

How Many Footsteps Do Dogs Need to Determine the Direction of an Odour Trail?

Peter G. Hepper and Deborah L. Wells

Canine Behaviour Centre, School of Psychology, Queens University Belfast, Belfast BT7 1NN, UK

Correspondence should be sent to: Peter Hepper, School of Psychology, Queens University Belfast, Belfast, BT7 1NN, UK.
e-mail: p.hepper@qub.ac.uk

Abstract

Dogs have the ability to determine the direction of an odour trail left by a human. This study examined how much olfactory information from this trail is required by dogs to determine direction. Six dogs, able to determine direction, were tested on a 21 footstep trail laid on 21 individual carpet squares, one footstep per square, by the same individual wearing the same shoes. Dogs brought in at right-angles to the trail at its centre were able to correctly determine direction better than chance ($P < 0.025$). Dogs were unable to determine direction when the order of the footsteps was randomized by rearranging the order of the carpet squares. When the individual odour cue was removed, but ground disturbance left, dogs were unable to determine direction, indicating that it was the odour of the individual that was used to determine direction. In the final experiment the number of footsteps made available to the dog was reduced from 21 to 11 and then 9, 7, 5 and finally 3. Dogs were able to determine direction from 5 footsteps but not 3. It was calculated that it takes $\sim 1\text{--}2$ s for the odour information in footsteps to change to provide discernible information that can be used by dogs to determine direction. The process by which dogs may determine direction from odour cues is discussed.

Key words: detection, dog, odour trail, olfaction, scent, tracking

Introduction

The ability to detect and follow an odour trail is of importance to many animal species, enabling them to locate food, prey, mates, home or avoid predators. Animals may come across an odour trail by chance or as a result of a search pattern and will need to determine the direction of the trail to move either towards the odour source (e.g. if prey), or away (e.g. if predator). Domestic dogs have the ability to follow an odour trail but little is known about the underlying mechanisms of this behaviour.

The olfactory abilities of dogs are utilized by many organizations to assist in their work, e.g. search and rescue (Fenton, 1992), identification of individuals (Schoon and De Bruin, 1994), location of cadavers (Komar, 1999), detection of drugs (Lorenzo *et al.*, 2003), explosives (Furton and Myers, 2001) and fire accelerants (Kurz *et al.*, 1994), and in conservation work to assess population size (Smith *et al.*, 2003). Their successful use in these tasks rests on two key factors: (i) dogs possess a more sensitive olfactory system than humans and thus are able to detect odours at lower concentrations; and (ii) the dog is trainable. Furthermore, following an odour trail is an essential part of the wild dog's behavioural repertoire, enabling it to locate food, and thus using this ability for human

purpose (e.g. search and rescue), is building on a finely honed natural ability.

Early, more anecdotal, reports (e.g. Romanes, 1887) that dogs can follow an odour trail have been superseded by experimental studies (e.g. Steen and Wilsson, 1990; Wells and Hepper, 2003) which have confirmed that dogs are able to track individuals by their odour. However what odour cue(s) dogs use remains open to speculation.

Although terminology may differ between authors (Syrotuck, 1972; Lowe, 1981; Pearsall and Verbruggen, 1982; Johnson, 1997), in broad terms there are two general types of odours that the dog may detect and use to follow an odour trail. First, the *individual odour* of the person being followed. This comprises their own personal smell arising from their skin, sebaceous, apocrine and eccrine secretions and the smell of their clothes, perfume, washing powder, etc. Second, is what may be termed *contact* or *disturbance odour*. As the individual walks over the ground their footsteps impact on the surface, crushing vegetation, insects, etc., releasing an odour based on this contact. Thus, as the individual moves through an environment their individual odour and that arising from contact/disturbance leaves a distinctive odour trail.

The dog may perceive odour from this trail by airborne currents or from its deposition on a surface. Thus, an individual odour may be detected in the air that blows over the individual and carries airborne scent rafts away from the individual, or from where the individual has deposited their odour either when contacting the ground or surrounding vegetation or when skin cells, for example, fall off the individual's body to the ground around where the individual has walked. Contact/disturbance odour may be detected directly from the surface affected or potentially in the air if the odour is volatile. Many factors may influence the salience of the odour that forms the trail, e.g. temperature, humidity, etc. (Syrotuck, 1972). It is not intended to review this aspect more fully here other than to note that many factors will influence the odour trail left behind by the individual which will affect the ability of the dog to detect and follow the trail.

