

VARIABLES INFLUENCING BEHAVIOUR AND
DETECTION EFFICIENCY IN EXPLOSIVES
DETECTOR DOGS

THESIS SUBMITTED FOR THE DEGREE “DOCTOR OF PHILOSOPHY”

BY

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SUBMITTED TO THE SENATE OF TEL-AVIV UNIVERSITY

APRIL, 2005

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*"... in life the firmest friend,
The first to welcome, foremost to defend,
Whose honest heart is still his master's own
Who labors, fights, lives, breathes for him alone..."*

Lord Byron.

Inscription on the Monument of a Newfoundland Dog
Newstead Abbey, October 30, 1808.

I would like to dedicate this work to my beloved family:

My parents, Raya and Zvika Gazit, who raised me to believe that I can succeed in anything I set out to do.

My husband Eliezer, for the years of encouragement and support, and our adorable kids – Nitzan, Raz and Ophir, who joined the family, one by one, along the course of this protracted study

My caring in-laws, Sima and Arie Parnafes, who gave me time to "play" with the dogs by devotedly babysitting their grandchildren.

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Acknowledgements

I would like in particular to thank the following people:

My supervisor, Prof' Joseph Terkel, for his guidance and ideas, for giving me complete independence to work, while always being there with advice and help when needed; who not only taught me to understand the behaviour of animals, but that of people too.

Dr. Allen Goldblatt, for his unique ideas, advice and help throughout, in the many drafts of this thesis.

Mr. Yitzhak Shelach, Head of the Human Engineering Unit, DDR&D Ministry of Defence, for his involvement and encouragement.

A special thank you to Ms. Naomi Paz, who became an expert on canine behaviour while editing my broken English and making it comprehensible, always with a smile, patience and kindness.

Dr. Amelia Terkel for her help in both language and logic.

The dog trainers: Dror Shikragi, Yael Golani, Joseph Leon, Merav Hadari and Maayan Fuchs; and all the dog handlers and the dogs themselves for their hard work and commitment to the study by day and by night, summer and winter.

Ms. Nurit Gazit and Ms. Idit Gunther, for their help with the analyses of a vast amount of data.

And finally, to my lab mates, Rony Rado, Uri Shanas, Ido Zuri, Ahuva Gottreich, Dafna Yanai, Tali Kimchi, Shani Doron, and Hillit Finkler, for all the good years we spent together.

Abstract

From the dawn of history dogs have accompanied humans in both their domestic life and their war activities. During the process of domestication, the bond between dog and human, for the benefit of both, has become tightly interwoven. Over the last century in particular, the use of dogs in many areas of detection has expanded and such use is now widespread throughout the world for a variety of military and civilian purposes. Based on the animal's highly developed sense of smell and its willingness to work with man, the dog has currently become the most efficient and common olfactory biodetector used by man.

Working dogs constitute a very important tool in the detection of explosives. They are highly accurate, rapid, mobile and as reliable as most existing machines. However, dogs, like humans, are biological systems and their performance is affected by various environmental, physiological and psychological factors. In the experiments that comprise this thesis, I investigated the effect of these factors on the search behaviour and detection efficiency of the dog.

Since the dog perceives odours mainly by sniffing, part of this study sought to examine this behaviour and its influence on the dog's detection efficiency. Consequently, we developed an electronic communication device that enables the dog's handler to hear and record the dog's sniffing sounds while it is searching. The device transmits sounds from the dog's muzzle area to earphones worn by the listener, enabling easy discrimination between active sniffing and non-sniffing or panting. The recorded signals can be analyzed later using a special computer software program, also developed for the purpose of this study, which discriminates between sniffing and panting and counts the signals according to the experimenter's requirements. Both the aural and the computerized sound analyses enabled a study of the dog's sniffing behaviour under the variety of conditions that were examined in the series of four experiments that followed and are included in this overall study. Development of this device comprised the first part of the study, and is referred to here as Experiment 1.

Experiment 2 investigated the relative contribution of olfaction and vision to explosives detection. Experiment 3 examined the effect of physical activity on sniffing rate and efficiency of detection. Experiments 4 & 5 examined two major variables affecting the dog's ability to effectively use olfactory cues in the

detection of explosives: the effects of context shifts on olfactory detection; and the effects of the relative target density on the probability of detection.

Experiment 1. *A simple system for the remote detection and analysis of sniffing in explosives detection dogs*

This section of the study presents the device developed, for both research and operational purposes, to assist handlers of sniffer dogs and improve efficiency of search, as described above. Correlation of the obtained data with the visually monitored behaviour of the working dog contributes additional and important information to our knowledge, and a greater understanding of detector dogs' behaviour and abilities.

Experiment 2. *Domination of olfaction over vision in explosives detection by dogs*

In this part of the study I examined the relative contribution of the senses of sight and smell to detection of explosives in dogs. Six sniffer dogs were required to detect explosives in a controlled (indoors) and uncontrolled (field track) environment, under both virtually dark (very low light intensity) and full light conditions. Detection percentages, search duration, and sniffing and panting frequencies were measured.

Olfaction was shown to be the main sense used by the dogs for detection not only when vision was possible but difficult, in very low light intensity, but also in full light. Furthermore, neither the presence nor the virtual absence of light was demonstrated to differentially affect the dogs' detection ability.

Experiment 3. *Explosives detection by sniffer dogs following strenuous physical activity*

This part of the study examined the effect of physical activity on sniffing rate and efficiency of detection by comparing the dogs' performances prior to and following strenuous physical activity. Here, I examined the sniffing and panting rates of the dogs and their ability to detect small explosives charges, under two conditions: 1. while relaxed and therefore only lightly panting; and 2. following exercise on a treadmill and therefore heavily panting. The results revealed an inverse ratio between rate of panting and efficiency of the dog's olfactory work, with increased panting resulting in a significant decrease in explosives detection. The decline in efficiency was also expressed in longer duration of search period. It was also found that dogs are able to

adjust to working under severe physiological conditions derived from extreme physical activity. Such adjustment can lead to improvement in the dog's abilities under strenuous conditions and can be obtained by suitable training.

Experiment 4. *The role of context specificity in learning: The effects of training context on explosives detection in dogs*

Various studies have revealed that if an animal learns a stimulus-response-reinforcer relationship in one context and is then tested in another context there is usually a lessening of stimulus control, and the same discriminative stimuli which reliably controlled the behaviour in the first context will have less effect in the new context. This reduction in performance is known as the “context shift effect”.

I investigated the effect of changing context on the probability of detecting explosives, using seven highly trained explosives detection dogs. In Part 1 of this experiment the dogs were trained on alternate days on path A, which always had five hidden explosives, as well as on path B, which was very similar but never had any explosives. Within a few sessions the dogs showed a significant decrease in search behaviour on path B, but not on path A. In Part 2 of the experiment the same dogs were trained only on path B, but now with a target density of one explosive hidden every fourth day. The dogs' motivation to complete the search and their probability of detecting the explosive was found to be significantly lower than in Part 1. In Part 3 of the experiment the effect of the low target density as used in Part 2 was investigated on a new but very similar path C. Both the detection probability for the one explosive every fourth day on the new path and the motivation to search were significantly higher than found in Part 2. In the final part of the experiment, Part 4, an attempt was made to recondition the dogs to search on path B. Although trained for 12 daily sessions with one explosive hidden every session, the dogs failed to regain the normal levels of motivation they had shown both on new paths and on paths that they knew usually contained explosives. The findings reveal that even a very intensively trained explosives detection dog will rapidly learn that a specific stretch of path does not contain explosives. The dog will then be less motivated to search and will miss newly placed targets. This learning is specific to the formerly always-clean path and is to some extent irreversible. However, the dog will search and detect normally on new paths even if they are very similar to the always-clean path. The data are discussed in terms of variables effecting renewal. The results suggest that

following training designed to make a behaviour “context independent”, any extinction training will not generalize beyond that specific context used during the extinction training. In addition, if the behaviour is extinguished in a specific context, it will be very difficult to restore that behaviour in that context. These conclusions should be considered by anyone attempting to extinguish well-established trans-context behaviours.

Experiment 5. Formation of an olfactory search image for explosives odours in sniffer dogs

The term “search image” refers to an animal’s heightened ability to detect a specific cryptic prey following experience with that prey. Formulated in 1960 by Tinbergen, the search image concept has been the subject of much research, albeit almost entirely based on visual search cues in birds of prey. Given the theoretical and practical importance of this concept for foraging or searching in general, I set out to investigate whether dogs could form an olfactory search images for explosive odours. Seven experienced explosives detector dogs were first tested for their ability to detect 30 grams of the explosives TNT, C4 or PENT placed in various containers randomly distributed along a 300 meter limestone track. In consecutive stages of the experiment, I altered the relative percentages of the three explosives. The results showed that the percentage of TNT containers detected by the dogs increased in trials that followed placing of a high percentage of TNT relative to other explosives and decreased in trials that followed placing of a relatively low percentage of TNT containers. Overall, these results suggest that dogs can form an olfactory search image that might aid in prey/target detection.

In summary, the dog’s detection efficiency is affected by various environmental, physiological and psychological variables. It is well known that sniffing activity enhances olfactory sensitivity mainly when odour concentration is low and close to detection threshold. In such cases, the dog must increase its effort and concentration on the detection task through increasing its sniffing frequency; whereas when odour intensity is above threshold, the dog will be able to detect the odour easily without performing extra sniffing. Consequently, the dog will adjust its sniffing frequency according to the requirements of the olfactory task.

However, despite the reports in the literature that suggest the importance of sniffing rate for successful olfactory detection, I suggest here that the influence of the dog's motivational level on its detection performance dominates that of the olfaction variables (i.e. sniffing frequency). Under motivated situations the dog will recruit all of its resources in order to fulfill the assigned task successfully, by fully focusing its attention on the olfactory cues available for detection of explosives. Consequently, a demonstrated motivation to work should be the main factor under consideration when selecting a detection dog.

Introduction

The origin of the dog

The Canidae comprise a biologically cohesive group of carnivores containing thirty-eight species, including the domestic dog. There has long been debate over the true ancestor of the domestic dog, whether it originated from the wolf (*Canis lupus*) or the golden jackal (*Canis aureus*). Darwin (1868) wrote as follows: "The chief point of interest is whether the numerous domesticated varieties of the dog have descended from a single wild species or from several. Some authors believe that all have descended from the wolf, or from the jackal, or from an unknown and extinct species. Others again believe, and this of late has been the favourite tenet, that they have descended from several species, extinct and recent, more or less commingled together. We shall probably never be able to ascertain their origin with certainty". Today, however, based on recent data, we are closer to such certainty. The combined results of multidisciplinary research areas, such as behaviour, vocalisations, morphology and molecular biology all indicate that the wolf, *Canis lupus*, is the main, if not the only, ancestor of the dog (for review see Clutton-Brock, 1995; Vila et al. 1997).

