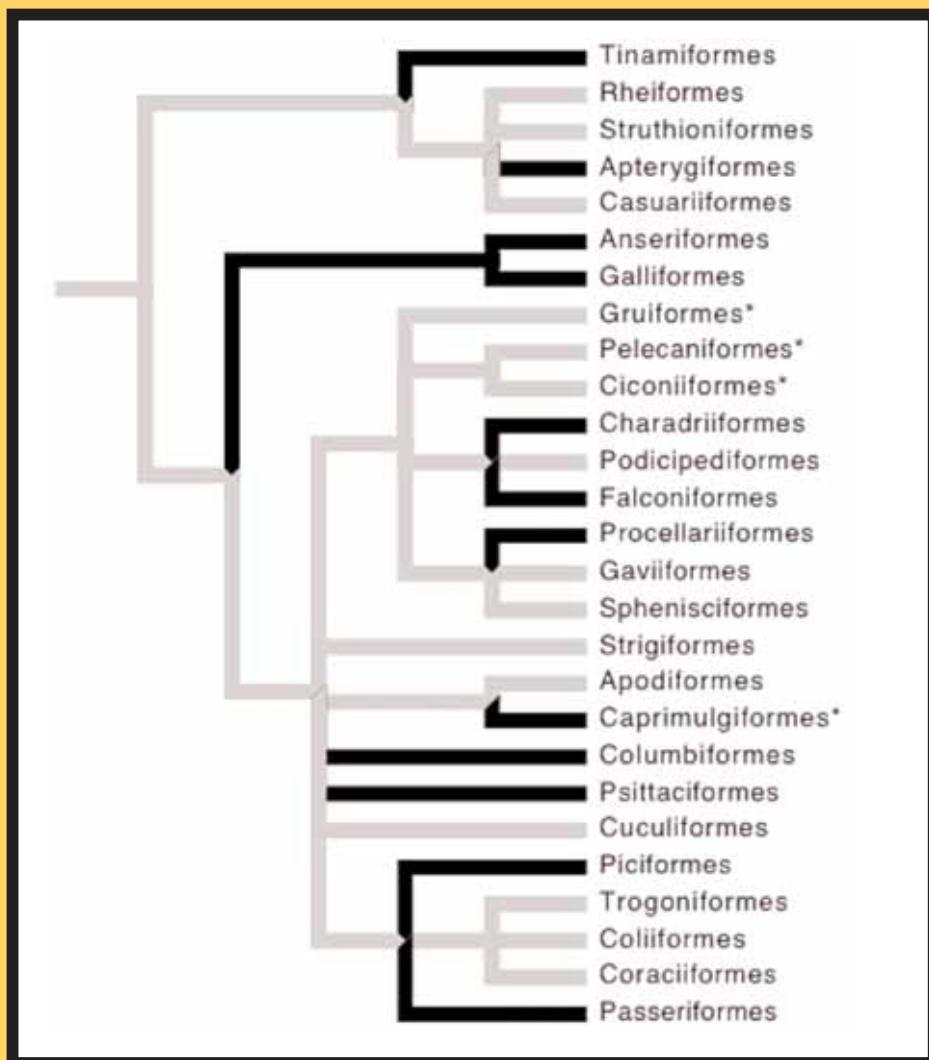


Figure 1. Simplified phylogeny of the major avian orders (after Cracraft et al. 2004) with black branches indicating groups containing species shown to have a behavioral response to odors. Asterisks indicate orders that may not be truly monophyletic.

assemblage that includes Procellariiformes (tube-nosed seabirds), Gaviiformes (loons), Podicipediformes (grebes), Ciconiiformes (storks and herons), Pelecaniformes (pelicans and cormorants), Charadriiformes (shorebirds and gulls), and Gruiformes (rails and cranes) (Cracraft 1988; Sibley and Ahlquist 1990; Hedges and Sibley 1994). Species within the waterbird assemblage show a range of specialized respiratory features that apparently serve as adaptations to an aquatic lifestyle but may also have an, as yet, unexplored relationship to olfactory ability. Gannets (*Sulidae*) and cormorants (*Phalacrocoracidae*), for example,

