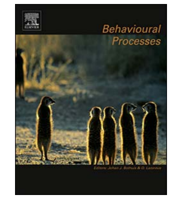
Behavioural Processes 141 (2017) 67–74

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Persistence and resistance to extinction in the domestic dog: Basic research and applications to canine training

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ARTICLE INFO

Keywords:
Behavioral persistence
Canine
Domestic dog
Working dog
Detection dog
Stereotypy

ABSTRACT

This review summarizes the research investigating behavioral persistence and resistance to extinction in the dog. The first part of this paper reviews Behavioral Momentum Theory and its applications to Applied Behavior Analysis and training of pet dogs with persistent behavioral problems. I also highlight how research on Behavioral Momentum Theory can be applied to the training of detection dogs in an attempt to enhance detection performance in the presence of behavioral disruptors common in operational settings. In the second part of this review, I highlight more basic research on behavioral persistence with dogs, and how breed differences and experiences with humans as alternative sources of reinforcement can influence dogs' resistance to extinction of a target behavior. Applied Behavior Analysis and Behavior Momentum Theory have important applications for behavioral treatments to reduce the persistence of problem behavior in dogs and for the development of enhanced training methods that enhance the persistence of working dogs. Dogs can also be leveraged as natural models of stereotypic behavior and for exploring individual differences in behavioral persistence by evaluating breed and environmental variables associated with differences in canine persistance.

1. Behavior momentum theory and applications to canine training

The domestic dog holds a unique position as a laboratory animal, a working animal, and a pet in modern society. Research in Behavioral Momentum Theory (BMT) and behavioral persistence highlights dogs' different roles as both animal models and the targets of applied research. In this section, I will provide a brief overview of BMT and translate the applications of BMT to Canine Stereotypic Behavior as a target for behavior reduction and a model for stereotypic and Obsessive-Compulsive behaviors in humans. I will also highlight the applications that BMT research has for enhancing the performance of working dogs.

2. Behavioral momentum theory and applications to canine training

BMT is a quantitative model that describes the strength of behavior, reflected by its resistance to disruptors such as extinction, non-contingent delivery of reinforcers, and reinforcer satiation (Nevin and Grace, 2000a; Nevin and Shahan, 2011; Pritchard et al., 2014). BMT proposes that the magnitude of disruption of a behavior is directly related to the magnitude of the disruptor, and inversely related to the richness of the reinforcement history for engaging in the disrupted behavior (Nevin and Grace, 2000b; Nevin et al., 1983; Nevin and Shahan, 2011). In one of the initial experiments in the BMT literature, Nevin et al. (1983) trained pigeons on a multiple schedule in which two or more components were alternated within a session, and each component was separated by an inter-component-interval. Each component was associated with a different schedule of reinforcement which was signaled by a unique discriminative stimulus (e.g. different colored lights). Nevin et al. (1983) trained the pigeons on a two-component multiple schedule in which a red and green key light signaled the reinforcement schedule (a richer or leaner schedule) in effect during each component. When performance was disrupted by providing response independent food between components or by extinction, responding consistently showed the greatest resistance to change (i.e. least disruption) in the component with the discriminative stimulus associated with the richer schedule of reinforcement (Nevin et al., 1983). This finding has been replicated and extended in a wide variety of species (For reviews, see: Nevin and Grace, 2000b; Nevin and Shahan, 2011).

Several lines of research suggest that the Pavlovian association between the discriminative stimulus and the reinforcer is important in these types of momentum effects (Bai et al., 2016; Mauro and Mace, 1996; Nevin and Grace, 2000a; Nevin et al., 1990; Podlesnik and Shahan, 2008, 2009; see also: Bell, 1999; Podlesnik and Shahan, 2008;

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http://dx.doi.org/10.1016/j.beproc.2017.04.001
Received 30 November 2016; Received in revised form 29 March 2017; Accepted 5 April 2017
Available online 06 April 2017
0376-6357/

Podlesnik and Fleet, 2014, Williams and Bell, 2000). In one study, Nevin et al. (1990) held the response contingent reinforcement schedule for both components of a two-component multiple schedule identical. In one component, however, additional food was delivered according to a variable-time schedule (response independently), thus strengthening the discriminative stimulus-reinforcer relation (Pavlovian association), but not the response-reinforcer relation. Resistance to disruption was greatest in the component that provided additional variable time reinforcers suggesting that the overall reinforcement rate in the presence of the discriminative stimulus (stimulus-reinforcer parings) was important in determining resistance to extinction (Nevin et al., 1990). Resistance to disruption, however, also seems to be influenced by response-reinforcer relations (Bell, 1999; Podlesnik and Shahan, 2008; Williams and Bell, 2000).