Recently, using genetic and biochemical methods, it was shown that domestic dogs are virtually identical in many respects to other members of the genus (Coppinger & Schneider, 1995). There is only little variation in karyotypes (the number and shape of the chromosomes) within the genus *Canis* (Chiarelli, 1975; Fischer, Putt & Hackel, 1976; Simonsen, 1976). Results from mitochondrial DNA (mtDNA) testing also reveal startling similarities among canids (Vrana, 1988, unpublished BA thesis, Hampshire College; in: Coppinger & Schneider, 1995). Mitochondrial DNA is passed from mother to daughter with no genetic recombination. This allows the evolutionary development of maternal lineages to be reconstructed. Greater mtDNA differences appeared within the individual breeds of Doberman pinscher or poodle, for example, than between dogs and wolves. These data indicate wolves as just another breed of dog. To keep the results in perspective, it should be pointed out that there is less mtDNA difference between dogs, wolves and coyotes than there is between the various ethnic groups of human beings, which are recognized as belonging to a single species (Coppinger & Schneider, 1995). The results are not surprising since, reproductively, wolves, coyotes, jackals and dogs are all interfertile, and cross-

breeding still occurs in the wild between wolves, coyotes and dogs (Lehman et al., 1991; Young & Goldman, 1944). Consequently, all these canines bear a genetic resemblance and wolves are not more closely related to any one particular breed than to another (Coppinger & Schneider, 1995).

Two recent publications in *Science* move our understanding to address key questions in the field. With their studies of dog mitochondrial DNA, Savolainen et al (2002) and Leonard et al (2002) effectively address how and when dogs and wolves diverged.

Based on the examination of mtDNA sequence variation among 654 domestic dogs (representing all major dog breeds worldwide) the researchers suggest an East Asian origin of the domestic dog from a wolf ancestor (Savolainen et al., 2002). They note that although their data indicate several maternal origins from the wolf, over 95% of all sequences were found to belong to three phylogenetic groups universally represented at similar frequencies. This suggests a common origin from a single gene pool for all dog breeds. The finding of a larger genetic variation in East Asia than in other regions and the pattern of phylogeographic variation suggest an East Asian origin for the domestic dog about 15,000 years ago (Savolainen et al., 2002).

Leonard et al. (2002) examined 452 base pairs of mtDNA from the remains of 37 dogs deposited in precolumbian archeological sites in Mexico, Peru, and Bolivia, and from Alaskan dogs buried before the arrival of Europeans to the region. These data were compared to sequences from 67 diverse modern dog breeds, and from wolves from 30 locations worldwide. The authors conclude that about five major founding canine lineages came to North America when humans colonized the New World 12,000–14,000 years ago, and that ancient American and Eurasian domestic dogs share a common origin from Old World grey wolves. They argue further that the large diversity of mtDNA lineages observed in dogs colonizing the New World implies a large, well-mixed ancestral population of Eurasian dogs. Together, these studies extend and confirm earlier data, establishing that the divergence of dogs from wolves stems from at least five different maternal wolf lineages (Acland and Ostrander, 2002).

Wayne and Ostrander (2004) reviewed the recent progress in the genome sequencing of the dog. They describe work by the Whitehead Institute, which proposed

sequencing of an additional 600 million base pairs from nine dog breeds and a gray wolf. This extensive comparative database will provide novel genetic markers for population, genetic and evolutionary studies of domestic and wild canids, and may lead to a new understanding of the genes associated with domestication.

Dogs' association with man - Historical review of canine use for military applications

Dogs have accompanied man's domestic life and war activities from the dawn of history. It has been hypothesized that the dog originally volunteered to associate with man without constraints, receiving in return only the small remuneration of food and attention (Budiansky, 1989). Other animals have also been trained by man, but they require capture, restraint, and taming by force. The association of dogs with man is manifold: they are kept as pets, for various civilian uses (e.g. as service dogs) and for military purposes.

Since the earliest days of recorded warfare, and up to and including the many recent hostile actions around the world, man has employed specially trained dogs in direct or indirect support of combat operations. With emerging and increased technology and the growing use of long-range explosive weapons, the effectiveness of attack dogs in combat has diminished significantly (Laird, 1979). However, their usefulness in other military applications has increased. During World War I large numbers of canines were utilised as sentries, scouts, messengers and ammunition bearers etc. It has been estimated that Germany employed over 30,000 dogs for such purposes, and approximately 20,000 animals served in similar capacities with the French Army (Mitchell, 1976). Dogs were employed on an even larger scale during World War II: Germany used over 200,000 canines in this war; the Russians employed about 60,000 dogs, mainly for mine detection and destruction of tanks; and around 20,000 dogs served in the U.S. army, many of which were decorated for their wartime performance (Laird, 1979; Mitchell, 1976). After World War II, the U.S. Army found that although use of dogs for pack and sled service, mine detection and as messengers was no longer needed, sentry dogs and silent scout dogs continued to be of great value. Since World War II dog-handler teams have been used extensively by the U.S. military to locate explosives. The Russian military still train dogs for mine detection and to locate wounded soldiers in the field. Gas masks with built-in radio receivers have been designed for dogs and the deplorable Russian program of teaching the dogs to

carry out suicide attacks against tanks persists (Lemish, 1996). Dogs have continued to serve the U.S. armed forces with distinction in many conflicts. In the Korean War the army used about 1,500 dogs, primarily for sentry duty. During the Vietnam War about 4,000 dogs were employed. After Vietnam, the number of dogs needed by the U.S. military began to decline. More recently, dogs were deployed to the Persian Gulf War, Afghanistan and Iraq. Currently, almost all of the U.S. security forces, such as the Coast guard, Border Patrol, Drug Enforcement Agency, Customs, Federal Aviation Administration, Secret Service and the Department of Agriculture, use dogs, mainly for explosives and drug detection but also for intruder detection along the borders. Finally, after the 11/9/2001 attack on the Twin Towers in New York, dogs have begun to play a renewed role in countering terrorism.

The Israeli security forces (IDF and police) have employed dogs for a variety of purposes since 1948. The IDF Dog Unit – *Oket'z*, operates dogs for Attack, Explosives Detection, Chase, Search and Rescue, and Weapons Detection. Each section of the Unit uses different types of dogs and trains them differently, according to its individual objectives. The Police Animal Unit currently comprises around 200 dogs, trained mostly for narcotics and explosives detection.

The variety of uses of detector dogs

Over the last century the use of detector dogs has expanded and is currently widespread throughout the world.

Detector dogs are used for both military and civilian purposes, relying primarily on their sense of smell to detect a variety of odours. Military working dogs are used as scouts (e.g. Laird, 1979), for the detection of explosives (e.g. Lovett, 1992; Phillips, 1971; Phillips et al., 1974) land mines and trip-wires (e.g. Breland & Bailey, 1971; Carr-Harris et al., 1969; Thal et al., 1970), and weapons etc. (for comprehensive review see Frost, 1990; Kelch, 1982). The civilian uses are manifold, such as to search for live or dead bodies in open field areas (Komar, 1999), for survivors buried beneath rubble at disaster areas (Komar, 1999; Weiss and Greenberg, 1997), for cross-match of human odours (Schoon and De Bruin, 1994; Schoon, 1996; Schoon, 1998) and for arson investigations (Gialamas, 1996; Kurz et al., 1994), as well as to detect smuggled agricultural products (Eastwood, 1990), drugs (Adams and Johnson, 1994), gas pipe leaks, cows in oestrus (Hawk et al, 1984; Jezierski, 1990), melanomas (Pickel et al., 2004; Williams and Pembroke, 1989), human bladder cancer (Willis et

al., 2004), termites, screwworms (Welch, 1990) etc. The dogs' ability to detect the revealing odours comes from their highly developed sense of smell, which derives from their possession of a very large number of olfactory receptor cells, together with a specialised behaviour called sniffing.

The canine sense of smell

Despite its importance to the survival of most animals, the sense of smell is the least understood of the sensory organs. Although considerable progress has been made in recent years there are still many unanswered questions.

Furton and Myers (2001) provide a simplified definition of the sense of smell as it relates to explosives detection, as follows: 1) odours come into contact with the olfactory receptors more efficiently by means of sniffing; 2) the odorants are dissolved in the mucus layers within the nasal cavity, which cover the olfactory epithelium and contain the olfactory receptors; 3) the binding of the odorants to the appropriate receptors creates a second messenger cascade via a G-protein coupled reaction or an inositol 1,4,5-triphosphate (IP3) reaction; 4) the second messenger then sets up a receptor potential via opening sodium channels, eventually to the point of causing an action potential; 5) the neurones of the olfactory nerve transmit the action potentials to a variety of sub-cortical and cortical structures in the brain for further encoding and, eventually, perception; 6) in order to avoid physiological adaptation, the odours, still present on the olfactory mucosa and elsewhere in the nasal cavity, must then be purged. This phenomenon enables the olfactory system to maintain sensitivity during continued stimulation; and 7) in addition to the olfactory system, the trigeminal nerve and the vomeronasal systems are also involved in the sense of smell, but their relative contributions are less well understood (Furton and Myers, 2001).

The nasal cavity: In vertebrates, the nasal cavity plays an important role in odour discrimination by influencing the distribution of odorant molecules to the olfactory receptors by means of several mechanisms (Keyhani, et al., 1997). First, the lining of the nasal cavity acts in a manner similar to that of a gas chromatography column, separating molecules on the basis of their partition coefficients into the mucosal layer along the length of the cavity (Mozell, 1964). The nasal cavity's second major influence is on the flow dynamics. The interior of the vertebrate nasal cavity is

typically convoluted, creating distinct flow paths and generating eddies and currents that result in uneven distribution of odorants to the receptors in the anterior and posterior regions of the cavity, thereby physically patterning the odours (Kauer, 1987; Moulton, 1976). There are also pockets of receptors that are not located in the main airflow, making diffusion the only mechanism for exposure. In these regions, analyte molecules are detected exclusively on the basis of their diffusion rates (Kauer, 1987). All of these mechanisms may play a role in odour perception and discrimination in vertebrate olfaction, and thus offer a rich area to exploit in developing sensor diversity (Stitzel et al., 2003).

The odorants: The dog perceives odour as a result of binding of the odorant to the olfactory receptors located in the olfactory mucosa in the nasal epithelium.

Odorants are molecules that elicit an olfactory response. They are usually small (with molecular weight up to approximately 300) and volatile. They show strong lipophilicity and are highly hydrophobic.

Estimations of the number of odorous compounds that can be detected by mammals vary from 10,000 (Fierstein, 1991) to more than 400,000 (Mori and Yoshihara, 1995).

The sniffing behaviour: The dog mainly perceives odours by sniffing, during which air is inhaled through the nostrils in short aspirations while the mouth remains closed (Neuhaus, 1981). Sniffing may be advantageous compared to normal breathing because it presumably creates more turbulent gas flow in the air passage and thus reduces the diffusion distance from fresh air to receptors in the nose (Neuhaus, 1981; Steen et al., 1996). This means that dogs have to sniff in order to smell at low concentrations, but at high concentrations diffusion of the molecules in the nose can also lead to odour sensations if the regular breathing inspiration time is long enough (more than 2 sec). Analysis of sniffing strategies in rats performing odour detection tasks revealed variations related to different odours and to different concentrations of the same odorant (Youngentob et al., 1987).

Laing (1983) showed that sniffing improves human sensitivity to odours compared with even airflow. A single sniff has been shown to be sufficient for humans to smell an odour (Laing, 1986). Other studies have shown that larger than normal flow rates of air through the nose enhance odour perception (Le Magnen, 1945; Rehn, 1978). Sobel et al. (1998) found that sniffing, whether an odorant is present or absent,

induces activation primarily in the piriform cortex of the temporal lobe and in the medial and posterior orbito-frontal gyri of the frontal lobe. The source of the sniff-induced activation is the somatosensory stimulation that is induced by airflow through the nostrils. Based on Le Magnen (1945) and Laing (1983), they emphasised the importance of sniffing to olfaction: "The sensation and perception of smell are largely dependent on sniffing, which is an active stage of stimulus transport and therefore an integral component of mammalian olfaction" (Sobel et al., 1998).

