

Chapter 1

Canine Olfaction: Scent, Sign, and Situation

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Abstract Canine olfaction is a rich field of study for the behavioural sciences and neurosciences, and it is rich in interdisciplinary connections. This chapter will explore the neurocognitive and neuroconative bases of olfaction (the neurophysiological foundations of cognition and motivation), and discuss the behavioural, psychological, and semiotic dimensions of scent processing. It will cover the basic psychophysics of olfaction and the methodologies allowing us to explore this sensory modality, as well as the complex cognitive and motivational dimensions of scent. This chapter will open with an overview of the different disciplines involved in the study of canine olfaction. Some basic anatomy and neuroscience will be reviewed, mostly with direct reference to behaviour and associated psychological processes (e.g., cognitive, motivational, and affective systems). For the behavioural aspect of olfaction, a discussion of the contrasting, yet complementary methods of ethology and experimental psychology will be examined. The importance of both field and laboratory research will be highlighted. Olfaction “in context” will also be discussed in reference to zoosemiotics and in order to understand the canine olfactory psychoethology in its most meaningful and functional dimension: processing “signs” (including symptoms as with dogs trained for biomedical applications such as symptom detection). We will conclude with a short commentary on the human-canine sensory symbiosis with sniffer dogs.

1.1 The Sciences of Canine Olfaction

Canids, like most mammals (and many other vertebrates, such as reptiles), live in an olfactory world. Their *Umwelt*, or “sensory world”, is impressively different from ours (see also Horowitz and Hecht, this volume). Observing our dogs exploring

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their social landscape by relentlessly sniffing scent marks (mostly invisible, unless you live where yellow snow is a possibility) left by others, we understand that we are not in the same sensory-perceptual world. We are just starting to understand the amount of information that animals process from chemical messages. Like us with our emails and social site postings, dogs and other canids have their own world of “peemails” and “Nosebook” to explore, create and manipulate (Harrington and Asa 2003; Bekoff 2001; Allen et al. 1999; Wells and Bekoff 1981).

The study of olfaction has traditionally focused on mammals and insects. In mammals, rats and mice have been the primary model systems, at least in experimental psychology and neuroscience. Recent focus on dogs, and working dogs more specifically, seems to have sparked an interest in the scientific study of olfactory processing in canines. Different theoretical, conceptual, and methodological perspectives have contributed to the science of canine olfaction over the past century or so, either directly or indirectly. Here, we will advocate a generalist, synthetic, and broad-reaching perspective on canine olfaction. We believe in a full integration of experimental psychology (mostly psychophysics and animal learning theory), behavioural biology (mostly ethology because of its strong focus on proximate questions), neuroscience (behavioural, cognitive, affective, and social) and zoosemiotics. Many new applications surface every year (from bed bug detection to telephone poll rot detection)—most either unknown by the scientific community, or known in their own parallel (non-academic) world of “research and development” (R&D) and applied types of research with low inter-disciplinary diffusion. An important part of the scientific contribution to canine olfaction has been fringe and marginal for decades. Canine olfaction can be discussed in relation to the natural environment of the animal or in the context of laboratory conditions. Applied canine olfaction is also a growing area of investigation and often relates to “quasi-experimental” approaches and the industrial, R&D model of applied research. We will discuss some of these applications later.

The field of ‘zoosemiotics’ deserves a brief introduction. Sebeok (1968, 1977) conceptualized the field around the idea of ‘semiotics’, or the ‘theory of signs’. This perspective applies well to “semiochemicals”: chemicals used as signs. At first glance, the field seems to duplicate the study of animal communication (e.g., Bradbury and Vehrencamp 2011). But interestingly, communication, according to zoosemioticians, is only one of three sign processes, or semiosis. Communication describes the “classical” perspective in the field of ethology: exchange of information between a sender and a receiver. Zoosemiotics also makes room for “representation” (when a sender is producing a sign without the presence of a receiver, arguably for an intended receiver or clearly identified receiver, or if you will, a “to whom it may concern” message) and “signification” (when a receiver is present and processing a sign, without the emitter or sender being present). A clear case of representation would be when a canine sender/emitter is urinating, potentially scent marking its territory, but without any other dog in the vicinity. Signification would be when a urine mark or defecation is found, and processed by the receiver, without the sender/emitter present, and without the assumption that the receiver was the intended target (see also Bekoff, this volume, on urination patterns). The elegant

nuance here is that intentionality in the processing of pheromones or allomones (pheromones crossing the species barrier) is not assumed in either signification or representation. In other words, a “sign” (including an olfactory one, or semiochemical) can provide information without being necessarily produced in the context of communication (in which case, the term “signal” is used).

This brings us to the title of this chapter, “Canine Olfaction: Scent, Sign, and Situation”. It goes without saying that the stimuli discussed here are odorants or scents. They are signs as defined by zoosemiotics, and they are always in context. Without having to take a radical “ecological” or behavioural ecology perspective on the issue, ethology, with its focus on direct observation of observable behaviours, and its interest in social and developmental issues, as well as neurophysiological and fine-grained analysis of motor patterns (Fentress and Gadbois 2001), provides tools and an “in-context” framework that complements zoosemiotics, not to mention the highly formalist approaches of psychophysics and animal learning research.

1.2 A Neurocognitive and Neuroconative Perspective on Olfaction

This section will address how mental processes (cognition) and motivations (conation) interact to produce and modulate olfactory behaviours. The neuroscience of mammalian olfaction is a vast area of research, but the work on canines is limited, mostly because of the potential invasiveness of the research. Much of what will be mentioned here emanates from rodent and human research: most vertebrates share the fundamental structure of the olfactory system, as well as its mechanisms, and the homogeneity within the mammalian brain is truly impressive (Panksepp 1998; Panksepp and Biven 2012). The olfactory system is fundamentally linked to the limbic system or paleo-mammalian brain (MacLean 1990). Our perspective in this chapter is neurocognitive. We will discuss two areas of theoretical interest in our lab: the neurocognitive issues behind olfactory processing and learning in relation to training scent processing canines and the issue of learning and motivation from a “soft” pharmacological perspective that one of us (SG) calls the “dopamine hypothesis” (Gadbois 2010).

Because of our neurocognitive focus we will redirect the reader interested in the neuroanatomical and neurophysiological foundations of olfaction to excellent reviews (e.g., Buck 2000; Menini 2009; Shepherd 1994; Wilson and Stevenson 2006; Zelano and Sobel 2005). For the purpose of this chapter, we will focus mostly on the olfactory cortex per se (Haberly 1998; Price 2003), that is, the cortical and peri-cortical part of the olfactory system (the neo-mammalian and paleo-mammalian parts of the olfactory system, respectively, per MacLean’s (1990) terminology). We will not get into the distinction between the primary (or main) olfactory system

and secondary (or accessory) olfactory system, well known from countless reviews on the mammalian vomeronasal organ (VNO) and processing of pheromones and allomones, but we will discuss one important neurocognitive distinction in olfactory processing: the distinction between smelling (implicit processing, involuntary) and sniffing (explicit processing, exploratory) as explained by Sobel et al. (1998). Although Sobel et al. studied human brains, it is reasonable to think that some aspects of this distinction between implicit and explicit neurocognitive processing could take place in canids.

1.2.1 Three Main Neuroanatomical Components of Olfactory Cognition and Conation

We will now describe briefly three main components of the olfactory system that are involved in more “cognitive” processing of olfactory information, as well as being involved in motivational mechanisms underlying olfaction.

1.2.1.1 Pyriform Cortex

The pyriform cortex is also called the ‘prepyriform cortex’ or ‘primary olfactory cortex’: information from the olfactory bulb (an integral component of the limbic system and the first sub-system involved in processing olfactory information from the primary and secondary olfactory systems) is directly wired to the pyriform cortex, which then feeds information to the frontal lobes and the orbitofrontal cortex (via the thalamus). The pyriform cortex is believed to play an important role in olfactory detection and discrimination (Price 2003; Wilson and Sullivan 2011), especially the posterior pyriform cortex. (The anterior pyriform cortex is more involved in the basic analysis of the chemical structure of the odorant. See [Sect. 1.3.1.1](#) below).

1.2.1.2 Entorhinal Cortex

The entorhinal cortex feeds directly into the hippocampus, frontal cortex, and orbitofrontal cortex. It has an important role in memory, especially spatial memory, and thus may play an important role in navigation and possibly tracking and trailing in dogs. It is often defined as the main interface between the hippocampus and the neocortex (frontal and orbitofrontal cortices). The structure is also linked to the amygdala and seems to be involved in autonomic nervous system responses to odours. Emotional memories driven or triggered by smell may involve the entorhinal cortex in significant ways. It is fundamentally part of the hippocampal complex and therefore involved in spatial memory and orientation. See [Sect. 1.3.1.2](#) below.

1.2.1.3 Orbitofrontal Cortex

Often labelled as the ‘secondary olfactory cortex’, this part of the cortex is known to be important in decision making, as well as some cognitive processing of reward, especially expectation and anticipation of rewards (Kringelbach and Berridge 2009). It is therefore involved in the explicit processing of odours (sniffing, as opposed to smelling).

