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Exploring breed differences in discrimination, reversal learning, and resistance to extinction in the domestic dog (*Canis familiaris*)

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Learning is crucial for shaping domestic dogs' behaviour through life experiences, yet not all breeds exhibit the same learning aptitude towards a particular task. The current study's objective was to identify differences in behaviour and learning performance across and within five breed clades and elucidate the underlying factors contributing into these variations. Dogs ($n = 111$) from five breed clades (UK Rural, Retrievers, Asian Spitz, European Mastiff, and New World) participated in a virtual learning task with their owners. Owners completed validated questionnaires of Impulsivity and Reward Responsiveness. The learning task comprised of reinforcing an arbitrary behaviour (hand-touch) through multiple sessions of Acquisition (reinforcing the hand-touch), Discrimination (reinforcing the hand-touch on one of two hands) and Reversal Learning (reinforcing the hand-touch on the opposite hand), followed by a single session of Extinction (hand-touch not reinforced). Results showed notable differences across the studied breed clades in certain learning and behavioural components. However, the observed disparities may not be entirely attributed to inherent cognitive differences among the breed clades but rather potentially influenced by contextual factors such as the human-dog communication dynamics associated with breeds' cooperativity. Furthermore, breed clades differed in the contributing factors predicting individual learning performances, which could highlight the potential effect of breeds' historical function.

Keywords Breed differences, Individual variation, Domestic dog, Discrimination, Reversal learning, Resistance to extinction

The domestic dog (*Canis lupus familiaris*) is one of the earliest domesticated animals, tracing its lineage back to the gray wolf (*Canis lupus*) over 15,000 years ago[50]. Over the last few hundred years, human intervention through artificial selection to create a wide range of human-desirable characteristics in domestic dogs, has given rise to a diverse array of modern dog breeds[1]. This deliberate breeding approach has created an extraordinary genetic and phenotypic diversity across dog breeds, and resulted in remarkable variations in their physical features, physiological characteristics, and distinctive behavioural profiles[26,63].

While the artificial breeding in domestic dogs has provided a unique opportunity for researchers to study the heritability of cognitive traits and breed-typical behaviour,[29], previous research has yielded inconclusive and conflicting findings. A large body of research found substantial differences in behavioural traits across different breeds, suggesting genetic factors as one of the main elements causing these differences[19,29,63]. On the other hand, some studies found that breed has little predictive value for the behaviour of individual dogs[2,35,39]. For instance[39] found behaviour of modern dog breeds to be more polygenic than previously thought. Their findings suggested that dog breeds do not predict behavioural traits as much as aesthetic traits such as the size of the dog,[39]. Thus, it is plausible that various aspects of dog behaviour might have changed in response to recent shifts in selective pressures and the processes involved in breed formation (e.g., human preference for the size or coat rather than the original behavioural function of the breed). However, it is still unclear whether these changes following only a few generations could alter all dimensions of breed-typical behaviour in the same way, or if behavioural traits have never been as consistent as aesthetic traits.

The complexity of learning and behavioural traits of the domestic dog results from a multifaceted interplay of factors, including genetic predispositions shaped by human selection and learning experiences influenced by diverse environmental interactions throughout a dog's life. These dynamics gave rise to distinctive variations

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within both breeds and individual purebred dogs[35]. As the capacity to learn may be genetically determined, behavioural differences across dog breeds can stem from not only differences in various innate expressions of behaviour (e.g., stalking behaviour) but also in learning capacity itself (e.g., how quickly something is learned or the value of a certain reward). In this regard, previous research findings indicated that cognitive abilities (e.g., problem-solving abilities) and working intelligence (i.e., the general ability to learn tasks) have strong potential to undergo selection and vary across breeds[19,29], with this potentially attributed to differences in genetically determined physical skill performance, such as running speed, jumping height, and physical strength when it comes to working-related tasks[23].

To make matters more complicated, the historical functional purpose of a breed may not only dictate the specific aspects of learning and behaviour in which the dog of a particular breed is naturally inclined to excel but also may reflect the types of experiences and stimuli they are likely to encounter throughout their lives furtherly shaping their behaviour[11,26,58]. For example, the owner of an Australian Shepherd is more likely to expose this dog to sport and herding-related activities compared to other breeds. Hence, the alignment between breeds' purposeful breeding for certain tasks and their environmental experiences can profoundly impact dogs' learning and behavioural performances, with this influence even extending beyond dogs' everyday behaviour and potentially affecting their behaviour within experimental settings as well[26,53].

Studies have also highlighted the importance of variations in motivational tendencies[8,30], which revolve around how individuals assess the potential benefit of displaying a behaviour relative to the effort it demands[51], as another important factor resulting in differences in the behavioural and cognitive performance across individuals (see[28] for a detailed discussion). However, the mechanism by which these factors contribute into the interplay between gene and environment is still questionable. Research studies on dogs have indicated that individual dogs display varying degrees of responsiveness for specific rewards such as food and ball/toys[18,46], which can impact their reward pursuing behaviour, motivation to engage in learning tasks, and subsequently influence their performance[30,55]. Previous research also found breed differences in reward responsiveness, with Herding dogs having the highest score on ball and toy responsiveness and Retriever dogs being rated as the most responsive breed group to food rewards[18]. Considering the documented differences in reward responsiveness both across breeds and individuals, there remains a degree of uncertainty regarding the extent to which these propensities may impact an individual dog's learning aptitude and contribute into the performance variations seen across individuals. Furthermore, it remains an open question as to whether variation in reward responsiveness and motivation towards certain reward types across different dog breeds can exacerbate or ameliorate this contribution.

Dogs' performance in learning tasks may also reflect underlying personality traits[30,47]. As a multidimensional cognitive construct, Impulsivity is one of these personality traits extensively studied in dogs, and which may influence several broad behavioural aspects such as arousal, attention, risk-taking, delay gratification, and inability to inhibit an action or withhold a response in dogs[3,13]. Studies found that dogs' impulsive predispositions may influence their baseline sensitivity to rewards [55], depending on whether a highly preferred reward is being used or not[30]. Notably, Gerencsér and colleagues[18] found extreme levels of responsiveness to various reward types (both food and ball/toy) being associated with high levels of inattention and hyperactivity-impulsivity. In another study, detection dogs behaved more impulsively when a more preferred reward was used in the task[30]. Furthermore, previous research identified a subtype of Impulsivity denoted as "Impulsive choice" as a factor influencing an individual's choice between rewards with different costs[3,52]. Therefore, the link between Impulsivity and Reward Responsiveness in dogs constitutes a crucial determinant influencing their learning and behavioural performance in experimental tasks[30], and consequently, their training outcome. Nevertheless, the extent to which these fundamental components interact with each other within distinct dog breeds, potentially leading to between-breed variations in learning outcomes, still remains a subject for investigation.

The aim of the current study was to explore variations in learning performance across and within certain breed clades of domestic dogs. Moreover, the current study also aimed to determine which contributing factors, including Reward Responsiveness scores, Impulsivity, training background, and owners' experiences with dogs can predict learning performance across and within these breed clades. We hypothesize that (1) breed clades would differ in their learning task performances, (2) dog-related factors such as Reward Responsiveness, training experiences (e.g., being a sport dog), and Impulsivity would significantly predict dogs' learning performances, and (3) variables contributing into learning task performances differ across the studied breed clades, depending on breed-specific genetic predispositions and historical function. For example, individual dogs exhibiting greater responsiveness to food rewards are anticipated to demonstrate enhanced learning performances, likely due to their heightened incentive motivation. Similarly, dogs with higher impulsivity scores are expected to display increased perseverance when faced with reward omission. However, these correlations are also expected to be influenced by variations between breed clades, reflecting breed-specific predispositions towards particular rewards and/or behavioural tendencies.

Materials and methods
Participants
Purebred companion dogs were recruited through community advertisements. Interested owners were required to sign a written informed consent form, filling out a questionnaire and performing a virtual behavioural task in their home with their dog. Owners were ≥18 years of age, have owned their pure-bred dog for a minimum of six months, and were the primary caretaker of the dog. The recruited dogs were assigned into five breed clades based on the breed clustering cladogram published by Parker and colleagues (2017), which targeted the genetic signatures of breed development in dogs considering the ancestry and geographical origin of the studied breeds[41]. Five breed clades were chosen for the study, based on their representations among the recruited dogs, including: (1) UK rural clade (Herding dog breeds), (2) Asian spitz clade (Ancient dog breeds), (3) Retriever

clade, (4) New world clade (only German Shepherd dogs were represented this breed clade in the current study), and (5) European Mastiff clade (Mastiff-like breeds). The final analysis was restricted to dogs who passed the learning task's criteria and successfully finished the task.