have a pair of secondary nostrils at the fleshy corners of the mouth, while the external nares of the maxilla become completely covered by hornified epithelium as the bird matures (Bang 1971; Nelson 1978). These secondary nostrils can be sealed to keep water from entering them when the bill is submerged, but do not provide as direct a pathway to the olfactory epithelium as in species with nares. By contrast, the Procellariiformes are pelagic seabirds that spend most of their lives flying over the open ocean. These birds are called 'tube-nosed' seabirds because many species possess horny tubes on the bill surface that

are extensions of the nares. In some species, the nares are fused into a single tube (e.g., Southern and Northern Giant Petrels (*Macronectes sp.*)). Bang (1966) suggested that the tubes increase airflow to the olfactory conchae, but the adaptive significance remains poorly understood.

Evolutionary Trends in Avian Olfaction

Given the variation in anatomical structures, several authors have suggested that the evolution of heightened olfactory ability has been driven by adaptation to specific ecological conditions such as an aquatic lifestyle (Cobb 1960b; Bang 1971) or activity under low light conditions (Healy and Guilford 1990). The implication is that a relatively narrow suite of ecological variables could be driving olfactory specialization. More recent evidence suggests that this is probably not the case. Roper (1999) reviewed much of the available behavioral and physiological evidence for all avian groups and categorized olfactory behavior in terms of navigation, foraging, reproduction, attachment and affiliation, and avoidance. This analysis shows that olfactory ability has been documented across a broad phylogenetic and behavioral spectrum, even in orders that are not typically associated with a well-developed sense of smell. To give several examples, among the Psittaciformes (parrots), an order typically assumed to be highly reliant on visual cues, preliminary studies suggest that the Yellow-backed Chattering Lory (*Lorius garrulus flavopalliatus*) and the Kakapo (*Strigops habroptilus*) may use olfactory cues to forage (Hagelin et al. 2003; Roper 2003). In the Passeriformes (song birds), an order comprised of species that have the smallest relative olfactory bulb sizes among birds, male Blue Tits (*Parus caeruleus*) have been conditioned to detect lavender odor through the use of food rewards (Mennerat et al. 2005). In the Charadriiformes (shorebirds), crested auklets (*Aethia cristatella*) emit a tangerine-scented odor that may be involved in chemical communication (Hagelin et al. 2003) or as a signal of mate quality by virtue of its properties as an ectoparasite repellent (Douglas et al. 2004). Finally, among the Procellariiformes, the use of scent in individual recognition has been shown in Antarctic prions (*Pachyptila desolata*)

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(Bonadonna and Nevitt 2004), European storm-petrels (*Hydrobaes pelagicus*) (De Leon et al. 2003) and Leach's storm-petrels (*Oceanodroma leucorhoa*) (O'Dwyer et al., in press). Together, these examples illustrate that olfactory abilities are common among birds and can serve diverse functions.

It has also been proposed that there is a tendency for relative bulb size to become reduced in more recently derived groups, such as the Passeriformes (song birds). This phylogenetic relationship suggested to Wenzel (1971) that olfactory acuity is an ancestral condition that has gradually been replaced by visual and aural acuity in some modern birds. Rigorous examination of a phylogenetic basis for olfactory acuity has been hampered, however, by the lack of a widely accepted phylogeny for modern birds. Sibley and Alquist (1990) generated an extensive avian phylogeny using DNA hybridization techniques that, although influential in many respects, was criticized for the analytical methods employed and for the underlying assumptions regarding traditional higher-order taxa (Houde 1987; Mindell 1992; Harshman 1994). Cracraft et al. (2004) have since formulated an alternative phylogenetic hypothesis for the modern birds based on a larger collection of taxa and molecular and morphological characters. The problematic nature of resolving higher order relationships is reflected in the topology of their summary tree, which shows a high degree of polytomy (nodes with multiple branches that cannot be resolved to a paired, hierarchical form) within most of the major clades. This lack of resolution reflects uncertainty in the evolutionary distinctiveness of traditional bird groups and their positions relative to one another (Cracraft et al. 2004).

