

# COMPARATIVE COGNITION & BEHAVIOR REVIEWS

## Behavioral and Cognitive Factors That Affect the Success of Scent Detection Dogs

**Camille A. Troisi, Daniel S. Mills, Anna Wilkinson,  
and Helen E. Zulch**

*School of Life Sciences  
University of Lincoln*

Scent detection dogs are used in a variety of contexts; however, very few dogs successfully complete their training, and many others are withdrawn from service prematurely due to both detection accuracy issues in the field and wider behavioral issues. This article aims to review our understanding of the factors affecting variation in scent detection dogs' learning of the tasks and performance in the field. For this we deconstructed the scent detection task into its key behavioral elements and examined the literature relating to the factors affecting variation in the dogs' success all across their development. We first consider factors that affect individuality and individual performance, in general, such as temperament, arousal, the handler–dog relationship, training regimes, and the housing and management of scent detection dogs. We then focus on tasks specific to scent detection dogs and critically appraise relevant literature relating to the learning and performance of these tasks by dogs. This includes prenatal and early life exposure and later environment, training regime, and the human–dog relationship, as well as performance limiting factors such as the need to pant in hot environments during work.

*Keywords: learning, performance, training, human–dog interactions, scent detection dogs*

---

### *Introduction*

Scent detection dogs are required to correctly identify a target odor, indicate its presence to their handler, and not indicate when the odor is absent. These dogs are used in a number of critically important roles to society, including the search for live people, cadavers, drugs, firearms, explosives, endangered species, and diseases (Browne, Stafford, & Fordham, 2006). A well-recognized problem in the production of animals for this work is that very few dogs successfully complete training (Maejima et al., 2007; Wilsson & Sundgren, 1997)

and many others are withdrawn from service prematurely (Evans, Herbold, Bradshaw, & Moore, 2007). Not only are these inefficiencies an economic problem in terms of cost and working efficiency, but poor performance by the dogs may reflect a range of ongoing welfare problems for the dogs involved, due to the disruptive effects of psychological distress (Cobb, Branson, McGreevy, Lill, & Bennett, 2015; Rooney, Clark, & Casey, 2016). In addition, in some contexts, unreliable performance can have catastrophic consequences for the

safety of both dogs and handlers working in the field, as well as those who depend on them, if a real threat is not detected. To develop sound strategies aimed at minimizing these risks, it is important to have a clear understanding of both the task required of the dog and how this is developed, together with the associated challenges; in this review we focus on the processes leading up to a successful working career. The scent detection exercise can be divided into four key performance tasks. The animal must

1. search an area, often indicated by its handler;
2. locate the target odor;
3. follow the target odor to its source; and
4. reliably alert at the source of the odor without alerting to nontarget odors.

Performance in each of these tasks is influenced by a diverse range of behavioral and cognitive factors from both a broad developmental perspective and more proximate task-execution perspective. Suboptimal activity in any of these has the potential to reduce performance in one or more of the four functional tasks just listed.

Our goal, by presenting this review and commentary on the current state of scientific knowledge in this area, is to encourage cooperation and synergy between academics interested in the purer aspects of animal cognition and professionals interested in either the preparation or deployment of dogs for scent detection in tasks. In the first part, we focus on environmental factors affecting the individual variation in behavioral predisposition seen within a population including personality and temperament, state-level factors, and broad environmental and management factors. In the second part, we focus more on the factors affecting the training of specific tasks associated with scent detection work.

---

**Author Note:** Daniel S. Mills, School of Life Sciences, University of Lincoln, Lincoln, LN6 7DL, United Kingdom.

Correspondence concerning this article should be addressed to Daniel S. Mills at [dmills@lincoln.ac.uk](mailto:dmills@lincoln.ac.uk).

**Acknowledgments:** We thank the Animal, Behaviour, Cognition and Welfare Research Group at the University of Lincoln. This research was supported by the Defense Science and Technology Laboratory.

## *Part 1: Factors Affecting Individual Variation Within the Population*

In this section, we examine factors that have an impact on behavioral variation within the dog population. We first consider how a dog's personality can affect its probability of successfully completing training and having a good performance in the field. We also investigate the impact of different levels of arousal on learning capabilities and performance and how individuals respond differently to stress. We then look at how handlers influence their dogs' behavior, before examining how different training regimes also affect dog behavior. Finally, we turn to the evidence showing how housing and more general management of dogs affect dogs' learning and performance.

### *The Personality of the Successful Scent Detection Dog*

There is evidence that an individual's personality (defined here as behavioral traits that are consistent over time and context) is linked to successful completion of training in scent detection dogs (e.g., Maejima et al., 2007), with a thorough review recently provided by Jamieson, Baxter, and Murray (2017). Accordingly we do not rereview the literature but do highlight some of the specific points of significance here. Traits that have consistently been identified as important in the selection of scent detection dogs include a strong motivation (to play or to search), boldness, and the ability to adapt and cope with stress stimuli (Jamieson et al., 2017; Maejima et al., 2007; McGarrity, Sinn, Thomas, Marti, & Gosling, 2016; Sinn, Gosling, & Hilliard, 2010; Svarterberg, 2002; Svobodová, Vápeník, Pinc, & Bartoš, 2008; Wilsson & Sinn, 2012). Working dogs also need to be cooperative with the handler, and obedient, but have some level of independence in making decisions (Diverio et al., 2017; Jamieson et al., 2017; Maejima et al., 2007). These latter features are likely to be affected by experience and training more than the more intrinsic personality traits reported, and thus the relative value of genetic selection versus experience management in shaping the optimal phenotype is likely to vary and needs further investigation. Another major challenge is the identification of the biological basis to these traits in terms of key underpinning processes or constructs. One approach to this is the reinforcement sensitivity theory of personality (Corr, 2004; Gray, 1970); this argues that ultimately an animal's behavior can be reduced to the tendency for approach or avoidance of given stimuli; likewise,

underpinning emotional processes must have a common currency to allow the trade-offs between different affective states to be evaluated and a final decision made. This is represented within the concept of core affect, which has a positive–negative dimension and arousal dimension (Mendl, Burman, & Paul, 2010).

Emotional valence has differential effects on learning (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Galea, Mallia, Rothwell, & Diedrichsen, 2015). Discrete emotional associations induced in training affect not only the readiness to form specific types of association but also memory consolidation and recall (Galea et al., 2015; Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012; Schwabe, Wolf, & Oitzl, 2010). In humans, this is clearly illustrated by the different areas of the brain activated during positive reinforcement or negative punishment (Delgado et al., 2000); the latter is mediated through the dorsal striatum, whereas the former is mediated through the insula (Wachter, Lungu, Liu, Willingham, & Ashe, 2009). Although punishment is often found to accelerate learning in humans (Galea et al., 2015; although see Wachter et al., 2009), this accelerated learning may relate to the change in arousal it brings rather than the processing of punishment per se. It is well established in humans that the use of positive reinforcements can increase memory retention (Galea et al., 2015; Penney, 1967), probably due to increased dopamine activity (Galea et al., 2015), but a review of the neurobiology of learning is beyond the scope of this review. In some cases, using rewards also has been shown to decrease reaction time in a learning task in humans, compared to using punishment (Wachter et al., 2009), potentially by engaging different behavioral motivational systems.

Within reinforcement sensitivity theory, three major systems are described that interact to influence the motivation of behavior in relation to appetitive (rewarding) or aversive (punishing) stimuli (Corr, 2013): the *behavioral approach system*, which responds to rewarding stimuli such as food or social partners; the *fight–flight–freeze system*, relating to aversive stimuli such as predators; and the *behavioral inhibition system*, relating to conflicting or uncertain stimuli. It is argued that there is considerable variability between individuals in the sensitivity of these systems that results in differences in personality/temperament (Corr, 2013). Accordingly, certain stimuli are perceived as more harmful or alternatively more rewarding by particular individuals due to differences in sensitivity relating to core affect (negative and positive activation sensitivity, sensu Sheppard & Mills, 2002). For example, individuals who score high

on *behavioral approach system* are more exploratory and strongly motivated by positive reinforcement (high in positive activation/extravert). They have high expectations of potential rewards; show high engagement when rewards can be earned; and are more likely to be affected by the lack of such a reward, which may be fueled by an incorrect response (Boksem, Tops, Kostermans, & De Cremer, 2008; De Pascalis, Varriale, & D’Antuono, 2010). It has recently been argued (Brady, Cracknell, Zulch, & Mills, 2018) that this focus on reward–aversion (positive–negative activation) sensitivity also provides a consistent framework for conceptualizing and classifying the behavior tests used to assess working dogs.

The concept of the “highly motivated/driven dog” can be deconstructed using this approach, but first it is worth noting that the term *motivation* is used in at least two distinct ways that need to be recognized to avoid poor decisions about the role of selection and training on performance. Motivation refers to a broad trait within an individual that leads to it taking action (the primary focus of the current section), but it can also refer to the intervening variable that leads to a specific action, for example, the tendency to eat or perform any other consummatory act at a given time (Hughes & Duncan, 1988). In this latter context, it reflects the current short-term changes in the individual’s physiological state, such as hunger or thirst in a given context, and so it is not a trait but a temporary state, and thus not directly related to personality (this form of motivation is considered later in relation to the incentivization and reinforcement of specific activities). When considering the “highly motivated dog,” there are obviously elements of motivation that are task specific (state-level motivation), but at the level of personality, there is almost certainly an element of reward sensitivity (positive activation) across a wide range of contexts (trait-level motivation). The variation in reward sensitivity between individuals is typically larger than that occurring within individuals for a given context; this means that it should be possible to predict an individual’s response across situations with some reliability (Braver et al., 2014; Ryan & Deci, 2000). Large interindividual variation also means that simple phenotypic characteristics, such as breed may be poor predictors on their own (Fadel et al., 2016). Given that part of the role of a scent detection dog is to explore areas and trace back odors to their source, it is unsurprising that motivation, as measured through personality questionnaires and behavioral coding, has often been associated with a higher probability of completing training (Maejima et al., 2007; McGarrity et al., 2016; Sinn et al.,

2010; Slabbert & Odendaal, 1999; Svobodová et al., 2008; Wilsson & Sinn, 2012). However, this may not predict success in the field as other characteristics, such as sensitivity to aversives may be important, for example, if the animal must work in a combat zone.

Although some behavioral traits have been associated with successful completion of training, the use of personality assessments on puppies to predict training success has had mixed results (Goddard & Beilharz, 1986; Slabbert & Odendaal, 1999; Svobodová et al., 2008). Goddard and Beilharz (1986) found weak correlations between three elements of a puppy test and training success in both military working dogs and potential guide dogs. Individuals that were more likely to pass the certification were found to be more willing to chase, catch and fetch a ball, and follow a rag drawn away from them when they were less than 7 weeks old (Svobodová et al., 2008), all indicative of a high level of positive activation. Likewise, in police dogs, Slabbert and Odendaal (1999) found a correlation between a positively reinforced retrieval test at 8 weeks and success in training; by contrast, the results of a startle test at 16 weeks (an assessment of negative activation) predicted aggression at 9 months. However, there is growing concern over the often implicit assumption in the literature (such as the aforementioned studies) that the behavioral measures used in puppy tests are reliable (i.e., results are replicable; Harvey et al., 2016; Riemer, Müller, Virányi, Huber, & Range, 2014) and the extent to which they might be generalized across working dog roles. However, we argue (Brady et al., 2018) that by focusing on the underlying emotional processes (such as that provided by reward sensitivity theory) involved across a range of tests rather than the specific behavior of dogs in particular contexts (such as the result from a single test like chasing a rag), greater generalization should be possible and genetic selection more reliable. This is because the underlying trait has a solid biological basis and its assessment is operationally defined across a range of tests designed to elicit that attribute, and so the effects of random error in the measure reduced.