Dogs that follow an odour trail may be broadly divided into three types, determined by their behaviour on the trail (Bryson, 1984; Johnson, 1997). *Air scenting* dogs follow the odour trail with their head up in the air and are considered to be following the airborne scent rafts emanating directly from the individual providing the odour and being carried away by air currents. It would follow that these dogs can only follow a trail up-wind. *Trailing* dogs follow the trail with their head up when moving into the wind and head down when following the trail in the same direction as the wind. They often do not follow directly on the path trodden by the individual laying the odour and at bends may overrun before turning. It is considered that these dogs are following the individual scent deposited by contact with the ground surface. *Tracking* dogs follow the trail with their head down and noses on the path and follow very closely the footsteps of the individual. It is assumed that tracking dogs are following the odour deposited on the ground and may be detecting contact or disturbance odour. It should be noted, however, that these three characterizations are based on the behaviour observed in the dog and as yet there is little experimental evidence to confirm or deny these observations; in particular there are few studies to determine what cues dogs actually employ.

Kalmus (1955) suggested that the dog detects and follows cues of individuality and found that dogs remain on the trail of a specific individual even when it is crossed by other individuals. Furthermore, when individual odours were prevented from being deposited through covering of the shoe (Romanes, 1887) or by the wearing of a whole body suit (Pearsall and Verbruggen, 1982) dogs were unable to follow the trail. However, others have observed that dogs were unable to track a trail of body odour cues, and could only follow a trail when there had been ground contact (Budgett, 1933). Indeed the odour cues caused by ground contact seem important for tracking on older odour trails (Johnson, 1977). Thus what cues dogs use in tracking odour is unclear. The fact that dogs can track on hard surfaces (Steen and Wilsson, 1990) where there may be little ground disturbance suggests that

individual odour cues are sufficient to enable a dog to follow a trail.

Once it has detected an odour trail, the dog has to make a decision about which direction to follow the trail. There has been no experimental study to elucidate the mechanisms used by dogs in following an odour trail. However, the ability to follow an odour trail and locate its source is essential for survival in many animal species and much progress has been made in identifying the mechanisms used to navigate to an odour source in some species, particularly certain crustaceans and insects.

Considerable work has been undertaken examining the dynamics of odour plumes, i.e. the path and spread of odours as they move away from their source (e.g. Weissburg, 2000). It is now recognized that odours do not disperse in a linear continuous gradient, but rather their dispersal is subject to turbulence, which creates a much more dynamic and complex odour stimulus. The odour plume is comprised of filaments and patches of odour, of varying concentrations, separated by areas of clean air or water where no odour is present (Murlis *et al.*, 2000; Weissburg, 2000). The stimulus the animal must decode in such conditions is one of varying temporal and spatial characteristics, in particular a stimulus that is erratically distributed (Moore and Atema, 1991). Thus animals are faced with a variable intermittent odour signal from which to determine direction. Under such circumstances sampling to obtain information on the odour gradient is very difficult and to be successful would have to be averaged over long time scales (Vickers, 2000): longer than the time observed for orientation responses in crustaceans and insects. This indicates that animals have evolved strategies and mechanisms to obtain information on direction and enable orientation to an odour source in this environment (Vickers, 2000).

A key problem presented by an odour plume is that of signal intermittency. One strategy employed by individuals to overcome this is odour-gated rheotaxis. The animal, upon detecting an odour it wishes to respond to (e.g. prey), moves upstream or upwind. Thus animals need to detect both flow and the odour. As the source is intermittent, the animal will experience persistent loss with the signal and therefore needs to have a strategy for either maintaining or regaining contact with the odour signal. Detailed study of crabs, lobsters and moths has revealed some of the complexity of mechanisms used to locate an odour source.

The blue crab (*Callinectes sapidus*) moves upstream upon detection of an appropriate odour (e.g. prey) and maintains its direction to the source by comparing odour stimulation received by receptors on its left and right legs (Weissburg and Zimmer-Faust, 1993, 1994; Weissburg and Dusenbery, 2002; Keller *et al.*, 2003). Lobsters (*Homarus americanus*) similarly move upstream upon contact with an appropriate odour but may also use the internal chemical and fluid dynamical structure of the odour plume (eddy chemorheotaxis; Atema, 1996) to maintain direction and locate odour source (Moore *et al.*, 1991; Atema, 1996). Moths

fly upwind upon detection of a relevant odour using optomotor anemotaxis (i.e. visual feedback during flight to assess direction of flow) coupled with a counterturning motor pattern generated within the central nervous system to jump from odour patch to odour patch within the plume (Mafra-Neto and Cardé, 1994, 1996; Baker and Vickers, 1997; Cardé and Mafra-Neto, 1997). The fine scale structure of the odour plume also influences navigational behaviour (Moore and Atema, 1991; Kozłowski *et al.*, 2001). The more complex the structure of an odour plume, the more efficient is the orientation of the crayfish (*Orconectes virilis*) to the odour source (Keller *et al.*, 2001). The intermittency of the odour signal — the time between patches of odour — is an important determinant of upwind progress in moths, who fly straighter and quicker to sources of higher pulse rate frequency and slower and adopt a more zigzag course to lower frequencies (Mafra-Neto and Cardé, 1994, 1998; Justus and Cardé, 2002). Moreover, examination of the receptors used to respond to odour reveals they have become adapted to use this intermittency information to determine direction, e.g. receptor cells of lobsters act as temporal filters and enable spatial information to be extracted from the odour plume (Gomez and Atema, 1996).