Despite the topological uncertainty, the Cracraft et al. (2004) phylogeny is currently the most complete picture of evolutionary relationships among birds, and provides the best evolutionary framework for illustrating how olfactory ability has spread throughout the modern birds. In Figure 1, we have used this tree to highlight groups that contain species where olfactory abilities have been implicated behaviorally or physiologically.

This illustration suggests that the sense of smell is neither limited to the more ancestral taxa nor restricted to only a few select groups. By contrast, olfactory abilities appear to be widespread within the modern birds.

Evolution and Development of Olfactory Ability in Procellariiform Seabirds

While persistent questions concerning the relationships among modern birds make it difficult to study the evolution of olfaction, we have found that a comparative approach is useful for investigating subgroups with better-developed phylogenies. The procellariiform seabirds are a model system for this type of investigation. First, this order has been the subject of several phylogenetic analyses (Imber 1985; Paterson et al. 1995; Bretagnolle et al. 1998; Nunn and Stanley 1998; Kennedy and Page 2002), and consequently much is known about the underlying phylogenetic relationships between the subgroups. Second, the olfactory abilities of procellariiform seabirds have been well characterized, particularly with respect to different olfactory-based foraging strategies. For example, working with a sub-Antarctic species assemblage near South Georgia Island (South Atlantic Ocean), Nevitt and co-workers have shown that differences in foraging strategy are linked to differences in how birds utilize olfactory or visual information (Nevitt et al. 1995; Nevitt et al. 2004). Procellariiforms tend to forage on a variety of prey types including squid, fish and Antarctic krill (*Euphausia superba*). Antarctic krill, in turn, forage on phytoplankton (Warham, 1996). Dimethyl sulfide (DMS) is produced from the breakdown of metabolic byproducts of phytoplankton, and emissions increase when phytoplankton are grazed by zooplankton (Dacey and Wakeham 1986). We have shown that several species of storm-petrels (*Oceanodroma sp.*), prions (*Pachyptila sp.*), and gadfly petrels (*Procellaria sp.*) are able to track this odor to its source in experimental trials, whereas other typically larger and more visible species are more responsive to visual cues and odors associated with crushed krill or fish (pyrazines and trimethylamine) (Nevitt et al. 1995; Nevitt 1999; Nevitt et al. 2004).

These and other results suggest that DMS-responders are adapted to forage opportunistically on small or less concentrated prey patches by tracking the scent of DMS whereas more aggressive species (e.g., albatross, *Diomedea*, and giant petrels, *Macronectes*) rely more heavily on multi-modal cues which include scents associated with crushed prey and visual cues associated with the activity of other birds.

Using a phylogenetic comparative analysis, we have recently revealed an evolutionary link between foraging strategy and nesting habit (Van Buskirk and Nevitt, *in press*). We have shown that DMS-responders tend to nest underground in deep burrows whereas multimodal foragers tend to nest above ground (Figure 2). Since chicks grow up in drastically different sensory environments, this suggested to us that the developmental environment could be shaping sensory systems over evolutionary time. The chick-rearing period is particularly long in procellariiforms, ranging from approximately 45 days in storm-petrels to 280 days in the largest albatrosses (*Diomedea*) (Warham 1990). Chicks reared in a burrow spend this time in a dark, underground nest, where smell is likely to be a dominant feature of their sensory world. By contrast, surface-nesting species grow up with direct access to light. Living above ground, these chicks are exposed to a wide range of stimuli, including visual, aural, and olfactory cues, as they complete their development at the nest. In an evolutionary framework, these differences in rearing environment could lead to differences in sensory function.

Though comparative analysis of the procellariiforms showed a relationship between nesting and DMS tracking behavior, this correlation did not hold up with respect to odors more directly associated with macerated krill or fish (pyrazines or trimethylamine, for example). (Van Buskirk and Nevitt, *in press*). Ancestral trait reconstruction indicates that procellariiforms arose from a burrow-nesting lineage, with the albatrosses and the fulmarine petrels independently adopting a surface-nesting strategy. The implication is that the move to the surface could have

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Figure 2: Wandering albatross (*Diomedea exulans*, Left) and blue petrel chick (*Halobaena caerulea*, Right). The blue-petrel chick was removed from its burrow, approximately 1.5 meters underground. As adults, blue-petrels will track odors associated with macerated phytoplankton (e.g., DMS) whereas wandering albatrosses are more likely to be attracted to visual cues provided by other birds or odor cues associated with macerated fish and krill (Nevitt et al. 2004).

been a life history innovation that presented new opportunities for selection to act on the development of visual systems, while relaxing the need to track prey by scent.