### *Arousal, Performance, and Learning Effects*

Arousal, like “motivation,” may also refer to a trait-level feature as well as a more proximate state of the individual. Arousal is believed to affect performance in a curvilinear way in accordance to the Yerkes–Dodson Law (Yerkes & Dodson, 1908). For example, when testing dogs selected and trained for low arousal levels (assistance dogs that are required to perform tasks that

require inhibitory control), it has been found that their performance on an inhibitory control task increased when their arousal level was artificially increased, but increasing the arousal level (in a similar way) in dogs that already had a higher level of arousal (pet dogs) led to decreases in their performance (Bray, MacLean, & Hare, 2015). Thus the conditions under which dogs are expected to complete a task can have considerable impact on their performance. It is therefore critical that scent detection dogs are trained to perform well in their working environment and that the selection tests used actually reflect field conditions. It is also important to pay attention to the individual baseline arousal of every dog (trait-level arousal) to adapt the training and working environment to the optimal level for that particular dog. As with tests designed to assess different qualities of personality, the issues of test reliability and prior experience that might help an individual pass a specific test need to be considered. For example, prior experience with transparent barriers can improve performance on inhibitory control tasks (van Horik et al., 2018), and such a barrier was used in Bray et al.’s (2015) study, but the dogs’ previous experience with this was unknown.

The concept of arousal is closely related to stress, and in some situations the two terms may be used synonymously (e.g., when referring to a change in cortisol as a change in stress); however, in other contexts stress refers specifically to negative emotional arousal, and cortisol is not a specific measure of stress in this context. A scent detection dog can experience a wide range of stressors across its life, such as housing conditions, social isolation, training methods, transport, novel environments, and more general environmental conditions in the field. Distress can inhibit learning and block memory retrieval (Wolf, 2009) and thus reduce performance, particularly in unfamiliar environments (Pritchard, Hurly, Tello-Ramos, & Healy, 2016), but it can be difficult to tease out the effects of negative emotional arousal from the effects of a change in the level of arousal, and often the two interact. In addition, wider neuroendocrine associations can have differential effects on specific memory encoding, consolidation, and retrieval processes (Schwabe et al., 2010, 2012). Multiple mechanisms may also explain an effect; for example, increased arousal in humans may result in increased sensitivity to prediction errors as well as an increase in exploratory activity, both of which can increase the speed at which a correct solution may be found (Galea et al., 2015). Accordingly, generalizations about the specific mechanisms underpinning an observed effect should only be made with caution,

especially if based on a limited range of contexts. Nonetheless, increased memory consolidation following increased arousal can occur regardless of the valence of the emotion (Liu, Graham, & Zorawski, 2008; Nielson & Lorber, 2009; Nielson & Powless, 2007), but these effects on memory may be indirect through altering attention to or perception of the stimulus or reward during encoding (Sharot & Phelps, 2004). When individuals are emotionally aroused, activation of cortisol receptors in the amygdala can result in enhanced memory consolidation (Roosendaal, 2002; Schwabe et al., 2010). In this regard, Sümegi, Oláh, and Topál (2014) found that pet dogs exposed to negatively valenced stressors prior to a learning task showed better performance in working memory tasks. By contrast, pet dogs that had owners who tended to play more with them during the manipulation phase of a task committed more errors when retested in a memory task (Sümegi et al., 2014). These results might be used to suggest that the valence of the arousal rather than the level of arousal per se affects memory; however, Kis et al. (2017) found no long-term effect of the play session on memory in a learning task despite finding decreased performance after a bout of play. This result suggests that the emotional arousal following play may not interfere with memory consolidation so much but instead might have more of an effect on other processes relevant to performance, such as attention. Indeed, Affenzeller, Palme, and Zulch (2016) found that their play activity between training sessions increased the speed of learning in pet dogs. Although the exact mechanism underlying this process is unknown, it is possible that the change in arousal associated with play or emotional congruence between play and training with positive reinforcement might improve memory consolidation. This finding implies that both the timing of emotional arousal during training and its valence may be crucial for predicting performance outcome. In this regard, stressors prior to testing appear to lead to impairment of memory retrieval (Roosendaal, 2002; Schwabe et al., 2010). It is therefore important to distinguish the observed effect from its proposed underlying cause when considering the application of research results in the field. Only systematic evaluation of a given phenomenon in a range of settings can really exclude competing mechanistic hypotheses, and the lack of this is a major limitation to much of the working dog literature.

In general, stressful arousal results in facilitation of memory consolidation, but memory retrieval, and thus performance of a learned task, may be impaired by this process (Schwabe et al., 2010). There is also an important

relationship between arousal during initial encoding and retrieval. In humans, information that is learned under high arousal levels appears to be best recalled when individuals are in the same state of arousal; the same is also true with more normal arousal levels (Cahill, Gorski, & Le, 2003; Clark, Milberg, & Ross, 1983). Although no such experiments have been conducted with dogs, it may be particularly important for scent detection dogs to operate in the field at arousal levels that are consistent with the training context, and vice versa.

Arousal affects not only what is learned or remembered but also the way that individuals respond (Schwabe et al., 2010). In humans, increased arousal (both chronic and acute) can modulate the memory system used during a task, tending to favor habitual (as opposed to more cognitively flexible) responding (Schwabe et al., 2010). Given that it is important for scent detection dogs to have a certain degree of autonomy, a training system that encourages more rigid “habitual” responding could impinge on performance; to retain an effective degree of autonomy in decision making, it is therefore important that arousal during training remains manageable for the dog.

In conclusion, both the intensity and the type of arousal have the potential to influence the performance of scent detection dogs in training and in the field. It is important to consider whether dogs are positively or negatively aroused, as different types of arousal activate different areas of the brain, which in turn have different effects on memory. Future work should also consider training scent dogs in a situation that results in a similar arousal level to that which the dogs would experience in the field and investigating whether this leads to longer working careers. However, given the growing evidence that the bond and relationship between an owner and his or her dog can affect arousal levels, especially under stressful circumstances (Gácsi, Maros, Sernkvist, Faragó, & Miklósi, 2013), it is important to extend our consideration of factors affecting performance to the dog–handler unit.

### *Response to Handler Cues*

Handlers have an important role to play in mitigating (and potentially exacerbating) the stress of working dogs, as well as how they perform in the field; for example, in the working environment it is important that dogs readily respond to their handler’s cues. Haverbeke et al. (2010) found that military working dogs that underwent a particular familiarization and training program that increased dog–handler contact performed better than control

military working dogs, even though they appeared to pay less attention to the task (based on head and/or body orientation). However, dogs that underwent this familiarization program were also selected at purchase as being more sociable and showing less fear of humans prior to the start of the program, which could have affected the findings. However, other studies that have investigated the influence of increased contact between the dog and the handler, such as dogs living at the handler's home, have also shown positive correlations with increased obedience (Lefebvre, Diederich, Delcourt, & Giffroy, 2007) and increased performance (Foyer, Bjällerhag, Wilsson, & Jensen, 2014; Haverbeke et al., 2010) in military dogs. Nonetheless, it should be noted that both the studies of Lefebvre et al. (2007) and Foyer et al. (2014) used behavioral questionnaire rather than experimental manipulations to determine the effects, which may be more subject to bias, especially if those reporting are not blind to the conditions being compared.

Although contact between dog and handler is important, scent detection dogs also need to retain a degree of independence from their handler to be successful in the field. This need gives rise to a potential problem when extrapolating from the pet dog literature to the working dog. Pet dogs appear to be more socially dependent on humans; for example, they follow and look more at humans than (unspecified) working dogs (Topál, Miklósi, & Csányi, 1997). Pet dogs pay more attention to humans with whom they have a strong relationship (Horn, Range, & Huber, 2013). Thus, it is not surprising that in pet dogs, time spent gazing at the owner correlates positively with obedience performance (Braem & Mills, 2010), but pet dogs have also been reported to perform worse in an independent problem-solving task (getting food from a box) compared to working dogs (Topál et al., 1997) and worse at an inhibitory control detour task (Bray et al., 2015). It is possible that increased dependence on humans reduces problem-solving ability. Regardless of the mechanism behind this difference in performance, these findings present an important consideration when extrapolating findings from pet dogs to working dogs and when trying to determine the optimal handler–dog relationship for working dogs. Clearly, a balance needs to be struck between responsiveness to the human and problem solving; however, there are no data on which to base this. It is also important to appreciate the multifaceted nature of the relationship between an owner or handler and their dog and not to think it can be fully characterized by a single dimension, such as attachment (Mills, van der Zee, & Zulch, 2014). The

comprehensive deconstruction of the dog–owner relationship and assessment of the effects of each are important areas for future research.

The handler's own emotions can also have an effect on the dog. Even with a small sample size ( $n = 19$ ), it has been found that pet dogs pay more attention to their owners when their owner is happy compared to when she or he is sad (Morisaki, Takaoka, & Fujita, 2009). When stress was induced in the owner, but not the dog, pet dogs performed better in an object hiding and finding task (Sümegei et al., 2014), as do scent detection dogs during a scent detection task (Zubedat et al., 2014). Despite the particularly small sample size of Zubedat et al.'s (2014) study ( $n = 5$ ), and the stressors used in the two studies being different, similar results were found with pet and working dogs. It has been suggested that when the handlers are distressed, they are more likely to be distracted and so exert less control over the dog and therefore potentially interfere less, which means there are fewer chances of forced false identifications (Zubedat et al., 2014). However, there is also evidence of a physiological response by dogs in response to their handlers' stress levels. In working dogs used in prisons, a negative correlation was found between the handler's baseline cortisol and testosterone levels and the changes in the cortisol level of their dogs before and after a test search (Dreschel & Entendencía, 2013). Thus, it might be that the dogs' behavioral response to their handlers' stress levels is mediated by an effect of handler stress on the dogs' arousal level or some other form of physiological effect.

In conclusion, scent detection dogs need to be both obedient to and independent from their handler, but the handler's behavior and arousal can also affect the performance of their dog. The handler's arousal has been found to directly affect scent detection dog performance. Nonetheless, the effect of handler arousal level and emotional state on the success of the team needs to be understood further. Indirect correlations have also been found between the time that military dogs spend with their handler and their obedience and performance. However, whether this generalizes to scent detection dogs still remains unknown.

### *Training Regimes*

It is essential that both trainers and academics share a common language and understanding of the reinforcement and punishment and their effects (Table 1). Animals are motivated by both intrinsic and extrinsic factors, and these have different underlying mechanisms (Kleen, Sitomer, Killeen, & Conrad, 2006). With extrinsic motivation, reinforcement contingencies associated

with the physical environment and individuals will affect the propensity for a dog to perform a specific task or act at a specific time. Externally derived rewards generally do not decrease intrinsic motivation to complete a task, and may enhance it (Cameron & Pierce, 1994; Deci, 1972a). For example, in humans, verbal praise, compared to tangible rewards, has been found to increase intrinsic motivation (Cameron & Pierce, 1994). Both of these are externally derived, but they may be represented internally in very different ways; in the former case, there may be added value from the strengthening of the relationship that may follow. It is also possible that praise plays a role as a secondary reinforcer. Although we do not know at what level dogs may be able to represent such phenomena, it seems that domestic dogs, having shared their evolutionary history with humans, are sensitive to the emotional signals of humans (Albuquerque et al., 2016), to the point that they may have developed specific human-directed responses (Albuquerque, Guo,

Wilkinson, Resende, & Mills, 2018). However, extrinsic reinforcements can, in some circumstances, decrease intrinsic motivation (Deci, 1972b) as can punishment for poor performance, or negative feedback on performance (Deci, 1972a; Dickinson, 1989). It is therefore essential that handlers and trainers are fully aware of how their own behavior and actions may impact on their dog's future performance, beyond the provision of any intended reinforcement. This area requires much more research, although it is clear from several survey-based studies with pet dogs (Eskeland, Tillung, & Bakken, 2007; Hiby, Rooney, & Bradshaw, 2004), working dogs (Arnott, Early, Wade, & McGreevy, 2014), and military dogs (Haverbeke et al., 2010) that there is a relationship between training method and undesired behavior; dogs subjected to more punishment-based training methods also engage in more unwanted behavior. However, the correlational nature of these studies means that the causal direction of this relationship (if any) cannot

**Table 1.** Definitions of Positive and Negative Reinforcement and Punishment Adapted From Chance (1994) with Dog-Related Examples.