The distribution of dogs included in the final analysis across the five studied breed groups was as follows: UK Rural ($n=22$), Asian Spitz ($n=20$), Retrievers ($n=23$), New World Dog (GSDs) ($n=22$), and European Mastiff ($n=24$). Furthermore, 54.5% of these dogs were Female. Table 1 shows a list of the breeds (within each clade) and sexual status of dogs included in the analysis.

Questionnaire

The questionnaire contained two separate sections, where the first part consisted of questions about the dog and owner's demographics, the training history of the dog (e.g., being a sport dog – only those engaged with Rally/obedience and/or agility were considered as sport dogs in the current study), and the owner's previous experiences with dogs (i.e., dog ownership experience based on how many dogs they have owned in the past, and knowledge of dog training by declaring whether they have passed any professional dog training courses or not). Items in the second part of the questionnaire consisted of two validated scales for measuring Impulsivity (Dog Impulsivity Assessment scale - DIAS) and Reward Responsiveness (Canine Reward Responsiveness Scale – CRRS: Ball/toy responsiveness [BTR] and Food responsiveness [FR]) in dogs[18,69].

Learning task procedure and measures

Each dog underwent a learning task including four phases: (1) Acquisition, (2) Discrimination Learning (DL), (3) Reversal Learning (RL), and (4) Extinction (EXT). The learning task was a modified version of the hand-touch extinction learning task used by[44]. Each dog was tested in their home by the owner while a researcher (AA) virtually guided the owner throughout the test. All sessions were video recorded via Zoom Video Communications, Inc. ("Zoom"), version of 5.3.0. Figure 1 shows the experimental setup for the hand-touch learning task.

The owner was instructed to wear sunglasses to prevent the potential influence of gaze tracking on dogs' responses[59], remain silent during the sessions except when they were allowed to do so (e.g., saying "YES" when the dog responded correctly – see below), and provide no other cues or directions to guide the dog or change their choice towards the target hand (e.g., moving the hand to get the dog's attention).

For the learning task, the preferred treat of the participating dog (as per the owner's report), which should have been cuttable into small pieces, were used as the primary reinforcer throughout the task. As treats should make up no more than 10% of a dog's daily calories[60], each dog's resting energy requirement (RER) was calculated using the following formula:

$RER = 70 \times \ Body\ Weight^{0.75}$[36], and the maximum amount of treats for the experiment were determined as 10% of the measured RER for the dog based on the manufacturer's caloric information for the treats.

Working classification	Breed Clades	Age range in years (mean ± Std. Deviation)	Sexual status	Breeds	Number of dogs	Total
Cooperative Working breed clades	UK rural clade	0.66–11.0 (3.63 ± 2.719)	Neutered Male: 2 Intact Male: 6 Spayed Female: 13 Intact Female: 1	Border Collie	4	22
				Pembroke Welsh Corgi	6	
				Australian Shepherd	11	
				Shetland Sheepdog	1	
	Retriever clade	0.75–11.58; 4.461 ± 2.757	Neutered Male: 11 Intact Male: 3 Spayed Female: 6 Intact Female: 3	Nova Scotia Duck Tolling Retriever Labrador Retriever Golden Retriever	7 8 8	23
	New World clade	0.75–9.0; 3.737 ± 2.07	Neutered Male: 4 Intact Male: 6 Spayed Female: 7 Intact Female: 5	German Shepherd Dog	22	22
Independent Working breed clades	European Mastiff clade	1.666–11.416; 3.981 ± 2.838	Neutered Male: 8 Intact Male: 8 Spayed Female: 5 Intact Female: 3	Rhodesian Ridgeback	4	24
				Great Dane	2	
				Cane Corso	2	
				Boerboel	1	
				Staffordshire Bull Terrier	6	
				English Bull Terrier	4	
				French Bulldog	1	
				Boston Terrier	2	
				Bulldog	2	
	Asian Spitz clade	0.5–11.25; 4.72 ± 3.048	Neutered Male: 4 Intact Male: 3 Spayed Female: 9 Intact Female: 4	Siberian Husky	16	20
				Alaskan Malamute	1	
				Shiba Inu	3	

Table 1. Distribution of the recruited dogs who successfully passed the task ($N=111$) across different working style categories and breed clades.

Fig. 1. Experimental setup for the virtual hand-touch learning task. Owners were instructed to present one hand during the Acquisition phase and switch between hands on a trial-to-trial basis, providing reinforcement for each correct response. In the subsequent phases, both hands were presented simultaneously, with reinforcement given only for responses to a particular hand depending on the specific learning phase at which the dog was performing.

Furthermore, owners were advised to make appropriate adjustments to their dogs' food intake on the day of experiment, should they wish to do so for compensating the extra food treats possibly added to the measured amount.

Acquisition phase

The aim of the Acquisition phase was to expose the dog to the behavioural response required for the task. The response in the learning task was defined as any touch on any part of the owner's hand by any part of the dog's head. During this phase, the owner stood still or sat on a chair (for small-sized dogs) in front of the dog while holding both hands behind themselves. The owner started the task by presenting their dominant hand, while the other hand stayed behind their back. The owner was then instructed to loudly say "YES" as soon as a response occurred on their hand and provide the dog with a treat using the same hand by tossing a small piece of food on the floor (behind the dog to re-position them).

Once the dog looked back at the owner, the owner was instructed to present the other hand (while the previously presented hand stayed behind) to start the next trial. The session continued with the owner alternating the presented hand across trials to ensure that the dog received similar quantity of food from both hands and reduce potential learning effect or side bias towards a specific hand on the subsequent phases. If the dog did not respond to the owner's hand, the experimenter instructed the owner to provide assistance by showing the dog a food treat with their hand, then holding the treat in between their fingers and using the verbal cue of calling the dog's name, followed by the command "Touch" to encourage a response.

Responding to the owner's hand for a minimum of four consecutive trials (two touches on each hand) within three seconds after the hand presentation, and without any assistance from the owner, was considered as the criteria for the Acquisition phase. If the dog did not meet the criteria after 20 trials, that given session of Acquisition was terminated and a new session was started after one minute, with a maximum of three sessions (60 trials) for each dog. If the dog did not meet the criteria after 60 trials of Acquisition, they were scheduled for another day (maximum of three days). Dogs who could not meet the criteria or were not motivated to perform the task after participating for three days were excluded from the experiment. After meeting the Acquisition criteria, each dog had a 1-minute time-break before performing the second part of the Acquisition. The second part of Acquisition had the same procedure and criteria and was mainly conducted to break any potential side bias towards a specific hand before starting the subsequent phase.

Discrimination learning (DL) phase
The DL phase was started immediately after finishing the second part of the Acquisition. The owner was instructed to present both hands at the same time, while only the dominant hand served as the target (discriminative stimulus; S^d). The dog was only reinforced for touching the S^d, while touching the other hand (non-dominant hand; extinction stimulus or S^Δ) resulted in no reinforcement (no verbal praise: i.e., no "YES" and no food). Once a correct response occurred, the owner loudly said "YES", delivered a food treat immediately with the target hand, and then removed both hands to start another trial after two seconds. After each touch on the S^Δ, the owner was instructed to remove both hands immediately, holding them behind their back, and start another trial after two seconds.

To meet the DL criteria, dogs were required to make a minimum of eight touches towards the S^d out of 10 trials within a given DL session. After each session, there was a time break of one minute. The DL phase continued for a maximum of six consecutive sessions (60 trials) per day and for a maximum of three days if the dog did not meet the DL criteria. Dogs that were unable to meet the criteria after attempting on three different days were excluded from the experiment.

Reversal learning (RL) phase
Once the dog met the DL criteria within six sessions or fewer in a given day, the RL phase started after a 2-minute time break. For this phase, the procedure remained the same, however, the contingency was reversed as touching the alternative hand (non-dominant hand) was reinforced while no reinforcement was provided for touching the previous target hand (dominant hand). All dogs performed six sessions of RL (10 trials/session; one minute of time break between sessions) regardless of the outcome to allow for the numbers of touches towards the new S^d to be a measure and to standardize the number of sessions across dogs, overcoming learning confounds in the next phase.