Using a comparative approach also leads to new and exciting questions about how olfactory foraging abilities are distributed among marine bird lineages. For example, the ancestral nature of nesting underground raises the possibility that a heightened reliance on smell may also have been an ancestral condition, present in the ancestors of the Procellariiformes and their sister order, the Sphenisciformes (penguins). Little penguins (*Eudyptula minor*), for example, not only nest underground but also show tube-like structures on their nostrils during development (Kinsky 1960). Does this mean that penguins also have a well-developed sense of smell? Though olfaction in penguins has rarely been considered, these birds also forage in productive areas that are characterized by high levels of DMS (Culik 2001).

To summarize, the sense of smell in birds does not seem to be associated with a particular lifestyle, such as nocturnality, nor

is it restricted to a particular evolutionary position within the ancestral groups. Instead, olfaction has likely evolved in a variety of ways throughout the avian lineage. Our understanding of the evolution of avian olfaction will improve as avian phylogenies become better established, and more research is completed on the use of olfaction by birds. Progress in this field will require a change in the commonly accepted point of view that 'birds can't smell.' To the contrary, there is much evidence to suggest that most birds have a functional sense of smell, and investigators working in the realms of sensory and behavioral ecology would be wise to take this sensory modality into account when designing experiments. In our example of the Procellariiformes, a comparative approach yielded unexpected associations between nesting habit and olfactory responsiveness, with broader implications for both foraging ecology and the evolutionary origins of different foraging strategies. Such associations may be more common than we think ■

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REFERENCES

Balthazart J (2001) Olfaction in birds: myth or reality? *Aves* **38**:105-126.

Bang BG (1965) Anatomical adaptations for olfaction in the Snow Petrel. *Nature* **205**:513-515.

Bang BG (1966) The olfactory apparatus of the tubenosed birds (Procellariiformes). *Acta Anat.* **65**:391-415.

Bang BG (1971) Functional anatomy of the olfactory system in 23 orders of birds. *Acta Anat.* **79** (Suppl.):1-76.

Bang BG, Cobb S (1968) The size of the olfactory bulb in 108 species of birds. *Auk* **85**:55-61.

Bang BG, Wenzel BM (1985). Nasal cavity and olfactory system. Pages 195-225. In: King AS, McLelland J (eds) *Form and Function in Birds*. Academic Press, London.

Benvenuti S, Iolo P, Papi F (1992) The olfactory map of homing pigeons. Pages 429-434. In: Doty RL, Mueller-Schwarze D (eds) *Chemical Signals in Vertebrates VI*. Plenum Press, New York.

Bonadonna F, Nevitt GA (2004) Partner-specific odor recognition in an Antarctic seabird. *Science* **306**:835.

Bretagnolle V, Attie C, Pasquet E (1998) Cytochrome-B evidence for validity and phylogenetic relationships of Pseudobulweria and Bulweria (Procellariidae). *Auk* **115**:188-195.

Cobb S (1960a). A note on the size of the avian olfactory bulb. *Epilepsia* **1**:394-402.

Cobb S (1960b). Observations on the comparative anatomy of the avian brain. *Perspect Biol Med.* **3**:383-408.

Cracraft J (1988) The major clades of birds. Pages 339-361 In: Benton MJ (ed) *The Phylogeny and Classification of the Tetrapods*, Vol 1: Amphibians, reptiles, birds. Clarendon Press, Oxford.

Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, Garcia-Moreno J, Sorenson MD, Yuri T, Mindell DP (2004) Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. Pages 468-489 In: Cracraft J, Donoghue MJ (eds) *Assembling the Tree of Life*. Oxford University Press, New York, NY.

Culik B (2001) Finding food in the open ocean: Foraging strategies in Humboldt penguins. *Zoology* **104**:327-338.