Despite the importance of sniffing to detection ability, dogs are able to detect an odour (albeit at a significantly lower rate) even when heavily panting. One possible explanation for this phenomenon is their ability to direct the stream of air through the nose or mouth or both, according to immediate needs (Goldberg et al., 1981). Dogs can also maintain an inward air stream through the nose even during heavy panting (Steen et al., 1996), thus enabling the binding of several odour molecules to the receptors.

Olfactory epithelium: Mammalian olfaction is mediated by the olfactory epithelium (or mucosa), the structure of which has been described in detail (Graziadei, 1971; Menco, 1983; Moulton and Beidler, 1967). It is 100-200 μm thick, and varies from a few square centimetres (in man) to more than 100cm^2 (in dog) (Lancet, 1986; Lovett, 1991; Moulton, 1977). Olfactory sensitivity to odours is not directly affected by the size of the olfactory epithelium (Laing, 1975; Moulton et al., 1970) but was found to be related to receptor density (Apfelbach et al., 1991). If the olfactory epithelium is destroyed, it can regenerate within 30-60 days (Lancet, 1986; Schwob et al., 1995; Simmons and Getchell, 1981). The olfactory epithelium is situated next to the cribriform plate and covers the turbulate bones on each side of the nasal cavity (Mori and Yoshihara, 1995). It consists of at least six morphologically and bio chemically distinct cell types (Huard et al., 1998), although additional classes of less well defined microvilli containing cells have been noted prenatally (Menco and Jackson, 1997) and postnatally (Carr et al., 1991). The three major cell types are: supporting cells, sensory neurones and basal cells. The supporting cells are glia-like in nature and have microvilli on their apical surface (Lancet, 1986). There are high levels of cytochrome-P450 and detoxifying enzymes in the supporting cells, which may play a part in removing odorants from the area (Jones and Rog, 1998). The sensory neurons are bipolar nerve cells with a nonbranching dendrite that terminates at the epithelial

surface with a slight enlargement (olfactory knob) bearing 5-20 long cilia (Lancet, 1986). The surface area of the cilia is quite large, estimated as over 22 cm² in the human (Doty, 1998) and 170 cm² in the German shepherd dog (Moulton, 1977). The receptors are located on the surface membrane of these cilia. The axons of the sensory neurones form bundles that join together to form the olfactory nerve, which passes through the cribriform plate and terminates in the brain, in the olfactory bulb. Sensory neurone cells have a lifespan of 30 days, after which they are replaced by new sensory neurone cells that are produced by dividing basal cells (Synder et al., 1988; see Mori and Yoshihara, 1995 for review). Some cells, however, can live longer, especially if they are not exposed to pollutants (Williams, 1995).

The olfactory system is unique in the central nervous system in being the only component in direct contact with the environment and in its ability to regenerate damaged or lost neurones (Firestein et al., 1996).

Mucus: The mucus covering the olfactory epithelium is produced by Bowman's glands. Its composition is complex and contains many different proteins, such as antibodies, antibacterial proteins, detoxifying enzymes, etc. (Pelosi, 1994). In order to bind to the receptors, the hydrophobic odorants have to penetrate the watery mucus. In some cases, the transport of odorants through the mucus to the cilia is aided by transporting molecules termed odorant-binding proteins (OBPs) (Doty, 2001; Pelosi et al., 1982). These are small soluble proteins secreted by the nasal glands and reversibly binding several odorants, specifically medium-size hydrophobic molecules. OBPs are therefore thought to have a mediating role (Herent et al., 1995; Pelosi, 1994; Pes and Pelosi, 1995; Snyder, et al., 1998). They have broad odour-ligand affinities, and normally enhance odour responses by concentrating odour molecules in the mucus, presenting them to the receptors, and facilitating their inactivation and removal (Hildebrand and Shepherd, 1997).

The receptors: One of the first steps in an animal's detection of a volatile compound in its environment is the binding of the odorant to G protein-coupled receptors expressed on the surface of olfactory neurones. The pattern of receptors to which the odorant binds, and thus the pattern of neurones that transmit an action potential to the olfactory bulb in the brain, allow the animal to identify the compound and respond to

its presence (Issel-Traver and Rine, 1996). The gene family that encodes these odorant receptors was identified over a decade ago (Buck and Axel, 1991). Using molecular cloning techniques, the researchers identified members of an extremely large multigene family that encoded 7 transdomain proteins whose expression was limited to the olfactory epithelium. These odorant receptors have very diverse amino acid sequences expressed from about 500 genes and, as they can discriminate between 10 times that number of odours, it is likely that each odour receptor interacts with several different odours (Jones and Rog, 1998). The size and diversity of the gene family make it possible for mammals to recognise and discriminate thousands of different odorants (Issel-Traver and Rine, 1997). It is uncertain whether the large number of compounds that can be recognised are matched by the number of specific receptor proteins, each a product of a separate gene and expressed on different cells (Lancet, 1994), or whether olfactory receptor neurons express several receptor proteins, or whether each olfactory receptor protein has broad binding specificities (Jones and Rog, 1998). Some researches indicate a stimulus-induced plasticity: repeated exposure to an odour increased peripheral olfactory sensitivity in mice (Wang et al., 1993) and rats (Yongentob and Kent, 1995). A stimulus-controlled gene expression was suggested, as was apoptosis, as possible mechanisms to adjust sensory neuron numbers in response to sensory stimuli (Najbauer and Leon, 1995). It was recently found that in mice, exposure to an odour-enriched environment doubled the number of newborn neurons surviving in the main olfactory bulb (Rochefort et al., 2002). The authors stated that enriched living affects only cell survival (Kempermann et al., 1997) whereas exercise increases both cell division and survival (Van Praag et al., 1999) in the hippocampus.

Consequently, when using the olfactory system of dogs as a detection tool, continuous training of the dogs on the odours they are intended to detect will enhance the availability of appropriate receptors (Schoon, 1997).

Transduction mechanisms: During the past decade there has been an impressive development in understanding the initial events of olfactory transduction, beginning with the identification by Buck and Axel (1991) of a large gene family that encodes olfactory receptors. Although a given receptor cell seems to express only one type of receptor derived from a single allele (Chess et al., 1994), each cell is electrophysiologically responsive to a wide, but circumscribed, range of stimuli

(Holley et al., 1974). This suggests that a single receptor accepts a range of molecular entities, and that coding occurs via a complex cross-fiber patterning of responses. Odorant binding leads to an inwardly depolarizing current within the cilia of the bipolar receptor cells which ultimately triggers the action potentials that collectively provide the neural code that is deciphered by higher brain centres (Doty, 2001). Two main signal transduction pathways have been distinguished: one through a cAMP cascade, and another through an IP₃ (Inositol triphosphate) cascade. Evidence shows that odorants can activate either of these pathways, and indications are that in vertebrates the cAMP pathway is excitatory, and the IP₃ pathway inhibitory (Breer, 1994). However, although it is generally thought that some odorants activate a second transduction pathway in vertebrates (namely, that associated with activation of the enzyme phospholipase C to produce the second messenger IP₃) (Breer and Boekhoff, 1991), recent data suggest that this may not be the case, at least in mice (Gold, 1999). Desensitisation of the liganded receptor proteins through phosphorylation and direct modulation of the cyclic nucleotide-gated channel are both thought to terminate the signal. The odour molecules in the mucus are probably transported by olfactory binding proteins into the supporting cells where they are converted into inactive chemicals (Mori and Yoshihara, 1995).

Olfactory receptor cell regeneration: The olfactory epithelium and its neuronal population are known to have a substantial capacity to recover after either direct injury or damage to the olfactory nerve. However, the mechanisms underlying this capacity for recovery and the limits to the recovery process are not well understood (Schwob et al., 1995).

Doty (2001) stated in a review of olfaction that "an important ongoing revolution in the field of olfaction is the elucidation of the nature of degeneration and regeneration within the olfactory neuroepithelium". The major uniqueness of the sensory neurons of the olfactory epithelium, unlike the sensory neurons of other major systems, is that they have a propensity to replace themselves after injury. Although it is accepted that the olfactory neuroepithelium undergoes complete cell turnover approximately every 30-60 days (Graziadei and Monti Graziadei, 1979; Lancet, 1986; Schwob et al., 1995; Simmons and Getchell, 1981), it appears, based on recent data, that the situation is much more complex. Thus, many receptor cells are relatively long-lived despite continuous neurogenesis within the olfactory epithelium (Hinds et al., 1984), and both

endogenous and exogenous factors promote receptor cell death or replenishment from progenitor stem cells (Mackay Sim and Kittel, 1990). It was recently found that the receptor cells of older animals appear to live longer than those of younger animals (Weiler and Farbman, 1999b).

Doty (2001) emphasizes several key points in recent neurogenetic findings. Biochemical or mechanical stress appear to induce subgroups of stem cells to differentiate into mature olfactory receptor cells (Feron et al., 1999), and differentiated neurons send back regulatory signals that inform the neuronal progenitor cells as to the numbers of new neurons that need to be produced in order to maintain equilibrium in the cell population (Calof et al., 1998). Recently, it has been shown that the mitral cells of the bulb may contain a trophic substance that helps to maintain the survival of olfactory receptor neurons (Weiler and Farbman, 1999a).

Olfactory bulb: The mammalian main olfactory bulb has a relatively simple cortical structure, containing thousands of signal-processing modules called "glomeruli" (Shepherd and Greer, 1998). The olfactory glomerulus is one of the clearest anatomical modules in the entire nervous system (Leise, 1990). Glomeruli are relatively large spherical neuropils (50 to 200 μm in diameter), within which axons of olfactory sensory neurons form excitatory synaptic connections on dendrites of mitral and tufted cells, the output neurons of the main olfactory bulb (Leise, 1990; Pinching and Powell, 1971). This is a unique feature of the olfactory system: the olfactory bulb is the only region in the brain that receives direct axonal input. An individual glomerulus can be viewed as an olfactory axon convergence centre for input originating from one type of odorant receptor; the odorant receptor-specific signal is transmitted to the mitral and tufted cells innervating the glomerulus. In mice, each glomerulus receives converging axonal inputs from several thousand olfactory sensory neurons and is innervated by primary dendrites of about 20 mitral cells (Royet et al., 1998). The number of glomeruli in the main olfactory bulb has been estimated at between 1000 - 1800 in mice (Hildebrand and Shepherd, 1997; Mori et al., 1999) and 5000 in dogs (Hildebrand and Shepherd, 1997). The odour molecule information is processed by the local neuronal circuit that mediates synaptic interactions within the module as well as among these modules in the main olfactory bulb. Axons of mitral and tufted cells then send the information to the olfactory cortex (Mori et al., 1999). The positions of specific glomeruli are topographically fixed and

conserved within a species in the brains of all animals. Thus, the olfactory bulb defines a two-dimensional map that identifies which of the numerous receptors have been activated within the sensory epithelium. This has led to an attractive model of olfactory coding in the brain, according to which discrimination of odour quality will result from the detection by the brain of specific patterns of glomeruli activity (Dulac, 1997; Hildebrand and Shepherd, 1997). For example, stimulation with peppermint odour in a learning paradigm activated an identifiable glomerulus in the lateral olfactory bulb (Coopersmith and Leon, 1984). At low odour concentrations, activity may be restricted to only one or a small group of glomeruli (Stewart et al., 1979). With increasing concentration, an odour activates an increasing number of glomeruli, a principle that could contribute to coding of odour concentration. These basic results have been confirmed and extended in a number of studies (e.g. Coopersmith and Leon, 1984) and maps are now available showing different glomerular patterns elicited by several different odour conditions (Hildebrand and Shepherd, 1997; summarized in Shepherd, 1994).