Extinction (EXT) phase
Once the dog completed all the six sessions of RL, the EXT phase started after a 2-minute time break. In this phase, both hands were considered as S^Δ and no reinforcement was provided upon touching either of the owner's hands. The EXT phase was continued (as a single session) until the dog completely disengaged from the behaviour (i.e., three consecutive trials without any response after 10 s).

Considerations for the experiment
If the dog did not respond to the owner's hands after 10 s, the owner was instructed to start the next trial after a delay of two seconds. Each trial with no response from the dog was counted as one trial out of the considered maximum number of trials per session. If the dog continued to not respond to the owner's hands after three consecutive trials, that session was terminated, and another session was started after one minute. For the new session, the dog first underwent another Acquisition session to encourage participation. Once the dog met the Acquisition criteria again, the new DL or RL session was started immediately. After three consecutive session terminations due to not responding to the owner's hands, the test was terminated for the day and rescheduled for another day (within a maximum of seven days depending on the owner's availability). The only exception was for the last three sessions of RL, where the RL phase was considered as complete, and EXT started after a 1-minute time break. All these re-scheduled dogs started the experiment from the beginning (Acquisition phase) on the second or third day. A subsequent failure to meet criteria after three experimental tests (in three different days) resulted in a termination of participation.

In the case of small dogs, if the dog jumps on the owner's lap while they are sitting on a chair, the owner was asked to stand up to encourage the dog to jump off and restart the trial. Owners were asked to perform the test in an area without any distraction, where there was enough space allowing the dog to move a few steps around them, and enough space in front of them enabling them to toss food on the floor for the dog.

Owners were instructed to re-position the dog and place them in a central position when necessary (e.g., the dog goes behind the owner). Following two touches on the S^Δ during both the DL and RL sessions, all dogs were re-positioned and placed in a central position in front of the owner. This approach aimed to offer the dogs an opportunity to observe both hands again, facilitating their choice between them and preventing potential frustration.

Measuring emotional responses
In addition to measuring different types of learning and behavioural persistence, this study also aimed to examine the emotional responses of dogs, specifically frustration-like behaviours, during instances of learning difficulty. The rationale behind this was that emotional responses and frustration-like behaviours, may provide critical insights into a dog's experience when facing challenges during learning or training tasks. By quantifying these responses, the study aimed to assess not only how individual dogs cope with learning difficulties but also explore potential breed differences in the expression of these behaviours. Furthermore, exploring factors predicting frustration-like behaviors may help identify whether certain dogs are more prone to emotional responses in learning contexts, which could have implications for training methods, welfare considerations, and behavioural resilience. Collecting these data also allows integrating emotional responses with other metrics, such as learning rates and persistence, to create a more comprehensive profile of how dogs respond to and overcome cognitive challenges. To measure frustration-like behaviours throughout the experiment, video recordings of the sessions (except the Acquisition phase) were further analyzed and coded for the percentage of trials with frustration-like

behaviours including vocalizations (e.g., barking and whining), jumping on the owner, pawing at the owner, and nipping within each phase of the test, except the Acquisition phase (see Table 2 for the list of emotional responses and definitions derived from[14,27,34,38].

Ethical considerations

Prior to each session of the experiment, the owners were reminded by the experimenter that if they find the dog or themselves experiencing any distress, the experiment can be terminated immediately and re-scheduled for another day or the dog can be excluded from participation, depending on severity.

All methods were carried out in accordance with relevant guidelines and regulations, and all experimental protocols were approved by the UBC *Behavioural Research Ethics Board* (H22-00509) and the Animal Care Committee (A22-0025). Additionally, informed consent was obtained from all dog owners for participating in the experiment, with their performance being recorded on a video.

Statistical analysis

Measures in the current study included four variables related to DL performance (number of sessions until meeting the DL criteria, % of sessions terminated due to having three consecutive No-response trials, and % of no-response trials throughout the DL phase), three related to RL (% of correct trials, % of No-response trials, and % of sessions terminated due to having three consecutive No-response trials in the RL phase), three related to EXT (total number of responses during EXT, % of No-response trials, and total number of times the dog switched their choice from one hand to another), and three related to frustration-like behaviours within each phase of the task, except the Acquisition phase (% of trials with emotional responses during DL, RL, and EXT).

To assess the inter-rater reliability for emotional responses, 30% of the videos were double coded and agreement was assessed via the Intraclass Correlation Coefficient (ICC) analysis. The analysis used a two-way mixed-effects model with absolute agreement, assuming the interaction effect is absent, which is typical for reliability studies where the raters are fixed but the subjects are random. For emotional responses during DL phase, Cronbach's Alpha, a measure of internal consistency, was calculated as 0.965, indicating excellent reliability between the two raters. The Average Measures ICC was 0.966, with a confidence interval between 0.931 and 0.983, representing the reliability of the average ratings between the two raters ($p < 0.001$). The inter-rater reliability between the two raters for emotional responses during RL (the Cronbach's Alpha: 0.959; the ICC values: Average Measures: 0.957, 95% CI [914, 979]; $p < 0.001$) and during EXT (the Cronbach's Alpha: 0.938; the ICC values: Average Measures: 0.940, 95% CI [878, 970]; $p < 0.001$) were also excellent, showing a highly consistent evaluation across the raters.

For dogs that successfully finished the task but engaged in the task for more than a single day (up to three days) either due to not meeting the criteria or lack of motivation, their learning outcomes were evaluated based on their overall performance. For instance, if a dog failed to meet the criteria of DL on the initial day after undergoing six sessions but managed to achieve it after two sessions on the second day and completed the task successfully on this day, the DL metrics (such as the % of correct trials and the number of sessions until meeting the DL criteria) for this dog was assessed considering the total of eight DL sessions they underwent.

Exploratory factor analysis with a varimax rotation (to maximize the variance of squared loadings within each factor and facilitate the interpretation of component loadings) was used to identify the underlying components contributing to the set of variables measured through the learning task. A combination of the Kaiser criterion (eigenvalues greater than 1) and the scree plot were used to determine the number of components to extract, suppressing small coefficients with absolute values below 0.4[49]. Components were labeled based on the variables loaded under each and the direction of the scores. The assumption of normality was assessed by a Q-Q Plot along with the Shapiro–Wilk test. The component scores were not normally distributed across the studied breed groups and the data had negative values; therefore, the data was shifted by adding a constant value of 1.5 to all observations to make them positive along with a subsequent logarithmic transformations (log10) to help normalize the data distribution.

Variables obtained from the questionnaire data included dog-related variables: demographic information, breed clade, breed cooperativity working type (Cooperative vs. Independent worker), training background (being a sport dog, having prior experience with the hand touch command, and predominant reward type used in training), along with DIAS and CRRS scores. Information regarding the owners' experience with dogs and

Behaviour	Definition
Vocalizations	Included barks, groans, snorts, whines, whimpers, yelps, and howls, which originate from the dog's throat and mouth.
Rearing (jumping)	To jump or to stand on hind legs with front paws on the owner.
Pawing	To generate pawing/scratching movement of a front paw on the owner
Pushy/nippy behaviour	To push against the owner with the muzzle or lightly bite the owner's sleeve/pockets/clothes, hand, or the treat bag

Table 2. List of emotional responses (frustration-like behaviours) recorded within each trial throughout the learning task. A trial, defined from the moment of hand presentation until either a response was received, or the maximum 10 s time limit was reached, was categorized as a trial with emotional responses if any of the mentioned behaviours occurred during that trial (without considering the cumulative frequency of each behaviour within each trial). The percentage of trials with emotional responses was then calculated within each phase of the task for each dog.

their knowledge of dog behaviour (whether they have a dog-related occupation, how many dogs they had in the past, and having passed any dog training courses) were also recorded as the owner-related variables.

Generalized linear models (GLM) were utilized, with each learning component serving as the dependent variable separately and the questionnaire-recorded factors as independent variables to determine significant predictors for each of the studied learning and behavioural components. Linearity was assessed by partial regression plots and a plot of studentized residuals against the predicted values. The independence of residuals was assessed by Durbin-Watson statistic. The visual inspection of a plot of studentized residuals versus unstandardized predicted values along with both the F-test and the Breusch-Pagan test were used to assess homoscedasticity in the data. Multicollinearity was assessed by tolerance values greater than 0.1. The studentized deleted residual greater than ± 3 standard deviation was used as a cut-off to assess the presence of outliers, and the leverage values greater than 0.2, and values for Cook's distance above 1 were used to assess other unusual points. In the event of finding heteroskedasticity in the data, the GLM was re-run with robust standard errors (HC3 robust estimator)[22].