BMT also extends to another measure of behavioral persistence, relapse. Under BMT, stimuli associated with higher rates of reinforcement are not only more resistant to extinction, they are more likely to re-occur following extinction. Podlesnik and Shahan (2009) showed that stimuli associated with additional response-independent food in a two-component multiple schedule with identical response dependent schedules of reinforcement was associated with greater resistance to extinction and increased relapse in a reinstatement, resurgence and renewal paradigms. The importance of the stimulus-reinforcer relation appears to extend to relapse similar to resistance to disruption (for a review see Podlesnik and DeLeon, 2015).

These findings have important applications to the field of Applied Behavior Analysis and canine training. In Applied Behavior Analysis, problem behaviors are targeted for reduction using a variety of procedures (See Cooper et al., 2007; Vollmer and Iwata, 1992). One such procedure is Differential Reinforcement of Alternative behaviors (DRA). In this procedure, a problem behavior is reduced by reinforcing a more appropriate target alternative behavior (DRA; Cooper et al., 2007). DRA procedures are often used with children with autism or individuals with developmental delays, as this procedure teaches an alternative, more favorable behavior, to the problem behavior targeted for reduction (Petscher et al., 2009; Vollmer and Iwata, 1992). DRA procedures are often used for functional communication training, which teaches more appropriate communication behaviors and can be implemented with or without extinction for the problematic behavior (for a review see Petscher et al., 2009; Vollmer and Iwata, 1992).

Critically, however, proponents of BMT have noted that providing a rich reinforcement schedule for alternative behavior in the same context in which problem behavior occurs might have unintended consequences in strengthening the stimulus-reinforcer relationship between the context and problem behavior (Ahearn et al., 2003; Mace et al., 1990; Pritchard et al., 2014). The Pavlovian Stimulus-Reinforcer interpretation of BMT suggests that additional reinforcers provided in the same context as problem behavior, although provided for an appropriate alternative response, may strengthen the stimulus-reinforcer relation, thereby increasing the overall resistance to disruption of the problem behavior.

Mace et al. (2010) compared extinction of problem behavior following a baseline condition (no DRA) to when it followed a condition including a DRA treatment. The authors found that extinction was more rapid (less resistant) following baseline than it was following the DRA condition. Ahearn et al. (2003) reached a similar conclusion in that problematic stereotypic behavior was more persistent following a condition in which additional reinforcers were provided in the context of problem behavior (but not as a consequence of problem behavior) compared to when no additional reinforcers were provided.

Together, these findings from the basic and applied literature on BMT have significant applications for the field of Applied Animal Behavior and canine training. One challenging problem canine trainers and veterinarians face is stereotypic behavior in pet dogs. Stereotypic behavior is a critical feature of Canine Compulsive Disorder (CCD), which can range in severity from mild annoyances to owners up to cases that require pharmacological intervention from the veterinarian (Luescher et al., 1991; Overall and Dunham, 2002). CCD has also been suggested as a natural animal model of human Obsessive Compulsive Disorder (Dodman et al., 2016; Luescher et al., 1991; Overall, 2000; Vermeire et al., 2012). Similar to Obsessive Compulsive Disorder, dogs will engage in ritualistic grooming. Dogs will also engage in a variety of topographies, such as tail chasing, flank sucking, repetitive licking and many more (Overall and Dunham, 2002; Vermeire et al., 2012; Wynchank and Berk, 1998). Interestingly, both Canine Compulsive Disorder and Obsessive-Compulsive Disorder appear to be related to serotonergic and dopaminergic neurotransmission (Vermeire et al., 2012), and are both susceptible to pharmacological treatments such as Clomipramine (a tricyclic antidepressant) and Selective Serotonin Reuptake Inhibitors (SSRIs) such as fluoxetine (Overall and Dunham, 2002; Wynchank and Berk, 1998).

The dog may therefore be a useful natural model for conditions such as Obsessive Compulsive Disorder and stereotypic behavior in humans. The dog is a particularly attractive model because it is a spontaneous ('natural') model requiring no pharmacological or surgical induction and occurs in enriched environments such as the human home, providing some face validity for the dog model. Furthermore, the dog is an ideal model for exploring both genetic and environmental causal mechanisms. Due to the high linkage disequilibrium (non-random association of alleles; see Sutter et al., 2004), dogs are an efficient model for investigating the genetic contributions to disease (Hall and Wynne, 2012; Karlsson and Lindblad-Toh, 2008; Ostrander et al., 2000; Sutter and Ostrander, 2004). Recently, in as few as 92 cases and 68 controls, Dodman et al. (2010) were able to identify putative genes associated with a compulsive behavior in Doberman Pincers, which has since been extended to additional candidate genes (Dodman et al., 2016; Tang et al., 2014).