1.2.2 Motor and Motivational Factors in Olfaction

The words ‘motor’, ‘motion’, ‘motivation’, and ‘emotion’ are etymologically related, from *movere*, “to move” in Latin. They all have a neuropharmacological connection as well: dopamine. This important excitatory brain neurotransmitter is of great importance in the motor system at the cortical level (e.g., frontal lobes) and subcortical level (the limbic system, the basal ganglia, and associated structures such as the ventral tegmental area, the substantia nigra, the nucleus accumbens, etc.). It is also implicated in activity in the olfactory system, including the olfactory tubercle in the olfactory cortex (where it plays a role in the overall “reward” system of the brain; the pyriform cortex is rich in dopamine and dopamine receptors), and finally the periglomerular cells in the olfactory bulb. Cognitively, dopamine is associated with a broad range of cognitive functions, including attentional processes, which are conceptually linkable to anticipatory processes at the conative level (in fact, those constructs may be less conceptually and practically distinguishable than currently believed).

Dopamine is involved motivational processes as well. As addiction to dopamine agonists (amphetamines, cocaine) may suggest, the role of dopamine in modulating the motivational system of addicts is remarkable. Interestingly, dopamine agonists are known to increase motivation and anticipation, as well as olfactomotor behaviours and olfactory activity in the olfactory system. In fact, dopamine activity in the lateral hypothalamus is associated with “stimulus-bound processes” (Panksepp 1998), such as exploratory olfactomotor behaviour—in other words, sniffing. Other behaviours may be associated with this as well, such as mouthing, licking, whisking (Deschênes et al. 2011) and more involved motor behaviours such as searching, exploring, and manipulating behaviours. Incentive salience is a characteristic of reward-predicting stimuli that define a system called the “WANTING system” by Berridge and associates (Berridge 2001, 2004). This system is discussed by Panksepp as being the SEEKING system, and similar theories exist elsewhere: Gray’s “Behavioural Activation System” (Gray 1987) and Depue’s “Behavioural Facilitation System” (Depue 2000). Berridge’s theory is more integrated in our opinion as it explains very well the balance between an arousal state of anticipation for the reward (wanting or seeking the reward: what ethologists labelled appetitive behaviours) and the opposing system that takes over when the reward is acquired and being consumed. Here Berridge and Panksepp agree on some of the details, including the

idea that those two systems are incompatible in the sense that if one is activated, the other one is not (in normal conditions, and as Berridge would explain, addiction would be an exception), and that what really motivate animals to do things, including learning, is anticipating the reward, not consuming it: it is wanting it, not liking it. Berridge explains well his integration of those two systems and their impact on behaviour and learning (Berridge 2001; Berridge and Robinson 1998; Berridge et al. 2009). Some neo-behaviourist theories of conditioning postulated such quasi-cognitive or cognitive factors in learning.

Neurocognitively and neuroconatively, “anticipations” and “expectations” seem to be modulated by the dopaminergic system—although it is not the only neurotransmitter system involved (see Table 1.1 showing how the LIKING system taps into endorphins, in fact suppressing the WANTING system, therefore suppressing behaviour). As a reminder, dopamine is the central neurotransmitter in the WANTING/SEEKING system. It is important in olfaction and motor behaviour in general, and therefore plays a role in olfactomotor behaviours, including the basic behaviour of sniffing that is enjoying its own scientific literature in recent years (in humans, rodents, and canines; see Mainland and Sobel 2006; Sobel et al. 1998; Kepecs et al. 2005; Panksepp 1998). Sniffing is an exploratory behaviour that has many important roles in olfaction: it actively participates in the input of the olfactory stimulus, it can be modulated to account for different odorant concentrations, and it can modulate the pattern of neural activity (e.g., brain waves).

In relation to canines, in 1992, Arons and Shoemaker demonstrated that some dog breeds have higher baseline levels of dopamine than others. Border collies and huskies have high dopamine levels; livestock guarding dogs’ levels are lower. It is difficult not to think about the role of dopamine in some human disorders when thinking of dopamine and dog breeds that seem to follow the pattern. Think of border collies. The terms “hyperactive”, “obsessive”, “compulsive”, etc., are frequently used to describe individuals of that breed. This basically translates into the intriguing possibility that individual differences and breed differences in baseline dopamine levels may have a direct impact on cognition, motivation, learning, and overall olfactory behaviour and performance. It is interesting to note that our most successful laboratory and field work dogs are Border collies. A selection bias may be at play here since we recruit dogs volunteered by their owners eager to find an occupation for their overactive pets who appear in need of stimulation, but if we look at the retention of individuals (the ones that make the cut for advanced laboratory or field training), Border collies dominate the roster. As a general rule, they are good and hard workers: motivated, persistent, good sniffers, and their attentional focus can be channelled (in most cases) very well.

Our “dopamine hypothesis” essentially highlights the possibility that “software”-level characteristics (neurochemical and neural-level mechanisms and processes) are more important than the often-touted “hardware” characteristics. For example, we never had any luck with Bloodhounds and other hunting “scent dogs” mostly because of motivational issues, resilience, ability to work long hours or consistently, and overall performance and energy levels. By contrast, the “work ethics” of high-dopamine breeds, like the Belgian Malinois, Jack Russell, and Parsons, is remarkable.

Table 1.1 Theoretical relationships between anticipatory and reward systems of the brain

	Appetitive behaviours	Consummatory behaviours
Traditional system(s)	<ul style="list-style-type: none"> • SEEKING system (Panksepp) • Behavioural activation system (Gray) • Behavioural facilitation system (Depue) 	“Reward system”
Berridge’s perspective	WANTING system	LIKING system
Associated brain areas	Hypothalamus, basal ganglia and associated structures	Limbic system: Amygdala, Hippocampus, Septum, etc.
Associated behaviours	Exploratory behaviours: foraging, stimulus-bound sniffing, mouthing, licking	“Feeling good”
Associated neurotransmitters	Dopamine	Endorphins

Although we have not yet had the opportunity to work with these breeds, some field biologists working with wildlife conservation canines believe Jack Russells are the ultimate detector breed: Engeman et al. (1998) calls them “the unique detector dogs”. We know local dog trainers and handlers in the Canadian Maritime provinces working in bed bug detection that would share that belief.

1.3 Between Nose, Brain, and Mind: Cognitive Processes

1.3.1 Neurocognitive Sub-Systems

The visual system has two pathways (or streams) of processing information from the outside world (Schneider 1969). One is the WHAT system for object recognition, and the other is the WHERE system for spatial vision and localization. From an evolutionary perspective it is believed that those systems evolved in order to make sense of the immediate threats and potential foraging opportunities afforded to the animal. In this section, we argue that the olfactory system can be conceptualized the same way. It may be too early to determine the neuroanatomical boundaries and localization of these subsystems (assuming it is even relevant), but at least the processes involved can be identified. To those two main systems, we will add one that may be of crucial importance to olfaction: HOW MUCH. Table 1.2 summarizes the perspective we propose.

1.3.1.1 The WHAT System

The psychophysics literature makes a clear case for the distinction between detection, discrimination, and identification. Those three processes are part of the “what” system. We will briefly describe the processes involved. Note that in terms of higher

Table 1.2 Olfactory neurocognitive systems and corresponding neuroanatomical centres

WHAT	WHERE	HOW MUCH
Detection	Searching	Scaling
Discrimination	Trailing	
Identification (e.g., matching)	Tracking	
<i>Pyrifom cortex</i>	<i>Entorhinal cortex</i>	<i>Olfactory bulb; cortical?</i>

level (cognitive) processing, we have already identified the pyrifom cortex as an important role player in the WHAT system.

Detection defines the identification of one stimulus (e.g., grapefruit oil) or stimulus category (e.g., citrus essential oil) among background noise or interference. Note that we recognize the importance of early stimulus generalization when inferring categorical detection.

Discrimination defines the identification of one stimulus (e.g., grapefruit oil, referred to as the S+ or positive stimulus) or stimulus category (citrus oils) as contrasted to another often similar stimulus (e.g., orange oil, the S− or negative stimulus) or another category (e.g., floral oils).

Identification is a process by which a more explicit knowledge of the stimulus is made. In humans, for example, “naming” the stimulus would be a demonstration of this level of discriminatory process. Matching-to-sample tasks attempt to get at that level of investigation; that is, the hope is that matching a sample with a target among many other choices is an indication that the animal explicitly “identifies” the target as the “same as” the sample. By definition, identification is preceded by detection and discrimination. We will use the laboratory technique of simultaneous matching-to-sample as an example. Imagine a set of four exemplars: lavender, grapefruit, sandalwood, and bergamot oils. Each of these odorants can be used as the sample to be matched with one or more instances of the same odours. For example, if presented with a lavender oil sample, a dog may be required to pick the matching sample in an array (matrix, line-up, or any other arrangement) of two, three, or x number of choices that can include any of the oils in the initial set and/or distractors. Another example is same-or-different judgments: dogs are trained to investigate two odours and simply indicate if the samples are the same or different (by pressing or poking a paddle, for example). This specific type of learning, although at first glance simple and elegant, has been found to be very difficult if not impossible to acquire by dogs in our lab. Colleagues in developmental psychology have pointed out to us that even children have a hard time with matching-to-sample (non-matching-to-sample tasks being often acquired more readily) and same-or-different judgment tasks (Diamond et al. 1999, Diamond 2006; Overman 1990; Premack 1983).