A comprehensive review of the navigation abilities in odour plume is beyond the scope of this paper but this brief introduction serves to illustrate two key points: (i) the information provided by the odour as it disperses from its source is complex; and (ii) animals have evolved behavioural and receptor mechanisms to enable orientation to the odour source from this information.

Little is known about the mechanisms underlying the ability of the dog to determine direction from an odour trail. Indeed there was (is) some debate over whether dogs can actually determine direction. Budgett (1933) claims dogs are unable to determine the direction of a trail, and anecdotal (Morrison, 1980; Schwartz, 1980) and some experimental studies (Mackenzie and Schultz, 1987) support this. Recent work has found, however, that dogs are able to determine the direction of a trail (Steen and Wilsson, 1990; Wells and Hepper, 2003). Moreover, they do this using olfactory cues. For example, Wells and Hepper (2003) opposed the visual and olfactory cues present in a trail, i.e. the olfactory cues indicated the trail went to the right but the visual cues indicated the trail went to the left, and observed that dogs followed the olfactory cue.

How dogs determine the direction of an odour trail is unknown. Given that dogs can determine the direction of an odour trail, it can be assumed information is present within the trail to enable this. In this paper we assess the dog's ability to use information available from the footsteps of an odour trail to determine direction. Specifically do footsteps provide sufficient information to determine direction (experiments 1–3) and how many footsteps are required to enable a dog to determine the direction of an odour trail (experiments 4 and 5).

Materials and methods and results by experiment

Subjects

Six dogs, able to track a human odour trail (see pre-screening), were used. All dogs were male, ~2 years of age and either German shepherd dogs ($n = 2$) or labrador retriever/golden retriever crosses ($n = 4$). Our previous research (Wells and Hepper, 2003) demonstrated that the ability to track direction appeared better in young male dogs. There was no difference in the performance of different breeds in this experiment and no further comparison is made between dog breeds.

Pre-screening

Dogs were included in the study if they could successfully determine direction on a 100 m trail laid on grass. The trail was laid by an individual walking across a field and marking the beginning and end with small wooden posts. Dogs were brought by their handlers, at right-angles to the trail at its centre, ~1 h after the trail was laid. Dogs and handlers were blind to the direction of the trail. At ~3 m from the trail, handlers were given the instruction to command their dog to track. Dogs were tested on 10 different trails. Each track was only used once. All dogs achieved a significant level of performance, i.e. correctly determined direction in a minimum of 9 of the 10 trails ($P < 0.025$, binomial test; Siegel, 1956). Thus all dogs were able to determine the direction of a trail better than expected by random chance.

Experiment 1

Procedure

A dark beige wool carpet (100% tufted wool, with jute hessian backing and pile length 10.5 mm) was cut into 45.8 cm squares. The carpet was stored externally prior to use and was slightly damp on use in the study. All studies took place outdoors. The carpet squares were laid in a straight line with edges touching to form a line of 21 squares on a large concrete surface (Fig. 1). All trails were laid on the carpet by the same individual (one of the experimenters) walking, one footstep per square, from one end of the carpet squares to the other. The individual wore the same shoes: ~2 year old hiking boots with well-worn leather uppers and rubber soles. To create the trail the individual walked from a point

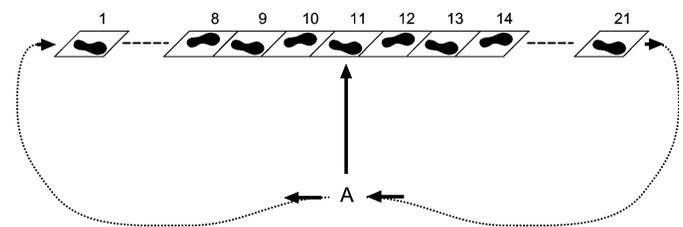


Figure 1 Diagrammatic representation of trail used in this experiment.

~10 m from the centre of a trail in a loop to one end with disposable plastic overshoes over their normal shoes and then removed the overshoes. After walking the trail, the individual replaced the overshoes and returned to the start point. The number of each square was marked using a black felt-tip pen in one corner, on the underside of the carpet square, with the number of the footstep, i.e. 1 = first step, 2 = second step and so on. The carpet trail was left for 60 min and then the dog was tested.