Action	Definition	Example
<b>Reinforcement</b>	<b>Procedures that strengthen or increase the long-term probability of behavior.</b>	<b>A specific desirable action is encouraged.</b>
Positive reinforcement	A response is followed by the appearance of or increase in the intensity of an attractive (appetitive) stimulus or event.	If a dog is asked to sit by a handler, and the handler gives it food, a toy, etc., after the correct behavioral response, the dog is likely to sit again when the same cue is provided.
Negative reinforcement	A response is followed by the removal of or decrease in the intensity of an aversive stimulus or event.	The pressure applied to the head of a dog through a head collar is relieved when the dog turns its head to the desired direction, so the dog is more likely to turn in the desired direction.
<b>Punishment</b>	<b>Procedures that weaken or decrease the long-term probability of behavior.</b>	<b>A specific undesirable action is discouraged, but no specific desirable alternative is encouraged.</b>
Positive punishment	A response is followed by the appearance of or increase in the intensity of an aversive stimulus or event.	A dog is given an electric shock, when it lunges on the lead toward sheep at such an intensity that the dog avoids sheep in future.
Negative punishment	A response is followed by the removal of or decrease in the intensity of an attractive stimulus or event.	A dog barking for its owner attention is completely ignored and so is less likely to perform this behavior in future.

be determined; each are equally plausible, despite the tendency for these authors to emphasize the possible role of punishment in the development of behavior problems. That said, it is worth noting that there is evidence that pet dogs that receive more rewards and less punishment during training, and with owners who play more with them, perform better at learning a novel task and are more obedient (Rooney & Cowan, 2011). Another study has compared the behavior of pet dogs trained at a school that used aversives extensively (pulled on the leash or physically forced to sit until responding as desired to a command) with one school that focused on positive reinforcement (rewarded with food or praise after a correct behavioral response); they reported that the latter dogs showed increased attentiveness toward their owner, but there was no effect on avoidance behavior (Deldalle & Gaunet, 2014), thus differences in performance may relate to differences in attention rather than the efficiency of positive versus negative reinforcement. Likewise, in military dogs, those trained with a shock collar showed more avoidance behavior than those that trained similarly but without the use of shock (Schilder & Van Der Borg, 2004). Given the importance of the handler–dog relationship and arousal discussed earlier, it seems reasonable to suggest that methods based on the use of positive reinforcement are preferable in terms of both performance outcome and potential risk to the subject; preferential attention should be given to how the behavioral goals required of a scent detection dog can be achieved maximizing the use these techniques.

Little is known about how training should be structured, but it is worth noting that the amount of time spent training (> 4 hr per week) has been shown to be positively correlated with completion of training in search dogs (Alexander, Friend, & Haug, 2011); in addition, both spacing and repetition of training sessions (training schedule) may be expected to affect the time to acquisition of a task but not necessarily the performance of dogs (Demant, Ladewig, Balsby, & Dabelsteen, 2011). In a study comparing training once a week to five times a week, laboratory dogs needed fewer sessions to learn tasks when trained only once a week (Meyer & Ladewig, 2008). The authors suggest that when training takes place only once a week, the dogs are more aroused during these sessions, which could help with retention and consolidation, but an alternative explanation may be found in studies examining other influences, such as sleep, on memory consolidation (e.g., Demant et al., 2011). It is therefore important to consider the structure of the training when attempting to make the training

more efficient, but as already mentioned, more research is necessary if we wish to fully understand the underlying mechanisms to the observed effects, particularly regarding the specific training of scent detection dogs.

Although most methods used for training working dogs rely on the routine application of operant conditioning principles (Lindsay, 2000; Pryor, 1999; see the Training Effect section for potential new, cognitive-based methods for this type of training), it is worth considering other methods. Given the explosion of interest in canine social cognition in the past 20 years, there is growing interest in the potential value of a range of more novel social-learning-oriented protocols. Comparison of learning through imitation (“Do as I do,” when a dog is first trained by operant conditioning techniques to match its behavior to familiar actions demonstrated by a human on command and is then able to use this rule to learn novel behaviors; Fugazza, 2011) to a simpler and more traditional individual reinforcement method found no difference in the subsequent performance of pet dogs in relation to simple tasks (Fugazza & Miklósi, 2014). Similarly, McKinley and Young (2003) found no advantage in the “model-rival” technique (in which the presence of a potential human rival is meant to enhance motivation to learn about the situation) over traditional associative techniques for establishing the retrieval of a named object by pet dogs. However, that said, Fugazza and Miklósi (2014) found that in the performance of more complex tasks (i.e., when pet dogs were required to perform a sequence of two actions), those trained on the “Do as I do” method outperformed those trained using traditional methods. Additional studies would be beneficial to further explore the comparative efficacy of specific techniques that take note of the dog’s remarkable social skills, especially given the degree of autonomous decision making required by scent detection dogs in the field. It may be that training paradigms that go beyond the rote learning of tasks but instead focus on the dog’s ability to appreciate the goal have the potential to be more efficient, once we can determine the best ways to do this.

In this regard, it should be noted that dogs can also learn from observing the behavior of a conspecific. Indeed, Slabbert and Rasa (1997) found that puppies that were allowed to observe their mother during a scent detection task between 6 and 12 weeks of age outperformed dogs that did not observe their mother, when tested at the age of 6 months. Further, pet dogs are more likely to investigate a location where a conspecific has just come from if they smelled a food odor on the conspecific’s snout, compared to when no such odor was



present (Heberlein & Turner, 2009). This result suggests that there may be novel ways to assist the development of scent detection dogs that have not yet been exploited.

Overall, exposure to nonspecific training has been found to be correlated with succeeding at a specific task. For instance, when comparing working dogs (agility-trained dogs, Schutzhund-trained dogs, search and rescue dogs, retriever working, and dogs trained in freestyle performances), which receive formal training, to pet dogs, which often do not, Marshall-Pescini, Valsecchi, Petak, Accorsi, and Previde (2008) found that the more widely trained dogs were more successful at completing a novel task (opening a box) and that untrained dogs spend more time looking at owners, potentially because they were less autonomous (Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato-Previde, 2009; Marshall-Pescini et al., 2008). These findings are reinforced by work with assistance dogs, which were also found to perform better than pet dogs on an inhibitory control detour task (Bray et al., 2015; although see earlier for the limitations of the inhibitory control detour task used). It is also worth noting that (unspecified) working dogs were not only better than pet dogs at performing a novel problem-solving task (pulling a dish containing meat from under a fence) but also more autonomous when they had to complete a task on their own (Topál et al., 1997). Thus it seems that a pet dog's dependence on humans might inhibit independent successful completion of tasks and that more general training might decrease this dependence on humans, potentially increasing the dog's autonomy when making decisions. Training is therefore essential not only for task-specific purposes but also to increase the dog's autonomy when encountering a novel situation. Autonomy is a critical ability in the scent detection dog.

To summarize, correlations have been identified between the training methods used and individual behavior and learning, in both pet and working dogs. However, the current literature has a heavy dependence on field reports rather than the experimental work that is required to establish causation. More experimental work is also needed not only to establish how training methods affect a scent dogs' specific performance but also to examine how the structure of the training program itself (including nonspecific training and experience) might affect a dog's potential in the long term. Finally, there is promising work on the use of more cognitive training methods, but these have yet to be incorporated in scent detection dog training. More comparative work on social and asocial learning would better inform trainers and handlers on the efficiency of these techniques.

### *Housing and General Management Effects on Learning and Performance*

Living conditions can affect learning ability, with enrichment producing developmental and physiological changes that result in improved performance of individuals in cognitive tasks. In rats, living in enriched environments (small social groups and with access to a variety of objects) can lead to an increase in the number of synapses and dendritic elaboration in the brain (Brienes, Klintsova, & Greenough, 2004). In this species, the benefits of enrichment include improved spatial working memory, stress coping, improved inhibitory control (for a review, see Stairs & Bardo, 2009), and reduced age-related deficits in attention (Harati et al., 2011). Certain forms of housing in dogs result in higher levels of anxiety and a greater tendency to be startled (see Rooney et al., 2016, for a review). It is therefore important to adapt the housing and working environment of dogs to minimize the risks and maximize the benefits. For example, separating dogs from conspecifics (Walker, Waran, & Phillips, 2014); putting dogs in small, dark rooms while cleaning their kennel (Gaines, 2008); and using noisy equipment (Mills, 2005) increase the distress of dogs and should be avoided in the housing of scent detection dogs (Rooney et al., 2016). Enrichment refers to the positive effect of a certain physical or social stimuli in the environment, but it is important to appreciate that increasing environmental complexity is not always enriching, regardless of the intention of the change. It is therefore important that the nature of the intervention and its impact are carefully assessed.

Social contact with humans or conspecifics both during working and nonworking time can potentially affect the development of fear responses of scent detection dogs. The likelihood of developing fear when encountering a new stimulus is believed to be increased if a dog encounters this new stimulus in the presence of a fearful conspecific (Landsberg, Hunthausen, & Ackerman, 2012), and some trainers use the presence of an unreactive dog to reduce fear in an individual exhibiting fear (Rooney et al., 2016). Nonetheless, the value of the presence of a calm individual in helping working dogs adjust to the range of stressors they encounter still needs to be assessed. Although there is consistent evidence that human interactions can provide a calming effect on pet dogs during stressful events (Gácsi et al., 2013; Hennessy, Williams, Miller, Douglas, & Voith, 1998; Tuber, Sanders, Hennessy, & Miller, 1996), specific interactions with humans can also increase a dog's fear response; for instance, after owners became angry, their

dogs' cortisol level has been reported to increase (Jones & Josephs, 2006).

Not only is there a proximate effect of social interactions on dog behavior, but there are longer term (ultimate) effects, especially as a result of early-life exposure. The seminal work of Scott and Fuller (1965) and others around this time (e.g., Fox, 1966) has highlighted the important role of deficits in the early environment on the normal behavioral development of dogs, but this work is often misrepresented, with its results being based on a very artificial environment, a very limited range of breeds, and often very small sample sizes. For example, the classic work of Freedman, King, and Elliot (1961), on which the definition and critical impact of the socialization phase of puppies were initially defined, had only one control puppy to establish the difficulty of later socialization, and subsequent work has largely sought to support rather than challenge this finding. In a more naturalistic setting using a retrospective study technique of clinical cases, Appleby, Bradshaw, and Casey (2002) found that puppies raised in nondomestic maternal environment between the ages of 3 and 6 months, and that did not have a lot of experience with urban environments during that time, were more likely to be aggressive toward unfamiliar people and show more avoidance behavior. Although there is evidence that socialization programs during the early life of dogs have a positive long-term effect on the dogs' behavior (Vaterlaws-Whiteside & Hartmann, 2017), the effects may not be as clear-cut or widespread as is often portrayed (Seksel, Mazurski, & Taylor, 1999), with adequate socialization often occurring naturally in the home. Using a longitudinal study, Vaterlaws-Whiteside and Hartmann (2017) found that puppies undergoing a particular socialization program based on nest stimulation theories had more desirable scores, associated with improved responsiveness toward humans and increased confidence within their environment (Asher et al., 2013). Responsiveness to humans and confidence are important qualities for scent detection dogs, given that they are likely to encounter many unfamiliar environments and people when in the field. However, whether the program used in the former study is relevant to or similarly effective for scent detection dogs compared to their normal management still needs to be assessed. Many studies on early life socialization have had mixed results, possibly because of the variability in the standard of the reference control condition. For instance, Gazzano, Mariti, Notari, Sighieri, and McBride (2008) found that the rearing environment (kennel vs. family home) had no major effect on puppies'

behavior tested other than vocalizations on separation. Likewise Seksel et al. (1999) found that structured socialization opportunities in early life above that naturally provided in a pet home had no effect on the puppies' obedience. Thus it seems that as long as animals are raised in good-quality social conditions (rather than the total isolation of the original experimental setups of the 1960s), general attempts at providing additional social enrichment may be less critical for the development of adaptive social skills than is widely implied. However, this does not mean that specific targeted interventions to produce the optimal socialization state for a given type of work will provide no benefit; more focused work is required to address this question and should begin with the operational definition of the "well-socialized" dog for the given task. In particular, there is a lack of work on early socialization effects in the scent detector dog (Bray, Sammel, Cheney, Serpell, & Seyfarth, 2017).