The dog is also a unique animal model for exploring causal mechanisms related to the environment and reinforcement contingencies. Dogs are one of a few species that live within our homes, engage in variety of social behaviors with humans (Udell and Wynne, 2008), and can be provided Applied Behavior Analytic treatments.

We recently investigated the function of canine stereotypic behavior (Hall et al., 2015a). Identifying the function of a behavior is to identify the reinforcer that maintains the problematic behavior. This is done by manipulating the consequences for the problem behavior to observe when the behavior is most likely to occur. This methodology, called Functional Analysis, has been used extensively in Applied Behavior Analysis working with humans engaging in problem behavior (Iwata et al., 1994a,b). Knowing the function of a problem behavior is important as it allows treatments to target the specific consequences maintaining problematic behavior. If the function of a behavior is unknown, proposed treatments may not address the reinforcer maintaining the behavior, or at worst, inadvertently continue to reinforce the problem behavior. Such an example might be an owner turning and telling their dog to "stop" barking, when the barking is reinforced by such attention from the owner. For canine stereotypic behavior, standard recommendations for all clients are generally to implement a DRA treatment such as training the dog to sit or lie down in the problem behavior context (see Overall and Dunham, 2002). Without knowing the function of the stereotypic behavior; however, it's unclear how well this standard treatment might address an individual dog's problem behavior.

To explore the function of canine stereotypic behavior, we first identified some of the common responses owners have to their dog's stereotypy. Some of the most common responses were, saying "Stop", ignoring the dog, attempting to block the response, giving the dog a desirable item, and giving the dog attention. This allowed us to evaluate whether owners might provide putative social or tangible reinforcers to dogs as a response to canine stereotypic behavior (Hall et al., 2015a). Based on these results, we conducted a Functional Analysis (Iwata et al., 1994a) for the stereotypic behavior of 5 dogs. To do this, we evaluated putative reinforcers for each dog. For example, one dog that showed persistent licking of floors, we tested whether the behavior showed the highest rates when social reinforcement was provided by the owner (i.e. attention in the form of "Stop") contingent on licking or was maintained in the absence of owner presence (i.e. alone, 'automatic reinforcement'). We also included a control condition in which social reinforcement was provided non-contingently for licking. In this dog's case, high rates of licking were observed only when attention was provided contingently. For two dogs that showed stereotypic responses to lights, we evaluated whether the behavior was maintained by contingent owner attention, movement of lights, or removal of lights. We found that for both of these dogs, light movement maintained stereotypy, but light removal (as a consequence of chasing) did not. Overall, we found that stereotypic behavior was maintained by owner attention for two dogs, automatic reinforcement for two dogs, and one dog's stereotypic behavior was not observed sufficiently to determine the function. Interestingly, in humans, stereotypic behaviors are largely maintained by automatic reinforcement (Rapp and Vollmer, 2005) rather than social reinforcement, potentially suggesting that canine stereotypic behavior may be heterogeneous in its function and might require more individual based behavioral treatments.

Following functional analysis, we implemented treatments for three dogs (a DRA treatment for 1 dog and a DRO and Time Out for two dogs). For the dog in DRA treatment, we observed a significant decrease in stereotypic behavior during treatment, however, when we attempted to fade the DRA we noted significant resurgence in stereotypic behavior. This may be related to the prediction of BMT that DRA treatments might increase the overall strength of problem behavior by strengthening the problem behavior stimulus-reinforcer relationship (Ahearn et al., 2003; Mace et al., 1990), thereby increasing the rate of relapse of the problem behavior (Bai et al., 2016). This study, however, was not designed to test this question, therefore it's unclear if the resurgence of problem behavior was related to the use of the DRA.

This preliminary study, however, is an initial step toward developing a canine model for exploring behavioral treatments. Future work is needed to systematically explore whether DRA treatments lead to more persistent stereotypic behavior and whether DRA treatments should be considered cautiously as part of a standard treatment package for all dogs showing stereotypic behavior.