The dog was brought by the handler at right-angles to the line of carpet at its centre; on approaching the carpet tiles the dog was instructed to track. Each dog was given 10 trials using a fresh trail (carpet squares), i.e. that had not previously been used by any dog, each time. For half the trails the direction ran to the dog's left and for the other half the direction ran to the dog's right. A minimum of 20 min was left between trials. The dog, handler and experimenter recording outcome were unaware of the direction of the trail. The experimenter remained at the start point to record the direction in which the dog tracked.

Analysis

The experimenter recorded whether the dog went in the correct direction, i.e. followed the trail moving to the end of the carpet squares at which the trail ended. The number of times the dog correctly determined the direction of the trail was recorded. Results were analysed individually for each dog by means of a binomial test (Siegel, 1956).

Results

The results are reported in Table 1. All dogs were successfully able to determine the direction of the trail at a level greater than chance ($P < 0.025$). It would thus appear that the cues provided by the individual walking on the carpet provided information on direction.

Table 1 The number of times each dog in experiments 1–3 correctly determined the direction of a trail

DOG	Experiment 1	Experiment 2a	Experiment 2b	Experiment 3
	Track	Jumbled track	Control track	Ground disturbance
A	10*	6	5*	4
B	9*	4	5*	7
C	9*	3	5*	3
D	10*	5	5*	6
E	10*	5	5*	6
F	9*	6	5*	4

In all cases 10 trials were offered to the dog with the exception of experiment 2b where only 5 trials per dog were used.

*Indicates a significant ($P < 0.025$) level of performance as determined by a binomial test.

Experiment 2a and 2b

In order to ensure that the dog's tracking ability was due to the odour cues left on the carpet squares and not an extraneous cue, the above procedure was repeated with the exception that after the trail was laid, the order of the carpet squares was randomized (experiment 2a). Randomization was achieved using a computer program to produce 10 different sequences for each dog and trial (Research Randomizer, 2002). Thus a different randomized sequence was used for each trial across all dogs. Squares were handled using rubber gloves to prevent any contamination with other odours being included. A polythene sheet was laid from the start point to the carpet squares and also parallel to the carpet squares to enable the experimenter to pick up the squares without leaving a trail. The experimenter randomly ordered the squares such that the trail now formed a random sequence of footsteps and not an ordered sequence. The heel-toe direction of the footprint on each square remained the same and ran in the direction the individual walked when laying the trail. The sheeting was removed following manipulation of the squares. The dogs were ordered to track in the same way as reported for experiment 1. As a control (experiment 2b) for the randomization procedure (experiment 2a) squares were picked up as in experiment 2a but replaced in the same order, i.e. handled but still presented an ordered trail. The number of times the dogs tracked in the correct direction was recorded. In experiment 2a ten trails per dog were used. It was intended to use a maximum of ten trails in experiment 2b but if the performance of the dog reached statistical significance at five trials (calculated at 100% success) the experiment would cease.

Results

When given the randomized tracks (experiment 2a) dogs performed at the level of chance (see Table 1). Only five trials were given on the handled but ordered track (Experiment 2b) as all dogs achieved 100% success (see Table 1).

The results indicate that dogs were using cues present in the footsteps to determine directionality and not some extraneous cue in the environment. The behaviour of the dogs in experiment 2a also differed. They back-tracked much more frequently and often changed the direction in which they tracked. This suggests the cues presented were more confusing for the animal and supports the experimental observation that dogs were unable to determine direction from the randomized trail.

Experiment 3

A final test was undertaken to examine the nature of the cues used by the dogs. The procedure was identical to that reported for experiment 1 with the single exception that the individual laying the trail placed clean rubber overshoes on their feet at the start of the trail and covered these with three layers of disposable plastic overshoes. This prevented

the trail-laying individual from depositing any individual foot or shoe odour, but retained any scent made by crushing ground disturbance.

Results

The dogs performed at the level of chance in this experiment (see Table 1). Thus, although information was still present from ground disturbance as the individual walked the trail, this cue did not provide sufficient information for the dogs to determine direction in this task.

In summary, experiments 1–3 indicate that dogs can determine the direction of a trail and use information present in the individual odour left by a footstep to do this.

Experiment 4

To determine how much information was required by the dogs to determine the direction of the trail, squares from the end of the 21 carpet line were removed in pairs (i.e. no. 1 and 21 together), thereby reducing the number of footsteps available to the dog (experiment 4). Thus, to provide 19 footsteps, the squares from each end were removed and replaced with identical but non-walked-upon, carpet squares. To provide 17 footsteps, the last 2 squares at each end were removed, and so on.

A pilot study using 11 steps (i.e. the last 5 squares/footsteps had been removed from each end and replaced with fresh non-walked-upon squares) found dogs were successfully able to determine direction from the remaining 11 footsteps and so the experiment proper began at 11, i.e. 11 footsteps. On initial trials dogs became ‘confused’ as the trail ended and began searching for its continuation. The handlers were then given instructions to encourage the dog to continue to the end of the line of carpet squares and the dogs were given positive social reinforcement (verbal praise and stroking) when they reached the end. After some 10–15 trials dogs continued to the end of the carpet with little hesitation following the cessation of the odour trail.