Independent variables were divided into two sets of variables depending on being dog-related or owner-related, and GLMs predicting each of the studied learning components were run for each sets separately. The models for both the dog-related and owner-related sets of variables were conducted while accounting for the variable "Breed clade" (UK rural, Asian Spitz, Retrievers, New World dogs, and European Mastiff dogs) alongside the other independent variables. Furthermore, separate GLMs for each learning component were conducted within each breed clade, including the same sets of independent variables (owner-related and dog-related - except the breed-related variables), to explore individual variation within each of the studied breed clades.

Given the significant variations in the proportion of dogs participating in sports across different breed clades, the impact of sports on dogs' learning performance was expected to be influenced by substantial variability across the breed clades. Therefore, an interaction term between "Breed clade" and "Sport engagement" was also added into the models including all dogs and running with the dog-related variables, while accounting for dogs' breed clade. Variables having low number of samples within one of their categories ($\leq$ 20% of the total cases for that variable) were excluded prior to running the models.

For post-hoc analysis of significant main effects, Least Significant Difference (LSD) tests were used to compare estimated marginal means. Although the LSD method does not control as strictly for Type I error compared to other methods (e.g., Bonferroni correction), it was selected in this study to maintain statistical power and sensitivity, given the exploratory nature of the research and the relatively small sample size. The goal was to detect potentially meaningful differences in dog behaviour across clades without overly conservative adjustments that could obscure possible important trends.

Statistical analyses were performed using the analytical software package SPSS 28.0 (SPSS, Chicago, IL, USA). Alpha level was set at 0.05 and p-values less than that were denoted as statistically significant. Data were presented as Mean $\pm$ Std. Error unless otherwise specified. Table 3 summarizes the statistical tests and approaches used in the study for the performance measures and questionnaire data. Only the statistically significant results were reported in the manuscript.

Results

A total of 151 dogs were initially enrolled in the study; however, 41 were excluded for either failing to meet the task criteria ($n = 40$) or due to a significant procedural error made by the owner during the task ($n = 1$). Among the 40 dogs that did not meet the criteria, six belonged to the UK Rural clade, 12 to the Asian Spitz clade, 10 to the Retriever clade, five to the New World clade, and seven to the European Mastiff clade.

A total of 111 dogs successfully finished the task and were included in the analysis. A total of 12 dogs out the 111 performed the task for more than one day (UK Rural = 3, Asian Spitz = 5, Retriever = 4), with only two dogs (Asian Spitz) out of the 12 using the maximum three-day limit to successfully finish the task. The duration of each daily session for dogs that successfully completed all phases of the task varied between 25 to a maximum of 75 min, depending on their individual performance.

Distribution across Age and categorical variables

The Age ranges (reported as min-max in years; Mean $\pm$ Std. Deviation) within the studied breed clades were as follows: UK Rural (0.66-11.0; 3.63 $\pm$ 2.719), Asian Spitz (0.5-11.25; 4.72 $\pm$ 3.048), Retrievers (0.75–11.58;

Statistical step	Variables included	Statistical Test	Details
Step 1: Determining learning and behavioural components	DL, RL, and EXT Performance Variables, and Emotional Response Variables	Exploratory factor analysis (EFA)	Varimax rotation, Kaiser criterion (eigenvalue > 1), scree plot, loadings below 0.4 suppressed.
Step 2: Studying predictors of learning and emotionality components generated from EFA	Questionnaire Data: - Dog-related variables (demographic data, breed clade, training background, and behaviour scores including DIAS and CRRS) - Owner-related variables (having a dog-related occupation, dog ownership experience, and dog training knowledge)	Generalized Linear Models (GLM)	Durbin-Watson test for residual independence, estimated marginal means used for pairwise comparisons in significant models with post-hoc Least Significant Difference (LSD), HC3 robust estimator used to account for heteroscedasticity

Table 3. Summary of the statistical tests performed in the study. The table provides an overview of the analytical framework applied to examine learning and emotional responses in dogs including the key variables analyzed, the corresponding statistical methods employed (e.g., generalized Linear models, Exploratory Factor Analysis), and any post-hoc procedures or adjustments made.

4.461 ± 2.757), New World Dog (GSDs) (0.75-9.0; 3.737 ± 2.07), and European Mastiff (1.666–11.416; 3.981 ± 2.838).

A total of 48.6% of dogs were sport dogs, and 81.9% were familiar with hand-touch behaviour prior to participating in the study. The variable "Main reward type used in training" were excluded from the analysis as the number of dogs within the two categories were significantly different and unequal (Dogs having food as the main reward $n = 102$; Dogs having non-food rewards in training $n = 9$). A total of 32.4% of dogs were owned by individuals having a dog-related occupation, and 13.5% were owned by individuals who declared they have not passed any dog training lessons.

Determining the main learning components

The exploratory factor analysis was run on 13 variables measured throughout the learning task based on dogs' performance within each phase of the task. Inspection of the correlation matrix showed that all variables had at least one correlation coefficient greater than 0.3. The overall Kaiser-Meyer-Olkin (KMO) measure was 0.714. Bartlett's test of sphericity was statistically significant ($p < 0.001$), indicating that the data was likely factorizable.

The factor analysis revealed four components that had eigenvalues greater than 1.0 explaining 29.42%, 20.86%, 19.48%, and 9.77% of the total variance, respectively. Visual inspection of the scree plot indicated that four components should be retained, and this four-component solution explained 79.54% of the total variance. The interpretation of the data was consistent with the learning features for which the task was designed to measure, with strong loadings of DL-related variables on Component 1, RL variables on Component 2, EXT variables on Component 3, and variables focusing on the frustration-like behaviours on Component 4. The loading directions of the variables were such that higher component scores indicated greater difficulty and poorer performance in Discrimination Learning (DL) and Reversal Learning (RL), as well as higher levels of Resistance to Extinction (EXT) and Emotionality. Component loadings and communalities of the rotated solution are presented in Table S1.

Differences in the learning performances across the breed clades

Discrimination learning (DL)

The model revealed no significant association between DL performance and any of the dog-related variables, including the breed clade of dogs (Table S2). None of the owner-related predictor variables also reached statistical significance (Table S3).

Reversal learning (RL)

Breed clade ($F(4, 95) = 2.564$, partial $\eta^2 = 0.097$, $p = 0.043$) was a significant predictor for the difficulty in RL scores. The remaining dog-related variables did not significantly predict the difficulty in RL scores. The pairwise comparisons based on the estimated marginal means revealed variations in the difficulty in RL scores across the studied breed clades, with certain breed clades demonstrating greater difficulties compared to others. The mean difficulty in RL score for the Asian Spitz clade, which had the lowest mean score (-0.110 ± 0.083), was significantly lower than that of the Retriever clade (which had the highest mean RL score: 0.187 ± 0.072) with a mean difference of -0.297 ($p = 0.007$), and the New World clade with a mean difference of -0.281 ($p = 0.011$), suggesting a better RL performance in the Asian Spitz compared to the latter two clades. Results are shown in Table S4, and Fig. 2 illustrate differences in RL performance across the studied breed clades. None of the owner-related variables included in the model showed a significant effect on predicting RL task difficulty (Table S5).

Resistance to extinction (EXT)

A significant effect was observed for the variable "Breed clade" ($F(4, 95) = 2.830$, partial $\eta^2 = 0.106$, $p = 0.029$). The pairwise comparisons of the estimated marginal means showed that dogs within the European Mastiff clade (with the highest mean across the breed clades: 0.336 ± 0.06) had a significantly higher mean Resistance to EXT score compared to dogs within the Asian Spitz clade (mean difference = -0.277, $p = 0.003$), who had the lowest mean score across the studied breed clades (0.058 ± 0.073). Dogs within the Asian Spitz clade also had a significantly lower mean Resistance to EXT score compared to dogs from the Retriever (0.277 ± 0.064) (mean difference = -0.219, $p = 0.023$) and UK Rural clades (0.299 ± 0.071) (mean difference = -0.241, $p = 0.014$). The effect of the remaining dog-related variables was not significant. Results were shown in Table S6, and Fig. 3 shows differences in EXT performance across the studied breed clades. None of the owner-related variables had a significant effect on Resistance to EXT scores (Table S7).