1.3.1.2 The WHERE System

The localization of olfactory stimuli is crucial in the context of finding food and mates, just to mention the most obvious. We have identified the entorhinal cortex as being an integral part in olfactory processing in the context of spatial memory

and likely localization of odours. It should be no surprise that canids, as predators, have been efficient at using their olfactory sense to survive and reproduce. What is less obvious is how this works beyond the WHAT system. Assuming the canine knows the target scent (can detect it from background interference, can discriminate it from similar odours that may be less relevant, and can identify it in more complex situations), the issue of finding it when no other sensory modality can help (especially vision and audition) is less obvious. This is where laboratory conditions fail to give a full sense of the complexity of the processes necessary to “find” target odours.

The “sniffer dog” literature often distinguishes between trailing and tracking dogs. There is in fact a significant confusion between these two processes, and in some ways the distinction may be somewhat artificial or irrelevant to brain and behavioural organization. But since it is an accepted conceptualization and often defines specific training methods, protocols, and even dogs, we will include the nuance in the WHERE system category. Not unlike the processes in the WHAT system, the WHERE system addresses an incremental level of complexity in terms of processing the stimulus. In this case, the stimulus is entirely “in context”: in a dynamic environment, meaning that the animal needs to be in foraging mode and move around. Our experience in lab conditions suggests that a motor involvement in active searching involving rooting and burying to find an odour source may be facilitating detection and identification, despite the added olfactory noise coming from the substrate. Our hypothesis is consistent with data presented by Hall et al. (2013). We are currently investigating this intriguing hypothesis further. This factor may also explain the “field effect”, that is, the often radical and counter-intuitive loss of performance in dogs that experience field conditions after laboratory training. Motor integration between basic locomotor functions and olfactomotor functions may be crucial for the system to work efficiently. Therefore, searching, trailing, and tracking are uncommon areas of research but promising behaviours to study. This is particularly evident with some of our dogs in the scent processing program at the Canid Behaviour Research Lab that are trained in the lab and later transferred to the field. For half of our dogs, at minimum, it is almost impossible to bring them back to work in lab conditions. They seem to have lost all motivation for the low stimulation (and contamination) of the laboratory environment (it is possible that the absence of cues associated with reward would be the cause). Alternatively, dogs may simply not be stimulated enough cognitively—something that we address often with Border collies that seem to need being constantly challenged. Our discussion of neurocognitive processes addresses the potential reasons behind this phenomenon documented by other teams (e.g., Smith et al. 2003) that we have labelled “field effect”. It is one type of “motivational collapse” (also our term) that is often reported by dog handlers and trainers familiar with working dogs.

Searching The first step in localization, before the stimulus is acquired, is to search. Searching requires the animal to have an identified target, and in applied settings, it may require the dog to memorize biologically irrelevant stimuli (e.g., looking for drugs or explosives). The important dimension of this step is that the

stimulus has not yet been detected. The early stages of foraging behaviour are essentially “searching” behaviours.

Trailing Trailing is often defined as searching, at least in the early stages, but also may suggest that the stimulus is acquired, but not yet localized. In other words, cues are detected that announce the presence of the target, but the exact localization or path taken by the target is not yet identified (and may never be). This process requires significant amount of “air scenting” or sampling the air, as opposed to “ground scenting” or investigating the ground.

Tracking Tracking is much more specific and there is a consensus on the definition of the term. In tracking, the target is acquired, and the path taken by the moving target is also identified and followed (with different levels of spatial accuracy).

1.3.1.3 The HOW MUCH System

There are at least two situations, natural and artificial, that may require the dog to assess the quantity of molecules present in the environment. Volatiles will be distributed according to a specific gradient influenced by contextual conditions (temperature, humidity, barometric pressure, and most importantly, air movements such as drafts and wind), not to mention the distance between the dog and the target (and obviously all this in relation to the actual saliency of the stimulus). Much of this category is akin to the “scaling” process known in psychophysics. Training and experimental conditions may require a dog to identify a threshold and, for instance, give a positive response if the stimulus is above threshold and give a negative response or no response if the stimulus is below that threshold. An example would be a dog trained to identify *Varroa destructor* (parasitic mites) and *Nosema apis* (fungus) in beehives. Both are potentially important factors in colony collapse disorder (CCD). Most beehives in North America are infected with some level of *Varroa* and *Nosema*, but the applied issue would be to train a dog to identify hives infected beyond a specific threshold, highlighting the need for an immediate intervention.

Interestingly, it is unclear whether the HOW MUCH system would actually be able to discriminate within the actual volumetric quantity of a given stimulus (of biological significance or having a primary incentive value—e.g., food). A study by Horowitz et al. (2013) suggests that pet dogs may not differentiate between low and high quantities of food based on olfactory cues alone. It is possible that a larger differential between small and large amounts would have resulted in more significant results (in terms of physical or chemical volatility), or perhaps the differential incentive value of the stimuli was minimal enough to keep them indifferent in their choice of food source.

The HOW MUCH system likely serves a function in processing gradients—in other words, helping the dog to determine the direction of a source of volatiles.

This specific question has been discussed in the context of directionality of tracks. The basic question is as simple as “Do dogs know if they backtrack or forward-track a target?”, and as a corollary, “Can they make a mistake?”. It seems logical that, in order to survive, wolves would have had to “know” where their prey was going, as backtracking would be counterproductive and maladaptive. A debate has been ongoing regarding this issue with dogs (Thesen et al. 1993; Steen and Wilson 1990; Wells and Hepper 2003; Hepper and Wells 2005). Interestingly, Wells and Hepper (2003) found that dogs were not good at “detecting” direction. Only 36.3 % of the dogs studied could do this consistently. Steen and Wilson (1990) suggested that the training (read “learning” for ethological, non-artificial contexts) may be of importance in determining if dogs track in the right direction. Thesen et al. (1993) identified three stages in tracking behaviour: a “searching” phase (before the stimulus or target is acquired, as described above), a “deciding” phase (when the dog determines the directionality of the moving target), and a “tracking” phase. They also found the dogs to be more accurate and consistent than those in the study by Wells and Hepper (2003). Note that this literature and perspective on the HOW MUCH system may link it directly to the WHERE system. It may even suggest that it is a sub-system of the WHERE system or simply needs to be fully merged with it.

Most of the traditional fundamental research on canine olfaction and applied research with sniffer dogs has focused on the WHAT system (e.g., odour discriminations) and the HOW MUCH system focusing on detection thresholds, in other words, more traditional psychophysics experiments (see Helton 2009a, b and Lit 2009 for reviews; see also the work of the Auburn University College of Veterinary Medicine group, e.g., Furton and Myers 2001). Research on tracking per se is at its infancy, mostly because of the methodological constraints imposed by moving subjects during searching, trailing, and tracking but also because of the challenges presented by field work.

1.4 Methodology: Psychophysics, Olfactory Learning, and Cognition

Section 1.3 presented our three-system perspective on the sensory and cognitive processes that work in synergy to process information. Now we move on to the methods to investigate olfactory capacity. Studying olfaction in animals has been a challenge in that what are salient odours for most non-human mammals (with exceptions, e.g., cetaceans) are for humans “invisible” and often undetectable stimuli. Experimental psychology has provided effective tools to study sensory processes in animals using mostly operant methods (Blough 1966; Blough and Blough 1977). Quantitative tools in human psychophysics have also contributed to the application of Signal Detection Theory (SDT) to olfactory stimuli, either in

detection tasks (one stimulus in a noisy environment) or discrimination and identification tasks (discriminating between two stimuli). While we are not covering it here, the basics of SDT for canine olfactory processing are discussed in Helton (2009a, b). McNicol (2005) is a short yet useful resource to cover the basics of SDT and MacMillan and Creelman (2005) is a comprehensive resource to cover advanced applications of SDT. The latter includes its use in designs such as two-alternative forced choice designs (2AFC) and multiple alternative forced choice (mAFC), same-different, matching-to-sample, and oddity design (triangular method) (Lit 2009). Although written with humans and mostly visual stimuli in mind, olfactory stimuli can be used with these approaches. It is also worth mentioning that although SDT is usually used as a parametric tool, a non-parametric version of SDT also exists (Pastore et al. 2003).