Compared to the social environment, the evidence concerning the effect of the physical environment on the long-term development of dogs is much clearer. Pluijmakers, Appleby, and Bradshaw (2010) compared the behavior of puppies raised with exposure to audio-visual playback of animate (people, dogs) and inanimate (traffic, vacuum cleaner) images for 20 min per day for 14 days between 3 and 5 weeks of age to those raised without. They found that puppies without exposure explored objects in familiar and unfamiliar environments more than those exposed to the playback at 5 weeks of age. When tested at 7–8 weeks of age, unexposed puppies also tended to explore objects more frequently (but not significantly more) and were more fearful in a novel environment than the exposed puppies. Thus, increased motivation to explore objects later in life was associated with increased fear (Pluijmakers et al., 2010). In addition, Lopes, Alves, Santos, and Pereira (2015) has found suggestive evidence (but no significant difference, potentially due to the small sample size;  $n = 6$ ) in military working dogs that puppies that experienced an enrichment park during early development, on top of their normal military dogs training, show reduced signs of stress (lower cortisol levels) and higher achievement scores.

There is good evidence of the potential beneficial impact of interventions on cognitive functioning in older dogs (Milgram, 2003; Milgram, Siwak-Tapp, Araujo, & Head, 2006), and this is of relevance if we wish to maximize the working life of military working dogs. In laboratory dogs, it has been found that enrichment effects interact with diet; for example, the beneficial effect of increasing antioxidant intake in aged dogs is greatly

increased when enrichment is added to the dogs' routine (Milgram et al., 2005). Both enrichment and diet have complex effects on cognitive functioning, and simple generalizations are unwise. A full review of the potential methods and interventions that might reduce aging is beyond the scope of this article.

Although there is no direct evidence that the rearing environment has an effect on the performance of scent detection dogs, the general effects described in dogs can potentially affect their search performance in the field. Overall there is a tendency in the literature to evaluate the effects of early rearing environment in terms of specific performance outcome measures or a limited range of general effects (most often exploration and avoidance due to fearfulness), but a wider appreciation of the potential emotional impacts (including on the expression of frustration) may provide valuable new insights. Tactile stimulation, because of its potential relationship with restraint, may be of particularly importance when considering the development of frustration tolerance, and there is growing interest in the role that early tactile stimulation has on neurological development and training of dogs. However, the work to date has produced mixed results. Battaglia (2009) suggested that early life tactile stimulation led to improved cardiovascular performance and more tolerance to stress, whereas Schoon and Berntsen (2011) found no effect of early life stimulation on later training results of mine detection dogs. As already mentioned in relation to other studies, a possible explanation for the discrepancies may be the quality of the control environments, which appear quite enriched in the study of Schoon and Berntsen. Gazzano et al. (2008) also reported a correlation between early life tactile stimulation and emotional development of puppies: Handled puppies were overall calmer, showed a longer latency to vocalize, and spent more time in exploratory activity in isolation compared to nonhandled puppies. Further investigation of this phenomenon is undoubtedly warranted to disentangle the effects of tactile stimulation from other forms of intervention and whether any effects are direct or through more general changes in physiology and stress reactivity.

### *Concluding Comments to Part 1*

In the first part of the review, we have evaluated the evidence relating to several socioenvironmental factors that can lead to individual differences in the

predisposition of dogs to training or field conditions, especially associated with scent detection work. In general, those working with dogs are having to extrapolate the science well beyond the available evidence; there is a particular lack of experimental studies aimed at elucidating the specific mechanism underpinning the effects seen. We have examined how some personality traits, which can be influenced by early experience as well as genetics, lead to differences in success both in training and in work. Motivation, as a trait, is particularly important in this regard but needs to be specifically defined if we wish to explore its mechanistic basis. Much work on personality and training success is correlational, or based on single measures with an assumption about their reliability; these seriously limit the depth of our understanding in this regard. Another key area for consideration is the role of arousal, which can have differential effects on learning and memory during training and field performance. It is particularly important that those working with scent detection dogs keep in mind how to develop the best possible dog *in the proposed field of operation* and not focus solely on the completion of training. This means attending to the role of the handler and the nature of the relationship with the dog. In general, time spent with a handler is positively correlated with obedience and performance, but there appears to have been little attention given to the wider cognitive skills and aptitudes that might make up the successful scent detection dog, especially how to instill the degree of autonomy required for the dog to be a confident decision maker in the field. Given the potential impact that the application of aversives may have on this, and the importance of the handler as a point of reference in the often stressful situations associated with scent detection work, we suggest, based on the available evidence, that the primary focus of training should be to train the correct response through the skillful use of positive-reinforcement-based methods. Nonetheless it is important that these dogs are resilient and able to cope effectively with stressors; the housing and general management of dogs may be particularly important in this regard, as well as providing the platform to the optimal working phenotype. Through this review it is clear that greater attention needs to be given, by both academics and dog professionals, to the wider aspects of the life of scent working dogs, which can affect their performance in the field beyond the task for which dogs are trained, if we wish to capitalize on their potential.

## *Part 2. Task-Specific Learning for Scent Detection Dogs*

We now focus on key factors that may influence training specific to scent detection dogs, which include searching an area, locating a target odor, following this target odor to its source, and reliably alerting at the odor's source. In this section, we first examine developmental process in odor discrimination with a focus on prenatal learning and the role of early life experience. We then investigate how different types of training affect dogs' performance at odor discrimination. We also look into how human cues influence performance in the field. We explore how to maintain the dogs' searching persistence in the field. We finish this part by discussing other factors that limit handler–dog performance in the field.

### *Developmental Processes Relating to Odor Perception and Discrimination*

Prenatal exposure has been found to help with odor discrimination and other preferences in a range of species, for example, rabbits (Bilkó, Altbäcker, & Hudson, 1994), cats (Hepper et al., 2012), humans (Mennella, Jagnow, & Beauchamp, 2001), sheep (Simitzis, Deligeorgis, Bizelis, & Fegeros, 2008), and rats (Smotherman, 1982). In dogs, individuals exposed prenatally to aniseed showed a preference for this stimulus 24 hr after birth (Wells & Hepper, 2006), but at 10 weeks of age, they no longer showed this olfactory preference (Hepper & Wells, 2006). However, when dogs were exposed to the odor both prenatally and postnatally, the preference for that odor remained when the dogs were 10 weeks old (Hepper & Wells, 2006). This result suggests that without postnatal exposure to the chemical stimulus, the effect of prenatal exposure may disappear when the pups wean (Hepper & Wells, 2006).

Early life exposure to stimuli generally improves sensory discrimination ability and related task learning later in life, and this clearly includes odor stimuli. In rats, after introducing odors in their home cage for 1-hr periods twice daily over 20 days, animals were better at discriminating between pairs of similar odors than they were before (Mandairon, Stack, & Linster, 2006). The authors suggest that this improvement is not necessarily specific to the odors used during the exposure period but that odors might have induced changes in the olfactory bulb network, which could have consequences on olfactory perception throughout the individuals' lifetime (Mandairon et al., 2006). Exposure to specific scents during early life not only might enhance

detection of these odors by detection dogs as a result of an initial preference but also could enhance the potential to discriminate and learn about them. Although this research was conducted in rats, it seems that odor enrichment, starting prenatally, would be beneficial to the training of scent detection dogs and could save time on later training.

### *Training Effects*

The number and diversity of odors that dogs have to learn to discriminate can have an impact on the individual's performance. Williams and Johnston (2002) found that when dogs (with unspecified backgrounds) learned to discriminate one odor after the other (up to 10 odors), there was no reduction in the number of odors they could detect and no increase in false alarms. Moreover, the amount of training required for each odor tended to decrease, as more odors were learned (Williams & Johnston, 2002). However, when dogs were trained to offer different alerts for each of two odors, they made more false positive alerts when both odors were present than when the dogs were trained to alert to only one of the two odors present (Lit & Crawford, 2006). This seems to demonstrate that the alert training itself and the decision-making process involved may influence performance. Alert training is an aspect of scent detection work that seems to have been largely overlooked in the research literature. When training scent detection dogs, Lit and Crawford (2006) suggested that trial runs in which no target odor is present might be very important to decrease the dogs' tendency to alert in any situation (negative control). In addition, higher performance can be achieved by including a positive control trial, in which the dog has to recognize an "easy" odor from several choices, prior to a scent detection task. This allows dogs to be more restrained in the subsequent task and make fewer errors when it comes to identifying the target odor (Schoon, 1996). Although the mechanism remains unclear, this increase in performance may be related to decrease in arousal.

There is also much potential to learn from the methods used in comparative psychology to improve training efficiency and retention (Wright et al., 2017). Wright et al. (2017) showed that dogs can learn to categorize odors, that they can generalize to novel stimuli from the same category, and that they can retain that information for more than 6 weeks. Wright et al. used both burned and unburned accelerants embedded in different odor stimuli, a situation similar to that encountered in the field. They found that animals with the categorical

information (accelerants, S+ counterbalanced across animals) performed significantly better than the pseudocategory control group, none of which could learn the task. This is the first evidence that nonhuman animals are able to learn to categorize nonbiologically relevant odors. Their results also suggest that the current scent detection dog training methods involving sequential rote learning might not be the most efficient, and further work should compare the two methods and explore the wider, well-established methods used in comparative cognition research for potential training innovations.

Recent work has revealed that pet dogs that learn an odor discrimination show greater improvement when the reward is delivered directly by the experimenter compared to when it was buried in the sand next to the correct odor (Hall, Smith, & Wynne, 2013). Close spatial contiguity between the odor and reward might elicit behavior that prevents dogs from performing as well or might interfere with target odor detection. Given that this research was performed with pet dogs, it is possible that the reward given by a human could influence the dogs' learning by making the reward more salient, and it is unclear how working dogs might respond in similar circumstances, as the handler may influence the performance of dogs in many ways as outlined in the next section.

#### ***Independent Problem Solving and Handlers' Influence***

Scent detection dogs have to generalize the search for one or more specific odor(s) from the training room to the field setting, detect that target odor from other odors, and work in novel environments. As they are working in a sensory domain that their handler cannot fully appreciate, they need to be able to work independently as well as in response to direction.

Pet and assistant dogs are able to use a lot of human cues such as pointing, nodding, and head turning when they are making choices (Miklósi, Polgárdi, Topál, & Csányi, 1998) and are very sensitive to potential cues from human behavior, but it is important that dogs selected and trained for scent detection work are not too reliant on human cues and indications. In avalanche-trained dogs, dogs performed better when they were less dependent on their handler as they spent more time exploring their environment (Diverio et al., 2017).

Owners are known to influence their dogs, and this can be counterproductive (Prato-Previde, Marshall-Pescini, & Valsecchi, 2008; Szetei, Miklósi, Topál, & Csányi, 2003; Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009). The implications of this in the working dog sphere have been well demonstrated by Lit,

Schweitzer, and Oberbauer (2011), who found that handlers erroneously called alerts on locations where they thought a target odor source was present, regardless of whether it really was.

Handlers also need to be trained appropriately to recognize their dog's alert signals, as Lasseter, Jacobi, Farley, and Hensel (2003) found that with cadaver dogs, handlers affected the reliability of the cadaver dog performance by missing the dog's signals and not recognizing the alert the dog was making. Although the sample size in that study was small ( $n = 5$ ), another small-sample-size study ( $n = 9$ ) similarly found that the majority of false negatives were due to the handler moving the dog away without realizing that the dog had detected the target (Wasser et al., 2004). In fact, even dog trainers are not always successful at correctly interpreting their dog's behavior, which might lead them to miss alerts in the field (Tami & Gallagher, 2009). A false negative while searching for a live person or for explosives can have catastrophic consequences in the field. Appropriate training of the handler is necessary to prevent poor performance due to these effects in the field. By contrast, false positives are not as detrimental, and it might be that the training should reflect the different costs of error in these choices. In humans it is well established that decision making is widely affected by the perceived risks involved associated with the consequences (Kahneman & Lovallo, 1993), but the implications of this do not appear to have been explored in, or applied to, working dog training.

#### ***Persistence***

While dogs attempt to locate an odor, the length of the search can affect their performance. Jezierski, Walczak, and Górecka (2008) found that for scent detection dogs, trials resulting in correct scent identification were shorter in time than those leading to incorrect identification. Although the sample size was small ( $n = 6$ ), the authors suggested that if dogs spend too long searching, they could "forget" the scent that they have to match during a match-to-sample test because they are distracted by other stimuli or because they are undecided and check the same stations several times (Jezierski et al., 2008). Whatever the reason, this work highlights the importance in scent detection dogs remaining motivated to search an area without being distracted until the whole area has been canvassed, regardless of whether any target odor has been detected. Previous studies have demonstrated that this is challenging for dogs and possibly handlers. For example, Porritt et al.