Emotionality

For the Emotionality scores, there was heteroskedasticity in the data, thus, the model was re-run using robust standard errors. The model showed no significant effect for the dog-related variables included the model. Table S8 in the Supplementary Material shows parameter estimates with robust standard errors. Moreover, the effect of none of the owner-related variables reached statistical significance (Table S9).

Differences in the learning performances within the studied breed clades

1. UK Rural clade:

The variable targeting dogs' prior experience with the hand-touch behaviour was removed from the model running with the dog-related variables as only 1 out of 22 UK Rural dogs did not know the hand-touch command prior participating in the current study.

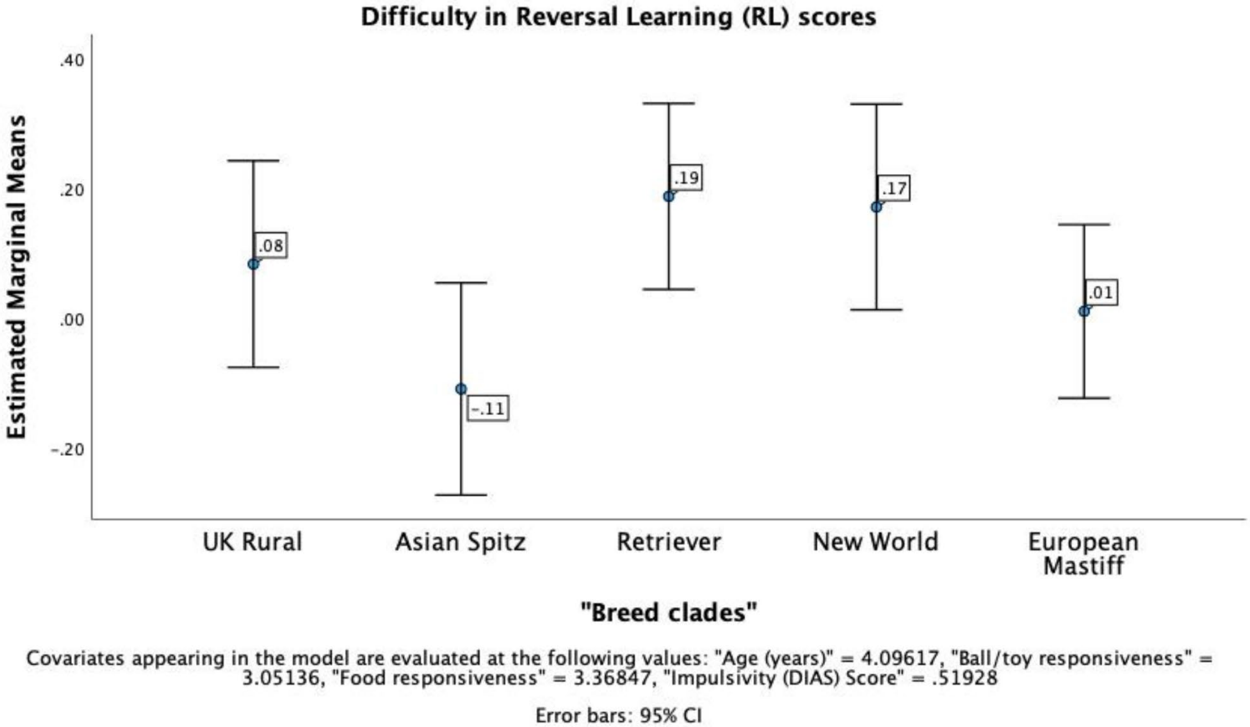

Fig. 2. Differences in the difficulty in Reversal Learning (RL) scores across the studied breed clades. Error bars are 95% Confidence Interval (CI) and values are the estimated marginal means.

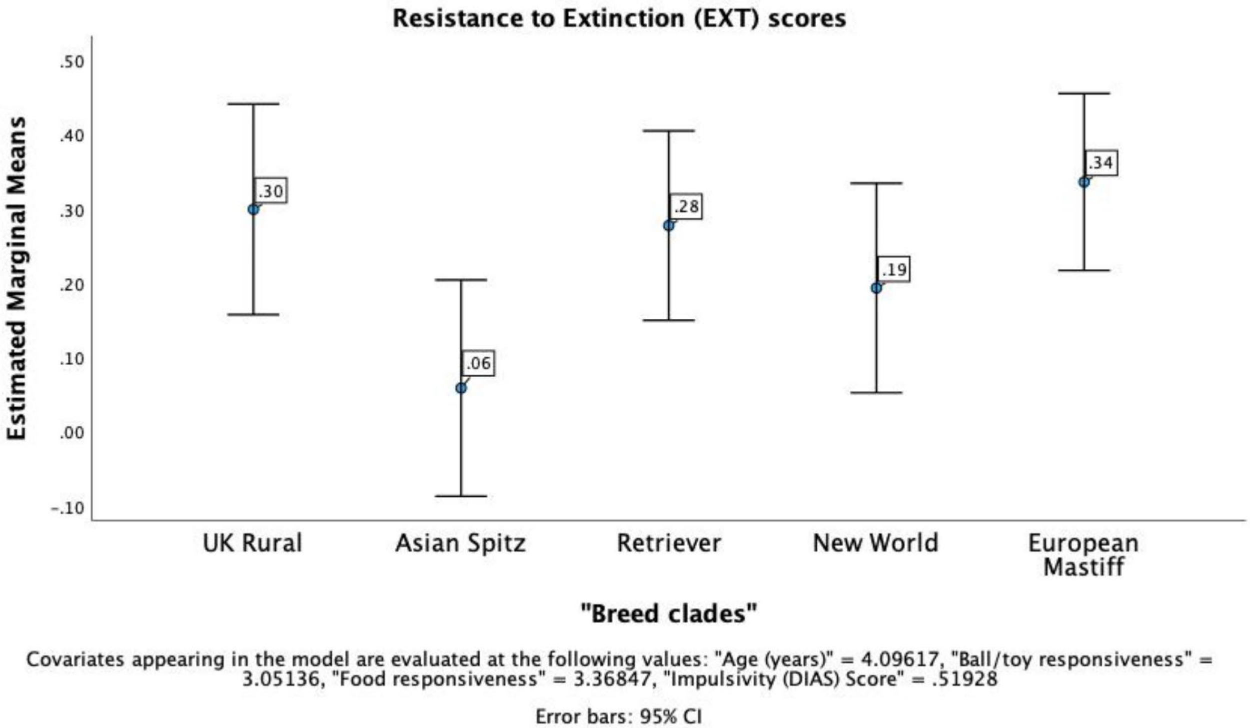

Fig. 3. Differences in the Resistance to Extinction (EXT) scores across the studied breed clades. Error bars are 95% Confidence Interval (CI) and values are the estimated marginal means.

Among the dog-related predictors, only the BTR had a statistically significant effect on the difficulty in RL scores (F(1, 15) = 5.839, t = -2.576, partial η^2 = 0.280, β = -0.613, p = 0.029), indicating that the UK rural dogs with lower BTR scores tended to experience more difficulties in RL (Figure S1). None of the remaining dog-related variables significantly predicted the component scores for dogs within the UK rural clade (Table S10-S13).

The owner-related variable concerning owners' knowledge of dog training (i.e., whether owners passed any dog training courses) was excluded from the set of the owner-related variables for dogs in the UK rural clade as only two out of 22 dogs were owned by individuals who reported not having taken any dog training lessons. Dogs owned by individuals having more dog ownership experiences (i.e., owning more dogs in the past) showed significantly lower levels of Emotionality score throughout the task (F(1, 19) = 6.652, t = -2.579, partial η^2 = 0.259, β = -0.543, p = 0.018) (Figure S2). None of the other owner-related predictors significantly contributed into the models predicting the studied learning components (Table S14-S17).

2. Asian Spitz clade:

The variable pertaining to prior experience with the hand-touch behaviour was eliminated from the model including the dog-related variables, given that only 3 out of 20 Asian Spitz dogs lacked experience with the hand-touch command before participating in the study. The effect of none of the dog-related variables on the studied learning and behavioural components' scores reached statistical significance (Table S18-S21).