1.4.1 Habituation-Dishabituation

Slotnick and Schellinck (2002) also review methodologies used with rodents, including an interesting non-operant technique called “habituation-dishabituation”. The method is often used in our lab before training dogs on a specific scent when we are in the early stages of a project. As habituation (and dishabituation) are non-associative, “simple” forms of learning, no training is required. We use this technique to test the ability of dogs to naturally detect two given odours. For example, in 2009, our laboratory started a project with Parks Canada that required sniffer dogs to find and potentially track Eastern Ribbon Snakes (*Thamnophis sauritus sauritus*), a species-at-risk in Nova Scotia. One of our worries was that Common Garter Snakes (*Thamnophis sirtalis*) are very common in the same habitat and areas where the dogs were going to work. Both species are of the same genus and to a human nose, smell quite the same. The procedure typically includes five trials. The first four are the habituation phase, when the dogs are exposed to the target scent for five minutes. During that time, the duration of sniffing (sniffing time) is recorded. The dogs are given a break of fifteen minutes between each exposure. Typically, by trial four, the sniffing time has been reduced dramatically. On trial five, the new scent (Common Garter Snake) is introduced. This is the dishabituation phase. If the dogs perceive the smell as different, it is assumed that the sniffing time will increase dramatically from trial four because of the novelty of the smell (Gheusi et al. 1997; Vaché et al. 2001). It is expected that the sniffing time would approach the sniffing time of the first trial. In our case (Gadbois et al. in prep), all dogs increased their sniffing time significantly, more than doubling the sniffing time for trial one (see the Fig. 1.1). This can be interpreted as a strong novelty effect, suggesting dogs can naturally discriminate the two smells. A control condition—a cotton ball without the smell—is always added within each trial. This immediate, within-trial control allows the experimenter to determine if the dog is sensing the target odours.

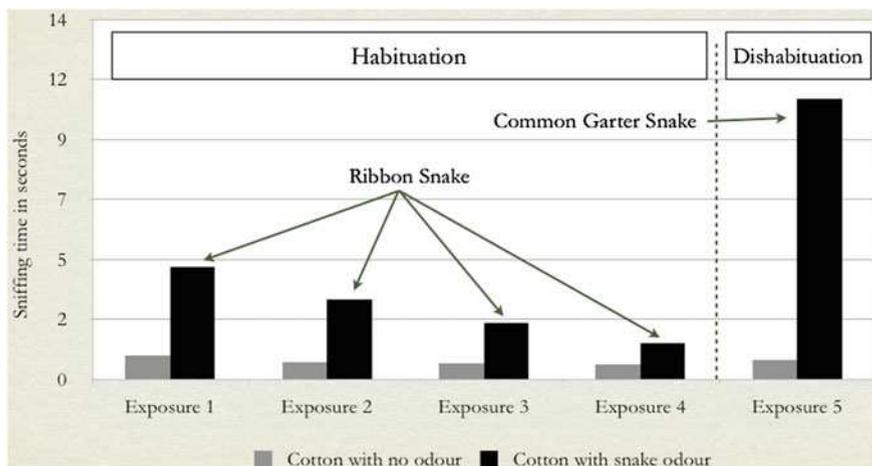


Fig. 1.1 Data showing Zyla’s (expert sniffer dog) habituation/dishabituation test comparing Eastern Ribbon Snake scent to Common Garter Snake scent (Gadbois et al. in prep)

1.4.2 Errorless Discrimination Training

Our lab has also worked on adapting Errorless Discrimination Training (EDT) (Terrace 1963a, 1963b, 1964, 1966) to olfactory discriminations with some success. Using the same example as above (training the Ribbon Snakes as the S+ or target scent versus Common Garter Snakes as S– or non-target scent) we use an adaptation of EDT. Terrace developed the procedure for colour (wavelength) discrimination in pigeons. As far as we know, EDT has never been applied to scent detection and discrimination. It differs from traditional discrimination training in a number of ways:

- There is no peak shift: i.e., gradual biases in discriminations away from the target stimulus do not occur.
- There is a large reduction of errors compared to traditional discrimination learning (~45 times fewer errors) (Terrace 1963a, b).
- EDT is based on excitatory conditioning only. In other words, mistakes (errors) are not required for learning. Thus, there are no negative emotions during training (e.g., frustration, helplessness, stress, anxiety, etc.), so the training does not become aversive.

In traditional discrimination training methods (TDT henceforth), a target odour is presented (S+) and a non-target odour is presented (S–). Presentations of S+ and S– can be simultaneous or sequential. Responses to S+ are always rewarded, at least initially, and responses to S– are never rewarded. EDT’s procedure is simpler, yet somewhat counterintuitive for most people familiar with TDT: initially, only S+ is presented, and a response specific to S+ (e.g., “sit”) is rewarded. Soon after the beginning of the training, S– is presented alongside S+ but in very low concentrations. The concentration of S– is gradually and slowly increased

until it is at the same level as S+. This process is called “fading-in”. Theoretically, dogs learn to ignore S−, and to only responded to S+. As mentioned above, errors made by animals with this type of training are radically reduced compared to TDT. The main drawback of this technique is that transfer of learning (during re-training) may be longer and more difficult for the dog. EDT dogs are more likely to become a “one-smell-dog” than TDT dogs, but they are very accurate for that one smell and the learned behaviour is very resistant to extinction.

The problem with EDT is to find a way to deliver the stimuli with a fading-in procedure in place. Olfactometers could be used, but we decided to explore a simpler and cheaper method. Our training used the Ribbon Snake odour (S+: a swab of a live animal). Part of the training takes place with the scent of other snake species or distractor odours (S−: food, dog smell, Common Garter Snake odour). A small rectangular aquarium is used to present the odours. Each sample (S+ and S−) sits at the bottom of the aquarium. Two containers (baby food jars or stainless steel spice containers) are placed in the aquarium, above water level, one containing the S+ (Ribbon Snake smell), the other the S− (e.g., Garter Snake smell). The location (left or right) of the S+ is randomly determined between trials. The Ribbon Snake sample is placed directly in the well, but the S− smell is contained in an ice cube that gradually melts, increasing ever so gradually the saliency of the smell. Since we do not control the presentation of the smell in discrete presentations, the dog is taken in and out of the testing room. In our case, ice cubes would take between 4 and 5 h to melt completely. Dogs are then invited to visit the experimental room and are rewarded (e.g. with play, food, or praise) for any attention paid to the S+ and simply ignored for any time spent sniffing the S−. The saliency of the S− (and the S+) can be increased towards the end of the exposures or accelerated overall to reduce the length of the session by using a hot plate or other heating device. The aquarium has a cover and multiple small holes allowing the scent to diffuse out of it. Time spent smelling the target side of the box is measured (and as mentioned above, counterbalanced between trials to avoid lateral preferences and learning) and rewarded. Within 3 to 5 h (or depending on the volume of the frozen sample), the dog typically sniffs only the S+ and ignores the S−. This type of learning can be transferred and generalized to procedures requiring the shaping of a more explicit response (e.g., nose poking and holding for a few seconds at the target stimulus). Our experience with this technique so far has been promising, although we often run into the problem of having a dog perfectly able to distinguish between the S+ and S−, but unable to then quickly learn a desired operant response to signal the presence of a target (unpublished data).

1.4.3 Line-Ups: Memory Load Issues in Scent Processing

The line-up is another very common method in olfactory discrimination and identification. It is traditionally used by the police forces and the military and has become common in many modern applications for training as well as experimental

and biomedical trials (e.g., cancer detection). For example, Schoon and Haak (2002) wrote what is often considered the standard for forensic work with canines. Their use of line-ups in the context of a matching-to-sample problem has many potential applications. In their case, they describe the training of dogs to match objects found at a crime scene with a potential perpetrator. At first glance, the concept seems to make sense as dogs act here as witnesses. Following discussions with a colleague at Dalhousie University, Dr. John Christie, a cognitive psychologist, we realized that the dogs may be “expert witnesses”, but they are not comparable to expert witnesses participating in a photo or person line-up as they were not at the crime scene. In other words, we are not testing their memory of a past event, but we are instead testing their sensory-perceptual matching of the odour of a person, and the odour of an object with which they were in contact. So the question then becomes: Why make this task a memory task?

In the early 1970s, a former mentor of one of us (SG), Werner Honig, introduced into animal learning, from human cognitive psychology, the concept of working memory. Honig was by training a traditional operant conditioning researcher who edited seminal books in the field (Honig 1966; Honig and Staddon 1977). Growing increasingly dissatisfied with a “pure”, traditional approach to instrumental conditioning, Honig became receptive to the memory literature in humans and applied many of the theoretical and conceptual foundations of human cognition to animal learning (he contributed a number of edited books on the topic, e.g., Honig and James 1971; Hulse et al. 1978; Honig and Fetterman 1992, and many articles addressing working memory in pigeons: Honig 1978, 1981, 1984). Although his work was never applied to canines and was largely restricted to pigeons (a traditional model in classical behaviourism), the concept of working memory in animals is now largely accepted in animal cognition textbooks. The basic idea is that information presented to animals may stay in memory for a short period of time, for the time necessary to complete a task. Working memory, as a specific type of short term memory, is prone to interference, and tends to fade rapidly when not in use.