(2015) found that, in the field, search runs with no target scent during training were associated with decreased vigilance and detection rate. Similarly, Gazit, Goldblatt, and Terkel (2005) found that dogs might learn that a path did not have a target odor present and decrease their search behavior on that specific path. There are a number of possible explanations for these observations: Search behavior may extinguish if the frequency of target odors is too low, the dogs may alter the way they search the environment, or the handler's behavior may alter in the expectation of no finds. Whatever the explanation, this observation has major implications for the use of scent detection dogs in the field, as in many situations the probability of finding target odors is low, suggesting that if a dog continuously searches the same specific area without finding any target odor, it will decrease its search behavior in this specific area. Hence it is important for the scent detection dog to have a frequent but variable schedule of reinforcement in training and for it to be trained to search a wider range of areas without target odors so as to not associate a particular area with a lack of presence of the target odor.

If dogs were trained under similar conditions to those found in the field, it might be expected that dogs would show higher performance once in the field, and extinction of search behavior would be less likely. On the other hand, behavioral momentum theory (a quantitative model that describes the strength of a behavior and its resistance to extinction, noncontingent delivery of reinforcers, and reinforcer satiation; Hall, 2017) predicts that richer schedules of reinforcement would lead to greater resistance to disruption (Hall, 2017). This was found to be the case for pet dogs in an odor discrimination task (Hall, Smith, & Wynne, 2015). So training dogs to a lower schedule of reinforcement may mean that the behavior is more likely to be susceptible to disruptors. The results of Porritt et al. (2015) and Gazit et al. (2005), alongside an appreciation of behavioral momentum theory (Hall, 2017; Hall et al., 2015), would indicate that increasing the schedule of reinforcement in the field could be highly beneficial to the performance of scent detection dogs. In fact, Porritt et al. suggested that this could be done by training dogs with an additional nondangerous odor as "target." These safe and innocuous targets, which can then be hidden during field runs, could be used to maintain search patterns and performance on target odors (Porritt et al., 2015). This would also allow training and field context to be more similar, with the provision of a higher rate of reinforcement, which should increase resistance to the extinction of search behavior.

The handler's behavior may also affect the dog's persistence. For instance, pet dogs that were told to lie down by their owner were found to obey for longer (stayed lying down more often and/or for longer) when their owner was watching them compared to when the owner was not (Schwab & Huber, 2006). Similarly, during an object manipulation task, pet dogs were found to manipulate an object for less time when the owner was absent compared to when he was present (Horn, Range, & Huber, 2013) and spent less time searching when they received a negative or fearful expression of emotion from the owner compared to a positive emotional expression (Merola, Prato-Previde, Lazzaroni, & Marshall-Pescini, 2014). Despite the caveats discussed earlier concerning the difference between pet and working dogs in relation to handler cues, it is possible that this is also the case for scent detection dogs: The handler's focus on the dog might be a predictor of the team's performance. However, the optimal balance between appropriate handler guidance of the dog and the dog's ability to make independent decisions still needs to be elucidated.

Further support for the importance of the dog-handler relationship is provided by the work of Horn, Huber, and Range (2013), who suggested that handlers should ensure that they act as a secure base for the dog, similar to the healthy bond found between parents and their children, which enables the child to be more confident in its exploration of a novel environment. A carer who acts as a secure base is sensitive to their child's needs but also consistently supportive of the child. In children, it was found that the secure base effect improves problem solving (Matas, Arend, & Sroufe, 1978), persistence, and exploration (Matas et al., 1978). The secure base effect is also associated with reduced distress and facilitates learning in humans (Passman, 1977). These are both desirable features in the scent detection dog, but we suggest that it is difficult to achieve if a handler is inconsistent in his or her behavior toward the dog (i.e., is associated with the intermittent delivery of negative reinforcement and/or punishment). In dogs of unspecified background, it has been found that in otherwise highly aroused individuals, the secure base effect of an owner may reduce heart rate and signs of distress when facing a threat (Gácsi, Maros, Sernkvist, & Miklósi, 2009). We do not know the extent of the secure base effect on scent detection dogs' performance and resilience, but this significant gap in our knowledge needs to be rectified, given the earlier comments on the effects of arousal on performance.

In conclusion, the available data suggest that similarity between training and field conditions, as well as

a high frequency of reinforcers, are important to maintaining persistence and resistance to extinction. The effects of handlers on the persistence of their dogs is less clearly defined. Nonetheless, there are specific measures that can be implemented on the basis of current findings, and the effect of these on scent detection dog training and performance in the field should be compared to current practices.

### *Performance-Limiting Factors*

Preexposure to strenuous exercise has been associated with reduced performance in an odor detection task in scent detection dogs (Gazit & Terkel, 2003). This may not be the result of any effect on arousal but rather because exercise increased panting, and dogs cannot pant and sniff at the same time. Panting may also result from the increased arousal (which itself might reduce performance in line with the Yerkes–Dodson Law) associated with distress, such as anxiety or frustration (Dreschel & Granger, 2005; Godbout, Palestrini, Beauchamp, & Frank, 2007; Landsberg, Mougeot, Kelly, & Milgram, 2015; McCobb, Brown, Damiani, & Dodman, 2001; Sheppard & Mills, 2003), and so stress management in scent detection dogs is of particular importance. Both exercise, particularly in hot conditions, and stress might have a direct impact on scent detection performance by physically limiting the amount that dogs are able to sniff.

Housing should provide a safe, secure environment for dogs and allow them to recover after work. Hewison, Wright, Zulch, and Ellis (2014) found that the living environment had a direct effect on the individuals' behavior and probably welfare. Prolonged exposure to kennel noise has also been shown to affect dogs' hearing, and hearing damage has been suggested to affect dogs' mental readiness and ability to respond to cues (Scheifele, Martin, Clark, Kemper, & Wells, 2012). Reducing noise levels could therefore serve to increase performance through this mechanism as well. Improved housing environments are also linked to improved performance, mediated by good welfare. For instance, in mice, enrichment enhances cognitive flexibility (for discrimination and reversal learning tasks; Zeleznikow-Johnston, Burrows, Renoir, & Hannan, 2017), and in captive pigeons, individuals exposed to an enriched environment (in this case, a large cage with three other pigeons for 4 hr a day) were less likely to make suboptimal and risky choices (Pattison, Laude, & Zentall, 2013). Pattison et al. (2013) suggested that nonenriched pigeons were less stimulated in their normal environment, and therefore their

arousal is increased during task performance. Enriched pigeons may exhibit better self-control during the task because of the increased stimulation. Enriched environments in scent detection dogs could therefore potentially reduce the number of errors during scent identification. In dogs, there are clear links between poor welfare and performance, as frustrated, apathetic, or fearful dogs have more difficulty in learning and decreased attention (Arnott et al., 2014; Haverbeke, Laporte, Depiereux, Giffroy, & Diederich, 2008; Rooney, Gaines, & Hiby, 2009). These findings were collected with working dogs from several sources—stock-herding dogs and military dogs, indicating a general effect in dogs, which can be expected to apply to scent detection dogs too. Clearly, given the diverse potential effects of kennel enrichment, there is a need for well-designed hypothesis-driven research on its effects on performance parameters of relevance to scent detection dogs.

### *Concluding Remarks on Part 2*

In this section we investigated socioenvironmental factors that particularly affect the behavior and performance of scent detection dogs. Innovations such as perinatal exposure to relevant odors and olfactory enrichment could help scent detection dogs achieve their biological potential. Subsequent training should focus on optimizing odor discrimination ability. In this regard, it is clear that dogs can be trained on a high number of odors without impacting their discrimination abilities, but they might not always alert correctly. Using novel training methods taken from well-established literature with other species is an important way to address this issue. Further, controlling arousal in the field might also be particularly important to minimize the risks here, as well as establishing the optimal balance between independent problem solving and reliance on handler-given cues. Dogs are clearly sensitive to human cues, but it is essential for working dogs to retain a degree of independence, and training programs should look to strike this balance. Therefore, there is also a need to improve the training of handlers to reduce the tendency for them to inadvertently force an alert from their dogs or miss their dogs. Handlers may also have a critical role to play in the persistence of scent detection dogs in the field. Training that matches training to field conditions, with the frequent use of positive reinforcers should increase resistance to extinction. There is also a need for greater awareness of three specific factors that affect the performance on scent detections dogs: panting, which prevents dogs from sniffing; hearing loss, which prevents dogs

from hearing commands; and appropriate stimulation while dogs are not being trained.

### *Conclusion and Future Directions*

We have reviewed the available evidence on how social and environmental factors affect the behavioral development and overall success of scent detection dogs. Domestic dogs are influenced by humans across all aspects of their development, and the impact of this should not be underestimated, but with the growing importance of the work of these dogs for security, it is essential that we ensure that their training makes best use of the available and growing scientific literature, rather than being based on traditional practice. The way dogs are trained, as well as the environment in which they live, affect what and how they learn. This must be considered alongside individual factors such as intrinsic motivation. These not only influence general learning and behavioral responses of the scent detection dogs but also affect performance on specific tasks necessary for the dogs to complete a scent detection exercise, such as (a) searching an area, (b) locating a target odor, and (c) following to it to its source, as well as (d) alerting to the handler at the source of the odor. These aspects must be taken into account to improve training success and reduce instances of premature withdrawal from service.

Regarding dogs searching an area, the results discussed here indicate that increasing the time spent by handlers with their dogs may improve obedience, which is essential when a handler indicates an area to be searched. An increased focus on the use of rewards to reinforce appropriate behavior may help to improve learning and attentiveness of the dog. Enrichment (both physical and social) may also help to improve memory and resilience. Setting up training so that a high frequency of reinforcement can be maintained in the field should be encouraged, as this is likely to lead to greater resistance to extinction of search behavior. This can be achieved by training to and using safe target odors in field searches. Regarding the location of target odor, dogs can be trained to discriminate a high number of odors, but there are potential changes in the training methods that are widely used, which could help improve the efficiency of training and decrease the probability of false alerts, not least the use of the training of olfactory categorical learning. Targeted olfactory exposure and enrichment early may be critical in maximizing the developmental potential of scent detection dogs. In the field, panting—due to either exercise or stress—should

be avoided, as it interferes with the sniffing of odors. Dogs should also be provided with stimulation outside the training context focused on improving their self-control in the field, allowing them to follow a target odor to its source more effectively. Stressful housing conditions should be avoided, as it decreases a dog's effectiveness. Scientific techniques developed to investigate memory and processing in other species should be harnessed to train detection dogs. Finally, there is also a need to specifically focus on the competence and skill set of handlers so that they fully appreciate how their behavior and relationship might impact the performance of scent detection dogs, both in training and in the field, as it seems they may be responsible for a notable proportion of apparent errors by the dog.