Dacey JWH, Wakeham SG (1986) Oceanic dimethyl sulfide production during zooplankton grazing on phytoplankton. *Science* **233**:1314-1316.

De Leon A, Minguez E, Belliure B (2003) Self-odour recognition in European storm-petrel chicks. *Behaviour* **140**:925-933.

Douglas HD, Malenke JR, Clayton DH (2004) Is the citrus-like plumage odorant of crested auklets (*Aethia cristatella*) a defense against lice? *J Ornith.* **146**:111-115.

Hagelin JC, Jones IL, Rasmussen LEL (2003) A tangerine-scented social odour in a monogamous seabird. *Proc Roy Soc Lond B Bio.* **270**:1323-1329.

Harshman, J (1994) Reweaving the Tapestry: What can we learn from Sibley and Ahlquist (1990)? *Auk* **111**:377-388.

Healy S, Guilford T (1990) Olfactory bulb size and nocturnality in birds. *Evolution* **44**:339-346.

Hedges SB, Sibley CG (1994) Molecules vs. morphology in avian evolution: The case of the "pelecaniform" birds. *Proc Natl Acad Sci USA* **91**:9861-9865.

Houde P (1987) Critical evaluation of DNA hybridization studies in avian systematics. *Auk* **104**:17-32.

Houston DC (1988) Competition for food between neotropical vultures in forest. *Ibis* **130**:402-417.

Imber MJ (1985) Origins, phylogeny and taxonomy of the gadfly petrels *Pterodroma* spp. *Ibis* **127**:197-229.

Kennedy M, Page RD (2002) Seabird supertrees: Combining partial estimates of Procellariiform phylogeny. *Auk* **119**:88-108.

Kinsky FC (1960) The yearly cycle of the Northern Blue Penguin (*Eudyptula minor novaehollandiae*) in the Wellington Harbour area. *Dominion Museum Record (New Zealand)* **3**:145-218.

Mennerat A (2005) Olfactory conditioning experiments in a food-searching passerine bird in semi-natural conditions. *Behav Proc* **70**:264-270.

Mindell DP (1992) DNA-DNA hybridization and avian phylogeny. *Syst Biol.* **41**:126-134.

Nelson B (1978) *The Sulidae: Gannets and Boobies*. Oxford University Press, Oxford.

Nevitt G (1999) Olfactory foraging in Antarctic seabirds: A species-specific attraction to krill odors. *Mar Ecol-Prog Ser.* **177**:235-241.

Nevitt GA (2000) Olfactory foraging by antarctic procellariiform seabirds: Life at high Reynolds numbers. *Biol Bull.* **198**:245-253.

Nevitt GA, Bonadonna F (2005) Seeing the world through the nose of a bird: New developments in the sensory ecology of procellariiform seabirds. *Mar Ecol-Prog Ser.* **287**:292-295.

Nevitt GA, Reid K, Trathan P (2004) Testing olfactory strategies in an Antarctic seabird assemblage. *J Exp Biol.* **207**:3537-3544.

Nevitt GA, Veit RR, Kareiva P (1995) Dimethyl sulfide as a foraging clue for Antarctic procellariiform seabirds. *Nature* **376**:680-682.

Nunn GB, Stanley SE (1998) Body size effects and rates of cytochrome b evolution in tube-nosed seabirds. *Mol Biol Evol.* **15**:1360-1371.

O'Dwyer T, Ackerman A and Nevitt GA Examining the development of individual recognition in a burrow-nesting procellariiform, the Leach's storm-petrel. *J. Exp. Biol.*, in press.

Papi F (1989) Pigeons use olfactory cues to navigate. *Ethol Ecol Evol.* **1**:219-231.

Papi F (1990) Olfactory navigation in birds. *Experientia* **46**:352-363.

Papi F (1991) Olfactory navigation. Pages 52-85. In: Berthold P (ed) *Orientation in Birds*. Birkhäuser Verlag, Basel.

Papi F, Wallraff HG (1992) Birds. Pages 263-319. In: Papi F (ed) *Animal Homing*. Chapman and Hall Ltd., London.