The procedure was identical to that reported above, i.e. dogs were given 10 trials on tracks containing 11, 9, 7, 5 and 3 footsteps. Dogs were given 10 trials with 11 steps, then 10 with 9, and so on. The direction of the trails was randomized across trials, ensuring half the trails were directed to the left, and half to the right, of the dogs. The direction of the trail was unknown to the dog’s handler.

Results

The results for each dog are presented in Table 2. All dogs were able to correctly determine direction using 11 and 9 footsteps. One dog’s performance did not reach significance with 7 footsteps, but all dogs, including the dog that only achieved 8/10 at 7 footsteps, were successfully able to determine direction with 5 footsteps. All dogs performed at chance level when presented with 3 steps.

Table 2 The number of times each dog in experiments 4 and 5 correctly determined the direction of a trail

DOG	Experiment 4					Experiment 5
	11 footsteps	9 footsteps	7 footsteps	5 footsteps	3 footsteps	3 and 5 footsteps
A	10*	10*	9*	9*	5	4
B	10*	9*	9*	9*	4	6
C	9*	9*	9*	9*	5	7
D	9*	10*	10*	10*	5	5
E	10*	9*	8	9*	6	2
F	9*	9*	9*	9*	3	6

In all cases 10 trials were offered to the dog.

*Indicates a significant ($P < 0.01$) level of performance as determined by a binomial test.

The results indicate that dogs require the information present in 5 footsteps in order to correctly determine direction.

Experiment 5

The trail presented to the dogs at 3 footsteps was very short and the dogs may have been confused and not perceived a trail present. That said, there was no observable difference in their behaviour on detecting the 3 footstep trail compared to the 5 footstep trail. However, to ensure that a trail was present for the dogs to perceive, a further experiment was run presenting dogs with a 5 footstep trail but with olfactory information from only 3 footsteps. To achieve this, when the trail was being laid, three extra carpet squares were placed alongside the middle three squares forming a 3×2 pattern (see Figure 2). As the individual approached these squares instead of walking one foot at a time on the three squares, they jumped two-footed onto the three pairs of carpet squares, one foot on each pair of carpet squares. This two-footed jump deposited three pairs of footsteps (one on each pair of squares), each pair being deposited at the same time. The trail was rearranged with the last nine squares at each end being replaced with blank squares. This left the middle three squares and their adjacent partner squares with footsteps. The blank square immediately preceding the first footstep was replaced with the partner square from the first of the footsteps deposited by the two-footed jumps (10L & 10R).

Thus there were now 2 footsteps (10L&R) deposited at the same time in a sequence. The middle square was replaced with its partner square (11L) to maintain the alternating left–right footstep sequence. The blank square immediately following the final footstep was removed and replaced with the partner square from the third paired footstep (12L). Thus, the dog was presented with 5 footsteps but the first 2 (10L&R) were deposited at the same time and the final 2

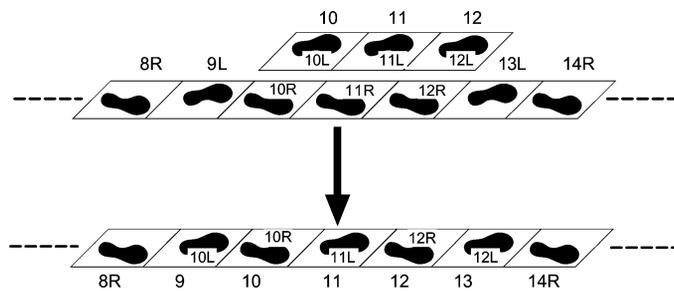


Figure 2 Diagrammatic representation of the configuration of footsteps used in experiment 5.

(12L&R) were deposited at the same time. Expressed in terms of time of deposition, with t being the middle square, the sequence of footsteps ran $t + 1, t + 1, t, t - 1, t - 1$. This presented the dog with an odour trail the same length as they successfully negotiated in the 5 footstep sequence, but only presented information regarding direction from 3 footsteps. This was an attempt to ensure the dog perceived a trail as being present.

Results

Dogs performed at chance level in this task when attempting to determine direction (see Table 2).

In summary, this experiment indicated that dogs require information from five sequential footsteps to successfully determine direction of an odour trail.

Discussion

The results confirm previous studies that dogs are able to determine the direction of a trail (Steen and Wilson, 1990; Wells and Hepper, 2003) and this is achieved using an odour cue (Wells and Hepper, 2003). This study extends these findings by demonstrating that footsteps provide sufficient olfactory information for the determination of direction and that five sequential footsteps are required to enable these dogs to determine directionality.