The model including the owner-related variables significantly explained variance in the difficulty in RL scores for dogs within the Asian Spitz clade (F(3, 16) = 4.249, p = 0.022, partial η^2 = 0.443, adj. R^2 = 0.339). Dogs owned by individuals with a dog-related occupation had a significantly higher mean difficulty in RL score (0.420 ± 0.157) compared to dogs owned by individuals without a dog-related occupation (-0.08 ± 0.086) (F(1, 16) = 9.599, t = -3.098, partial η^2 = 0.375, β = -0.623, p = 0.007; mean difference = 0.5) (Figure S3). The effect of dog ownership experience on the difficulty in RL scores was also significant (F(1, 16) = 5.445, t = -2.333, partial η^2 = 0.254, β = -0.047, p = 0.033), with dogs owned by individuals having more dog ownership experience in the past experiencing less difficulty in the RL phase (Figure S4). Results are shown in Table S22-S25.

3. Retriever clade:

Increasing age had a positive correlation with the Emotionality score when Age was the only independent variable included in the model (F(1, 21) = 5.771, t = 2.402, β = 0.464, p = 0.026) (Figure S5). The remaining dog-related variables did not significantly contribute into the models predicting the Emotionality and learning components' scores. Age was also found as a significant predictor of the difficulty in RL for the Retriever dogs, however, only when BTR and the overall DIAS score were also accounted in the model (F(1, 19) = 5.064, t = 2.250, β = 0.475, p = 0.036 – Table S30). Notably, older Retriever dogs were more likely to experience difficulty during the RL phase (Figure S6). Results are shown in Table S26-S29.

The variable concerning whether dog owners are employed in a dog-related profession was removed from the list of the owner-related factors for dogs in the Retriever clade, as only three out of 23 Retriever dogs belonged to individuals who reported having a dog-related occupation. None of the included owner-related variables had a statistically significant effect on the studied learning components' scores (Table S31-S34).

4. New World clade (German Shepherd dogs):

Having previous experience with the hand-touch command was removed from the dog-related variables for the New World clade as only 2 out of 22 GSDs lacked this experience before participating in the study. Higher overall DIAS scores were associated with lower difficulty in DL scores for dogs within the New World clade (F(1, 15) = 8.097, t = -2.846, partial η^2 = 0.351, β = -0.666, p = 0.012) (Figure S7). None of the other dog-related predictors emerged as a statistically significant predictor for the remaining learning components and the Emotionality scores (Table S35-S38).

The variable concerning whether the owners passed any dog training lessons was removed from the list of the owner-related variables for the New World clade as only one GSD out of 22 was owned by an individual declaring they had not passed any dog training lessons. Nevertheless, none of the included owner-related variables significantly predicted the studied learning components and the Emotionality scores. Results are shown in Tables S39-S42.

5. European Mastiff clade:

The model predicting the Resistance to EXT for the European Mastiff clade was statistically significant (F(7, 16) = 4.099, p = 0.009,, partial η^2 = 0.642, adj. R^2 = 0.485). Further analysis identified significant effects for certain predictors (Figure S9-S11). Specifically, increasing age (F(1, 16) = 11.525, t = 3.395, partial η^2 = 0.419, β = 0.625, p = 0.004) and lower FR scores (F(1, 16) = 5.737, t = -2.395, partial η^2 = 0.264, β = -0.434, p = 0.029) were found to be significantly associated with higher Resistance to EXT scores. Furthermore, sporting dogs had a significantly higher mean Resistance to EXT score (0.427 ± 0.059) compared to non-sport dogs (0.224 ± 0.036) (F(1, 16) = 7.801, t = -2.793, partial η^2 = 0.328, β = -0.535, p = 0.013; mean difference = 0.203). The effects of the other dog-related variables were not significant. Results of the models incorporating the dog-related variables are shown in Table S43-S46.

The FR score (without accounting for the other dog-related variables) had also a significantly positive correlation with the Emotionality scores of dogs in the European Mastiff clade (F(1, 22) = 5.905, t = 2.43, partial η^2 = 0.212, β = 0.46, p = 0.024), with dogs having higher FR scores showing more emotional responses throughout the task (Figure S8).

The variable related to dog owners' dog training knowledge was excluded from the set of the owner-related factors for the European Mastiff clade, as only two dogs out of the 24 belonged to individuals who reported not having undergone any dog training courses. The effect of none of the included owner-related variables on the studied learning components reached statistical significance. The overall model predicting the Emotionality score, however, was statistically significant ($F(2, 21) = 4.375$, $p = 0.026$, partial $\eta^2 = 0.294$, adj. $R^2 = 0.227$), and dogs owned by individuals having a dog-related occupation had a significantly lower mean Emotionality score (-0.018 ± 0.044) compared to those owned by individuals who don't (0.127 ± 0.023) ($F(1, 21) = 8.695$, $t = 2.949$, partial $\eta^2 = 0.293$, $\beta = 0.541$, $p = 0.008$; mean difference = -0.145; Figure S12). Results are shown in Tables S47-S50.

Discussion

Breed clade differences in learning performance

Behavioural persistence and social cognition may have gone through diversifying artificial selection in different dog breeds[29,32]. In support of this, we found differences in learning and behavioural performances across distinct dog breed clades. Dogs in the Asian Spitz clade (e.g., Siberian Huskies, Shiba Inus) were better at matching their behaviour to the contingencies – they showed better performance in the reversal learning (RL) task and less resistance to extinction (EXT; i.e., stopped responding quickly when no reward was provided), compared to dogs in the Retriever (e.g., Labrador Retriever, Nova Scotia Duck Tolling Retriever, Golden Retriver) and New World (German Shepherd Dogs; GSDs) clades. The better performance in the Asian Spitz clade could be attributed to their historical role as independent workers, having the ability to adapt and change their behaviour without relying on human communicative signals[17]. On the other hand, dogs belonging to the cooperative breed clades, such as Retrievers and GSDs, which are bred for their inclination towards collaboration with humans and maintaining visual contact with them[17], might have faced challenges in the hand-touch learning task. These dogs might have paid less attention to environmental contingencies, such as the rewarding schedule, and more attention to the (lack of) owner's body cues or visual communicative signals, thereby reducing their performance.

Our results also prompt questions as to whether previous research findings, which highlight differences in various measured cognitive traits across dog breeds, might be more attributed to the context or the nature of the tasks rather than innate cognitive differences. Certain breeds might excel in tasks that suit their natural inclinations, while others may struggle due to mismatched contextual factors resulting in performance variations, rather than solely due to selective pressures for specific cognitive traits. This aligns with previous research findings, which support the idea that physical capability plays a more significant role in interpreting perceived breed differences in working intelligence or trainability, rather than attributing it solely to cognitive factors[23].

Furthermore, the low resistance to extinction levels found in the Asian Spitz clade might also reflect their cost-effective behavioural strategy as an Independent working breed clade, having stronger reward-maximizing tendencies and being sensitive to reward-omission[11]. The Cooperative working breed clades, on the other hand, tend to show higher behavioural persistence in response to reward omission or extinction[33].

Nevertheless, not all breed differences may be explained by breeds' functional selection such as cooperativity, and breeds within the same breed group can still exhibit behavioural variations due to (intentional or unintentional) selection for different traits[29]. In this context, previous research has also highlighted the subjective nature of breed stereotypes as a significant limitation of the cooperative-working categorization approach. This raises the question: how do we accurately determine whether a particular breed should be labeled as cooperative or independent? For instance (see[64] for detailed discussion), Siberian Huskies were categorized as independent workers and less socially sensitive to human communicative signals by[17], while[68] classified them as cooperative workers, exhibiting considerable social sensitivity to humans.

A similar situation may apply to the European Mastiff clade, as in several respects, they may align more closely with the Cooperative breed groups than with the Asian Spitz breeds. While categorized as an Independent working breed clade in the current study, the European Mastiff clade (e.g., Staffordshire Bull Terriers, Rhodesian Ridgebacks, English Bull Terriers) showed considerably high levels of Resistance to extinction, which was significantly higher than the other Independent working breed clade in the current study (i.e., Asian Spitz). Hence, the high levels of persistence shown by the European Mastiff clade could indicate their notable perseverance to pursue the reward type used in the current study, either due to their high motivation to interact and respond to the owner or having a potentially higher level of incentive motivation compared to the Asian Spitz clade. Therefore, breed differences in learning and behavioural performance may not entirely be in line with the cooperative-independent working classification. Furthermore, the differences across breeds may also depend on the type of learning feature or cognitive trait being studied, for which different breeds might still have been selected with different intensities.