Paterson A, Wallis GP, Gray RD (1995) Penguins, petrels, and parsimony: Does cladistic analysis of behavior reflect seabird phylogeny? *Evolution* **49**:974-989.

Petit C, Hossaert-McKey M, Perret P, Blondel J, Lambrechts MM (2002) Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecol Lett.* **5**:585-589.

Roper TJ (1999) Olfaction in birds. *Adv Stud Behav.* **28**:247-332.

Roper TJ (2003) Olfactory discrimination in Yellow-backed Chattering Lories *Loriurus garrulus* flavopalliatus: first demonstration of olfaction in Psittaciformes. *Ibis* **145**:689-691.

Sales J (2005) The endangered kiwi: a review. *Folia Zool.* **54**:1-20.

Sibley CG, Ahlquist JE (1990) *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, CT.

Stager KE (1964) The role of olfaction in food location by the turkey vulture (*Cathartes aura*). *Los Angeles County Museum Contributions in Science* **81**:1-63.

Van Buskirk RW, Nevitt GA (in press) The influence of developmental environment on the evolution of olfactory foraging behavior in Procellariiform seabirds. *J Evol Biol.*

Waldvogel JC (1989) Olfactory orientation in birds. *Curr Ornith.* **6**:269-321.

Wallraff HG (2001) Navigation by homing pigeons: Updated perspective. *Ethology Ecol Evol.* **13**:1-48.

Wallraff HG (2005) *Avian Navigation: Pigeon Homing as a Paradigm*. Springer, Berlin.

Warham J (1990) *The Petrels: Their Ecology and Breeding Systems*. Academic Press, London.

Warham J (1996) *The Behavior, Population Biology and Physiology of the Petrels*. Academic Press, London.

Wenzel BM (1971) Olfaction In Birds. Pages 432-448. In: Beidler LM (ed) *Handbook Of Sensory Physiology IV*. Springer-Verlag, Heidelberg.



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NEWS

Sweet-smelling odour can increase tolerance of pain.

Enduring ongoing pain can be a necessity in people with chronic pain and in situations where relief cannot be easily obtained or when it is inappropriate to administer drugs. There are many situations where this might happen, including during childbirth; where someone is trapped under a heavy weight (road accident, building collapse); or in situations when medical help is slow in arriving.

Recent research has shown that activating the chemical senses in such situations may induce an analgesic effect and increase tolerance of the presence of pain. It has been known that sweet tastes (whether nutritive or not) and some odours (vanilla, caramel) have an analgesic effect and can increase pain tolerance, but little is known of how or why this may be so. Explaining the analgesic effect of odour has been confounded by the pleasantness of the odorants.

In a report published in *Psychological Science* (2007), John Prescott and Jenell Wilkie of James Cook University, Cairns, Australia, using 94 healthy undergraduate student volunteers, found that odors that are sweet-smelling through prior association with tasted sweetness, similarly influence pain by activating the same analgesic mechanisms as sweet tastes. Inhalation of a sweet-smelling odor during a cold-pressor test

(keeping one's arm immersed in very cold water) increased tolerance for pain compared to pleasant or unpleasant low-sweetness odors, and to no odor. While tolerance of the pain increased, there were no significant difference in pain ratings between the odor conditions.

These results suggest that smelled-sweetness can produce a naturally occurring, conditioned increase in pain tolerance. Controlling for odour hedonics, they demonstrated that an odour chosen on a basis that it was 'sweet-smelling', selectively increased tolerance for cold-induced pain. That the effect was specific to this odour quality, points to an olfactory mechanism involving associative conditioning that takes advantage of the innately analgesic effects of tasted sweetness. Their findings support the interpretation that odour-sweetness and other odour-taste qualities have a perceptual reality in which these qualities can be functionally equivalent to tastants experienced via oral receptors. Secondly, they reinforce the idea that it may be worthwhile to investigate claims for odours having alerting, relaxing, or other effects on mood in terms of associative conditioning mechanisms.