In this study dogs used an odour left by an individual's footstep to determine direction. Air scent cues were not available as the individual laying the trail was not at either end of the trail. Two odour cues may be left as an individual walks: a direct contact cue that arises from the bottom of the shoe touching the ground; and a more indirect cue from body odour that falls to the ground (Szinak, 1985; Fenton, 1992) around the individual. Clifford (1958) suggests such indirect odour may spread out ~5 yards for 'heavy particles of scent' and 25 yards for 'medium particles of scent' from the body. Pearsall and Verbruggen (1982) argue that this indirect body odour is important for enabling the dog to track. However, the dogs in experiment 2 were unable to determine direction where cues from this general body odour deposition were available but footsteps were not. This supports the suggestion of Budgett (1933) that it is contact odour cues that are important for de-

termining direction. When the individual odour was removed from the odour trail (experiment 3), but contact/disturbance odour was left, the dogs were unable to determine direction. Thus dogs in this study were using the individual odour cue deposited by a footstep to determine direction.

The study found that five sequential footsteps were needed to determine direction. This corresponds with the observation of Thesen *et al.* (1993), who reported dogs sniffed at 2–5 footprints when making a decision about directionality, although more footsteps were available.

How the dog determines directionality is unknown. Direct comparison with studies of navigation in an odour plume (see Introduction) may be inappropriate due to differences in the olfactory signal and species under question.

Footsteps provide a series of discrete odour cues that differ in time of deposition and hence may form a reasonably uniform stepwise olfactory gradient. Observations of the dogs' performance here, and by others (Steen and Wilsson, 1990; Thesen *et al.*, 1993; Wells and Hepper, 2003), indicate that dogs perform this task with their nose just above the ground and not in the air. This suggests they are using the ground-based olfactory cues rather than airborne scents subject to turbulence. Previous observations (Steen and Wilsson, 1990) suggest that dogs are unable to determine direction from a continuous olfactory trail but can do so when discrete separate olfactory stimuli are present, e.g. footsteps. Studies of insect navigation in odour plumes have found that some moths require intermittency in the olfactory plume and are unable to locate the odour source in a continuous odour plume (Justus and Cardé, 2002). It has been suggested that the internal fine structure of an odour plume provides an important source of information regarding direction. A footstep may also provide some information regarding direction. In a normal footstep the heel touches the ground before the toe and potentially provides an internal cue to direction. However, dogs in this study did not appear to use this information as they were unable to determine direction with the 3 footstep sequence – where heel-toe information would be present.

It should also be noted that the 'cognitive processing' capacity of the dog is different to that of the insects and crustaceans previously studied and this may have implications for how direction is determined. It is most likely that the dog determines direction, in this task, through processing elements of the olfactory signal contained within a footstep. Flow may be unimportant as dogs here were able to determine direction upwind, downwind and crosswind.

Two possible mechanisms would allow the dog to determine directionality. Firstly, the odour cue(s) somehow encode absolute information about time. This would be the equivalent of a time code stamped on a photograph. Dogs would then 'read' this information from each footstep, compare the absolute times of different steps and then determine direction. This is most unlikely and it is virtually impossible to envisage a mechanism for this level of time encoding in an

olfactory cue. Secondly, and much more likely, the dog compares the cues offered by each individual footstep which differ systematically with direction. Footsteps present a number of possibilities for an odour gradient to be followed. The individual odour may smell stronger with more recent footsteps, and thus the dog has to determine the strongest smell, which equates to the most recent, and move in that direction. Alternatively, it could be a product of decay that provides the relative information. With time, as decay increases, this provides a stronger smell and thus, comparatively, the more recent footstep smells less decayed than the preceding footstep. To determine direction the dog moves in the direction of least decay. The fact that discrete patches of olfactory information may be required to determine direction supports further the possibility of a comparative process.

Having detected the direction of the trail, what causes the dog to move towards the source is unknown. It may be the result of an innate response; however, these were trained dogs and so it may represent a result of their training.

Recording the time taken to complete the 21 footsteps enables an estimate of the time, and hence olfactory decay rate, between steps to be made. The time taken to complete 100 trails of 21 footsteps reveals an average time between footsteps of 0.486 s (SD \pm 0.25). For 5 footsteps there is a time difference of 1.9 s between the first footstep and the fifth, whereas for 3 footsteps the time difference is 0.9 s. Thus, in this study, a time of \sim 1–2 s is required for the olfactory information contained in a footstep to change on exposure to the environment to provide a sufficient difference in its olfactory signature for the dog to determine the trail's direction. Interestingly lobsters also take about 1–2 s to make a decision about which direction to turn when tracking a plume (Atema, 1996).