Early olfactory experience leads to structural changes in the olfactory bulb. Leon (1992) found that such early olfactory experience led to changes in the size of the glomeruli involved: early odour training of rat pups led to 19% more relevant sensory neurons, and to a 20% increase in the size of the related glomerulus. Continued exposure to an odour was found to lead to selective degeneration in mitral cells in the olfactory bulb, even though there was no significant difference in response to this odour (Dalland and Doving, 1981). Olfactory experience also leads to structural changes in the mitral cells, as was found for the glomerular cells. For example, the size of the mitral cells was found to be affected by prolonged exposure to odour in rats (Panhuber and Laing, 1987). The term "neural plasticity" defines the ability of the adult brain to respond to environmental and internal challenges, inducing significant functional and anatomical modifications. This has been well documented for the perinatal ("critical") period, in which sensory-driven activity patterns are able to induce long-term changes in specific neural circuits that last throughout adulthood (Bareradi et al., 2000). Interestingly, recent analysis of this plasticity indicates that a developmental mismatch between inhibition and extinction could provide a time frame during which the reorganisation of cortical circuitry can be particularly influenced by sensory experience (Fagiolini and Hensch, 2000; Huang et al., 1999). The self-renewing capacity of the olfactory bulb's inhibitory neuronal network leaves

open the possibility that the critical period may in fact be indefinite in the olfactory system (Rocheffort et al., 2002). Indeed, odour experiences have been reported to modulate adult olfactory bulb functions (Rabin, 1988; Rosselli-Austin and Williams, 1990; Woo and Leon, 1995).

Based on the above, it would seem necessary to continually train dogs on the odours they are intended to be able to find in order to maintain the appropriate olfactory bulb structures (Schoon, 1997).

Further processing in the brain: Discrimination among odours requires a specific interaction between odorant molecules and receptors and the precise recognition by the brain of which subset of receptors has been activated by a given odorant.

Processing of the sensory information requires the coding of sensory inputs into specific patterns of neuronal activity. Independent molecular and functional approaches have recently provided a model for the specific recognition of odours by the brain, which involves the translation of odorant quality into an array of topographically segregated stimuli (see: Dulac, 1997). The signal is transported to the brain from the mitral/tufted cells by the axonal projections in two main ways: one to the thalamus (medialis dorsalis) and on to the orbitofrontal cortical region in the neocortex (cognitive processing); and one to the preoptic/lateral hypothalamic region (non-cognitive processing, limbic system) (Stoddart, 1990).

The processing of odour information is often studied using learned behaviour. Studies on the pathways from the olfactory bulb to the forebrain and brainstem using lesions in different parts of the brain have revealed that there is no single pathway or locus (other than the olfactory bulb) that is essential for odour detection. There are at least three direct bulbar pathways and a number of indirect ones. The projections of the olfactory cortex are diffuse: any one area of the cortex may receive input from different regions of the bulb. The anatomical organisation of these projections indicates that the information may be represented according to a spatial pattern. The redundancy inherent in this organisation may explain why only massive lesions produce deficits in olfaction (Slotnick and Schoonover, 1992).

Odours also have significant physiological effects. This processing is thought to take place in the limbic system that controls emotion and sexual behaviour. The limbic system receives input not only from the olfactory epithelium through the olfactory bulb, but also from the vomeronasal organ through the accessory olfactory bulb.

Olfactory information into the limbic system occurs prior to further processing in the cerebral hemispheres, and is thought to be responsible for many different effects, as summarised by Stoddart (1990).

Vomeronasal organ: The anatomist Ludvig Jacobson (1813) was the first to describe an organ in the mammalian nasal cavity that had not been noticed previously.

Although he assumed that the organ was secretory in nature he suspected that it might also be a sensory organ. Today, this organ in mammals is recognized as a chemosensory organ for pheromones (Doving and Trotier, 1998). The vomeronasal organ (VNO) is a chemoreceptor organ enclosed in a cartilaginous capsule and separated from the main olfactory epithelium. It is located at the base of the nasal cavity and has the appearance of a paired, tubular structure divided by the nasal septum, each side having a crescent-shaped lumen (Doving and Trotier, 1998). This crescent-shaped lumen is lined with receptor neurons on the medial concave side and is filled with fluid from the vomeronasal glands. The vomeronasal neurons have two distinct types of receptor which differ from each other and from the large family of odorant receptors. The VNO receptors constitute seven-transmembrane receptors coupled to GTP-binding protein, but appear to activate inositol 1,4,5-triphosphate signaling as opposed to cyclic adenosine monophosphate. The receptor neurons possess apical microvilli as opposed to the cilia seen on the main olfactory receptors, and their axons merge together, forming vomeronasal nerves that run between the paired olfactory bulbs and enter the accessory olfactory bulb at the posterior dorsal aspect of the main olfactory bulb. The nature of stimulus access suggests that the VNO responds to non volatile cues, leading to activation of the hypothalamus by way of the accessory olfactory bulb and amygdala. The innervated areas of the hypothalamus regulate reproductive, defensive and ingestive behaviour as well as neuroendocrine secretion (Keverne, 1999).

The VNO is involved mostly in reproduction, by detecting pheromones. However, in some animals, such as snakes, it also mediates the tracking of prey and food detection (Halpern, 1987). Since research into the function of the VNO is still in its beginnings, there are probably many more functional aspects to be revealed (Doving and Trotier, 1998).

Comparison of instrumental methods with detector dogs

The attempts to detect odours have led scientists to recognise the effectiveness of incorporating biological principles into the design of artificial detection devices or systems. One modern example of this approach is the development of electronic "artificial noses" (Yinon, 2003). "Artificial noses" are vapour detection systems that mimic key principles of vertebrate olfaction (Stitzel et al., 2003). Like the natural system, artificial noses are able to quantify and discriminate between odours. Drawing on a wide range of disciplines, from chemistry and biology to material science and chemometrics, the goal of creating an artificial nose represents an integrative approach to device design (Dickinson et al., 1998).

There are several hundred commercial electronic-nose instruments currently in use throughout the world and, although nearly all of these are bench-top, laboratory scale instruments, a number of second-generation instruments that are smaller, faster and more sensitive are beginning to evolve, primarily in academic and government laboratories (for more comprehensive overview see: Dickinson et al., 1998; Keith et al., 2001; Maruyama, 2000; Yinon, 1999; Yinon, 2003).

Although certain of these electronic instruments and systems have proven reasonably effective in the detection of metallic land mines, they are not always effective against non-metallic mines and related explosive devices. A variety of techniques have been developed for detection of ultra trace quantities of specific vapours emanating from primary explosives; for example, fluorescence, nuclear magnetic resonance, nuclear quadrupole resonance, plasma chromatography, gas chromatography, spectrochemical emission spectroscopy, IR absorption, Raman spectroscopy, chemiluminescence, bioluminescence, energy-dispersive X-ray diffraction, ion mobility spectrometry and enzymatic catalysis (e.g. Dickinson et al., 1998; Keith et al., 2001; Maruyama, 2000; Yinon, 1999). Recently, Krausa and Schorb (1999) have shown the effectiveness of sensor systems based on cyclic voltametry for personal security and mine detection. However, each has drawbacks which limit its deployment under actual operational conditions.

The continuing military need for an effective real-time capability for detection of concealed battlefield threats such as buried or camouflaged land mines and similar explosive ordnance devices etc., could be met by the use of specially trained dogs. From an operational point of view, biodetectors, such as dogs specially trained for olfactory detection of explosive substances, have demonstrated tremendous value as

mine/booby trap detectors (Mitchell, 1976). The advantage of dogs over instruments as a better tool for detection is based on the mammalian olfactory system, which has long been recognised as one of the most effective sensory systems, together with the dog's extraordinary capacity to combine high sensitivity with broad-band detection and discrimination (Dickinson et al., 1998). The dogs' selectivity is generally superior to instrumental methods, with dogs being able to generalise an odorant signature, enabling detection of target odours in the presence of significant distracting odours without the false alerts commonly encountered with many instruments (Furton and Myers, 2001). According to Furton and Myers (2001), dogs use highly sophisticated neural networks to confirm explosives from the overall pattern of odour chemicals emanating from their representative parent molecules, rather than relying on the parent molecule as required by current instrumental methods. Another major advantage of detector dogs is the speed of detection, which is generally significantly faster than instrumental methods, and their ability to go to source and discover the explosive, unlike machines, which need the source brought to them. Overall, detector dogs are highly cost effective; the cost of a trained dog versus a calibrated instrument is significantly less in terms of initial purchase as well as annual maintenance costs (Furton and Myers, 2001). Furthermore, most breeds of dogs are good learners, motivated to perform, respond reliably to verbal and non-verbal commands, and can be trained to execute complex tasks (Mitchell, 1976). For certain types of devices (e.g. non-metallic mines, trip wires) and in certain scenarios (e.g. trails over rough terrain, railroads, buildings), dogs that have been specially trained for explosives detection appear to constitute the best all-round detection system currently available. At present, trained dogs are thought to be the most dependable land mine detectors (Keith et al., 2001). However, much research continues to be focused on furthering our understanding of olfaction, and its potential extension to artificial sensing devices (Dickinson et al., 1998).

Training procedure for detector dogs and the principal challenges encountered

It will become obvious from the following brief description that the training and maintenance of an explosives detector dog, under field conditions, is not only very complex, but is actually more complicated than most experiments by learning theorists, and the degree of stimulus control required is greater than that found in most operant conditioning paradigms. Yet trainers, who are neither extensively nor

academically trained in experimental psychology, continue to design, control, analyse, and implement these training procedures. Working dogs are a very important tool in the detection of explosives. They are highly accurate, rapid, mobile and as reliable as most existing machines (Furton and Myers, 2001). Unfortunately, however, the training of explosives detection dogs (EDDs) is still being approached as an art rather than a science. There is very little if any research into the training, maintenance and effective use of EDDs. Different national, state, local, and private organisations all zealously stick to their own in-house methodologies, often based on the fact that if “it works” don’t tamper with it (Frost, 1990). Because each group is trying to either establish a reputation or sell or rent its EDDs, there is very little open discussion of methodologies in regard to EDDs. This results in minimal cross-talk between academics (such as behaviourists), and trainers in the field. The academics often feel that these “real world” problems are either uninteresting or unimportant or too complex for analysis, and experimental control over “irrelevant” variables is often lacking. Another very real problem in working with dogs, especially EDDs, is that research is time consuming, and the number of available animals is limited. Given that demand for EDDs is greater than the supply, operational use tends to have a higher priority than research.

On the other hand, trainers often fail to consult with academics, believing the latter live in an ivory tower out of touch with the real world. However, in every aspect of the training, maintenance and use of EDDs, academic researchers can make a vital contribution and improve efficiency of the EDD. One of the areas in which academic research and applied training converge is in the study of the establishment and maintenance of stimulus control in EDDs. In other words, how trainers can maximise the probability of detections while minimising both misses and false positives.

Obviously, this problem, while theoretically very interesting, is even more important from the practical side. A miss can be fatal, and too many false positive responses can also have severe consequences.

In order to understand the variables that affect EDDs it is necessary to briefly describe how they are trained. The following focuses on the commonalities between various organisations and not on the divergences. A comparative study of methodologies can be found in Frost (1990).