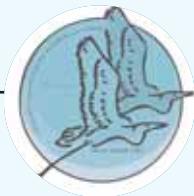
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Olfaction Abstracts from IBRO Satellite Meeting: Brain Mechanisms, Cognition and Behaviour in Birds, 19-23 July 2007, Heron Island, Queensland, Australia



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AFFERENT CONNECTIVITY OF THE OLFACTORY TUBERCLE IN THE DOMESTIC CHICK

Andras Csillag and Eszter Balint

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Olfactory sensation is considered to play an important role in the orientation of birds in general, in addition to those species that have been classically thought to utilise olfactory cues at feeding. We therefore find it increasingly important to clarify the neural connectivity of relevant areas in the domestic chick, commonly used in various behavioural experiments. The olfactory tubercle (TuO) is a ventral striatal region that receives input from the olfactory bulb and resembles the TuO of mammals in its neurochemistry and known connectivity. Deposits of the retrograde tracer Fast Blue (FB) were stereotactically placed by pressure injection in the TuO of one-week-old domestic chicks. Following a survival period of one week, the birds were perfused by 4% paraformaldehyde, the brains were removed and sectioned and the section series were viewed and photographed by fluorescent microscopy to demonstrate the location of retrogradely labelled perikarya of cells. The most consistent sites of labelling were as follows. In the telencephalic pallium, retrogradely filled cells were distributed in the intermediate arcopallium (both ventral and dorsal subdivisions), anterior arcopallium, and in particular the nucleus taeniae of the amygdala. Further important pallial projections arise from the piriform cortex, hippocampal formation, parahippocampal and dorsolateral corticoid areas, and also from the hyperpallium apicale and intermedium. Minor projections originate from nidopallial and mesopallial regions. Of the subpallial nuclei, the bed nucleus of stria terminalis (lateral part), nucleus of the diagonal band, medial striatum and septal divisions were found to be the main sources of TuO-bound projections. Scattered FB-labelled cells were consistently found in the septopallial-mesencephalic tract. In the diencephalon, retrogradely labelled cells were observed in the habenular region, dorsal thalamus, primarily the dorsolateralis anterior but also the dorsomedial nuclei, and in the paraventricular and ventromedial hypothalamic nuclei, as well as the lateral hypothalamic area. In addition to the reported projection from lateral mamillary nucleus, backfilled cells were found also in the medial mamillary nucleus of the chick. Of the brainstem cell groups, the subthalamic nucleus, midbrain central gray, ventral tegmental area, interpeduncular and pedunculopontine nuclei were found to contain labelled neurons in most cases, while additional labelled cells were observed, in some specimens, in the substantia nigra, locus caeruleus, solitary nucleus and the raphe nuclei. One of the novel findings was the representation of lateral and medial vestibular nuclei among the sources of TuO input. The observations are consistent with the assumption that the majority of the pathways afferent to TuO are similar to those of mammals, and, in many cases, they

participate in reciprocal circuits. The data will be discussed in terms of their relevance to the organisation of avian limbic corticoid areas and the 'visceral forebrain system'.

THE PERIPHERAL OLFACTORY SYSTEM OF CHICKS: PHYSIOLOGY AND DEVELOPMENT

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The chick olfactory system begins development at embryonic day 8 (E8) and is known to be functional by E15. Studies have shown that chick embryos exposed to odorants *in ovo* can recognize these odorants after hatching, suggesting that the olfactory system perceives and decodes odor stimuli during development. This *in ovo* experience may shape the animals' behavior upon hatching, presumably to make them more well-adapted to their immediate surroundings. We employed physiological, anatomical and behavioral approaches to study the timecourse of development of the olfactory system. The physiology of isolated olfactory sensory neurons (OSNs) from E18-21 and newborn chicks was studied using ratiometric measurements of odorant-elicited calcium fluxes. Chick OSNs displayed properties similar to those found in mature OSNs of other vertebrate species, indicating that the OSNs are fully functional *in ovo* and at birth. Since information from the OSNs is initially processed in the olfactory bulb, we also studied the development of the glomerular of olfactory bulb. Our studies show that glomerular structures are organized during a critical time period (E15 through E18), during which embryonic chicks can form behavioral associations with odorants introduced *in ovo*. Anatomical staining patterns and behavioral tests suggest differences in odorant-elicited bulbar activation corresponding to this time window. These results collectively suggest that odor imprinting occurs late in embryonic development, highlighting the importance of the sensory environment in shaping the developmental pathways of the olfactory system.