### *References*

- Affenzeller, N., Palme, R., & Zulch, H. (2016). Playful activity post-learning improves training performance in Labrador Retriever dogs (*Canis lupus familiaris*). *Physiology & Behavior*, *168*, 62–73. doi:10.1016/j.physbeh.2016.10.014
- Albuquerque, N., Guo, K., Wilkinson, A., Resende, B., & Mills, D. S. (2018). Mouth-licking by dogs as a response to emotional stimuli. *Behavioural Processes*, *146*, 42–45. doi:10.1016/j.beproc.2017.11.006
- Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*, *12*(1), 20150883. doi:10.1098/rsbl.2015.0883
- Alexander, M. B., Friend, T., & Haug, L. (2011). Obedience training effects on search dog performance. *Applied Animal Behaviour Science*, *132*, 152–159. doi:10.1016/j.applanim.2011.04.008
- Appleby, D. L., Bradshaw, J. W. S., & Casey, R. A. (2002). Relationship between aggressive and avoidance behaviour by dogs and their experience in the first six months of life. *Veterinary Record*, *150*, 434–438.
- Arnott, E. R., Early, J. B., Wade, C. M., & McGreevy, P. D. (2014). Environmental factors associated with success rates of Australian stock herding dogs. *PLoS ONE*, *9*(8). doi:10.1371/journal.pone.0104457



- Asher, L., Blythe, S., Roberts, R., Toothill, L., Craigon, P. J., Evans, K. M., ... England, G. C. W. (2013). A standardized behavior test for potential guide dog puppies: Methods and association with subsequent success in guide dog training. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8, 431–438. doi:10.1016/j.jveb.2013.08.004
- Battaglia, C. L. (2009). Periods of early development and the effects of stimulation and social experiences in the canine. *Journal of Veterinary Behavior: Clinical Applications and Research*, 4, 203–210. doi:10.1016/j.jveb.2009.03.003
- Bilkó, Á., Altbäcker, V., & Hudson, R. (1994). Transmission of food preference in the rabbit: The means of information transfer. *Physiology and Behavior*, 56, 907–912. doi:10.1016/0031-9384(94)90322-0
- Boksem, M. A. S., Tops, M., Kostermans, E., & De Cremer, D. (2008). Sensitivity to punishment and reward omission: Evidence from error-related ERP components. *Biological Psychology*, 79, 185–192. doi:10.1016/j.biopsycho.2008.04.010
- Brady, K., Cracknell, N., Zulch, H., & Mills, D. S. (2018). A systematic review of the reliability and validity of behavioural tests used to assess behavioural characteristics important in working dogs. *Frontiers in Veterinary Science*, 5, 103. doi:10.3389/fvets.2018.00103
- Braem, M. D., & Mills, D. S. (2010). Factors affecting response of dogs to obedience instruction: A field and experimental study. *Applied Animal Behaviour Science*, 125, 47–55. doi:10.1016/j.applanim.2010.03.004
- Braver, T. S., Krug, M. K., Chiew, K. S., Kool, W., Westbrook, J. A., Clement, N. J., ... Somerville, L. H. (2014). Mechanisms of motivation-cognition interaction: challenges and opportunities. *Cognitive, Affective & Behavioral Neuroscience*, 14, 443–472. doi:10.3758/s13415-014-0300-0
- Bray, E. E., MacLean, E. L., & Hare, B. A. (2015). Increasing arousal enhances inhibitory control in calm but not excitable dogs. *Animal Cognition*, 18, 1317–1329. doi:10.1007/s10071-015-0901-1
- Bray, E. E., Sammel, M. D., Cheney, D. L., Serpell, J. A., & Seyfarth, R. M. (2017). Effects of maternal investment, temperament, and cognition on guide dog success. *Proceedings of the National Academy of Sciences*, 201704303. doi:10.1073/pnas.1704303114
- Briones, T. L., Klintsova, A. Y., & Greenough, W. T. (2004). Stability of synaptic plasticity in the adult rat visual cortex induced by complex environment exposure. *Brain Research*, 1018, 130–135. doi:10.1016/j.brainres.2004.06.001
- Browne, C., Stafford, K., & Fordham, R. (2006). The use of scent-detection dogs. *Irish Veterinary Journal*, 59, 97–104.
- Cahill, L., Gorski, L., & Le, K. (2003). Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. *Learning & Memory*, 10, 270–274. doi:10.1101/lm.62403
- Cameron, J., & Pierce, W. D. (1994). Reinforcement, reward, and intrinsic motivation: A meta-analysis. *Review of Educational Research*, 64, 363–423.
- Chance, P. (1994). *Learning and behaviour* (3rd ed.). Belmont, CA: Brooks/Cole.
- Clark, M. S., Milberg, S., & Ross, J. (1983). Arousal cues arousal-related material in memory: Implications for understanding effects of mood on memory. *Journal of Verbal Learning and Verbal Behavior*, 22, 633–649. http://dx.doi.org/10.1016/S0022-5371(83)90375-4
- Cobb, M., Branson, N., McGreevy, P., Lill, A., & Bennett, P. (2015). The advent of canine performance science: Offering a sustainable future for working dogs. *Behavioural Processes*, 110, 96–104. doi:10.1016/j.beproc.2014.10.012
- Corr, P. J. (2004). Reinforcement sensitivity theory and personality. *Neuroscience and Biobehavioral Reviews*, 28, 317–332. doi:10.1016/j.neubiorev.2004.01.005
- Corr, P. J. (2013). Approach and avoidance behaviour: Multiple systems and their interactions. *Emotion Review*, 5, 285–290. doi:10.1177/1754073913477507

- Deci, E. L. (1972a). The effects of contingent and noncontingent rewards on employee satisfaction and performance. *Organisational Behavior and Human Performance*, 8, 217–229. doi:10.1080/00223980.1982.9915335
- Deci, E. L. (1972b). Intrinsic motivation, extrinsic reinforcement, and inequity. *Journal of Personality and Social Psychology*, 22, 113. doi:10.1037/h0032355
- Deldalle, S., & Gaunet, F. (2014). Effects of 2 training methods on stress-related behaviors of the dog (*Canis familiaris*) and on the dog-owner relationship. *Journal of Veterinary Behavior: Clinical Applications and Research*, 9(2), 58–65. doi:10.1016/j.jveb.2013.11.004
- Delgado, M. R., Nystrom, L. E., Fissell, C., Noll, D. C., & Fiez, J. A. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. *Journal of Neurophysiology*, 84, 3072–3077.
- Demant, H., Ladewig, J., Balsby, T. J. S., & Dabelsteen, T. (2011). The effect of frequency and duration of training sessions on acquisition and long-term memory in dogs. *Applied Animal Behaviour Science*, 133, 228–234. doi:10.1016/j.applanim.2011.05.010
- De Pascalis, V., Varriale, V., & D'Antuono, L. (2010). Event-related components of the punishment and reward sensitivity. *Clinical Neurophysiology*, 121, 60–76. doi:10.1016/j.clinph.2009.10.004
- Dickinson, A. M. (1989). The effects of extrinsic reinforcement on intrinsic motivation. *The Behavior Analyst*, 12, 1–15. doi:10.1007/BF03392473
- Diverio, S., Menchetti, L., Riggio, G., Azzari, C., Iaboni, M., Zasso, R., ... Santoro, M. M. (2017). Dogs' coping styles and dog-handler relationships influence avalanche search team performance. *Applied Animal Behaviour Science*, 191, 67–77. doi:10.1016/j.applanim.2017.02.005
- Dreschel, N. A., & Entendencia, K. (2013). Stress during certification testing in prison drug detection dogs and their handlers. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8(4), e28. doi:10.1016/j.jveb.2013.04.005
- Dreschel, N. A., & Granger, D. A. (2005). Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers. *Applied Animal Behaviour Science*, 95, 153–168. doi:10.1016/j.applanim.2005.04.009
- Eskeland, G. E., Tillung, R. H., & Bakken, M. (2007). The importance of consistency in the training of dogs. The effect of punishment, rewards, rule structures and attitude on obedience and problem behaviors in dogs [Abstract]. *Journal of Veterinary Behavior: Clinical Applications and Research*, 2(3), 99. doi:10.1016/j.jveb.2007.04.040
- Evans, R. I., Herbold, J. R., Bradshaw, B. S., & Moore, G. E. (2007). Causes for discharge of military working dogs from service: 268 cases (2000–2004). *Journal of the American Veterinary Medical Association*, 231, 1215–1220. doi:10.2460/javma.231.8.1215
- Fadel, F. R., Driscoll, P., Pilot, M., Wright, H., Zulch, H., & Mills, D. (2016). Differences in trait impulsivity indicate diversification of dog breeds into working and show lines. *Scientific Reports*, 6, 1–10. doi:10.1038/srep22162
- Fox, M. W. (1966). Neuro-behavioral ontogeny: A synthesis of ethological and neurophysiological concepts. *Brain Research*, 2, 3–20. doi:10.1016/0006-8993(66)90059-X
- Foyer, P., Bjällerhag, N., Wilsson, E., & Jensen, P. (2014). Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test. *Applied Animal Behaviour Science*, 155, 93–100. doi:10.1016/j.applanim.2014.03.006
- Freedman, D. G., King, J. A., & Elliot, O. (1961). Critical period in the social development of dogs. *Science*, 133(3457), 1016–1017. doi:10.1126/science.133.3457.1016

- Fugazza, C. (2011). *Do as I do—Il cane impara guardandoci* [Do as I do—The dog learns by watching us]. Fenegro, Italy: Haqihana.
- Fugazza, C., & Miklósi, Á. (2014). Should old dog trainers learn new tricks? The efficiency of the Do as I do method and shaping/clicker training method to train dogs. *Applied Animal Behaviour Science*, *153*, 53–61. doi:10.1016/j.applanim.2014.01.009
- Gácsi, M., Maros, K., Sernkvist, S., Faragó, T., & Miklósi, Á. (2013). Human analogue safe haven effect of the owner: Behavioural and heart rate response to stressful social stimuli in dogs. *PLoS ONE*, *8*(3). doi:10.1371/journal.pone.0058475
- Gácsi, M., Maros, K., Sernkvist, S., & Miklósi, Á. (2009). Does the owner provide a secure base? Behavioral and heart rate response to a threatening stranger and to separation in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, *4*, 90–91. doi:10.1016/j.jveb.2008.09.042
- Gaines, S. A. (2008). *Kennelled dog welfare—Effects of housing and husbandry*. Bristol, England: University of Bristol.
- Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. *Nature Neuroscience*, *18*, 597–602. doi:10.1038/nn.3956
- Gazit, I., Goldblatt, A., & Terkel, J. (2005). The role of context specificity in learning: The effects of training context on explosives detection in dogs. *Animal Cognition*, *8*, 143–150. doi:10.1007/s10071-004-0236-9
- Gazit, I., & Terkel, J. (2003). Explosives detection by sniffer dogs following strenuous physical activity. *Applied Animal Behaviour Science*, *81*, 149–161. doi:10.1016/S0168-1591(02)00274-5
- Gazzano, A., Mariti, C., Notari, L., Sighieri, C., & McBride, E. A. (2008). Effects of early gentling and early environment on emotional development of puppies. *Applied Animal Behaviour Science*, *110*, 294–304. doi:10.1016/j.applanim.2007.05.007
- Godbout, M., Palestini, C., Beauchamp, G., & Frank, D. (2007). Puppy behavior at the veterinary clinic: A pilot study. *Journal of Veterinary Behavior: Clinical Applications and Research*, *2*, 126–135. doi:10.1016/j.jveb.2007.06.002
- Goddard, M. E., & Beilharz, R. G. (1986). Early prediction of adult behaviour in potential guide dogs. *Applied Animal Behaviour Science*, *15*, 247–260. doi:10.1016/0168-1591(86)90095-X
- Gray, J. A. (1970). The psychophysiological basis of introversion–extraversion. *Behaviour Research and Therapy*, *8*, 249–266. doi:10.1016/0005-7967(70)90069-0
- Hall, N. J. (2017). Persistence and resistance to extinction in the domestic dog: Basic research and applications to canine training. *Behavioural Processes*, *141*(Part 1), 67–74. doi:10.1016/j.beproc.2017.04.001
- Hall, N. J., Smith, D. W., & Wynne, C. D. L. (2013). Training domestic dogs (*Canis lupus familiaris*) on a novel discrete trials odor-detection task. *Learning and Motivation*, *44*, 218–228. doi:10.1016/j.lmot.2013.02.004
- Hall, N. J., Smith, D. W., & Wynne, C. D. L. (2015). Pavlovian conditioning enhances resistance to disruption of dogs performing an odor discrimination. *Journal of the Experimental Analysis of Behavior*, *103*, 484–497. doi:10.1002/jeab.151
- Harati, H., Majchrzak, M., Cosquer, B., Galani, R., Kelche, C., Cassel, J. C., & Barbelivien, A. (2011). Attention and memory in aged rats: Impact of lifelong environmental enrichment. *Neurobiology of Aging*, *32*, 718–736. doi:10.1016/j.neurobiolaging.2009.03.012
- Harvey, N. D., Craigon, P. J., Sommerville, R., McMillan, C., Green, M., England, G. C. W., & Asher, L. (2016). Test–retest reliability and predictive validity of a juvenile guide dog behavior test. *Journal of Veterinary Behavior: Clinical Applications and Research*, *11*, 65–76. doi:10.1016/j.jveb.2015.09.005