The dog has two pieces of information which it uses to determine the direction of a trail: (i) a number of discrete pieces of information, i.e. the number of footsteps; and (ii) the difference in the odour cue due to time. The interaction between these on the ability of the dog to determine direction has yet to be fully explored. For example, walking more slowly would increase the time difference between steps and may reduce the amount of discrete pieces of information required by the dog to determine direction. If time difference were the only factor involved, it should be theoretically possible for a dog to determine direction from 2 footsteps separated in their deposition by 2 s. However, the determination of direction is not just reliant on a difference in cues as provided by a difference in time. The dog also has to make a comparison between the different sources of information and it may be that a certain number are required (e.g. 5 footsteps in this study) for an accurate comparison to be made. Indeed pilot studies exploring this reveal that both the time difference between footsteps and the number of footsteps is important. Despite increasing time between footsteps we have been unable to observe dogs determining direction correctly from just 2 footsteps.

Caution must be expressed in reaching these conclusions. The influence of training on the dog's performance cannot be underestimated (cf. Schoon and De Bruin, 1994). The dogs used in this study were trained to determine directionality on 100 m tracks laid in grass, thus providing a large amount (for the dog) of olfactory information. Although dogs were able to perform the task in this study, specific training on the above task may reduce the amount of information required to make a determination of direction. Environmental conditions will influence the change in olfactory stimuli over time. The experiments here were conducted in the absence of strong winds on days, which were dull, not sunny and not raining (a typical Belfast day!). Differences in wind, humidity and temperature could all be expected to change the rate, and perhaps the way, that the olfactory information present in a footstep changes with time. Hence both training and environment may influence the dog's performance.

In summary, dogs trained to determine directionality required 5 sequential footsteps, i.e. discrete pieces of information, to determine the direction of an odour trail. It is likely that dogs use a comparative process comparing the odours of discrete footsteps to determine direction and require a 1–2 s time difference to 'decay' or change the odour within a footstep to provide the dog with an olfactory gradient it can use to determine direction. Further work is underway to explore the interaction between time and the amount of discrete information on the dog's ability to determine direction.

References

- Atema, J.** (1996) *Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors*. Biol. Bull., 191, 129–138.
- Baker, T.C. and Vickers, N.J.** (1997) *Pheromone mediated flight in moths*. In Cardé, R.T. and Minks, A.K. (eds), *Pheromone Research: New Directions*. Chapman and Hall, New York, pp. 248–264.
- Bryson, S.** (1984) *Search Dog Training*. Boxwood Press, Pacific Grove, CA.
- Budgett, H.M.** (1933) *Hunting by Scent*. Charles Scribner: New York.
- Cardé, R.T. and Mafra-Neto, A.** (1997) *Mechanisms of flight of male moths to pheromone*. In Cardé, R.T. and Minks, A.K. (eds), *Pheromone Research: New Directions*. Chapman and Hall, New York, pp. 275–290.
- Clifford, R.J.** (1958) *Some notes and theories on 'scent'*. J. R. Army Vet. Corps, 29, 145–152.
- Fenton, V.** (1992) *The use of dogs in search, rescue and recovery*. J. Wilder. Med., 3, 292–300.
- Furton, K.G. and Myers, L.J.** (2001) *The scientific foundation and efficacy of the use of canines as chemical detectors for explosives*. Talanta, 54, 487–500.
- Gomez, G. and Atema, J.** (1996) *Temporal resolution in olfaction: stimulus integration time of lobster chemoreceptor cells*. J. Exp. Biol., 199, 1771–1779.
- Johnson, G.R.** (1977) *Tracking Dogs. Theory and Method*. Arner, New York.
- Justus, K.A. and Cardé, R.T.** (2002) *Flight behaviour of males in two moths, Cadra cautella and Pectinophora gossypiella, in homogenous clouds of pheromone*. Physiol. Entomol., 27, 67–75.