Let us go back to the line-up: Remember that a line-up is a special case of matching-to-sample—the sample being the “cue” given to the dog, i.e., what to find. The general procedure in a formal test of “expert canine testimony” would be to present the dog with the smell of a suspect, or sample (e.g., sweat sample on a cotton ball) and ask the dog to walk a line-up of containers containing objects, one of which could be the potential target. Conversely, the object found at the crime scene could be the sample, and a line-up of sweat samples from different people (including the suspect) could be available for investigation. Note that the most standard procedure includes six containers with samples to sniff: one target and five foils or distractors. The position of the target is typically randomly determined by throwing a die. Note also that dogs are typically trained to not respond to blank line-ups, so they should know that a “no target” condition is possible, thus reducing false alarms. In addition, they should be trained to identify two instances of the same target in the same line-up to encourage them to complete the sampling of the line-up even if the target is in an early position.

Table 1.3 Sequential position of target and performance of two expert detection dogs in a line-up procedure

	Position 1	Position 2	Position 3	Position 4	Position 5	Position 6
Dog 1	97.7 %	93.7 %	90.6 %	82.7 %	28.5 %	10.5 %
Dog 2	97.7 %	90.6 %	93.7 %	79.3 %	35.7 %	13.1 %
# trials	45	32	32	29	28	38

The working memory issue is easy to miss. Taking into consideration that the dog is not an actual witness of a crime trying to remember information about a crime scene, it is puzzling that we would increase interference with such a procedure. Added interference comes from the information in working memory after the inspection of each station containing a sample to inspect. Since this is done sequentially in one scan of all six containers, you can imagine that by the time the dog inspects the fifth and sixth samples, it may not remember the characteristics of the cue or initial sample.

We decided to put this hypothesis to the test with a mini-experiment with two dogs that were considered experts at line-ups and were of equal overall performance (80–100 %, averaging 90 %). Dogs were trained on diluted essential oils and in this case, we identified a specific target (lavender oil) to find in the line-up. We measured the accuracy of the dogs based on the position of the target in the line-up. The position of the target was randomly determined by throwing a die over 200 trials. As expected, if the target was early or close in the line-up (positions 1 and 2), accuracy was high (>90 %). But if the target was late or far in the line-up (positions 5 and 6), accuracy dropped significantly (<40 %) (Table 1.3). To go back to the forensic example with canine “expert witnesses”, imagine now that the target associated with a perpetrator has been randomly assigned to position 6. The dogs have less than a 15 % chance of making an accurate match. Note also that we are not working with degraded stimuli. In fact, even if significantly diluted, essential oils are so strong and salient that we stopped using them a few years ago in favour of tea and other infusions in the early training phases of detection-, discrimination, or matching dogs.

After realizing this pattern was common when using line-ups, and since we are not interested in mnemonic performance but rather psychophysical accuracy at the sensory and perceptual level, we started using simpler tasks with a reduced number of potential choices. Simplicity is our best ally in those situations. If possible, using simple designs and procedures (e.g., go/no-go, a single-scent task, or 2AFC or 3AFC if more than one operant response is necessary) is preferable. In other words, as discussed in Lit (2009), reducing the cognitive demand of the task will accelerate learning and likely increase performance. By analogy, in the case of the line-up, making sure that the matching-to-sample is simultaneous (i.e., the options are made available immediately, as opposed to a delayed matching-to-sample), and a small number of options is offered, would help performance. In other words, the spatial and temporal contiguities should be such that the task does not tax memory processing resources, but only sensory-perceptual processing resources.

1.4.4 Remote Scenting: Attentional Load Issues in Scent Processing

Sometimes the presence of the dog “on site”, especially in applied settings, is not desirable or even safe. Field conditions are sometimes too hazardous for the dogs to be present (land mine detection dogs can get injured or killed in the field), sample collection of rare species sign with wildlife conservation canines may be infrequent and occur over large expanses of terrain or in remote and difficult to access areas (collecting scats and identifying potential latrine sites for Eastern Cougars), or the dog is simply not able to easily work on premises (e.g., in clinics and hospitals for diagnostic detection or in interactions with patients). In those examples, practical reasons would normally exclude dogs from being part of the detection, searching, tracking, etc. Remote-scenting protocols were developed with these cases in mind, and an important historical first case was the development of Remote Explosive Scent Tracing (REST) with land mine detection in mind (Fjellanger et al. 2002; McLean et al. 2003; see Helton 2009a, b for a short review). One other clear advantage of this method addresses the issue of attention and an attempt with remote scenting to reduce attention demands by having the dogs work in controlled, consistent, and familiar indoor conditions. Microclimatic and micrometeorological conditions (temperature, humidity, air movements) can be controlled and delivery methods can be designed to optimize scent perception.

1.4.5 Ethological Approaches and Future Lines of Investigation

The study of canine olfactory psychophysics and learning has certainly benefited from the tradition of behaviourism and behaviour analysis, including applied behaviour analysis. Indeed, applied research with sniffer dogs seems to be the main impetus for funding and research opportunities in olfactory cognition, especially if an experimental approach is favoured. Unfortunately, there is an immense gap in the study of olfaction in canines: The true ethological field approach when looking into mid- to long-range tracking and trailing processes. Potential approaches to this may include the use of optical tracking methods (as used in path integration in canines by Séguinot et al. 1998) and GPS/GIS technology, when the technology becomes less expensive and more accessible.

A clear understanding and deep knowledge of animal learning and cognition is without a doubt useful to the development of experimental programs seeking to understand the fundamental and applied dimensions of canine olfaction.

1.5 Medical Detection and Assistance Canines: Cancer, Diabetes, and Epilepsy

The challenges of applied research are numerous. Although not our primary applied research area, we will present a quick review of a fascinating emergent area of biomedical research involving the training of dogs for detection of and assistance for medical problems.

The relationship between owner and pet can be a very fulfilling and rewarding experience. Recent advances in the field of health research suggest that dogs may soon be more than just our pets and that the nature of our relationship with them could change drastically.

1.5.1 Cancer Detection

The first evidence of a dog's ability to detect disease came from the well-known report by Williams and Pembroke (1989) in the *Lancet*, in which a woman sought medical attention after her dog persistently sniffed a mole on her leg. Upon clinical examination, the spot was discovered to be malignant melanoma. What was it the dog smelled that interested it so much? Advances in technology suggest that diseases such as cancer likely have a "signature scent", characterized by the volatile organic compounds (VOCs) being released (Szulejko et al. 2010).

In the 1970s, Linus Pauling et al. (1971) found 200 VOCs in exhaled human breath. Since then, more than 3400 VOCs have been documented in human breath (Phillips et al. 1999). VOCs released in the breath, urine, and tissues may provide a window into biological processes, with certain biological markers indicating specific medical conditions (Bijland et al. 2013; Buszewski et al. 2012; Miekish et al. 2004; Szulejko et al. 2010).

In 1999, Phillips et al. obtained breath samples from 50 healthy individuals and analyzed the biological components of the samples using an analytical technique called Gas Chromatography—Mass Spectrometry. The analysis revealed a total of over 3400 different VOCs. Importantly though, each individual breath sample was found to have an average of 204.2 VOCs, and only 27 VOCs were found to be present in every sample. This demonstrates a huge level of variability between individuals' breath samples. Such variation is likely due to differences in diet, drugs, medication, metabolism, and health status, to name a few factors (Phillips et al. 1999).

Can dogs detect differences in the VOCs being emitted by their owners? Can they even smell the VOCs? Evidence would suggest that this is the case. The burgeoning science of canine olfaction has elucidated just how sensitive the nose of a dog is. For example, using an olfactometer, Waggoner et al. (1998) showed that dogs were able to detect a target odour present in one part per billion in the presence of a distracting odour at a concentration of twenty parts per million, and

Pearsall and Verbruggen (1982) reported that dogs can smell some odours at one part per trillion.

The ability of dogs to sniff out melanoma was empirically tested by Pickel et al. (2004). Using two well-trained dogs, one of which was experienced in cancer detection, Pickel et al. first confirmed the dogs' ability to detect melanoma tissue using a variety of search tasks. Researchers then placed between 8 and 30 adhesive bandages on human participants, one of which covered the site of the cancerous tissue. The first dog successfully identified the correct bandage on 6 out of 7 patients, while the second dog was successful in sniffing out melanoma on 3 out of 4 patients.

Horvath et al. (2008) showed that a naive Riesenschнауzer (neither the dog's previous level of training, or experience in olfactory detection was mentioned) was able to detect ovarian cancer from cancerous ovary tissues with 100 % sensitivity and 97.5 % specificity. Moreover, control tissues in this study included abdominal fat, muscle, small bowel tissue, healthy postmenopausal ovarian tissue, and some tissues from an area just adjacent to the tumor. Given the impressive results, this study serves as excellent evidence that cancerous cells have a distinct odor that is reportedly detectable by dogs.

Detection of cancer in urine and fecal samples has yielded more conflicting results. Willis et al. (2004) reported that after a seven month training period, dogs with no prior experience could detect bladder cancer in urine samples at 41 % accuracy (as compared to 14 % expected by chance). Using urine samples to test dogs' ability to detect breast or prostate cancer, Gordon et al. (2008) had ten dogs trained by professional dog trainers. The reported successful detection rate for breast cancer was 22 % and only 18 % for prostate cancer.