- Haverbeke, A., Laporte, B., Depiereux, E., Giffroy, J. M., & Diederich, C. (2008). Training methods of military dog handlers and their effects on the team's performances. *Applied Animal Behaviour Science*, *113*, 110–122. doi:10.1016/j.applanim.2007.11.010
- Haverbeke, A., Messaoudi, F., Depiereux, E., Stevens, M., Giffroy, J. M., & Diederich, C. (2010). Efficiency of working dogs undergoing a new Human Familiarization and Training Program. *Journal of Veterinary Behavior: Clinical Applications and Research*, *5*, 112–119. doi:10.1016/j.jveb.2009.08.008
- Heberlein, M. T. E., & Turner, D. C. (2009). Dogs, *Canis familiaris*, find hidden food by observing and interacting with a conspecific. *Animal Behaviour*, *78*, 385–391. doi:10.1016/j.anbehav.2009.05.012
- Hennessy, M. B., Williams, M. T., Miller, D. D., Douglas, C. W., & Voith, V. L. (1998). Influence of male and female petters on plasma cortisol and behaviour: Can human interaction reduce the stress of dogs in a public animal shelter? *Applied Animal Behaviour Science*, *61*, 63–77. doi:10.1016/S0168-1591(98)00179-8
- Hepper, P. G., & Wells, D. L. (2006). Perinatal olfactory learning in the domestic dog. *Chemical Senses*, *31*, 207–212. doi:10.1093/chemse/bjj020
- Hepper, P. G., Wells, D. L., Millsopp, S., Kraehenbuehl, K., Lyn, S. A., & Mauroux, O. (2012). Prenatal and early sucking influences on dietary preference in newborn, weaning, and young adult cats. *Chemical Senses*, *37*, 755–766. doi:10.1093/chemse/bjs062
- Hewison, L. F., Wright, H. F., Zulch, H. E., & Ellis, S. L. H. (2014). Short term consequences of preventing visitor access to kennels on noise and the behaviour and physiology of dogs housed in a rescue shelter. *Physiology and Behavior*, *133*, 1–7. doi:10.1016/j.physbeh.2014.04.045
- Hiby, E. F., Rooney, N. J., & Bradshaw, J. W. S. (2004). Dog training methods: Their use, effectiveness and interaction with behaviour and welfare. *Animal Welfare*, *13*, 63–69.
- Horn, L., Huber, L., & Range, F. (2013). The importance of the secure base effect for domestic dogs - Evidence from a manipulative problem-solving task. *PLoS ONE*, *8*(5). doi:10.1371/journal.pone.0065296
- Horn, L., Range, F., & Huber, L. (2013). Dogs' attention towards humans depends on their relationship, not only on social familiarity. *Animal Cognition*, *16*, 435–443. doi:10.1007/s10071-012-0584-9
- Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological "need", models of motivation and animal welfare. *Animal Behaviour*, *36*, 1696–1707. doi:10.1016/S0003-3472(88)80110-6
- Jamieson, L. T. J., Baxter, G. S., & Murray, P. J. (2017). Identifying suitable detection dogs. *Applied Animal Behaviour Science*, *195*, 1–7. doi:10.1016/j.applanim.2017.06.010
- Jezierski, T., Walczak, M., & Górecka, A. (2008). Information-seeking behaviour of sniffer dogs during match-to-sample training in the scent lineup. *Polish Psychological Bulletin*, *39*, 71–80. doi:10.2478/v10059-008-0010-y
- Jones, A. C., & Josephs, R. A. (2006). Interspecies hormonal interactions between man and the domestic dog (*Canis familiaris*). *Hormones and Behavior*, *50*, 393–400. doi:10.1016/j.yhbeh.2006.04.007
- Kahneman, D., & Lovallo, D. (1993). Timid choices and bold forecasts: A cognitive perspective on risk taking. *Management Science*, *39*, 17–31. doi:10.1287/mnsc.39.1.17
- Kis, A., Szakadát, S., Gácsi, M., Kovács, E., Simor, P., Török, C., ... Topál, J. (2017). The interrelated effect of sleep and learning in dogs (*Canis familiaris*). An EEG and behavioural study. *Nature Scientific Reports*, *7*, Article 41873. doi:10.1038/srep41873

- Kleen, J. K., Sitomer, M. T., Killeen, P. R., & Conrad, C. D. (2006). Chronic stress impairs spatial memory and motivation for reward without disrupting motor ability and motivation to explore. *Behavioral Neuroscience, 120*, 842–851. doi:10.1037/0735-7044.120.4.842
- Landsberg, G. M., Hunthausen, W. L., & Ackerman, L. J. (2012). *Behavior problems of the dog and cat*. New York, NY: Elsevier Health Sciences.
- Landsberg, G. M., Mougeot, I., Kelly, S., & Milgram, N. W. (2015). Assessment of noise-induced fear and anxiety in dogs: Modification by a novel fish hydrolysate supplemented diet. *Journal of Veterinary Behavior: Clinical Applications and Research, 10*, 391–398. doi:10.1016/j.jveb.2015.05.007
- Lasseter, A. E., Jacobi, K. P., Farley, R., & Hensel, L. (2003). Cadaver dog and handler team capabilities in the recovery of buried human remains in the southeastern United States. *Journal of Forensic Sciences, 48*, 617–621. doi:10.1520/JFS2002296
- Lefebvre, D., Diederich, C., Delcourt, M., & Giffroy, J. M. (2007). The quality of the relation between handler and military dogs influences efficiency and welfare of dogs. *Applied Animal Behaviour Science, 104*, 49–60. doi:10.1016/j.applanim.2006.05.004
- Lindsay, S. R. (2000). *Handbook of applied dog behavior and training, adaptation and learning*. New York, NY: Wiley & Sons.
- Lit, L., & Crawford, C. A. (2006). Effects of training paradigms on search dog performance. *Applied Animal Behaviour Science, 98*, 277–292. doi:10.1016/j.applanim.2005.08.022
- Lit, L., Schweitzer, J. B., & Oberbauer, A. M. (2011). Handler beliefs affect scent detection dog outcomes. *Animal Cognition, 14*, 387–394. doi:10.1007/s10071-010-0373-2
- Liu, D. L. J., Graham, S., & Zorawski, M. (2008). Enhanced selective memory consolidation following post-learning pleasant and aversive arousal. *Neurobiology of Learning and Memory, 89*, 36–46. doi:10.1016/j.nlm.2007.09.001
- Lopes, B., Alves, J., Santos, A., & Pereira, G. D. G. (2015). Effect of a stimulating environment during the socialization period on the performance of adult police working dogs. *Journal of Veterinary Behavior: Clinical Applications and Research, 10*, 199–203. doi:10.1016/j.jveb.2015.01.002
- Maejima, M., Inoue-Murayama, M., Tonosaki, K., Matsuura, N., Kato, S., Saito, Y., ... Ito, S. (2007). Traits and genotypes may predict the successful training of drug detection dogs. *Applied Animal Behaviour Science, 107*, 287–298. doi:10.1016/j.applanim.2006.10.005
- Mandairon, N., Stack, C., & Linster, C. (2006). Olfactory enrichment improves the recognition of individual components in mixtures. *Physiology and Behavior, 89*, 379–384. doi:10.1016/j.physbeh.2006.07.013
- Marshall-Pescini, S., Passalacqua, C., Barnard, S., Valsecchi, P., & Prato-Previde, E. (2009). Agility and search and rescue training differently affects pet dogs' behaviour in socio-cognitive tasks. *Behavioural Processes, 81*, 416–422. doi:10.1016/j.beproc.2009.03.015
- Marshall-Pescini, S., Valsecchi, P., Petak, I., Accorsi, P. A., & Previde, E. P. (2008). Does training make you smarter? The effects of training on dogs' performance (*Canis familiaris*) in a problem solving task. *Behavioural Processes, 78*, 449–454. doi:10.1016/j.beproc.2008.02.022
- Matas, L., Arend, R. A., & Sroufe, L. A. (1978). Continuity of adaptation in the second year: The relationship between quality of attachment and later competence. *Child Development, 49*, 547–556. doi:10.2307/1128221
- McCobb, E. C., Brown, E. A., Damiani, K., & Dodman, N. H. (2001). Thunderstorm phobia in dogs: An Internet survey of 69 cases. *Journal of the American Animal Hospital Association, 37*, 319–324. doi:10.5326/15473317-37-4-319

- McGarrity, M. E., Sinn, D. L., Thomas, S. G., Marti, C. N., & Gosling, S. D. (2016). Comparing the predictive validity of behavioral codings and behavioral ratings in a working-dog breeding program. *Applied Animal Behaviour Science*, *179*, 82–94. doi:10.1016/j.applanim.2016.03.013
- McKinley, S., & Young, R. J. (2003). The efficacy of the model-rival method when compared with operant conditioning for training domestic dogs to perform a retrieval-selection task. *Applied Animal Behaviour Science*, *81*, 357–365. doi:10.1016/S0168-1591(02)00277-0
- Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2895–2904. doi:10.1098/rspb.2010.0303
- Mennella, J. A., Jagnow, C. P., & Beauchamp, G. K. (2001). Prenatal and postnatal flavor learning by human infants. *Pediatrics*, *107*(6), e88.
- Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2014). Dogs' comprehension of referential emotional expressions: Familiar people and familiar emotions are easier. *Animal Cognition*, *17*, 373–385. doi:10.1007/s10071-013-0668-1
- Meyer, I., & Ladewig, J. (2008). The relationship between number of training sessions per week and learning in dogs. *Applied Animal Behaviour Science*, *111*, 311–320. doi:10.1016/j.applanim.2007.06.016
- Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, *1*, 113–121. doi:10.1007/s100710050016
- Milgram, N. W. (2003). Cognitive experience and its effect on age-dependent cognitive decline in beagle dogs. *Neurochemical Research*, *28*, 1677–1682. doi:10.1023/A:1026009005108
- Milgram, N. W., Head, E., Zicker, S. C., Ikeda-Douglas, C. J., Murphey, H., Muggenburg, B., ... Cotman, C. W. (2005). Learning ability in aged beagle dogs is preserved by behavioral enrichment and dietary fortification: A two-year longitudinal study. *Neurobiology of Aging*, *26*, 77–90. doi:10.1016/j.neurobiolaging.2004.02.014
- Milgram, N. W., Siwak-Tapp, C. T., Araujo, J., & Head, E. (2006). Neuroprotective effects of cognitive enrichment. *Ageing Research Reviews*, *5*, 354–369. doi:10.1016/j.arr.2006.04.004
- Mills, D. (2005). Management of noise fears and phobias in pets. *In Practice*, *27*, 248–255. doi:10.1136/inpract.27.5.248
- Mills, D., van der Zee, E., & Zulch, H. (2014). When the bond goes wrong. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behavior and cognition* (pp. 223–245). New York, NY: Academic Press. doi:10.1016/B978-0-12-407818-5.00008-5
- Morisaki, A., Takaoka, A., & Fujita, K. (2009). Are dogs sensitive to the emotional state of humans? [Abstract]. *Journal of Veterinary Behavior: Clinical Applications and Research*, *4*(2), 49.
- Nielson, K. A., & Lorber, W. (2009). Enhanced post-learning memory consolidation is influenced by arousal predisposition and emotion regulation but not by stimulus valence or arousal. *Neurobiology of Learning and Memory*, *92*, 70–79. doi:10.1016/j.nlm.2009.03.002
- Nielson, K. A., & Powless, M. (2007). Positive and negative sources of emotional arousal enhance long-term word-list retention when induced as long as 30 min after learning. *Neurobiology of Learning and Memory*, *88*, 40–47. doi:10.1016/j.nlm.2007.03.005
- Passman, R. H. (1977). Providing attachment objects to facilitate learning and reduce distress: Effects of mothers and security blankets. *Developmental Psychology*, *13*, 25–28. doi:10.1037/0012-1649.13.1.25