The first stage in the training of a working dog is the selection of the dog. Different units use different criteria and the rejection rate varies from 90% to 10%. The breed

of dog has traditionally been determined by the chief trainer, who will generally believe that his preferred breed and his selection methods are the best. Since there are compelling financial reasons for better selection methods, scientific breeding and behavioural analysis techniques are becoming more popular. After the dog is selected it is first given simple discrimination training in a near-laboratory environment. The dog is trained to put its nose in a can for either food or the opportunity to play with a ball or towel. Then the explosive odour is introduced as a discriminative stimulus (SD) and the dog is trained to place its nose in the container with explosive. At this stage the dog is required to sit after the detection in order to receive reinforcement (reward). (The sit response is almost universally used as the response to detection of explosives). Negative stimuli called distractors are then placed in other cans and the dog does a sequential search. When the dog detects the explosive odour it sits and is reinforced by the trainer. Once the dog has learned the initial discrimination it is trained on other explosives. This basic discrimination training continues until the dog has learned all of the relevant explosive odours.

The next stage is usually a move out of the simple laboratory setting to more complex, naturalistic environments. The dog is now trained to search the area (with or without a trainer and on or off leash, depending on the final goals of the training). The dog knows when it is in “search mode” because it is given a different leash, may have a different collar and/or harness and is verbally instructed to search. The trainer will often encourage the dog by periodically calling out “search” or “where is it?”. Trainers particularly do this when they consider that the dog is not actively searching or if its motivation is low.

The target-cans at this stage are then phased out and the explosive is hidden in many different types of containers.

Distractors are also used at this stage but much less frequently than in the initial training. The trainer will gradually increase the distance between explosives, make the stimulus more difficult to detect, and extend the time interval between detections. The extension of these parameters is usually by intuition and no strict criteria are used for transitioning from stage to stage. Most training sessions last less than one hour and are usually around 20 minutes or less. The number of possible detections will be fewer than 20 but very rarely will the dog be trained without any explosive being present. Once the dog has been shown to reliably search for and detect the explosive odours it is considered operational and the trainer shifts to a maintenance schedule.

An operational dog will be brought to new areas where it will be instructed to search. Since the probability of detecting an actual explosive is very low, in order to maintain motivation the trainer will, when possible, plant an explosive where he knows the dog will find it. In the terminology of instrumental conditioning, the dog is performing a chain of behaviours: primary reinforcement (either food or play) is given when the animal sits in the presence of an explosive odour. The search behaviour (trotting and sniffing) is remotivated by either the “search” command of the trainer or by the leash and collar and general context. Reinforcement of the search behaviour is effected through detecting the explosive odour.

A major problem in maintaining stimulus control is that, in a real operational situation, when the dog sits the trainer does not know if it is a correct hit or a false positive. He or she also does not know whether the dog might have missed an explosive. Should it be reinforced or not? The trainer, and everyone else, must put their faith in the dog and this means that stimulus control must be continuously maintained at a very high level. Unfortunately (or perhaps fortunately), during operations, EDDs, especially those searching roads in hostile areas for mines and bobby traps, usually do not make any detections because there is usually no target to detect. In many cases, for security reasons, the trainer cannot plant explosives for the dog to detect and be reinforced because of operational considerations (the area may be too dangerous to linger around and train a dog). The usual solution to this dilemma is to take the dog to a safe area and provide more training with planted targets. Sometimes the dog will be rotated out of the operational area and go back to “boot camp” to bring its performance back to optimal level.

One aspect of training and maintenance that is critical to stimulus control is that of the environmental context. As mentioned above, dogs are often not reinforced in operationally relevant areas but instead receive reinforcement in “safe” areas. In other words, in one context dogs seldom or never detect the explosive odour that they do detect in several other contexts. Since it is well known that stimulus control can break down when the context is changed (Balsam and Tomie, 1986), it is important to understand the effect on the search and detection ability of a dog if it is inadvertently conditioned to perceive that no reinforcement will occur in one specific context. Furthermore, will any such effect generalise to other, new contexts? In addition to the practical reasons outlined above, there are several interesting theoretical implications to this question in regard to context as a modulator of instrumental behaviour. When

an animal is trained in one context and tested in another there is usually a reversible decrease in stimulus control (e.g. Thomas, 1985; Thomas et. al. 1993). This decrease is usually known as the context effect. The effects of the dog's inadvertent conditioning to expectations regarding particular characteristics of familiar searched tracks are discussed in the paper "The role of context specificity in learning: the effects of training context on explosives detection in dogs" (Gazit et al., 2005)".

Another critical aspect of training and maintenance of EDDs is to maximise detection probability of explosives under different conditions and with different explosive types and frequencies. Sniffer dogs are trained to identify and detect several types of explosives. According to circumstances such as availability, "popularity" etc., one particular explosive type may be used more frequently during a certain period. Thus, the ability of the dog to increase its detection ability for the specific explosive, as a result of suitable training, would be of great advantage. On the other hand, from an operational point of view, it is highly important that any increase in one explosive detection ability will not decrease the ability to detect another type of explosive. In this respect, a highly relevant model is that of the "search image". This term was first used by L. Tinbergen (1960) to explain why foraging songbirds sometimes focus on one common cryptic prey species among several possibilities. As a result of initial chance encounters with the cryptic prey, the predator "learns to see", and selectively attends to those cues that enable it to distinguish the prey from the background (Croze, 1970; Dawkins 1971a; Lawrence and Allen, 1983; Pietrewicz and Kamil 1979). Previous experiments have demonstrated that visual predators can rapidly exchange one search image for another when the prey type changes (Bond, 1983; Bond and Riley, 1991; Pietrewicz and Kamil, 1979, 1981; Reid and Shettleworth, 1992). The adaptive significance of search image formation might be that cryptic prey can be found more effectively when the predator concentrates on one prey type alone (Lawrence and Allen, 1983). The majority of studies on search images have dealt with visual search image in birds. Although olfaction is one of the major senses used for detecting food items by mammals, and although foraging behaviour is as common in mammals as in birds, few studies have examined the existence of a search image in mammals in general, and of a mammalian olfactory search image in particular. Indeed, the only study to have tested search image in mammals is that of Nams (1997) who found that skunks improved day-by-day their ability to detect a food odour. This occurred even when the animals were exposed to the food odour only once per day.

However, Nams did not use two types of prey and therefore could not determine if there were any effects of runs.

Demonstration of an olfactory search image in other mammals would thus greatly contribute to an understanding of the power and scope of the search image concept. There were several advantages to using explosives detection dogs in the present investigation. First, dogs have proven olfactory capabilities and are known to use olfaction while hunting. Second, the sniffer dogs we used were already well trained in searching for specific odours and were very familiar with the experimental paradigm, i.e. searching a track for olfactory stimuli, and therefore needed no prior training. In addition, the dogs were already familiar with searching large outdoor areas off leash, thus enabling us to place sequences of odours in a manner analogous to that of “runs” in laboratory simulations. Finally, determining the dogs’ ability to form an olfactory search image could have important practical consequences for the utilization and maintenance of explosives detection dogs. The paper "Formation of an olfactory search image for explosives odours in sniffer dogs" (Gazit et al., 2005), reports an experiment that investigated whether dogs are able to form an olfactory search image while searching for explosive charges.

In addition to the motivational and contextual factors that effect the dogs' search behaviour and detection ability, environmental and physiological factors also play a role. The dog perceives odours by sniffing, during which air is inhaled through the nostrils in short aspirations while the mouth remains closed (Neuhaus, 1981). Since dogs do not possess sweat glands, panting is the main means of cooling the body (Crawford, 1962). During panting most of the air passes through the mouth (Schmidt-Nielsen et al., 1970). Since the dog can either sniff or pant, but can never perform both actions simultaneously, panting causes a decrease in sniffing rate, and a consequent decrease in olfaction efficiency. As a result of overheating, therefore, physiological and behavioural resources are diverted from attention and concentration on the assigned task and applied instead to conscious or unconscious ways of body cooling. The paper "Explosives detection by sniffer dogs following strenuous physical activity" (Gazit and Terkel, 2003b), examines the dogs' ability to detect explosives under two extreme physiological conditions: 1) while calm and relaxed, and 2) following strenuous activity. The possibility of improving the dogs' performance by training them to adjust to the energetic requirements of the assignment is also investigated.

Another physiological factor influencing search efficiency is the extent to which vision is used during the search task. The canine visual system has adapted to exploit a particular ecological niche by enhancing visual performance under low light conditions while still retaining good function under a wide array of lighting conditions, including daylight (Miller and Murphy, 1995). Dogs are much more sensitive to moving objects than they are to stationary ones (Miller and Murphy, 1995). Unfortunately, the significant advantage of canine vision remains mostly unexploited when searching for a stationary object, e.g. explosives, drugs etc. In contrast to vision, olfaction is not considered to be affected by object mobility or lighting conditions. Despite the extensive use of dogs for a wide variety of olfaction tasks, however, the relative contribution of olfaction and vision in dogs during search has never been investigated. Many military operations are carried out at night. It is therefore essential to determine whether the dogs' search behaviour and detection ability are affected by the absence of light, and to find the best way to operate these dogs in such situations. In light of the above, the paper "Domination of olfaction over vision in explosives detection by dogs" (Gazit and Terkel, 2003a), examines the relative contribution of the senses of sight and smell in dogs searching for partially concealed explosives.

Since the dog perceives odours mainly by sniffing, a major part of this study focused on examining this phenomenon and its influence on the dog's detection efficiency. Consequently, we developed an electronic communication device that enables the handler to hear and record the dog's sniffing sounds while searching. The device transmits sounds from the dog's muzzle area to earphones worn by the listener, enabling the listener to easily discriminate between active sniffing and non-sniffing or panting. The uniqueness of the apparatus lies in its ability to monitor the dog's behaviour from a great distance (up to 500m in an open wooded area), while it is moving through a particular area. This in turn allows an informed decision about directing the dog to re-search specific areas. The signals are also recorded and can be analyzed later using a special computer software program, also developed for the purpose of this study, which discriminates between sniffing and panting and counts the signals according to the experimenter's requirements. Both the aural and the computerized sound analyses enable study of the dog's sniffing behaviour under a variety of conditions. The apparatus specifications along with the algorithm details are

presented in the paper "A simple system for the remote detection and analysis of sniffing in explosives detection dogs" (Gazit et al., 2001).

In an attempt to answer all of the above-mentioned challenges encountered in training and maintenance of efficient search behaviour, this study examined the influence of various psychological, physiological and environmental factors on the behaviour and detection efficiency of the sniffer dog. In addition, the main olfactory behaviour - sniffing - was examined under various scientific and operational conditions, using a device especially developed for this study.

Aims

The aims of the study:

1. To examine the relationship between a dog's motivation to search for an odour and its detection probability under various physiological, behavioural and psychological conditions.
2. To examine the significance of a dog's sniffing frequency on odour detection probability.
3. To establish a detection performance envelope for the explosives detector dog under various conditions.
4. To determine whether a dog's search behaviour is affected by context, and if so, whether this "context effect" interferes with the dog's detection success rate in other contexts.
5. To determine whether dogs can acquire an olfactory search image, and if so, whether this would increase their detection success rate.