More promisingly, Cornu et al. (2011) were able to train a Belgian Malinois with no prior experience to detect prostate cancer from urine samples with a sensitivity and specificity of 91 % in a period of 24 months. Furthermore, Sonoda et al. (2011) tested a trained cancer-detection Labrador retriever's ability to detect colorectal cancer in both breath and watery stool samples from patients with different stages of colorectal cancer. Control samples were obtained from patients with other colorectal conditions such as chronic inflammatory disease and various forms of colitis. The dog was able to detect colorectal cancer in the breath samples with 91 % sensitivity and 99 % specificity, and in the watery stool samples with 97 % sensitivity and 99 % specificity.

Still, based on the available literature, it would appear that testing the detection of cancer by dogs is more consistently successful with the use of breath samples. McCulloch et al. (2006) used a three-phase training program that spanned only a couple of weeks to train naive sniffing dogs to detect lung and breast cancer from breath samples. Testing revealed the dogs' ability to detect breast cancer with a specificity of 98 and 88 % sensitivity, and lung cancer with 99 % specificity and sensitivity.

Ehmann et al. (2012) had four family dogs trained by professional dog trainers to detect lung cancer from breath samples (no mention of length of training). In this study, sample controls were from patients with a non-malignant lung disease.

Here, dogs were reported to successfully detect lung cancer at a sensitivity of 72 % and specificity of 94 %.

Empirical studies of the ability of dogs to detect cancer are still in their infancy. Inconsistent findings are likely the result of differing training programs and sample collection techniques (Moser and McCulloch 2010), as well as breed-specific behavioural profiles as suggested by our dopamine hypothesis (Sect. 1.2). However, given the reported ability of dogs to successfully detect cancer despite potential confounds and biologically comparable control stimuli (Ehmann et al. 2012; Horvath et al. 2008), these studies provide an extremely promising and intriguing area of study that warrants much further investigation.

1.5.2 Diabetes Detection

Anecdotal evidence suggests that dogs (and cats) may be able to prevent health complications in individuals with insulin-dependent diabetes by signaling impending hypoglycemic events in their owners (Chen et al. 2000; Wells et al. 2008, 2011). In a series of case studies, anecdotal evidence from individuals with diabetes suggests that their dogs were aware of fluctuations in their blood sugar levels before they experienced symptoms. Furthermore, some dogs woke owners during the night, and one even signaled through a closed bedroom door (Chen et al. 2000).

Although there are companies claiming to train hypoglycemia detection dogs (e.g., CARES, Canine Assistance Rehabilitation Education and Services), there are currently no empirical studies confirming this ability in dogs, and there is only speculation as to what the dog is detecting before a hypoglycemic event. Researchers hypothesize dogs may be using olfactory cues such as a change in the chemical composition of their owners' sweat (sweating is a common symptom of hypoglycemia), or that signaling dogs are acutely aware of the behavioural changes accompanying hypoglycemia in their owners (Wells et al. 2008).

In an attempt to elucidate the mechanism with which dogs may detect hypoglycemia, our Canid Behaviour Research Team at Dalhousie University has teamed-up with colleagues at the IWK Health Centre in Halifax, Drs. Elizabeth Cummings and Elizabeth McLaughlin. We began in early 2013 a series of projects to examine potential biochemical routes of detection. Our dogs are selected based on motivation levels and their performance in detecting low-saliency stimuli. Those dogs that are selected are tested on their ability to detect glycemic changes in breath, sweat, and saliva samples from individuals with Type 1 diabetes. The dogs are presented with a forced choice task that requires them to match hypoglycemic samples with hypoglycemic samples, in the presence of normoglycemic samples from the same individual. Successful matching would indicate the dog's ability to discriminate between glycemic levels from samples in vitro, in the absence of the actual patient. Although the project is still very young, preliminary results are inconclusive. In the future, we would like to test the hypothesis that

what dogs may be detecting in their owner is actually a myriad of physiological and behavioural changes, therefore detection would only be possible in vivo. If this is found to be the case, we would also like to test the idea that hypoglycemia-detection dogs are responding to a generalized stress response. Anecdotal evidence may suggest that trained hypoglycemia detection dogs respond to a variety of biologically stressful events (e.g., asthma attack) in their owners and others and this may be an indication that physiological stress markers (e.g., increase in adrenalin, cortisol levels, etc.) may be detected, and not glycemic VOCs per se (e.g., personal communication, Sarah Holbert of CARES, March 2013).

1.5.3 Seizure Alert Dogs

Until recently, only anecdotal reports of dogs signalling oncoming seizures in their owners existed. However, recent empirical evidence has shown that dogs can indeed detect seizures and can be trained to do so reliably (Kirton et al. 2008, and for reviews see Brown and Goldstein 2011; Dalziel et al. 2003).

Strong et al. (1999) successfully trained six dogs to anticipate and signal an impending seizure in a family member. Following a training period of six months, the dogs learned to associate seizures with pleasurable events and consistently signalled 15–45 min before a seizure. An unexpected result was that owners reported a reduction in the frequency of seizures. Therefore, in 2002, Strong et al. examined this directly by following epileptic patients 24 weeks after acquiring a trained seizure detection dog. As reported by patients in the 1999 study, a reduction in the frequency of seizures in almost all patients was observed (9 out of 10 patients, mean reduction of 43 %). Given that seizures are often preceded by anxiety (Betts 1981) and that owners of seizure detection dogs have reported increases in well-being (Kersting et al. 2009), it is possible that owning a trained seizure detection dog provides feelings of comfort and safety (as discussed above), thereby reducing anxiety and as a result, seizure frequency.

As with hypoglycemia detection dogs, it is not known what signals from the owner alert the dog before a seizure. However, in this case, researchers appear confident that trained dogs are recognizing and responding to minute changes in the behaviour of their owner (Brown and Strong 2001), but detection of physiological changes cannot be ruled out without further investigation (Wells 2007).

1.5.4 Where to Go From Here?

Canine detection of disease and the use of dogs as assistance dogs is an extremely intriguing field. Evidence suggests that dogs can be trained to detect different forms of cancer using olfactory cues from multiple biological channels. Testing the VOCs in human biological samples provides an interesting alternative to

current screening methods for cancer. Depending on the cancer being tested for, current screening techniques can be expensive, inaccurate, increase exposure to radiation, and can result in unnecessary biopsies (Jett 2005; Gotzche and Nielsen 2006). The ability of dogs to detect impending hypoglycemic events in diabetic owners is a phenomenon that merits further study. Based on the successful training of seizure detection dogs, there is reason to believe that the validity of hypoglycemia-detection dogs may be empirically confirmed in the near future. Taken together, the literature presented here suggests that in the future we will see dogs not only as human's best friend, but as our partners in health care, providing detection of, assistance for, and treatment of disease.

1.6 Human-Canine Sensory Symbiosis and Appeal for a Renewed (Situated) Science of Canine Olfaction

Much of our applied work at the Canid Behaviour Research Lab at Dalhousie University is based on wild canid research and the use of sniffer dogs as “wildlife conservation canines”, helping us find our target species (e.g., coyotes, various species-at-risk, or invasive species) in unobtrusive and non-invasive ways. Although one of us (SG) has been using dogs in this capacity since the early 1990s, it was not until a student (Flannery and Gadbois, unpublished manuscript) decided to write a literature review on the topic that we realized the potential of this association between humans as field researchers and dogs as research assistants. As Hewes (1994) discusses, the symbiosis between humans and wolves or early dogs may have been a question of survival, and the complementarity of our sensory ecologies—visual humans, olfactory wolves—may have been the start of a remarkable (mutualistic) symbiosis. This never became more obvious to me than when a few years ago, in the scenic and majestic scenery of the Cape Breton Highlands in Nova Scotia, we were looking for a pack of coyotes and a suspected moose carcass site. Our sniffer dog Zyla was air scenting to localize the coyotes, pulling in one direction, and ravens were converging in a slightly different direction (towards, we realized later, the moose carcass). I could not stop thinking about how this all made sense. Early humans would have relied on scavengers and predators to locate food, and would have quickly realized that the keen sense of smell of wolves was an asset.

As suggested and highlighted in our discussion of the biomedical (and companionship, when assistance complements the detection work) applications of canine olfaction, we are only at the beginning of the realization of the amazing potential this partnership can offer.