3. Persistence in working dogs

Unlike persistence of stereotypy and other problem behavior, persistence of behavior in many situations is highly desirable. One particular situation is in the training of detection dogs. Detection dogs are trained to search for a wide variety of targets such as narcotics (Dean, 1972), explosives (Goldblatt et al., 2009), or even wildlife (Cablk and Heaton, 2006). Dogs are required to work in a variety of natural scenarios in which distractors and disruptors are in the search environment. Furthermore, in operational searches (non-training searches), dogs are worked under extinction conditions (Sargisson and McLean, 2010). This is also true for the giant pouched rats that have been trained to detect landmines (Mahoney et al., 2012; See also 2014). Although extinction in operational settings may lead to disruption of search behavior, it is done to avoid reinforcing potential false alerts, as well as to avoid providing dogs reinforcers in potentially dangerous environments (Mahoney et al., 2014; Porritt et al., 2015). Lastly, dogs must remain vigilant in real world scenarios even when the probability of finding a target is minimal. This is particularly true in the case of an explosives dog in which the detection of explosives in an operational environment is rare. Thus, detection dogs (and rats) must have highly persistent search behavior in the presence of a variety of behavioral disruptors, such as environmental distractors, extinction, and a low probability of a search target being present.

Methods to maintain highly persistent and accurate search is an active question for training detection dogs. Training organizations typically utilize intermittent schedules of reinforcement to enhance resistance to extinction, exemplifying the Partial Reinforcement Extinction Effect (PREE; (See Mackintosh, 1974)). However, it's unclear as to what would be the appropriate schedule of reinforcement. BMT would predict that richer schedules of reinforcement will lead to greater resistance to disruption. This apparent discrepancy between the predictions of BMT and PREE during extinction results from the discrimination of the transition from a continuous reinforcement schedule to extinction (See Nevin, 2012). The PREE effect can be accommodated within BMT if one assumes that a transition from continuous reinforcement to extinction is a more discernable disruptor (hence a greater disruptor) than transitioning from intermittent reinforcement to extinction. Importantly, BMT further predicts richer schedules of reinforcement will lead to greater resistance to a variety of disruptors other than extinction such as reinforcer satiation and non-contingent reinforcer presentation.

BMT suggests that resistance to disruption can be enhanced by simply strengthening the stimulus-reinforcer relationship. Hall et al. (2015b) tested this prediction of BMT on dogs working on an odor discrimination task. Dogs were trained on a standardized olfactory discrimination task between two different pairs of odorants (Odor A vs Odor B and Odor C vs Odor D) in a multiple schedule. Twelve dogs were trained on both discriminations using a two-choice discrete trials operant procedure until reaching an accuracy of 85% or greater on both discriminations. Half of the dogs then received Pavlovian conditioning trials to Odor A in separate sessions where the presentation of an odor was correlated with food presentation while the dog rested in a crate or behind a baby gate. The remaining half of dogs received explicitly unpaired stimulus-reinforcer presentations to Odor A. If stimulus-reinforcer relationships enhance resistance to disruption, we expected dogs that received Pavlovian conditioning to Odor A would show less disruption on the Odor A vs Odor B discrimination in comparison to the Odor C vs Odor D discrimination. In contrast, for the dogs that received unpaired conditioning, we expected no differential disruption. We evaluated resistance of odor discrimination accuracy to three disruptors: pre-session feeding, an odor distractor condition in which food odors were used to distract the dogs, and extinction. Fig. 1 shows the overall results in terms of mean proportion of baseline odor discrimination accuracy averaged across all three disruptors. Pavlovian conditioning to the target odor in separate sessions to the operant discrimination task led to enhanced resistance to disruption compared to the unexposed odor pair but there was no effect of unpaired odor-food presentations. These results indicated that Pavlovian conditioning trials alone can enhance resistance to disruption, and specifically enhance resistance to performance decrements in odor detection dogs.

3.1. Generalization between training and operational settings

Other research has focused on enhancing generalization between training and operational settings to support higher performance in the field. Under operational settings, dogs are under extinction conditions with a low probability of finding a target during search. Perhaps by training dogs under these near extinction conditions, such that the training and operational testing conditions are highly similar, dogs will show higher performance in the field. Using rodents as a model for detection dogs, Thrailkill et al. (2016) investigated extinction of heterogeneous behavior chains as a model of searching behavior to investigate whether training subjects to search for longer durations under intermittent reinforcement schedules led to greater resistance to extinction. In this task, rodents were required to engage in a chain pull which was consider similar to a detection dog's search behavior. The chain pull would lead to the presentation of a discriminative stimulus (according to an intermittent schedule of reinforcement). Lever pressing in the presence of the discriminative stimulus would lead to food. The researchers investigated procedural variants that produced greater