Discussion

Over the last century the use of detector dogs has expanded and is currently widespread throughout the world for a variety of military and civilian purposes. Particular use is made of the canine sense of smell, which is one of the most sensitive and discriminative senses among all mammals due to the enormous number of olfactory receptors located in the olfactory epithelium. The area of the canine olfactory epithelium has been estimated at around 100 - 170cm² in the German shepherd, in comparison to 3-22cm² in humans (Doty, 1998, Lovett, 1991; Moulton, 1977). This huge number of sensors may come into play in the detection of compounds with low odour thresholds. Because the dog's nostrils are completely separated by a septum it has an essentially bilateral separation of olfactory stimuli, which allows it to determine the direction or location of an odour's source (Terner, 1991). These capabilities, plus the ability to be trained and motivation to work for humans, have made the dog an extremely valuable biodetector for odour materials.

Although the last few decades have witnessed significant developments in certain scientific areas related to olfaction, and in sensor technology in particular, researchers have not yet succeeded in developing a mobile device that can reliably emulate the dogs' capabilities (e.g. Dickinson et al., 1998; Keith et al., 2001; Myers, 1992; Rouhi, 1997). Indeed, to date, the selectivity of detector dogs for specific odours is generally superior to that of instrumental methods, with dogs being able to both generalise and differentiate an odorant signature, enabling detection of target odours in the presence of significant distracting odours without the false alerts commonly encountered with many instruments (Furton and Myers, 2001). Thus, detector dogs still represent the fastest, most versatile, reliable and cost-effective real-time explosives "detection device" available.

There is no doubt that the performance of the explosives detector dog is as good as, if not better, than any currently available commercial detection machine. A machine, however, unlike a dog, does not vary in vigilance, nor get tired or bored (Yinon, 2003). Animal vigilance does vary, and the dog's effectiveness as a detector is affected by many variables, such as time spent searching, environmental variables such as heat and humidity, "mental" state such as motivation, the dog's particular

nature and temperament, its degree of training, and its previous experience with similar situations. In addition, since the sniffer dog "detection device" does not work independently but in cooperation with a handler, the handler's influence on the dog is also significant, and includes such variables as his/her own extent of expertise, previous experience with the required task, the quality of the bond between handler and dog, and even the handler's mood. Recently it was shown that dogs are very sensitive to the different visual cues presented by humans and are able, for example, to use even a novel social cue to find hidden food (Byrne, 2003; Hare et al., 2002).

Given the importance of the above-mentioned factors to the performance and search efficiency of the dog, the current study focused on the two traits whose development throughout the processes of evolution and domestication have made the dog the most efficient biodetector to date for work alongside man: its highly developed sense of smell, and its motivation and willingness to work with man. Under various conditions I examined the influence of different psychological, physiological and environmental factors on the behaviour and detection efficiency of the "explosives detection tool" that we call a "sniffer dog". In addition, since the dog perceives odours mainly by sniffing, a part of this study focused on examining this phenomenon and its influence on the dog's detection efficiency, using an electronic communication device especially developed for this study.

Many studies have shown that sniffing enhances olfactory sensitivity. The sensation and perception of smell are largely dependent on sniffing, which is an active stage of stimulus transport and therefore an integral component of mammalian olfaction (e.g. Laing, 1983; Le Magnen, 1945; Neuhaus, 1981; Rehn, 1978; Sobel et al., 1998, 2000). It has been found that sniffing increases olfaction sensitivity in comparison to smelling without sniffing (Neuhaus, 1981; Steen et al., 1996). However, most such studies were done under controlled laboratory conditions and focused mainly on threshold detection of various odours. Only a few studies have examined canine olfaction under more naturalistic uncontrolled conditions, with the dog exposed to and influenced by wind, temperature, background odours, etc. (e.g. Blade et al., 1996; Carr et al., 1993; Steen and Wilsson, 1990; Thesen et al., 1993). Given the extended use of detector dogs, examining the dogs' performances under operational field conditions is of great advantage. In order to study the dog's search mechanism under

more natural conditions, I improved an apparatus developed by Thesen et al. (1993) that enables the handler to hear and record the dog's sniffing sounds while searching. The device transmits sounds from the dog's muzzle area to earphones worn by the listener, enabling the listener to easily discriminate between active sniffing and non-sniffing or panting. The recorded signals can be analyzed later using a special computer software program, also developed for the purpose of this study, which uses neural networks to discriminate between sniffing and panting and counts the signals according to the experimenter's requirements. During the development of the software it was found that those parameters that characterise and differentiate sniffing signals from panting are not identical for every dog. Thus, in order to achieve reliable discrimination between the auditory signals representing sniffing and panting, each learning stage of the software is performed separately for each dog and individual parameters are extracted and used by the neural network. In our paper, Gazit et al., (2001), we describe in detail the apparatus components and algorithm specifications. Both the aural and the computerized sound analyses enabled a study of the dog's sniffing behaviour under the variety of conditions that were examined in the experiments performed throughout this study.

It was found that under severe physiological conditions, there was a direct relationship between sniffing frequency performed by the dog and its detection performance. Examination of the dogs' performances following strenuous physical activity revealed that the reduction of sniffing frequency consequent to intensive exercise on a treadmill resulted in low target detection (Gazit and Terkel, 2003b). These results support Carr et al. (1993), who found that following brief exercise in a gym, the dogs' performances in determining the correct direction of human footprints diminished to 68% accuracy in comparison to the 90-100% accuracy achieved when working when calm and non exercised (Steen and Wilsson, 1990; Thesen et al., 1993). Under non-stressful working conditions, in the present study, an increase in detection was not, however, always accompanied by a similar increase in sniffing frequency. Studying the dogs' behaviour under different lighting conditions in the field, revealed no difference in target detection between dark and light conditions, although sniffing frequency during dark was higher than during light sessions (Gazit and Terkel, 2003a). This finding (of no equivalence between sniffing frequency and detection percentages) was also reached when studying the effect of environmental context on the dogs' performances (Gazit et al., 2005). During this latter study the

dogs were differentially motivated to complete searches along three familiar paths. In this experiment the dogs were trained on the three paths that only differed in the number of explosives hidden along each path, which significantly affected the dogs' motivation to search. It was found that motivated situations led to an increase in detection percentages in comparison to low motivational situations. Surprisingly, no difference in sniffing frequency was found during searches between the two situations (data of sniffing rate not published). A similar finding was revealed in our separate study of dogs' search performances prior to and following strenuous physical activity (Gazit and Terkel, 2003b); When analysing the dogs performances according to the location of the targets along the track (first, second or third target), it was found that under both stressed and non-stressed conditions, the dogs detected the third target at a higher rate than the two targets hidden closer to the beginning of the track, without increasing their sniffing frequency.

Consequently, the findings of the current study combined with those of previous studies (e.g. Thesen et al., 1991; Youngentob et al., 1987) suggest that mammals have the ability to adjust their sniffing frequency according to the requirements of the olfactory task. In general, there is an inverse relation between panting and sniffing frequencies; elevation of panting results in reduction of sniffing. However, in our study of the dogs' performances prior to and following strenuous physical activity (Gazit and Terkel, 2003b) I found that under non-stressed conditions, when the dogs were anticipating ending their mission and being given rest upon completing the search (with which they had become highly familiar), they managed to maintain sniffing frequency even though this was paralleled by a slight increase in panting during this final period. The contention that dogs adjust their sniffing frequency according to the requirements of the olfactory task is also based on our study monitoring the sniffing frequency of the dogs while searching for small amounts (10 grams) of three types of explosives: TNT, C4 and PETN, under controlled conditions (unpublished data). More sniffing was performed by the dogs when searching for TNT, which is more difficult to detect, compared to when searching for PETN, which is easier to detect for the dogs. This sniffing adjustment by dogs was also shown by Thesen et al. (1993), who examined the ability of tracker dogs to determine the direction of a footprint track after being brought at a right angle to the track. The researchers recognised three phases in the dogs' behaviour while tracking: search, decision and track. During the decision phase, which is the most difficult one, when

the dogs have to determine the direction of the track, the duration of sniffing was 3-fold longer than during the other two phases. Laing (1986) examined the ability of humans to discriminate between various concentrations of two odourants and showed that sniffing duration influences identification over a narrow range of concentrations that is just above the recognition threshold. Youngentob et al. (1987) hypothesized that, in rats, by taking increasingly larger numbers of sniffs and sampling for a longer period of time as the task became more difficult, the animals were attempting to increase the total quantity of odorant reaching and interacting with the receptor epithelium.

It was previously found that sniff volume is inversely related to odour concentration (Johnson et al., 2003; Laing, 1983; Sobel et al., 2001; Walker et al., 2001; Warren et al., 1994). When smelling a concentrated odorant, mammals perform a smaller volume sniff, but when smelling a diluted odorant, they perform a larger volume sniff. Johnson et al., (2003) concluded that this phenomenon implicates a neural feedback mechanism that measures sensory input (odour concentration) and modulates motor output (sniffing) accordingly. The authors also suggest that sniffing is the primary sensory motor component of olfaction. Similar to fine control over ears and eyes, a sniff is accurately and rapidly modulated in accordance with sensory content.

As already mentioned, the canine sense of smell is highly developed and indeed is generally more sensitive than actually needed for the detection of most common explosives (Myers, 1992). Consequently, it is likely that increased sniffing is only employed when necessary, when odour concentration is very low (near threshold), or under severe physiological or environmental conditions.

It is known that the natural sniffing frequency is quite constant, with an average of 6 ± 2 sniffs per second both for dogs (Goldberg et al., 1981; Thesen et al., 1993) and for rats (Welker, 1964). Similar to sniffing, if a dog pants at the resonance frequency of the respiratory system, it will produce the greatest ventilation with the least effort. This would certainly be in the interest of the animal's energy and heat economy (Crawford, 1962). Since the natural sniffing frequency is constant, sniffing behaviour is modulated by the duration of the sniffing bouts. A dog's respiratory behaviour comprises three main components: 1) regular breathing, 2) sniffing, and 3) panting. Increasing one component will necessitate a decrease in the others. Theoretically, when extra sensitivity is not required, the dog will act in a manner that will minimize

energy expenditure and will not perform additional sniffing when this is unnecessary, since more sniffing means less panting, which is essential for body cooling.

The modulation of sniffing behaviour is similar to the vehicle kick-down mechanism, which enables instant acceleration by pressing strongly on the gas pedal. The majority of modern cars are sufficiently strong and fast for most road conditions. However, in extreme cases, when immediate acceleration is necessary, a swift, sharp depression on the gas pedal will instantly speed up the car, thus enabling a quick escape from a potentially dangerous situation. The cost of using this mechanism is higher fuel consumption. Therefore, it is obvious to every driver that in order to save fuel (e.g. energy) there is no need to use this mechanism under normal driving conditions. The same applies to the canine olfactory system. The dog will employ the "kick-down device" (more sniffing) only when such is really necessary for detection. In all other situations, when odour concentration is above threshold, the dog will perform according to the natural resonance frequency of its respiratory system, thus conserving energy and maintaining the olfactory system at optimal conditions for as long as possible.

As noted above, since the vapour pressure of most explosives is above the canine olfactory threshold, the dog generally does not have to increase sniffing frequency above its natural level for their detection. This might explain our finding in which a demonstrated increase in explosives detection rate, under ordinary conditions, was not accompanied by a parallel increase in sniffing frequency (Gazit and Terkel, 2003a; Gazit and Terkel, 2003b; Gazit et al., 2004). We suggest, therefore, that despite the importance of sniffing frequency to olfactory sensitivity and efficiency, the increase found in explosives detection rate was mainly a consequence of the dog's mental state, achieved through motivational rather than physiological changes.