Differences across breed clades in dog-related predictors

Results of the current study showed intriguing effects of dog-related variables on certain learning components, which varied in the type of predictor and the direction of the effect across the studied breed clades. Dogs within the UK Rural clade (e.g., Australian Shepherds, Pembroke Welsh Corgis, Border Collies) with higher Ball/Toy Responsiveness scores experienced less difficulty in reversal learning, suggesting higher cognitive flexibility in these responsive dogs. Forasmuch as dogs within the UK Rural clade were selectively bred for their high responsiveness to human commands[67], the reduced difficulty level in reversal learning, despite the task's context hindering communication with the owner, might be linked to the social element of Ball/Toy Responsiveness for these cooperative dogs. For these dogs, perhaps the interaction with their human partner acted as an alternative source of reinforcement[18], compared to dogs with lower Ball/Toy Responsiveness, and led to a greater motivation to persist in responding and figuring out the task criteria despite facing errors and reward loss for their responses towards the previous S^d.

Alternatively, previous research found that different dogs, depending on the function for which they have been selectively bred and trained (e.g., extensive breeding and training for self-regulation in working dogs), may have different baseline level of arousal[6], which may also be linked to their reward preference[30]. For example,[30] suggested ball-preferring detection dogs to potentially have higher baseline level of arousal. Thus, it is conceivable that individuals with higher Ball/Toy Responsiveness within this breed clade may also naturally possess a higher level of baseline arousal.

Within the European Mastiff clade, engagement with sports was associated with higher resistance to extinction, suggesting higher perseverance and reward expectancy in these dogs following their engagement with recreational activities. For this clade, the sport-related training activities might have subsequently resulted in heightened responsiveness to humans and motivation to interact with humans. Consequently, this increased responsiveness could be the reason why these dogs, despite the reward omission, might have shown a higher persistence to continue interacting with their owner compared to other European Mastiff dogs without experience in sport-related training.

It is also possible that having a high baseline level of arousal for some individuals within the European Mastiff clade, which could also be the primary reason leading the owners to place these dogs into sport activities to satisfy their need (as dogs with high arousal levels might be more suited for sports), might have subsequently lead to the significant variability between the sport and non-sport European Mastiff dogs.

Optimal arousal levels, following an inverted U-shaped trend, may enhance cognitive performances in individuals, while extreme levels may increase errors, and an under-stimulated arousal level may lead to either slow performances or lack of interest in the task[10,55]. Research has also shown that optimal arousal levels can be task-specific [55]. More challenging tasks tend to be executed more effectively at lower arousal levels, whereas simpler tasks can be accomplished successfully even at higher arousal levels[55].

It is possible that the higher baseline level of arousal in the highly Ball/Toy Responsive UK Rural dogs might have contributed to reaching an optimal arousal level when a less arousal-inducing reward, such as food, was utilized in the task[30]. Furthermore, if the high baseline arousal in these dogs led them reaching an over-stimulated level of arousal in the task, the interaction with the owner might have helped them overcome the challenge by sustaining their engagement, enhancing their ability to stay focused and displaying greater cognitive adaptability. Conversely, sporting European Mastiff dogs could have struggled with regulating their optimal arousal levels throughout the task, which could potentially result in increased persistence and decreased flexibility and adjustment to the reward omission. This challenge could have possibly stemmed from a potential mismatch between the task's demands and their accustomed style of sport training.

Nevertheless, the effect of sport training on extinction performance also highlights the significant contribution of training history on the behavioural shaping process, which might be more pronounced for breeds that are not naturally (genetically) selected for working and sport-related tasks. Recent studies have discovered that the effectiveness of training in enhancing executive function skills might vary depending on dogs' working background. This effect appears to be more pronounced within the non-working dog population compared to working dogs[15]. This aligns with previous findings indicating significantly higher "Responsiveness" scores in working dogs compared to non-working dogs (e.g., those coming from show lines of breeding)[13], suggesting that high levels of responsivity and executive function skills could be a crucial criterion for selective breeding of working dog breeds.

Considering that herding dog breeds are often employed as working dogs and have specific working lines of breeding,[70] along with their physical structural suitability for canine sport-related activities[24], it is plausible that factors for which they may have genetic predispositions (e.g., Ball/Toy Responsiveness) could overshadow the influence of training experiences such as engagement with sports on their learning and behavioral performances. Conversely, for the European Mastiff clade, having a high level of executive function skills may not have been a specific criterion for breeding, at least until recently. Consequently, these dog breeds may exhibit a more pronounced effect of training history on their learning and behavioural performances. In the current study, the European Mastiff clade had a significantly lower proportion of sporting dogs compared to UK Rural clade, which had one of the highest proportions (only about 33% of European Mastiff dogs were engaged in sports compared to 72% of UK Rural dogs). That being said, the low rates of sport engagement among these dogs could also potentially lead to more variability in training background across individuals and a more pronounced effect of this factor on their learning performance. While for UK Rural dogs, having a high proportion of sport dogs might have masked the effect of this factor due to a high rate of similarity regarding training history across individuals along with their natural capability of performing similar tasks even without having these training experiences.

While these discussions are speculative based on current findings and previous research studies, the interconnections between Ball/Toy Responsiveness, sport-related training, arousal, and learning performance warrant further investigation, particularly to identify the reasons behind the varying effects across different breeds with distinct selective pressures.

Interestingly, the dog-related factors evaluated in the current study did not contribute into the difficulty in discrimination learning (DL) across the studied breed clades, except for the New World clade (i.e., German Shepherd Dogs; GSDs). Notably, GSDs with higher overall impulsivity (DIAS) scores learned the discrimination easier. This is somewhat surprising as impulsivity has been previously indicated in poor cognitive and behavioural performance[57]. However, perhaps impulsivity is not a limiting factor when it comes to the initial learning of a task. Previous research found that working dogs are usually selectively bred and rigorously trained for a heightened sense of task-oriented responsiveness to cues from handlers, which is usually associated with high impulsivity, impacting different aspects of their learning and behavioural expressions (Juntilla et al., 2022).

Given that previous studies also found the GSDs to have one of the highest impulsivity scores among their studied dog breeds[48,57], it appears likely that this trait along with its related component "Responsiveness"[69] are one of the main traits for which this breed (which is often used as a working dog breed[16,25]) had been selectively bred[5,29]. In the context of the DL phase of the hand-touch learning task, being highly impulsive may specifically manifest as a dog being quick to respond to stimuli without much hesitation or deliberation. Given that the primary stimuli in the DL phase was the owner's dominant hand, to which the dog may already have a strong previous learning history, either from receiving commands or rewards, having an innate tendency towards high impulsivity and responsiveness, combined with this established connection, likely contributed to their enhanced performance in choosing the target hand to respond and learning the initial discrimination.

The Food Responsiveness (FR) score, another component of the Canine Reward Responsiveness Scale (CRRS), did not influence dogs' performances within any of the studied learning components except for the resistance to extinction scores in the European Mastiff clade. Interestingly, contrary to the hypothesis of the current study regarding the potential impact of higher value and preferred rewards on incentivizing greater motivation in dogs, leading to more persistent behaviour, resistant to disruptors such as EXT [20], [21,46], the European Mastiff dogs with higher Food Responsiveness scores showed less resistance to extinction. Decreased resistance to extinction in highly food-responsive individuals might have stemmed from the European Mastiff dogs' reward maximizing tendencies as independent working breeds. They could be highly sensitive to the omission of a reward type that is of high value to them[11], resulting in ceasing to respond when the reward stops. Although, as previously discussed, there could be notable behavioural similarities between Mastiff-like breeds and other cooperative breeds, warranting further investigation into the potential negative correlation between responsiveness to food and Resistance to extinction in this clade.

Effect of age on learning performances across breed clades

We found that age did not influence dogs' learning performance in the hand-touch learning task. These findings are not in line with previous research showing that older age worsens cognitive function in domestic dogs[43,65]. The hand-touch learning task may heavily incorporate the influence of dog breeds' historical functions, such as cooperativity, and a strong social component, given the direct involvement of a human in the task procedure as the target for the dog's response. In contrast, other cognitive tasks previously used in measuring cognitive aging might lack this strong social component. Consequently, the effect of age may not be as pronounced in this task, despite its inclusion of discrimination and reversal learning measures. Thus, this lack of age effect could be attributed to breed-specific behavioural tendencies towards interaction with humans[17,26],[39],[64], which may significantly influence dogs' performances in this task and remain unaffected by age.