AVIAN OLFACTION AND A NEW E-NOSE ALGORITHM CAN COMBINE IN NOVEL "FLYING NOSE" MACHINES

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The science of olfaction has provided important guidance for invention and development of artificial devices for detecting and identifying odour. In turn, success with the devices has suggested possible mechanisms for biological olfactory systems. This paper describes what aspects of physiology have influenced e-nose development and how a recent breakthrough might be applied to generate physiological hypotheses.

Birds have impressive olfactory capability. The basic anatomy and physiology of avian noses are highly conserved in higher animals including mammals and

man. Therefore the bird can be a useful model for basic science of olfaction and how olfaction is used by birds can generate important insights into how very mobile or airborne artificial "sniffing" devices (e-noses) might be designed.

This paper will briefly review the history of important progress in thinking about olfaction which has come mainly from receptor binding biochemistry, patch clamp electrophysiology, and molecular genetic techniques. Most important for development of artificial chemical sensors and sensor arrays is the demonstration by Linda Buck and co-workers (she and Richard Axel shared the 2004 Nobel Prize for their work on olfactory receptors) that combinations of several receptors are required to encode the identity of an odorant. This implies that arrays of sensors rather than single sensors are more likely to be needed to make valid and reliable identifications of odours and their concentration, be they single compounds or complex mixtures of compounds. The problem then arises as to how the complex information from a sensor array can be rapidly transformed into "correct" information upon which to base useful actions. A human can tell within a fraction of a second that the odour is "nice or nasty" and can, within a few seconds recognise the likely source (and therefore the identity) of the odour and its significance for the individual. Central nervous system mechanisms that determine olfactory phenomena, such as recognition of odour quality, ("rose", "lemon" etc) remain relatively poorly understood. Technology now has something to suggest about these.

Small arrays of broadly tuned sensors have proved useful in addressing tasks where the odorant mixtures have been relatively limited, such as to a particular industrial source, e.g. an abattoir or sewage plant. Recently a real-time odour recognition algorithm has been discovered, proved and patented. Its capacity to perform rapidly across a wide library of "remembered" odours suggests that an analogous mechanism might be found in the olfactory neuronal architecture and physiology of the forebrain. In addition, the speed of execution of this new algorithm means that a device can make rapid passes through an odour plume (as a bird would) and identify the odour from memory, or reject it as irrelevant if not in its memory. E-Noses can now enter the realm of "airborne sniffers", travelling towards the source of the odour, having identified an odour of interest, and using feedback of concentration information and appropriate flight corrections to reach it. The E-Nose thus moves to the odour source, rather than waiting passively for the odorant molecules to come to it. A "flying nose" has many important potential applications. Further study of avian olfaction and how birds use their noses will play an important role in these technological developments.

Upcoming Events

20-24 January 2008

15th Joint Conference on Applications of Air Pollution Meteorology
American Meteorological Society
New Orleans, USA
Info: www.ametsoc.org/meet/annual

28-30 March 2008

Smell and Taste 01 Course
Physiology and Pathology of the Chemical Senses Dresden Medical School
Info: <http://www.tu-dresden.de/medkhno/riechen>

6-8 May 2008

Enviro 08
Melbourne
Info: rvquit@bigpond.com

6-8 July 2008

International Conference on Environmental Odour Monitoring and Control – NOSE2008
Rome, Italy
<http://www.aidic.it/nose2008/>

21-25 July 2008

International Symposium on Olfaction and Taste (ISOT) and AChemS Meeting
Hyatt Regency Hotel at the Embarcadero
San Francisco, California, USA
<http://www.ISOT2008.org>

8-10 October 2008

The 3rd IWA Specialist Conference on Odours and VOC
Barcelona, Spain
Contact: r.steutz@unsw.edu.au

4-6 December 2008

Australasian Association for ChemoSensory Science (AACSS)
Annual Scientific Meeting
Griffith University, Brisbane
Contact: j.reinhard@uq.edu.au ■

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