The effect of the dog's motivation on its performance was demonstrated in several experiments performed as part of this dissertation. In my examination of the context effect on dogs' behaviour during a search for olfactory targets (Gazit et al., 2005) the dogs had to search three identical tracks which differed only in the number of explosives hidden along each track. Significant differences were found in explosives detection rate between the three tracks, although no differences in sniffing rates were found. In all cases, the differences in detection rates reflected alterations in the level of the dogs' motivation to search. By the time that one explosive was hidden along

what the dogs had previously come to recognise as a “clean track”, their motivation to search this track had diminished, and detection percentage was only 52.5%. However, when a single similar explosive was hidden along an unfamiliar track, which the dogs had never searched before, detection percentages rose to 96%. The only difference between the two situations was the dogs' previous familiarity with the "clean" track as opposed to their introduction to an unfamiliar track. The familiarity had led to their low motivational level to search the clean track whereas a regular motivational level was displayed when they were asked to search a novel track. Additional evidence for the effect of motivation on a dog's detection performance comes from the findings when the dogs were sent to search prior to or following strenuous physical activity (Gazit and Terkel, 2003b). It was suggested that various motivational factors, such as the dog's desire to rest in a cool place following completion of the search, or even its knowledge that it was about to complete the search track (the dogs were fully acquainted with the search track and its termination point), influenced the probability of detecting the explosives. This occurred both when the dogs were calm and only lightly panting as well as when they were physically stressed and thus heavily panting. Furthermore, the same study suggested that the dogs were able to adjust to working under severe physiological conditions and could improve their detection probability by being encouraged to concentrate on the task of detection. This indeed led to their maintaining the number of sniffs per minute, in spite of an increase in panting (which normally results in decrease of sniffing). Previous studies have revealed that focusing attention on a given task is associated with increased activation of the neurons processing this task, suppressed activity of other neurons, and enhanced behavioural performance for the attended task (e.g. Behrmann and Haimson, 1999; Corbetta et al., 1990; Desimone, 1998; Kastner et al., 1998; Spitzer et al., 1988). Spitzer et al. (1988) investigated whether the amount of attention, or cognitive "effort", devoted to a stimulus affects how it is coded within the visual system of rhesus monkeys (*Macaca mulatta*). Those authors examined the responses of neurons in the visual system to stimuli presented within the same perceptual task at different levels of difficulty. They concluded that increasing the amount of attention directed toward a stimulus can enhance the responsiveness and selectivity of the neurons that process it. Kastner et al. (1998) used functional magnetic resonance (fMRI) in humans to test for the presence of suppressive interactions among stimuli presented simultaneously within the visual field in the absence of direct attention, and

to investigate the influence of spatially directed attention on these suppressive interactions. They found that in the absence of direct attention, multiple stimuli in the visual field interact with each other in a mutually suppressive way; while spatially directed attention reduces these interactions by partially cancelling out their suppressive effects. Corbetta et al. (1990) instructed human subjects to report whether the moving bars in two successive briefly presented computer displays were identical. In the focused attention treatment, the subjects had been told what visual attribute might differ between the bars on each display (colour, shape, or velocity). In the divided attention treatment, the subjects had only been told that the bars could differ in one of the three attributes. It was found that focusing attention on a single attribute was correlated with increased neuronal activation in the area of the visual cortex that processes this attribute compared to the divided attention treatment. The significance of motivational factors on behaviour in rats was shown by Clarke and Trowill (1971), who demonstrated that rats can increase their sniffing frequency as a result of receiving - or even only anticipating - a positive hypothalamic stimulation. Anticipation of hypothalamic stimulation, which acts as a positive motivational factor, was sufficient to induce a response (more sniffing), resulting in improved odour detection.

The final part of this dissertation examined the phenomenon of search image. Search image is a well documented concept that explains the higher success in detection of one common particular prey type in comparison to other prey possibilities. As a result of initial chance encounters with the cryptic prey, the predator "learns to see", and selectively attends to those cues that enable it to distinguish the prey from the background (Croze, 1970; Dawkins, 1971a; Lawrence and Allen, 1983; Pietrewicz and Kamil, 1979). The majority of studies on search images have dealt with visual search image in birds. However, although olfaction is one of the major senses used for detecting food items by mammals, and although foraging behaviour is as common in mammals as in birds, few studies have tested for the existence of a search image in mammals in general, and a mammalian olfactory search image in particular. Given the widespread use of detector dogs for a variety of purposes for the benefit of mankind, it was of interest to determine whether dogs can acquire an olfactory search image, and if so, whether this would increase their detection success rate. Consequently, I conducted a series of experiments in order to determine whether sniffer dogs can develop such an olfactory search image (Gazit et al., 2005). Specifically, I asked

whether extensive training with one explosive would improve the dogs' ability to detect that explosive and also whether it would reduce their ability to detect other explosives. The results of this study provide evidence that dogs can develop an olfactory search image, as they clearly demonstrated both an improvement in their ability to detect a particular target (TNT) as a result of extended experience with that target, and a reduced detection rate of the same target when its probability of occurrence was reduced. These results support the usefulness of the search image concept beyond that solely of birds searching for visible prey. It has been suggested that the acquisition of a search image is part of the more general concept of perceptual learning, where exposure to a stimulus improves the ability of the subject to discriminate and detect that stimulus from the background (Goldstone, 1998). After an animal has acquired a search image for a specific target, its maintenance seems to be dependent on the relative target probability. I have shown here that the dogs' probability of detection of TNT was dependent on the relative percentage of TNT to other targets. This result, which is analogous to that found in foraging birds, supports a two-stage search image. After an animal acquires the search image, another mechanism, possibly selective attention, is responsible for its continued maintenance.

The findings achieved in this dissertation, combined with those of previous studies, support the following contentions:

- 1) Sniffing activity enhances olfactory sensitivity mainly when odour concentration is low and close to detection threshold. In such cases, the dog must increase its effort and concentration on the detection task through increasing its sniffing frequency.
- 2) Consequently, the dog will adjust its sniffing frequency according to the requirements of the olfactory task. "Difficult" olfactory tasks characterized by threshold intensity odour will produce high sniffing frequency, whereas when odour intensity is above threshold, the dog will be able to detect the odour easily without performing extra sniffing.
- 3) Despite the proven importance of sniffing for olfactory sensitivity, the influence of the dog's motivational level on its detection performance dominates that of the olfaction variables (i.e. sniffing frequency). This may explain the occasions on which I found improved detection rate not to be accompanied by elevated sniffing frequency. Thus, a motivated dog may

perform well without increased sniffing, whereas when less motivated, or stressed, it might perform badly despite high sniffing frequency.

- 4) While searching for the odour targets the dog may employ a search image that increases detection probability of the previously most frequently encountered target. This dissertation provides evidence, for the first time, of the existence of an olfactory search image in canines.

In summary, working dogs constitute a very important tool in the detection of explosives. They are highly accurate, rapid, mobile and as reliable as most existing machines. However, dogs, like humans, are biological systems, and their performance is affected by various environmental, physiological and psychological factors. In the current study, I investigated the effect of these variables on the search behaviour and detection efficiency of the dog. As a consequence of the strong bond between the dog and its handler, the dog's willingness to work for its handler, and its anticipation of reward in exchange for successful detection, the dog will recruit all of its resources and focus its attention in order to fulfill the assigned task successfully.

I suggest here therefore, that the dog's ability to adjust its search behaviour according to the necessities of the task, promotes efficiency of search and improves detection success. In addition, although the literature reports the importance of sniffing rate for olfactory detection, I suggest here that sniffing is much less important than the motivational and attention variables that influence olfactory search. Consequently, a demonstrated motivation to work should be the main factor under consideration when selecting a detection dog,

This behavioural flexibility of the dog, together with its highly developed sense of smell and eagerness to please its handler, make it an effective and valuable biodetector, when given the appropriate training and operated under the appropriate regime.

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תקציר

הקשר בין הכלב לאדם קיים משחר ההיסטוריה וחובק תחומים רבים. קשר זה, שהתהווה במהלך תהליך הביות הממושך, לתועלת שני הצדדים, הוא כיום קשר בל יינתק.

במהלך המאה ה-20 התרחב השימוש בכלבי הרחה בעולם כולו למטרות צבאיות ואזרחיות כאחת. השילוב בין הרגישות הגבוהה של חוש הריח של הכלב, יכולת הניידות המאפשרת תנועה לאורך גרדיאנט ריכוז הריח עד הגעה למקור הריח, ביחד עם רצונו של הכלב לעבוד לצד האדם, מייחד את הכלב כ- biodetector הטוב ביותר הקיים כיום. במהלך עשרות השנים האחרונות מושקעים מאמצים ומשאבים רבים בניסיונות לפתח מריחנים מלאכותיים המחקים את אף הכלב. אולם, על אף ההתקדמות הטכנולוגית, עדיין לא פותח מכשיר נייד המסוגל להגיע לרמת הרגישות וליכולת ההבחנה של הכלב. לכן, כלבי הרחה מהווים כיום "אמצעי" חיוני לזיהוי חומרי נפץ.

על אף שלכלבים יתרונות רבים על פני המכשור המכאני הקיים, הכלבים, כמו האדם, הם מערכות ביולוגיות, ותפקודם מושפע ממגוון גורמים סביבתיים, פיזיולוגיים ופסיכולוגיים. במחקר הנוכחי נבחנה השפעתם של גורמים אלו על התנהגות החיפוש של הכלבים, על רגישות ההרחה שלהם ועל סיכוייהם לאתר את מטרות הריח. מכיוון שלהתנהגות הרחרוח שמבצע הכלב בעת איתור מקור ריח תפקיד חשוב בקליטת מולקולות הריח, התמקד חלק מהמחקר הנוכחי בבחינת התנהגות הרחרוח והשפעתה על יעילות גילוי הריח. לצורך כך פותחה מערכת קשר אלקטרונית, המאפשרת לנוהג הכלב להאזין ולהקליט את קולות הרחרוח, המבוצעים על ידי הכלב במהלך חיפוש אחר מטרות אולפקטוריות. המערכת, המעבירה אותות קוליים מחלקו העליון של אף הכלב אל אוזניות המורכבות על אוזני הנוהג, מאפשרת לנוהג להבחין בין אותות קוליים האופייניים לרחרוח לבין אותות האופייניים להלחתה או לנשימה רגילה. תוכנת מחשב שפותחה לצורך מחקר זה ומבחינה בין סיגנלים המייצגים רחרוח לבין סיגנלים המייצגים הלחתה, מאפשרת לנתח את הסיגנלים המוקלטים ולסווגם לקבוצות על פי הגדרת החוקר. הניתוח הממוחשב של האותות הקוליים מאפשר לחקור את התנהגות הרחרוח של הכלבים במגוון מצבים שבהם נבחנו במהלך עבודה זו. פיתוח מערכת זו מהווה את החלק הראשון של הדוקטוראט ומתואר במאמר הראשון בסדרת המאמרים המרכיבים את התזה.

תחילה, נבחנה התרומה היחסית של חושי הריח והראיה לסיכויי הכלבים לאתר את מטעני חומר הנפץ. לאחר מכן בחנתי את ההשפעה של מידת המאמץ הפיזי שמבצעים הכלבים הן על תדירות הרחרוחים והן על סיכוייהם לאתר חומרי הנפץ. לבסוף, נבחנה השפעתם של שני גורמים שונים על יכולת הכלבים להיעזר ברמזי הריח לצורך איתור המטענים: ראשית, נבחנה השפעת שינוי ההקשר שבו בוצעה הלמידה על סיכויי גילוי המטענים, ולאחר מכן נבחנה השפעת היחס הכמותי בין סוגי המטענים השונים על סיכויי הכלבים לאתר את אותם מטענים.