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References

- Allen, J. J., Bekoff, M., & Crabtree, R. L. (1999). An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. *Ethology*, *105*, 289–302.
- Arons, C. D., & Shoemaker, W. J. (1992). The distribution of catecholamines and beta-endorphin in the brains of three behaviorally distinct breeds of dogs and their F1 hybrids. *Brain Research*, *594*, 31–39.
- Bekoff, M. (2001). Observations of scent-marking and discriminating self from others by a domestic dog (*Canis familiaris*): Tales of displaced yellow snow. *Behavioural Processes*, *55*(2), 75–79.
- Berridge, K. C. (2001). Reward learning: Reinforcement, incentives and expectations. In D. L. Medin (Ed.), *Psychology of learning and motivation* (Vol. 40, pp. 223–278). San Diego: Academic Press.
- Berridge, K. C. (2004). Motivation concepts in behavioral neuroscience. *Physiology & Behavior*, *81*(2), 179–209.
- Berridge, K. C., & Robinson, T. E. (1998). What is the role of dopamine in reward: Hedonics, learning, or incentive salience? *Brain Research Reviews*, *28*(3), 308–367.
- Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: ‘Liking’, ‘wanting’, and learning. *Current Opinion in Pharmacology*, *9*, 65–73.
- Betts, T. (1981). Epilepsy: Questions and answers. *Nursing Mirror*, *153*, 6–9.
- Bijland, L. R., Bomers, M. K., & Smulders, Y. M. (2013). Smelling the diagnosis. A review on the use of scent in diagnosing disease. *The Netherlands Journal of Medicine*, *71*(6), 300–307.
- Blough, D., & Blough, P. (1977). Animal psychophysics. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behaviour* (pp. 514–539). Englewood Cliffs, NJ: Prentice-Hall Inc.
- Blough, D. S. (1966). The study of animal sensory processes by operant methods. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 345–379). New York, NY: Meredith Publishing Company.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer Associates Inc.
- Brown, S. W., & Goldstein, L. H. (2011). Can seizure-alert dogs predict seizures? *Epilepsy Research*, *97*, 236–242.
- Brown, S. W., & Strong, V. (2001). The use of seizure-alert dogs. *Seizure*, *10*, 39–41.
- Buck, L. B. (2000). Smell and taste: The chemical senses. In E. R. Kandel, J. H. Schwartz, & T. M. Jessell (Eds.), *Principles of neural science* (4th ed., pp. 625–647). New York, NY: McGraw-Hill Companies.
- Buszewski, B., Ligor, T., Jezierski, T., Wenda-Piesik, A., Walczak, M., & Rudnicka, J. (2012). Identification of volatile lung cancer markers by gas chromatography-mass spectrometry: Comparison with discrimination by canines. *Analytical and Bioanalytical Chemistry*, *404*, 141–146.
- Chen, M., Daly, M., & Williams, G. (2000). Non-invasive detection of hypoglycaemia using a novel, fully biocompatible and patient friendly alarm system. *British Medical Journal*, *321*, 1565–1566.

- Cornu, J. N., Cancel-Tassin, G., Ondet, V., Girardet, C., & Cussenot, O. (2011). Olfactory detection of prostate cancer by dogs sniffing urine: A step forward in early diagnosis. *European Urology*, *59*, 197–201.
- Dalziel, D. J., Uthman, B. M., McGorray, S. P., & Reep, R. L. (2003). Seizure-alert dogs: A review and preliminary study. *Seizure*, *12*, 115–120.
- Depue, R. (2000). *Neurobehavioral systems, personality and psychopathology*. New York, NY: Springer.
- Deschênes, M., Moore, J., & Kleinfeld, D. (2011). Sniffing and whisking in rodents. *Current Opinion in Neurobiology*, *22*, 1–8.
- Diamond, A. (2006). Bootstrapping conceptual deduction using physical connection: Rethinking frontal cortex. *Trends in Cognitive Sciences*, *10*, 212–218.
- Diamond, A., Churchland, A., Cruess, L., & Kirkham, N. (1999). Early developments in the ability to understand the relation between stimulus and reward. *Developmental Psychology*, *35*, 1507–1517.
- Ehmann, R., Boedeker, E., Friedrich, U., Sagert, J., Dippon, J., Friedel, G. et al. (2012). Canine scent detection in the diagnosis of lung cancer: Revisiting a puzzling phenomenon. *European Respiratory Journal*, *39*, 669–676.
- Engeman, R. M., Vice, D. S., Rodriguez, D. V., Gruver, K. S., Santos, W. S., & Pitzler, M. E. (1998). Effectiveness of the detector dogs used for deterring the dispersal of Brown Tree Snakes. *Pacific Conservation Biology*, *4*, 256–260.
- Fentress, J. C., & Gadbois, S. (2001). The development of action sequences. In E. M. Blass (Ed.), *Handbooks of behavioral neurobiology: Developmental psychobiology, developmental neurobiology and behavioral ecology: Mechanisms and early principles* (Vol. 13, pp. 393–431). New York: Kluwer Academic Publishers.
- Fjellanger, R., Andersen, E. K., & McLean, I. G. (2002). A training program for filter-search mine detection dogs. *International Journal of Comparative Psychology*, *15*, 277–286.
- Flannery, M., & Gadbois, S. (2013). *The use of scent detection dogs in wildlife conservation*. Manuscript in preparation.
- Furton K. G., & Myers L. J. (2001). The scientific foundations and efficacy of the use of canines as chemical detectors for explosives. *Talanta*, *54*(3), 487–500.
- Gadbois, S. (2010). Canine behavioural neuroscience: From canine science in shackles to new opportunities. In Proceedings of the 2nd Canine Science Forum, Vienna, Austria.
- Gadbois, S., Demontfaucon, M., Mousse, D., & Flannery, M. (in prep). *Ribbon Snake Conservation Canines in Kejimikujik National Park*.
- Gheusi, G., Goodall, G., & Dantzer, R. (1997). Individually distinctive odours represent individual conspecifics in rats. *Animal Behaviour*, *53*, 935–944.
- Gordon, R. T., Schatz, C. B., Myers, L. J., Kosty, M., Gonczy, C., Kroener, J. et al. (2008). The use of canines in the detection of human cancers. *The Journal of Alternative and Complementary Medicine*, *14*, 61–67.
- Gotzsche, P. C., & Nielsen, M. (2006). Screening for breast cancer with mammography. *Cochrane Database of Systematic Reviews*, *4*, CD001877.
- Gray, J. A. (1987). *The psychology of fear and stress*. New York, NY: Cambridge University Press.
- Hall, N. J., Smith, D. W., Wynne, C. D. L. (2013). Training domestic dogs (*Canis lupus familiaris*) on a novel discrete trials odor-detection task. *Learning and Motivation*, *44*(4), 218–228.
- Haberly, L. B. (1998). Olfactory cortex. In G. M. Shepherd (Ed.), *The synaptic organization of the brain* (4th ed.), (pp. 377–416). New York, NY: Oxford University Press.
- Helton, W. S. (2009a). Attention in dogs: Sustained attention in mine detection as case study. In W. S. Helton (Ed.), *Canine ergonomics. The science of working dogs* (pp. 83–97). Boca Raton, FL: Taylor and Francis Group.
- Helton, W. S. (2009b). Overview of scent detection work. In W. S. Helton (Ed.), *Canine ergonomics. The science of working dogs* (pp. 83–97). Boca Raton, FL: Taylor and Francis Group.

- Hepper, P. G., & Wells, D. L. (2005). How many footsteps do dogs need to determine the direction of an odour trail? *Chemical Senses*, *30*, 291–298.
- Harrington, F. H., & Asa, C. S. (2003). Wolf communication. In D. Mech & L. Boitani (Eds.), *Wolves. Behaviour, ecology, and conservation*. (pp. 66–103). Chicago, IL: University of Chicago Press.
- Hewes, G. W. (1994). Evolution of human semiosis and the reading of animal tracks. In W. Nöth (Ed.), *Origins of semiosis. Sign evolution in nature and culture* (pp. 139–149). Berlin, Germany: Walter de Gruyter & Co.
- Honig, W. K., & James, P. H. R. (1971). *Animal memory*. New York, NY: Academic Press.
- Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 211–247). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Honig, W. K. (1966). *Operant behavior: Areas of research and application*. New York: Appleton-Century-Crofts.
- Honig, W. K. (1981). Working memory and the temporal map. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 167–197). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Honig, W. K. (1984). Contributions of animal memory to the study of animal learning. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 29–44). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Honig, W. K. & Fetterman, J. G. (1992). *Cognitive aspects of stimulus control*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Honig, W. K. & Staddon, J. E. R. (1977). *Handbook of operant behavior*. Englewood Cliffs, NJ: Prentice-Hall.
- Horowitz, A., Hecht, J., Dedrick, A. (2013). Smelling more or less: Investigating the olfactory experience of the domestic dog. *Learning and motivation*, *44*, 207–217.
- Horvath, G., Järverud, G. K., Järverud, S., & Horváth, I. (2008). Human ovarian carcinomas detected by specific odor. *Integrative Cancer Therapy*, *7*(2), 76–80.
- Hulse, S. H., Fowler, H., & Honig, W. K. (1978). *Cognitive processes in animal behavior*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Jett, J. R. (2005). Limitations of screening for lung cancer with low-dose spiral computer tomography. *Clinical Cancer Research*, *11*, 4988s–4992s.
- Kepecs, A., Uchida, N., & Mainen, Z. F. (2005). The sniff as a unit of olfactory processing. *Chemical Senses*, *31*, 167–179.
- Kersting, E., Belényi, B., Topál, J., & Miklósi, A. (2009). Judging the effect of epilepsy-seizure alert dogs on human well-being by a self-administered questionnaire. *Journal of Veterinary Behavior*, *4*(2), 84.
- Kirton, A., Winter, A., Wirrel, E., & Snead, O. C. (2008). Seizure response dogs: Evaluation of a formal training program. *Epilepsy & Behaviour*, *13*, 499–504.
- Kringelbach, M. L., & Berridge, K. C. (2009). Towards a functional neuroanatomy of pleasure and happiness. *Trends in Cognitive Sciences*, *13*, 479–487.
- Lit, L. (2009). Evaluating learning tasks commonly applied in detection dog training. In W. S. Helton (Ed.), *Canine ergonomics. The science of working dogs* (pp. 99–114). Boca Raton, FL: Taylor and Francis Group.
- MacLean, P. D. (1990). *The triune brain in evolution: Role in paleocerebral functions*. New York: Plenum Press.
- Macmillan, N. A., & Creelman, C. D. (2005). *Detection theory. A user's guide* (2nd ed.). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.
- Mainland, J., & Sobel, N. (2006). The sniff is part of the olfactory percept. *Chemical Senses*, *31*, 181–196.
- McCulloch, M., Jezierski, T., Broffman, M., Hubbard, A., Turner, K., & Janecki, T. (2006). Diagnostic accuracy of canine scent detection in early- and late-stage lung and breast cancers. *Integrative Cancer Therapies*, *5*(1), 30–39.