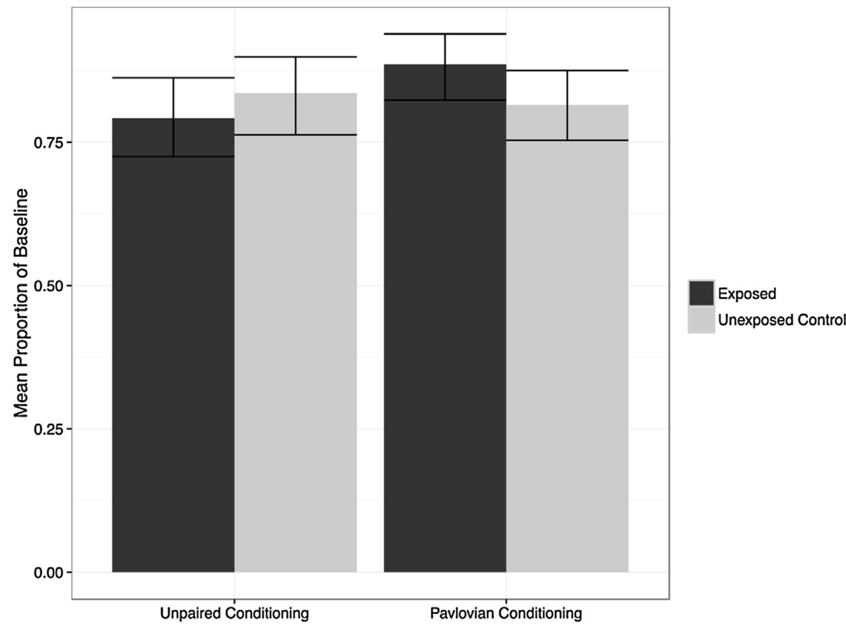

Fig. 1. Mean Proportion of Baseline Accuracy. Shows the mean proportion correct and 95% confidence interval for the odorant pair that was exposed and the control odorant across all three disruptors in the study by Hall et al. (2015b). For the Pavlovian conditioning group, Pavlovian conditioning (the exposed odor) led to enhanced resistance to disruption whereas for the unpaired conditioning, there was no significant difference between the exposed (unpaired conditioning) and unexposed odor pair.

resistance to search extinction (i.e. search responses did not produce the discriminative stimulus associated with the target response and the terminal reinforcer). Rodents showed the greatest resistance to extinction in the final sessions of extinction when the rodents were trained using longer search durations and partial reinforcement for searching compared to shorter search durations and/or continuous reinforcement for search responses. Furthermore, in a subsequent experiment, the authors investigated whether the presentation of non-contingent reinforcers would enhance resistance to extinction. Resistance to extinction was only enhanced when non-contingent reinforcers were presented both during training and extinction, indicating that performance was maintained by enhancing the similarity between training and testing settings.

The importance of enhancing generalization between the training and operational context is further exemplified by a study conducted by Gazit et al., 2005. The researchers utilized professionally trained explosives detection dogs trained to search along roadside paths. In the study, along one path, Path A, explosives were concealed at a high density, which could be considered typical of a training context. Along a second path, Path B, explosives were never placed ('search extinction'), which is more typical of an operational context. Search rapidly extinguished along path B, such that, when explosives were placed along Path B, dogs showed poor detection performance. Interestingly, this poor search did not generalize to another Path, Path C, where explosives were placed every 4th day. These results suggest that the search behavior of professionally trained explosives detection dogs is susceptible to rapid context specific extinction when no targets are found.

Together, these studies highlight the importance of maintaining the similarity between training and operational settings. This is largely done by training with very lean schedules of reinforcement, such that training more closely approximates extinction. BMT theory, however, suggests that as the schedule is thinned, behavior will become more susceptible to other disruptors such as reinforcer satiation or perhaps distractors in the environment (Hall et al., 2015b). To avoid this, generalization between training and operational contexts could be enhanced by increasing the schedule of reinforcement in operational settings by placing hides. Placing explosives or narcotics in operational contexts is logistically challenging. Porritt et al. (2015) evaluated a novel training procedure in which dogs were trained to both operationally relevant and non-relevant, but safe, target odors. The authors evaluated whether planting only the safe odors during simulated operational searchers would maintain dogs' search for both the relevant and non-relevant odors in the operational context. In a test, Porritt et al. found that by providing dogs with non-relevant odors in operational contexts, dogs were significantly more vigilant and more likely to detect relevant odorants compared to dogs that did not receive supplemental training with the non-relevant odors in operational contexts.