על מנת לבחון את התרומה היחסית של חושי הריח והראיה ליכולת איתור מטעני חומר הנפץ, בדקתי את תפקודם של שישה כלבים בשני מצבי תאורה קיצוניים: אור מלא וחשכה, ובמהלכו נבדקו אחוזי גילוי החומרים, משך הסריקה עד איתור החומר ותדירות ביצוע רחרוחים והלחתות במהלך הסריקה. בבחינת הכלבים תחת תנאים מבוקרים לא נמצא הבדל בכל הפרמטרים שנבדקו, בין חיפוש הנערך בתנאי תאורה מלאים לבין חיפוש המבוצע בחושך. מכאן, שחוש הריח הוא החוש העיקרי שבו נעזר הכלב לצורך איתור מטעני חומר הנפץ הן בתנאי חשכה והן בתנאי תאורה מלאה. עבודה זו מסוכמת במאמר מספר 2.

במחקר השלישי נבחנה השפעת מידת המאמץ הגופני שמבצעים הכלבים על תדירות הרחרוחים ועל סיכוייהם לאתר את המטענים, תוך השוואת רמת התפקוד של הכלבים לפני ואחרי ביצוע פעילות גופנית מאומצת. כיוון שלצורך ביצוע רחרוח נדרש הכלב לסגור את פיו ואילו הלחתה מבוצעת בפה פתוח, אין באפשרות כלב לבצע את שתי ההתנהגויות בו זמנית. בשלב ראשון של המחקר נבחנו הכלבים כאשר הם "רגועים", ללא כל מאמץ גופני, כך שתדירות ההלחתות שלהם נמוכה ביותר. לאחר מכן הורצו הכלבים על treadmill עד התייצבותם בדרגת מאמץ קבועה. לאחר ביצוע המאמץ הפיזי, נבחנו הכלבים שנית, כאשר הם מלחיתים בכבדות. במהלך המחקר אשר בוצע תחת תנאים מבוקרים ותנאי שדה נרשמו אחוזי גילוי החומרים, משך הסריקה עד איתור החומר ותדירות ביצוע הרחרוחים וההלחתות. נמצא שקיים יחס הפוך בין תדירות ההלחתות לבין יעילות עבודת ההרחה של הכלב: ככל שעלתה תדירות ההלחתות, עלה משך

בהמשך העבודה נבחנה השפעתם של גורמים פסיכולוגיים/מנטליים על רמת התפקוד של הכלבים. סיכויי הכלב לאתר את מקור הריח מושפעים גם ממידת המוטיבציה שלו לבצע את המטלה וממידת עמידותו למצבי תיסכול. על מנת לבחון את השפעת המוטיבציה של הכלב על סיכויי גילוי החומר, יצרנו אצל הכלב קישור בין מיקום הפעילות לסיטואציה. כתוצאה מכך נוצר מצב שבאזור מסויים רמת המוטיבציה שלו לחפש את החומר גבוהה, בעוד באזור אחר, הזחה לראשון בכל מאפייניו, רמת המוטיבציה של הכלב לחפש את החומר נמוכה. תופעה זו המוכרת בספרות כ- "context shift effect" מתייחסת למצבים בהם בעלי חיים משנים את התנהגותם בהתאם למקום ביצועה כתוצאה מהיכרות עם אותו המקום. כאשר בעל החיים למד לקשר בין גירוי-תגובה-תגמול המבוצעים באזור מסויים, ונבחן על אותו הקשר באזור אחר, קיימת ירידה בחוזק הקשר בהשוואה לחוזקו במקום בו נוצר.

השפעת שינוי ההקשר בו נלמדה ההתנהגות על התנהגות החיפוש של הכלב וסיכויי גילוי המטרות, נבחנה בסדרת ניסויים עוקבים. בניסוי הראשון הכלבים נשלחו לסרוק לאורך שני מסלולים זהים: מסלול א' – שלאורכו הוטמנו חמישה מטענים, ומסלול ב' – שלאורכו לא הוטמנו מטענים כלל. לאחר מספר פעמים שהכלבים סרקו לאורך שני המסלולים לסירוגין רמת המוטיבציה שלהם לסרוק לאורך מסלול ב' ירדה באופן מובהק בהשוואה לרמת המוטיבציה שלהם לסרוק לאורך מסלול א'. בניסוי השני נבחנו אותם הכלבים לאורך מסלול ב' בלבד, כאשר בשלב זה הוטמן לאורך מסלול זה מטען אחד בלבד, אחת לארבעה ימים. נמצא שרמת המוטיבציה של הכלבים לסרוק לאורך המסלול בשלב זה וסיכויי גילוי המטענים היו נמוכים באופן מובהק מאלה שנמצאו לאורך מסלול א' בניסוי הראשון. על מנת לבחון האם תוצאות אלו נובעות כתוצאה ממינוע המטענים שנמצא בשלב זה, חזרתי בניסוי הבא על נוהל הניסוי השני אולם הפעם לאורך מסלול שלישי (מסלול ג'), שהכלבים אינם מכירים. נמצא, שרמת המוטיבציה של הכלבים לסרוק לאורך המסלול השלישי וסיכויי גילוי המטענים היו גבוהים באופן מובהק מאלה שנמצאו לאורך מסלול ב' בניסוי השני ואף גבוהים מאלה שהתקבלו מסריקת מסלול א' בניסוי הראשון. לבסוף, בניסוי

הרביעי, בחנתי האם ניתן לשפר את ביצועי הכלבים לאורך מסלול ב' לאחר שלמדו שמסלול זה ריק ממטענים. נמצא, שלמרות שהכלבים מצאו מטענים לאורך המסלול 12 פעמים ברציפות, רמת המוטיבציה שלהם לבצע את הסריקה לאורך מסלול זה נשארה נמוכה בהשוואה לזו שנמצאה כאשר סרקו לאורך מסלולים א' או ג'. בניסוי זה הוכח שתופעת ה- context shift effect מתקיימת אצל הכלבים בעת חיפוש אחר מטרות אולפקטוריות לאורך מסלולים בעלי מאפיינים שונים. הכלבים למדו לקשר בין המסלול שלאורכו הם סורקים לבין מאפייניו, וללמידה זו השפעה מכרעת על המוטיבציה של הכלבים לבצע את הסריקה ועל סיכוייהם לאתר את המטרות. למידה זו מקושרת למסלול מסוים, אינה מועתקת למסלולים אחרים וקשה מאוד להכחדה.

סדרת ניסויים זאת מתוארת במאמר מספר 4.

בסדרת ניסויים נוספת, המתוארת במאמר מספר 5, בחנתי האם ניתן ליצור אצל כלבים "תבנית חיפוש אולפקטורית" (olfactory search image) של ריחות חומרי הנפץ אותם הם מחפשים. תופעת ה-search image מוכרת בספרות, ונחקרה בעיקר בהקשר של חיפוש מזון אצל ציפורים באמצעות שימוש בערוץ חזותי (ויזואלי). כאשר בעל החיים מפתח search image נוצרת במוחו תמונה של סוג המזון הנפוץ בשטח. כך מסוגל בעל החיים לאתר את אותו סוג מזון ביתר קלות בהשוואה לבעלי חיים אחרים המתחרים על אותם משאבי מזון, וסיכויי הישרדותו גדלים. למרות חשיבותו של חוש הריח להישרדותם של בעלי החיים מחקר אחד בלבד בחן קיום תופעת ה- search image לגבי חוש זה. בהתחשב בשימוש הנרחב בעולם בכלבי הרחה למגוון משימות כגון איתור מטעני נפץ, סמים, דליפות גז, חיפוש נעדרים ועוד, נשאלת השאלה האם יכול להיווצר אצל כלבים olfactory search image והאם היווצרותו במוח הכלב משפרת את סיכויי הכלב לאתר את החומר עליו נוצרה תבנית החיפוש האולפקטורית.

במהלך מחקר זה נבחנה יכולתם של 7 כלבי הרחה לאתר מטעני C4, TNT, PETN שהוסתרו לאורכו של מסלול. בסדרת ניסויים עוקבים שונו היחסים הכמותיים בין החומרים השונים, ונבחנו סיכויי הגילוי של הכלבים לגבי כל חומר בהתאם. נמצא שסיכויי הכלבים לאתר את מטעני ה-TNT היו נמוכים משני החומרים האחרים, ועלו באופן מובהק לאחר חזרות רבות על חומר זה בלבד. אולם, לאחר מספר חזרות, שבהן הוצגו לכלבים 25% TNT ו-75% PETN פחתו סיכויי

הכלבים לגלות את מטעני ה-TNT במידה ניכרת. מכאן, שסיכויי הכלב לאתר את ריח חומר הנפץ הרצוי מושפעים ממידת נפיצותו של החומר בשטח. ניסוי זה הדגים לראשונה, שניתן ליצור אצל כלבים olfactory search image של הריח הנפוץ שאותו הם מחפשים. כתוצאה מהיווצרות תבנית חיפוש אולפקטורית במוחו של הכלב, גדלים סיכוייו לאתר ריח זה בהשוואה לריחות אחרים. עוד נמצא, שהחלפת תדירות הריחות שבהם נתקל הכלב גורמת להחלפת ה-search image בהתאם להחלפת הריחות.

לסיכום,

סיכויי הכלב לאתר את המטרות מושפעים ממגוון גורמים סביבתיים, פיזיולוגיים ופסיכולוגיים. עובדה ידועה היא שפעולת הרחרוח משפרת את הרגישות האולפקטורית של הכלב. ואכן, מחקרים רבים הראו שפעולת הרחרוח מגבירה את רגישות ההרחה, בעיקר כאשר ריכוז הריח קרוב לסף ההרחה של הכלב. במקרים כאלה, נאלץ הכלב להגביר את המאמץ האולפקטורי באמצעות העלאת תדירות הרחרוחים. לעומת זאת, כאשר ריכוז הריח גבוה, מסוגל הכלב לאתר את המטרה ללא מאמץ מיוחד תוך שמירה על תדירות רחרוחים טבעית. מכאן ניתן להסיק, שהכלב מסוגל להתאים את תדירות ביצוע הרחרוחים בהתאם למידת הקושי האולפקטורי של המשימה בפניה הוא ניצב. אולם, מתוצאות עבודה זו נראה שלמרות חשיבותם של הרחרוחים לשיפור יעילות ההרחה, המשתנה המשמעותי המשפיע על סיכויי הכלב לאתר את חומרי הריח הוא מידת המוטיבציה שלו לבצע את הסריקה. כאשר רמת המוטיבציה של הכלב גבוהה, עולים סיכויי איתור המטרות האולפקטוריות כתוצאה מהפניית תשומת הלב של הכלב לקליטה ופיענוח של רמזי הריח הנחוצים לצורך איתור המטרה. לכן, המשתנה המשמעותי ביותר לבחירת כלב עבודה הינו מידת המוטיבציה של הכלב לעבוד למען האדם ולבצע את העבודה.

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תקציר בעברית

עבודה זו נעשתה בהדרכת

פרופ' יוסף טרקל

גורמים המשפיעים על התנהגות כלבי הרחה

ועל סיכויי גילוי בעת חיפוש חומרי נפץ

חיבור לשם קבלת התואר "דוקטור לפילוסופיה"

מאת

עירית פרנפס – גזית

הוגש לסנאט של אוניברסיטת תל-אביב

אדר ב, התשס"ה