- McLean, I. G., Bach, H., Fjellanger, R., & Akerblom, C. (2003). Bringing the minefield to the detector: Updating the REST concept. *Proceedings of EUDEM2-SCOT, 1*, 156–161.
- McNicol, D. (2005). *A primer of signal detection theory*. Mahwah, NJ: Lawrence Erlbaum Associates, Inc.
- Menini, A. (2009). *The neurobiology of olfaction*. Boca Raton, FL: CRC Press.
- Miekish, W., Schubert, J. K., & Noeldge-Schomburg, G. F. E. (2004). Diagnostic potential of breath analysis—focus on volatile organic compounds. *Clinica Chimica Acta*, *347*, 25–39.
- Moser, E., & McCulloch, M. (2010). Canine scent detection of human cancers: A review of methods and accuracy. *Journal of Veterinary Behaviour*, *5*, 145–152.
- Overman, W. H. (1990). Performance on traditional matching to sample, non-matching to sample, and object discrimination tasks by 12–32-month-old children. In A. Diamond (Ed.), *The development and neural bases of higher cognitive functions, annals of the New York academy of sciences* (Vol. 608, pp. 365–393). New York, NY: New York Academy of Sciences.
- Panksepp, J., & Biven, L. (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. New York, NY: W.W. Norton.
- Panksepp, J. (1998). *Affective neuroscience. The foundations of human and animal emotions*. New York, NY: Oxford University Press.
- Pastore, R. E., Crawley, E. J., Berens, M. S., & Skelley, M. A. (2003). “Nonparametric” A’ and other modern misconceptions about signal detection theory. *Psychonomic Bulletin & Review*, *10*(3), 556–569.
- Pauling, L., Robinson, A. B., Teranishi, R., & Cary, P. (1971). Quantitative analysis of urine vapor and breath by gas–liquid partition chromatography. *Proceedings of the National Academy of Science*, *68*, 2374–2376.
- Pearsall, M. D., & Verbruggen, H. (1982). *Scent. Training to track, search, and rescue*. Loveland, CO: Alpine Publications.
- Phillips, M., Herrera, J., Krishnan, S., Zain, M., Greenberg, J., & Cataneo, R. N. (1999). Variation in volatile organic compounds in the breath of normal humans. *Journal of Chromatography B*, *729*, 75–88.
- Pickel, D., Manucy, G. P., & Walker, D. B. (2004). Evidence for canine olfactory detection of melanoma. *Applied Animal Behaviour Science*, *89*, 107–116.
- Premack, D. (1983). The codes of man and beasts. *Behavioral and Brain Sciences*, *6*(1), 125–137.
- Price, J. L. (2003). The olfactory system. In: G. Paxinos (Ed.), *The human nervous system* (2nd ed.), (pp. 1198–1212). San Diego, CA: Elsevier Academic Press.
- Schneider, G. E. (1969). Two visual systems. *Science*, *163*(3870), 895–902.
- Schoon, G. A., & Haak, R. (2002). *K9 suspect discrimination: Training and practicing scent identification line-ups*. Calgary, Alberta: Detselig Enterprises.
- Sebeok, T. A. (1968). *Animal Communication: Techniques of study and results of research*. Bloomington, IN: Indiana University Press
- Sebeok, T. A. (1977). *How animals communicate*. Bloomington, IN: Indiana University Press.
- Séguinot, V., Cattet, J., & Benhamou, S. (1998). Path integration in dogs. *Animal Behaviour*, *55*, 787–797.
- Shepherd, G. M. (1994). *Neurobiology* (3rd ed.). New York, NY: Oxford University Press.
- Slotnick, B., & Schellinck, H. (2002). Methods in olfactory research with rodents. In S. A. Simon & M. Nicolelis (Eds.), *Frontiers and methods in chemosenses* (pp. 21–61). Boca Raton, FL: CRC Press.
- Smith, D. A., Ralls, K., Hurt, A., Adams, B., Parker, M., Davenport, B., et al. (2003). Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes (*Vulpes macrotis mutica*). *Animal Conservation*, *6*, 339–346.
- Sobel, N., Prabhakaran, V., Desmond, J. E., Glover, G. H., Goode, R. L., Sulliva, E. V., et al. (1998). Sniffing and smelling: Separate subsystems in the human olfactory cortex. *Nature*, *392*, 282–286.
- Sonoda, H., et al. (2011). Colorectal cancer screening with odour material by canine scent detection. *Gut*, *60*, 814–819.

- Steen, J. B., & Wilson, E. (1990). How do dogs determine the direction of tracks? *Acta Physiologica Scandinavica*, 139(4), 531–534.
- Strong, V., Brown, S., & Walker, R. (1999). Seizure-alert dogs - fact or fiction? *Seizure*, 8, 62–65.
- Strong, V., Brown, S., Huyton, M., & Coyle, H. (2002). Effect of trained Seizure Alert Dogs[®] on frequency of tonic-clonic seizures. *Seizure*, 11, 402–405.
- Szulejko, J. R., McCulloch, M., Jackson, J., McKee, D. L., Walker, J. C., & Touradj, S. (2010). Evidence for cancer biomarkers in exhaled breath. *IEEE Sensors Journal*, 10(1), 185–210.
- Terrace, H. S. (1963a). Discrimination learning with and without errors. *Journal of Experimental Analysis of Behavior*, 6, 1–27.
- Terrace, H. S. (1963b). Errorless transfer of a discrimination across two continua. *Journal of Experimental Analysis of Behavior*, 6, 223–232.
- Terrace, H. S. (1964). Wavelength generalization after discrimination learning with and without errors. *Science*, 144, 78–80.
- Terrace, H. S. (1966). Stimulus control. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 271–344). New York: Appleton-Century-Croft.
- Thesen, A., Steen, J. B., & Doving, K. B. (1993). Behaviour of dogs during olfactory tracking. *Journal of Experimental Biology*, 180, 247–251.
- Vaché, M., Ferron, J., & Gouat, P. (2001). The ability of Red Squirrels (*Tamiasciurus hudsonicus*) to discriminate conspecific olfactory signatures. *Canadian Journal of Zoology*, 79, 1296–1300.
- Waggoner, L. P., Jones, M., Williams, M., Johnston, J. M., Edge, C., & Petrusky, J. A. (1998). Effects of extraneous odors on canine detection. *SPIE Proceedings*, 2575, 355–362.
- Wells, D. (2007). Domestic dogs and human health: An overview. *British Journal of Health Psychology*, 12, 145–156.
- Wells, D. L., & Hepper, P. G. (2003). Directional tracking in the domestic dog, *Canis familiaris*, 84(4), 297–305.
- Wells, D. L., Lawson, S. W., & Siriwardena, A. N. (2008). Canine responses to hypoglycemia in patients with Type 1 Diabetes. *The Journal of Alternative and Complementary Medicine*, 14(10), 1235–1241.
- Wells, D. L., Lawson, S. W., & Siriwardena, A. N. (2011). Feline responses to hypoglycemia in people with Type 1 Diabetes. *The Journal of Alternative and Complementary Medicine*, 17(2), 99–100.
- Wells, M. C., & Bekoff, M. (1981). An observational study of scent-marking in coyotes, *Canis latrans*. *Animal Behaviour*, 29(2), 332–250.
- Williams, H., & Pembroke, A. (1989). Sniffer dogs in the melanoma clinic? *Lancet*, 333(8640), 734.
- Willis, C. M., Church, S. M., Guest, C. M., Cook, W. A., McCarthy, N., Bransbury, A. J., et al. (2004). Olfactory detection of human bladder cancer by dogs: Proof of principle study. *British Medical Journal*, 329, 712–714.
- Wilson, D. A., & Sullivan, R. M. (2011). Cortical Processing of Odor Objects. *Neuron* 72, 506–519.
- Wilson, D. A. & Stevenson, R. J. (2006). *Learning to smell: Olfactory perception from neurobiology to behavior*. Baltimore: John Hopkins University Press.
- Zelano, C., & Sobel, N. (2005). Humans as an Animal Model for Systems-Level Organization of Olfaction. *Neuron*, 48, 431–454.