- Pattison, K. F., Laude, J. R., & Zentall, T. R. (2013). Environmental enrichment affects suboptimal, risky, gambling-like choice by pigeons. *Animal Cognition*, *16*, 429–434. doi:10.1007/s10071-012-0583-x
- Penney, R. K. (1967). Effect of reward and punishment on children's orientation and discrimination learning. *Journal of Experimental Psychology*, *75*, 140–142. doi:10.1037/h0024921
- Pluijmakers, J. J. T. M., Appleby, D. L., & Bradshaw, J. W. S. (2010). Exposure to video images between 3 and 5 weeks of age decreases neophobia in domestic dogs. *Applied Animal Behaviour Science*, *126*, 51–58. doi:10.1016/j.applanim.2010.05.006
- Porritt, F., Shapiro, M., Waggoner, P., Mitchell, E., Thomson, T., Nicklin, S., & Kacelnik, A. (2015). Performance decline by search dogs in repetitive tasks, and mitigation strategies. *Applied Animal Behaviour Science*, *166*, 112–122. doi:10.1016/j.applanim.2015.02.013
- Prato-Previde, E., Marshall-Pescini, S., & Valsecchi, P. (2008). Is your choice my choice? the owners' effect on pet dogs' (*Canis lupus familiaris*) performance in a food choice task. *Animal Cognition*, *11*, 167–174. doi:10.1007/s10071-007-0102-7
- Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*, *105*, 41–55. doi:10.1002/jeab.195
- Pryor, K. (1999). *Don't shoot the dog! The new art of teaching and training*. New York, NY: Bantam Books.
- Riemer, S., Müller, C., Virányi, Z., Huber, L., & Range, F. (2014). The predictive value of early behavioural assessments in pet dogs—A longitudinal study from neonates to adults. *PLoS ONE*, *9*(7). doi:10.1371/journal.pone.0101237
- Rooney, N. J., Clark, C. C. A., & Casey, R. A. (2016). Minimizing fear and anxiety in working dogs: A review. *Journal of Veterinary Behavior: Clinical Applications and Research*, *16*, 53–64. doi:10.1016/j.jveb.2016.11.001
- Rooney, N. J., & Cowan, S. (2011). Training methods and owner-dog interactions: Links with dog behaviour and learning ability. *Applied Animal Behaviour Science*, *132*, 169–177. doi:10.1016/j.applanim.2011.03.007
- Rooney, N. J., Gaines, S. A., & Hiby, E. (2009). A practitioner's guide to working dog welfare. *Journal of Veterinary Behavior: Clinical Applications and Research*, *4*, 127–134. doi:10.1016/j.jveb.2008.10.037
- Rooszendaal, B. (2002). Stress and memory: Opposing effects of glucocorticoids on memory consolidation and memory retrieval. *Neurobiology of Learning and Memory*, *78*, 578–595. doi:10.1006/nlme.2002.4080
- Ryan, R. M., & Deci, E. L. (2000). Intrinsic and extrinsic motivations: Classic definitions and new directions. *Contemporary Educational Psychology*, *25*, 54–67. doi:10.1006/ceps.1999.1020
- Scheifele, P., Martin, D., Clark, J. G., Kemper, D., & Wells, J. (2012). Effect of kennel noise on hearing in dogs. *American Journal of Veterinary Research*, *73*, 482–489. doi:10.2460/ajvr.73.4.482
- Schilder, M. B. H., & Van Der Borg, J. A. M. (2004). Training dogs with help of the shock collar: Short and long term behavioural effects. *Applied Animal Behaviour Science*, *85*, 319–334. doi:10.1016/j.applanim.2003.10.004
- Schoon, G. A. A. (1996). Scent identification lineups by dogs (*Canis familiaris*): Experimental design and forensic application. *Applied Animal Behaviour Science*, *49*, 257–267. doi:10.1016/0168-1591(95)00656-7
- Schoon, G. A. A., & Berntsen, T. G. (2011). Evaluating the effect of early neurological stimulation on the development and training of mine detection dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, *6*, 150–157. doi:10.1016/j.jveb.2010.09.017
- Schwab, C., & Huber, L. (2006). Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology*, *120*, 169–175. doi:10.1037/0735-7036.120.3.169

- Schwabe, L., Joëls, M., Roozendaal, B., Wolf, O. T., & Oitzl, M. S. (2012). Stress effects on memory: An update and integration. *Neuroscience and Biobehavioral Reviews*, *36*, 1740–1749. doi:10.1016/j.neubiorev.2011.07.002
- Schwabe, L., Wolf, O. T., & Oitzl, M. S. (2010). Memory formation under stress: Quantity and quality. *Neuroscience and Biobehavioral Reviews*, *34*, 584–591. doi:10.1016/j.neubiorev.2009.11.015
- Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog*. Chicago, IL: University of Chicago Press.
- Seksel, K., Mazurski, E. J., & Taylor, A. (1999). Puppy socialisation programs: Short and long term behavioural effects. *Applied Animal Behaviour Science*, *62*, 335–349. doi:10.1016/S0168-1591(98)00232-9
- Sharot, T., & Phelps, E. A. (2004). How arousal modulates memory: Disentangling the effects of attention and retention. *Cognitive Affective & Behavioral Neuroscience*, *4*, 294–306. doi:10.3758/CABN.4.3.294
- Sheppard, G., & Mills, D. S. (2002). The development of a psychometric scale for the evaluation of the emotional predispositions of pet dogs. *International Journal of Comparative Psychology*, *15*, 201–222. doi:10.5811/westjem.2011.5.6700
- Sheppard, G., & Mills, D. S. (2003). Evaluation of dog-appeasing pheromone as a potential treatment for dogs fearful of fireworks. *The Veterinary Record*, *152*, 432–436. doi:10.1136/vr.152.14.432
- Simitzis, P. E., Deligeorgis, S. G., Bizelis, J. A., & Fegeros, K. (2008). Feeding preferences in lambs influenced by prenatal flavour exposure. *Physiology & Behavior*, *93*, 529–536. doi:10.1016/j.physbeh.2007.10.013
- Sinn, D. L., Gosling, S. D., & Hilliard, S. (2010). Personality and performance in military working dogs: Reliability and predictive validity of behavioral tests. *Applied Animal Behaviour Science*, *127*, 51–65. doi:10.1016/j.applanim.2010.08.007
- Slabbert, J. M., & Odendaal, J. S. J. (1999). Early prediction of adult police dog efficiency—A longitudinal study. *Applied Animal Behaviour Science*, *64*, 269–288. doi:10.1016/S0168-1591(99)00038-6
- Slabbert, J. M., & Rasa, O. A. E. (1997). Observational learning of an acquired maternal behaviour pattern by working dog pups: An alternative training method? *Applied Animal Behaviour Science*, *53*, 309–316. doi:10.1016/S0168-1591(96)01163-X
- Smotherman, W. P. (1982). In utero chemosensory experience alters taste preferences and corticosterone responsiveness. *Behavioral and Neural Biology*, *36*, 61–68. doi:10.1016/S0163-1047(82)90245-X
- Stairs, D. J., & Bardo, M. T. (2009). Neurobehavioral effects of environmental enrichment and drug abuse vulnerability. *Pharmacology Biochemistry and Behavior*, *92*, 377–382. doi:10.1016/j.pbb.2009.01.016
- Sümegei, Z., Oláh, K., & Topál, J. (2014). Emotional contagion in dogs as measured by change in cognitive task performance. *Applied Animal Behaviour Science*, *160*, 106–115. doi:10.1016/j.applanim.2014.09.001
- Svartberg, K. (2002). Shyness-boldness predicts performance in working dogs. *Applied Animal Behaviour Science*, *79*, 157–174. doi:10.1016/S0168-1591(02)00120-X
- Svobodová, I., Vápeník, P., Pinc, L., & Bartoš, L. (2008). Testing German shepherd puppies to assess their chances of certification. *Applied Animal Behaviour Science*, *113*, 139–149. doi:10.1016/j.applanim.2007.09.010
- Szetei, V., Miklósi, Á., Topál, J., & Csányi, V. (2003). When dogs seem to lose their nose: An investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science*, *83*, 141–152. doi:10.1016/S0168-1591(03)00114-X



- Tami, G., & Gallagher, A. (2009). Description of the behaviour of domestic dog (*Canis familiaris*) by experienced and inexperienced people. *Applied Animal Behaviour Science*, *120*, 159–169. doi:10.1016/j.applanim.2009.06.009
- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., & Miklósi, Á. (2009). Differential sensitivity to human communication in dogs, wolves, and human infants. *Science*, *325*, 1269–1272. doi:10.1126/science.1176960
- Topál, J., Miklósi, Á., & Csányi, V. (1997). Dog-Human relationship affects problem solving behavior in the dog. *Anthrozoos*, *10*, 214–224. doi:10.2752/089279397787000987
- Tuber, D. S., Sanders, S., Hennessy, M. B., & Miller, J. A. (1996). Behavioral and glucocorticoid responses of adult domestic dogs (*Canis familiaris*) to companionship and social separation. *Journal of Comparative Psychology*, *110*, 103–108.
- van Horik, J. O., Langley, E. J. G., Whiteside, M. A., Laker, P. R., Beardsworth, C. E., & Madden, J. R. (2018). Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences*, *285*(1875). doi:10.1098/rspb.2018.0150
- Vaterlaws-Whiteside, H., & Hartmann, A. (2017). Improving puppy behavior using a new standardized socialization program. *Applied Animal Behaviour Science*, *197*, 55–61. doi:10.1016/j.applanim.2017.08.003
- Wachter, T., Lungu, O. V., Liu, T., Willingham, D. T., & Ashe, J. (2009). Differential effect of reward and punishment on procedural learning. *Journal of Neuroscience*, *29*, 436–443. doi:10.1523/JNEUROSCI.4132-08.2009
- Walker, J. K., Waran, N. K., & Phillips, C. J. C. (2014). The effect of conspecific removal on the behaviour and physiology of pair-housed shelter dogs. *Applied Animal Behaviour Science*, *158*, 46–56. doi:10.1016/j.applanim.2014.06.010
- Wasser, S. K., Davenport, B., Ramage, E. R., Hunt, K. E., Parker, M., Clarke, C., & Stenhouse, G. (2004). Scent detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. *Canadian Journal of Zoology*, *82*, 475–492. doi:10.1139/z04-020
- Wells, D. L., & Hepper, P. G. (2006). Prenatal olfactory learning in the domestic dog. *Animal Behaviour*, *72*, 681–686. doi:10.1016/j.anbehav.2005.12.008
- Williams, M., & Johnston, J. M. (2002). Training and maintaining the performance of dogs (*Canis familiaris*) on an increasing number of odor discriminations in a controlled setting. *Applied Animal Behaviour Science*, *78*, 55–65. doi:10.1016/S0168-1591(02)00081-3
- Wilsson, E., & Sinn, D. L. (2012). Are there differences between behavioral measurement methods? A comparison of the predictive validity of two ratings methods in a working dog program. *Applied Animal Behaviour Science*, *141*, 158–172. doi:10.1016/j.applanim.2012.08.012
- Wilsson, E., & Sundgren, P. E. (1997). The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. *Applied Animal Behaviour Science*, *53*, 279–295. doi:10.1016/S0168-1591(96)01174-4
- Wolf, O. T. (2009). Stress and memory in humans: Twelve years of progress? *Brain Research*, *1293*, 142–154. doi:10.1016/j.brainres.2009.04.013
- Wright, H. F., Wilkinson, A., Croxton, R. S., Graham, D. K., Harding, R. C., Hodgkinson, H. L., ... Zulch, H. E. (2017). Animals can assign novel odours to a known category. *Scientific Reports*, *7*, 3–8. doi:10.1038/s41598-017-09454-0
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, *18*, 459–482. doi:10.1037/h0073415

Zeleznikow-Johnston, A., Burrows, E. L., Renoir, T., & Hannan, A. J. (2017). Environmental enrichment enhances cognitive flexibility in C57BL/6 mice on a touchscreen reversal learning task. *Neuropharmacology*, *117*, 219–226. doi:10.1016/j.neuropharm.2017.02.009

Zubedat, S., Aga-Mizrachi, S., Cymerblit-Sabba, A., Shwartz, J., Leon, J. F., Rozen, S., ... Avital, A. (2014). Human-animal interface: The effects of handler's stress on the performance of canines in an explosive detection task. *Applied Animal Behaviour Science*, *158*, 69–75. doi:10.1016/j.applanim.2014.05.004