Together these results highlight the difficulty in training detection dogs to find dangerous or controlled substances that are rarely detected in operational contexts. When rich schedules and a high probability of a target is used in training, but under operational contexts, dogs are run under extinction with the probability of finding a target being low, dogs will distinguish between these contexts. By making training and operational contexts more similar by either reducing the reinforcement rate in training to be more similar to extinction during operation or by increasing the reinforcement rate during operational contexts using non-target odors, enhances performance. According to BMT, maintaining higher rates of reinforcement will lead to greater resistance to disruptors, suggesting that developing novel methodologies that both enhance generalization between training and operational contexts and maintain higher rates of reinforcement will be ideal for maintaining canine search performance in the field.

4. Part 2: basic research in canine perseveration

Basic research in animal perseverative responding has investigated whether differences in resistance to extinction is indicative of general individual differences in the ability to inhibit responding of a previously reinforced behavior. Several animal studies have identified that resistance to extinction on an arbitrary task is associated with the presence or rate of stereotypic behaviors (For a review see: Garner, 2006). For example, measures of resistance to extinction in Asiatic and Malayan sun bears (Vickery and Mason, 2005), horses (Hemmings et al., 2007), bank voles (Garner and Mason, 2002), rhesus macaques (Lutz et al., 2004; Pomerantz et al., 2012), and dogs (Protopopova et al., 2014) has been shown to correlate with stereotypic behavior. Poor behavioral disinhibition has also been implicated in disorders in humans such as

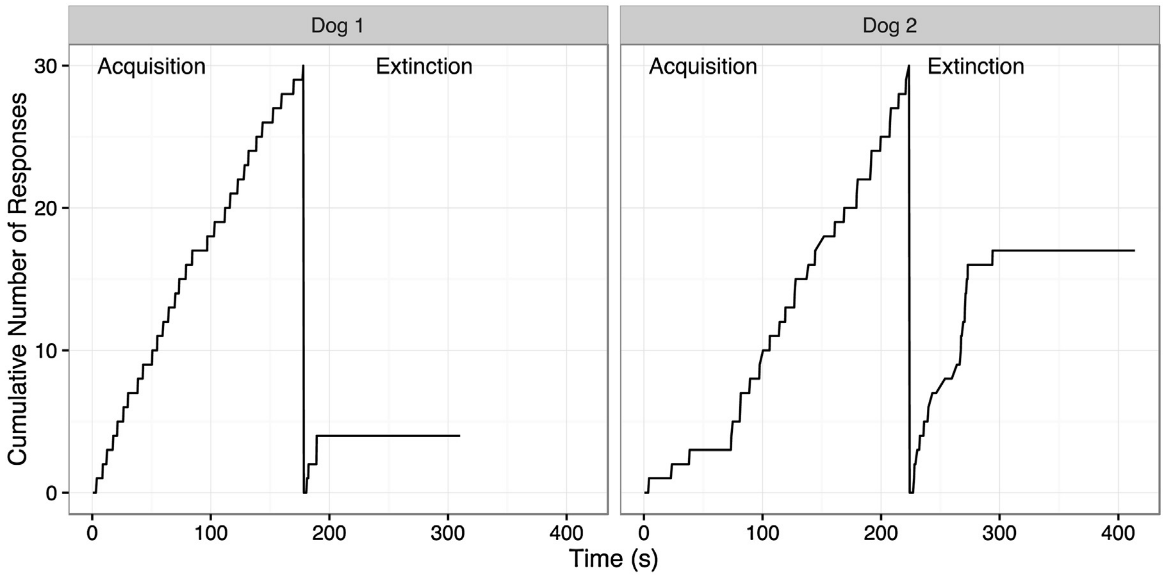

Fig. 2. Resistance to extinction task in dogs. Shows the cumulative number of responses during acquisition and extinction. Count re-sets to zero during extinction. Graph shows the acquisition and extinction of two dogs with different levels of responding during extinction.

Autism and Schizophrenia (Frith and Done, 1983; Garner, 2006; Russo et al., 2007). Individuals diagnosed with Autism or ADHD show more preservative responding with the changing contingencies of the Wisconsin Card Sorting Task (WCST) compared to matched controls (for a review see Russo et al., 2007). This suggests that abnormal levels of perseveration is related to abnormal behavior, such as stereotypic behavior, across a wide variety of species (for a review see Garner, 2006).