- Kalmus, H.** (1955) *The discrimination by the nose of the dog of individual human odours and in particular of the odours of twins*. Br. J. Anim. Behav., 3, 25–31.
- Keller, T.A., Powell, I. and Weissburg, M.J.** (2003) *Role of olfactory appendages in chemically mediated orientation of blue crabs*. Mar. Ecol. Prog. Ser., 261, 217–231.
- Keller, T.A., Tomba, A.M. and Moore, P.A.** (2001) *Orientation in complex chemical landscapes: spatial arrangement of chemical sources influences crayfish food-finding efficiency in artificial streams*. Limnol. Oceanogr., 46, 238–247.
- Komar, D.** (1999) *The use of cadaver dogs in locating scattered, scavenged human remains: preliminary field trial results*. J. Forensic Sci., 44, 405–408.
- Kozłowski, C., Yopak, K., Voigt, R. and Atema, J.** (2001) *An initial study on the effects of signal intermittency on the odor plume tracking behavior of the American lobster, Homarus americanus*. Biol. Bull., 201, 274–276.
- Kurz, M.E., Billard, M., Rettig, M., Augustiniak, J., Lange, J., Larsen, M., Warrick, R., Mohns, T., Bora, R., Broadus, K., Hartke, G., Glover, B., Tankersley, D. and Marcouiller, J.** (1994) *Evaluation of canines for accelerant detection at fire scenes*. J. Forensic Sci., 39, 1528–1536.
- Lorenzo, N., Wan, T.L., Harper, R.J., Hsu, Y.L., Chow, M., Rose, S. and Furton, K.G.** (2003) *Laboratory and field experiments to identify Canis lupus var. familiaris active odor signature chemicals from drugs, explosives and humans*. Anal. Bioanal. Chem., 376, 1212–1224.
- Lowe, B.** (1981) *Hunting the Clean Boot. The working bloodhound*. Blandford Press, Poole.
- Mackenzie, S.A. and Schultz, J.A.** (1987) *Frequency of back-tracking in the tracking dog*. Appl. Anim. Behav. Sci., 17, 353–359.
- Mafra-Neto, A. and Cardé, R.T.** (1994) *Fine scale structure of pheromone plumes modulates upwind orientation of flying moths*. Nature, 369, 142–144.
- Mafra-Neto, A. and Cardé, R.T.** (1996) *Dissection of the pheromone-modulated flight of moths using single pulse response as a template*. Experientia, 52, 373–379.
- Mafra-Neto, A. and Cardé, R.T.** (1998) *Rate of realized interception of pheromone pulses in different wind speeds modulates almond moth orientation*. J. Comp. Physiol. A, 182, 563–572.
- Moore, P.A. and Atema, J.** (1991) *Spatial information in the three-dimensional fine structure of an aquatic odor plume*. Biol. Bull., 181, 408–418.
- Moore, P.A., Scholz, N. and Atema, J.** (1991) *Chemical orientation of lobsters, Homarus americanus, in turbulent odor plumes*. J. Chem. Ecol., 17, 1293–1307.
- Morrison, H.** (1980) *He went that-a-way*. Off Lead, 6, 10–11.
- Murlis, J., Willis, M.A. and Cardé, R.T.** (2000) *Spatial and temporal structures of pheromone plumes in fields and forests*. Physiol. Entomol. 25, 1–12.
- Pearsall, M.D. and Verbruggen, H.** (1982) *Scent – Training to Track, Search and Rescue*. Alpine Publications, Colorado.
- Research Randomizer** (2002) <http://www.randomizer.org>.
- Romanes, G.J.** (1887) *Experiments on the sense of smell in dogs*. Nature, July 21, 273–274.
- Schoon, G.A.A. and De Bruin, J.C.** (1994) *The ability of dogs to recognize and cross-match human odours*. Forensic Sci. Int., 69, 111–118.
- Schwartz, C.** (1980) *Project: which way?* Off Lead, 7, 22–25.
- Siegel, S.** (1956) *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, Tokyo.
- Smith, D.A., Ralls, K., Hurt, A., Adams, B., Parker, M., Davenport, B., Smith, M.C. and Maldonado, J.E.** (2003) *Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes (Vulpes macrotis mutica)*. Anim. Conserv., 6, 339–346.
- Steen, J.B. and Wilsson, E.** (1990) *How do dogs determine the direction of tracks?* Acta Physiol. Scand., 139, 531–534.
- Syrotuck, W.G.** (1972) *Scent and the Scenting Dog*. Arner, New York.
- Szinak, J.** (1985) *Identification of odours*. Int. Crim. Pol. Rev., 58–63.
- Thesen, A., Steen, J.B., and Døving, K.B.** (1993) *Behaviour of dogs during olfactory tracking*. J. Exp. Biol., 180, 247–251.
- Vickers, N.J.** (2000) *Mechanisms of animal navigation*. Biol. Bull., 198, 203–212.
- Weissburg, M.J.** (2000) *The fluid dynamical context of chemosensory behavior*. Biol. Bull., 198, 188–202.
- Weissburg, M.J. and Zimmer-Faust, R.K.** (1993) *Life and death in moving fluid — hydrodynamic effects on chemosensory-mediated predation*. Ecology, 74, 1428–1443.
- Weissburg, M.J. and Zimmer-Faust, R.K.** (1994) *Odor plumes and how blue crabs use them in finding prey*. J. Exp. Biol., 197, 349–375.
- Weissburg, M.J. and Dusenbery, D.B.** (2002) *Behavioral observations and computer simulation of blue crab movement to a chemical source in a controlled turbulent flow*. J. Exp. Biol., 205, 3387–3398.
- Wells, D.L. and Hepper, P.G.** (2003) *Directional tracking in the domestic dog, Canis familiaris*. Appl. Anim. Behav. Sci., 84, 297–305.

Accepted January 28, 2005