The experimental procedure to measure perseveration in the dogs is quite simple (Protopopova et al., 2014). The experimenter briefly trains a nose touch response such that every time the dog touches the experimenter's hand with their nose, the dog is given a treat. After 40 training trials, extinction is implemented such that food is no longer delivered following a nose touch. The number of responses in extinction are then counted until no response is made for some duration. Fig. 2 shows a cumulative record of a nearly identical procedure with dogs, in which the extinction phase continues until 2 min pass without a response. In Fig. 2, both dogs show typical acquisition responding on the continuous reinforcement schedule. One dog, dog 2, shows a high rate of responding during extinction, whereas the other dog, dog 1, shows rapid extinction of responding. Protopopova et al., 2014 showed a correlation between the number of responses in extinction and stereotypy. Furthermore, Protopopova et al. noted interesting breed differences in overall perseveration. Hounds and Working breeds showed the most perseverative responding whereas terrier and herder breeds showed the least responding (see Fig. 3). It's not clear at this point, however, to what extent environmental contingencies increase or decrease the behavioral persistence differences observed between breeds. If clear breed differences can be further confirmed, this would serve as a useful naturalistic model for exploring what developmental, genetic, and long-term environmental variables are related to perseverative responding by comparing breeds raised in controlled environments or before and after training aimed at increasing or decreasing behavioral persistence on a task.

4.1. Persistence on the 'Unsolvable' task

The unsolvable task is another rapid way to measure persistence in the dog, and allows for the observation of alternative behaviors that occur when a previously reinforced response is placed on extinction. In the Unsolvable task, a dog is given some type of toy that by manipulating in specific ways, the dog can access a treat. After several successful trials, the toy is then switched for a highly similar toy, except that it has been modified to be 'unsolvable' and treats will never become accessible. Researchers then score how long the dogs works on the unsolvable task and measures what others behaviors the dog emits. This procedure, is therefore highly similar to the previously used extinction task in dogs except that a toy is used as the manipulandum.

Miklósi et al. (2003), conducted this procedure on both wolves and dogs and found that dogs were more likely to look back at the owner than human socialized wolves during the extinction phase. The authors suggest that the differential propensity for dogs to look at the human is a key factor underlying dogs' ability to form complex dog-human social communication that does not readily occur in the wolf. Evaluating the task as an extinction-task, however, suggests that the wolves are more perseverative, whereas the dogs are more likely to engage in alternative food obtaining behaviors such as looking back towards the human. Extinction induced variability in behavior is a documented finding in both humans and animals (Antonitis, 1951; Kinloch et al., 2009; Neuringer et al., 2001), suggesting that the dogs might simply be displaying extinction induced variability towards a person, which has presumably been a rich source of reinforcement in the past. These results, suggest that more comparative investigation is necessary to identify whether the observed differences in looking towards the human reflects a domestication processes for human-directed social behavior, as suggested by Miklosi and colleagues, or reflects differences in perseveration and extinction induced variability.

Since the use of the unsolvable task by Miklósi et al. (2003), several other researchers have utilized the task to explore what researchers consider to be socio-cognitive differences in dogs. Marshall-Pescini et al. (2009) investigated the looking behavior of agility trained dogs, search and rescue dogs, and pet dogs during the unsolvable task. Search and rescue dogs showed the highest rates of alternating gaze between the owner and the manipulandum followed by agility and pet dogs. Similarly, heightened gazing has been observed in water rescue dogs compared to pet dogs (D'Aniello et al., 2015). Furthermore, dogs have even been shown to account for the attentional state of the audience when looking back during extinction (Marshall-Pescini et al., 2013). These results suggest the importance of considering the dogs' experiences with alternative sources of reinforcement (such as human intervention) when one schedule is placed on extinction (the toy is unsolvable). These studies suggest that dogs with more specialized training with humans will more rapidly engage in looking towards humans when the primary reinforcement contingency is placed on

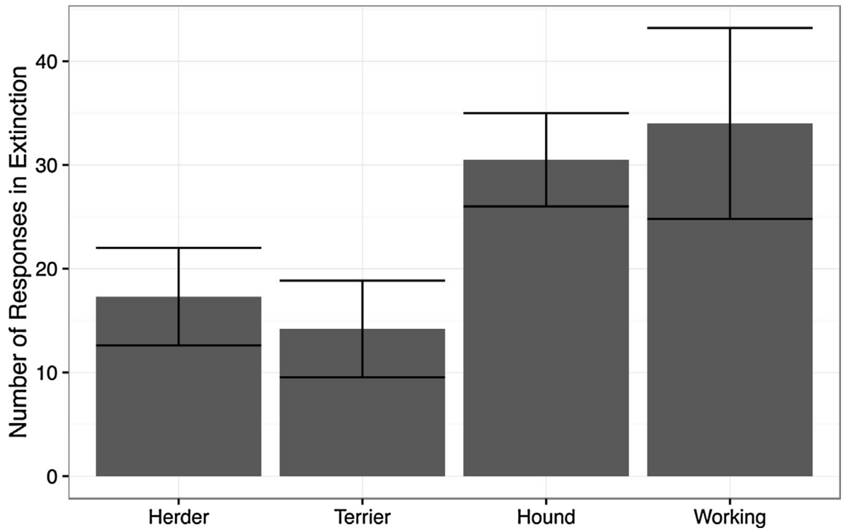

Fig. 3. Mean number of responses in extinction by breed. Shows the mean and standard error of the mean for the number of responses in extinction for the breeds tested in Protopopova et al. (2014).

extinction. One important caveat, however, is that some researchers have raised concerns regarding the stringency of the coding definitions used for scoring looking back (Smith and Litchfield, 2013).

Miller et al. (2010) used the unsolvable task to investigate the concept of self-control depletion in dogs. In this study, dogs were given a toy manipulandum from which the dogs could access treats. After a few trials with the manipulandum, half of the dogs were either given a cue by their owners to sit and stay for 10 min and thereby presumably utilizing self-control, whereas the other half were simply placed in a crate for 10 min which did not require self-control. It was hypothesized that the sit and stay required the dog to exert self-control, thereby depleting energy resources and would lead to less persistence during extinction with the toy. This is what Miller and colleagues showed, with dogs being required to stay showing less persistence. In a subsequent experiment, Miller showed that these differences could be alleviated by simply giving dogs a glucose supplement compared to a placebo following the sit-stay phase, suggesting that persistence in dogs could be directly manipulated via a glucose supplement. Although the mechanism is unclear, the results from Miller and colleagues suggest that (1) persistence on a subsequent task is decreased when it proceeds another task requiring persistence and (2) persistence can be recovered for the second task with a glucose supplement immediately before.

Together, these studies have identified several interesting findings related to dogs' behavior during the unsolvable task, which I argue is a measure of resistance to extinction. First, wolves are more perseverative than dogs, and dogs are more likely to engage in an alternative behavior of looking towards an owner than wolves. Furthermore, dogs highly trained to work with humans, such as search and rescue dogs, are also more likely to engage in the alternative behavior of looking toward the human than pet dogs with presumably less history of reinforcement for looking towards their owner. Lastly, having dogs engage in a task requiring them to sit and stay immediately prior to the unsolvable task, led to less persistence, which could be ameliorated with a glucose supplement. Although much of this research has been framed from a perspective of investigating social cognition in the dog, these results can also be interpreted as measure of resistance to extinction. This highlights the importance of experience with alternative sources of reinforcement (such as looking back toward humans) and the richness of those schedules, such that when extinction is implemented on the primary task, behaviors such as looking towards an owner are likely to occur at high rates.

5. Conclusions

Research on behavioral persistence and resistance to extinction has several applications for pet and working dogs. For the treatment of behavioral problems in the dog, BMT suggests that a potential unintended consequence of treatments that provide additional reinforcers in the context of problem behavior may make problem behavior more persistent and resistant to extinction. However, in some situations, such as with odor detection dogs, it is desirable to make behavior more persistent and resistant to extinction. The reviewed research suggests that, as predicted by BMT, increasing the number of odor-reinforcer pairings enhances dogs' resistance to disruption on an odor detection task. Research using a rodent model of detection dogs suggests that intermittent schedules of reinforcement in addition to the presentation of non-contingent reinforcers during training and extinction may enhance the persistence of searching behavior, by enhancing generalization between the training context and extinction. These findings can be reconciled by identifying that the rate of extinction depends on both the strength of the behavior (related to the number of reinforcers delivered) and the size of the disruptor (the change from the reinforcement contingency to extinction). Transitioning from continuous schedules of reinforcement to extinction is more discriminable and therefore a larger disruptor than transitioning from a very lean schedule to extinction. This indicates the need for novel training procedures that both enhance generalization between training and operational contexts, while also providing rich schedules of reinforcement to maintain high and consistent levels of performance in the presence of a variety of disruptors such as odor distractors.

Research in dogs has also highlighted individual differences in resistance to extinction on a rapidly learned task. The number of responses made during extinction has been shown to correlate with stereotypic behavior in the dog and with breed. This suggests that dogs might be a fruitful model for further exploration of phenotypic variability in general resistance to extinction across breeds. In addition, research using the unsolvable task in dogs highlights the importance of experience with humans as being an alternative source of reinforcement when a target response is placed on extinction.

Overall, the results reviewed suggest that there are several lines of applied and basic research directions for exploring behavioral persistence and resistance to extinction in dogs. Applications of Applied Behavior Analysis and Behavior Momentum Theory can be applied to canine behavioral problems to reduce problematic behaviors in pet dogs and enhance the performance of working dogs. Dogs can also be leveraged as natural models of stereotypic behavior and to explore breed and environmental variables associated with behavioral persistence.

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