The within-breed clade analysis revealed an effect of age on the reversal learning performance within solely the Retriever clade; but only when Ball/ Toy Responsiveness and Impulsivity (overall DIAS score) were accounted in the same model. Previous studies found differences in the risk of age-related behavioural and cognitive dysfunction across dogs with different body sizes[62], with reversal learning being particularly highlighted as one of the early appearing cognitive functions to be influenced by aging[37]. However, studies have also shown that cognitive abilities develop along comparable age-related trajectories among different dog breeds, even though there are significant differences in the developmental rates and dog breeds' lifespan [66]. Therefore, it is unlikely for the Retriever clade to show a more pronounced decrease in their RL performance following the aging process compared to other dog breeds.

Previous research found Retrievers to struggle more with cognitive flexibility and adaptation to changing reinforcement contingencies compared to other breeds[31]. Hence, the notable effect of age on reversal learning in Retrievers could stem from their breed's inherent challenge with this type of learning feature. Consequently, this could also explain why the impact of age on this type of learning was particularly pronounced and observable in Retrievers rather than the other studied breed clades. Furthermore, considering that Ball/Toy Responsiveness and overall Impulsivity scores were among the final predictors in the model demonstrating a significant effect of age, it is plausible that these factors significantly contributed to the observed effect of age. While the effect of age could potentially be an artifact stemming from the small sample size within the Retriever clade, exploring the interaction between age, Ball/Toy Responsiveness, and Impulsivity in Retriever dogs, and how they collectively impact learning performance, warrants further investigation.

Studies focusing on canine cognitive aging have found greater levels of perseverative responding by increasing age in dogs[65], with this increased behavioural persistence in older dogs being mainly due to the difficulty in adjusting to the outcome of their responses. In our data, the age of dogs had a curious association with resistance to extinction, however, only within the European Mastiff clade. The older European Mastiff dogs exhibited higher resistance to extinction (when accounting for some additional variables), while other breed clades did not show any considerable effect of age. This discrepancy suggests that age-related changes in perseverance may also vary across breeds, depending on breed-specific predispositions.

Nevertheless, in the European Mastiff clade, age itself, without accounting for the engagement with sport and Ball/ Toy Responsiveness, did not directly contribute to resistance to extinction. Therefore, it appears likely that the impact of age in the European Mastiff clade was significantly mediated by these two factors. After excluding one outlier, results revealed a statistically significant negative relationship between Age and Ball/Toy Responsiveness in the European Mastiff clade. We found that older European Mastiff dogs were less responsive to balls or toys. Interestingly, a similar decrease in Ball/Toy Responsiveness was observed within the Asian Spitz clade, which represents another Independent working breed clade studied in the current study. However, none of the Cooperative working breed clades exhibited this association between age and Ball/Toy Responsiveness, which might be due their potentially genetic predisposition towards leisure rewards. While the link between Age and Ball/Toy Responsiveness may not be present across the Cooperative working breed group, suggesting a consistent interest for this reward type despite becoming older, for the breed clades categorized as Independent workers, increasing age might have decreased their interest towards balls and toys. However, further data analysis on the European Mastiff dogs showed that those engaging with sports had a significantly higher Ball/Toy Responsiveness compared to the non-sporting dogs while also accounting for the effect of age. Thus, the effect of age on Ball/Toy Responsiveness might be eliminated in the European Mastiff breeds upon their engagement with sports. It is possible that sports engagement may preserve physical strength and the motivation required for playing, or the European Mastiff dogs who engage in sports may be more similar to Cooperative breeds, as described above. Results of these additional analysis for dogs within the European Mastiff clade has been provided in the supplementary material (Table S51-53 and Figure S13-15).

Emotional responses across breed clades

Forasmuch as learning and reward omission are potentially frustrating events, we were also able to collect data on negative emotional behaviour of the breed clades. Among Retrievers, age emerged as the sole predictor, with older Retriever dogs displaying elevated emotionality levels. Within the UK Rural and European Mastiff clades, food responsiveness played a significant role in emotionality. Dogs that had higher food responsiveness scores showed greater emotional responses throughout the task.

This correlation between food responsiveness and emotionality is consistent with previous research suggesting that preferred reward types, such as those of high value to individuals, can intensify incentive motivation, leading to heightened emotional reactions towards reward loss[7,9,12,46,47]. However, the absence of a significant relationship between food responsiveness and emotionality in the other breed clades suggests breed-specific variations in factors that are of predictive value for dogs' frustration-like behaviour towards rewards. For instance, the lack of this link in the GSDs may be due to their generally low food motivation as these dogs had the lowest mean food responsiveness score across the studied breed clades, which was significantly lower than that of the European Mastiff and Retriever clades (Table S54 and Figure S16).

Furthermore, the increased food responsiveness and the limited individual variability among individuals in the Retriever clade may account for the lack of effect of food responsiveness on the Emotionality scores within this clade. Given the high levels of food responsiveness among individuals within the Retriever clade as documented in previous studies[18,45], other biological factors such as age or life experiences may rather exert a more substantial influence on their individual variability in frustration-like behaviours associated with learning difficulty or reward omission. For example, Retrievers might have become more sensitive to reward loss and exhibit increased frustration as they age. However, this outcome could still be attributed to the greater difficulty that older Retrievers encountered during the reversal learning phase in the current study. Overall, these breed-specific dynamics underscore the need for further investigation into the interplay of various cognitive and physiological factors driving emotional and frustration-like behaviours towards reward loss across different dog breeds.

Differences across breed clades in owner-related predictors

Owner-related variables also played a significant role in predicting learning and behavioural performance across breed clades in the current study. Our findings suggest that owners' dog ownership experience (i.e., having owned more dogs in the past) may influence behaviour of dogs, which is consistent with previous research findings[61]. Notably, owning more dogs in the past was associated with less difficulty in the reversal learning for the Asian Spitz clade. However, this relationship did not hold for the other clades, and it appears likely that this effect is particularly pronounced in breeds having less general responsivity to humans and work independently of humans. Given that the Asian Spitz clade also had one of the lowest mean DIAS sub-scale "Responsiveness" scores across the studied breed clades, which was significantly lower than some of the Cooperative working breeds such as the UK Rural and New World clades (Table S55 and Figure S17), experienced owners may possess the skills and knowledge necessary to effectively manage the behaviour of these less interactive dog breeds by training them to stay motivated and continue performing the task or interacting with them despite errors and reward loss.

Nevertheless, the impact of the other owner-related variables did not follow the same direction, as the Asian Spitz dogs owned by individuals having a dog-related occupation experienced more difficulty in reversal learning. As a great proportion of the owners with dog-related occupation (more than 80%) in the Asian Spitz clade were professional dog trainers, this might be due to their more advanced training practices, teaching the Asian Spitz dogs to make eye contact and follow their communicative signals, which might have then led to the same confusion the Cooperative working breeds experienced throughout the task.

The contribution of the owner-related variables to dogs' emotionality were also considerable, with the European Mastiff dogs owned by individuals having a dog-related occupation, and UK Rural dogs belonging to owners with more dog ownership experiences showing less emotional responses throughout the task. It is possible that these experiences and expertise of the owners contributed to a more controlled and less emotionally reactive behaviour in these dogs. Further research exploring the nuanced dynamics of human-dog relationships and their impact on dog behaviour is warranted to deepen our understanding of owners' contribution into dogs' behavioural and emotional development, and how these effects could vary across different breeds.

Limitations and future directions

Although results of the current study offer valuable insights into the significant impact of dog breeds' historical function and working context on their learning and behavioural performance, as well as the predictive value of various factors influencing behaviour, there are limitations that should be considered before interpreting the findings.

The restricted sample size within each breed clade, coupled with the utilization of breed clusters, could be viewed as a significant limitation in the present study. The current study used dog breeds' genetic clusters instead of studying each dog breed separately. Previous research discussed the disadvantages of using the breed grouping approaches, potentially masking important differences between breeds that are clustered within a particular group or clade[29,58]. This is particularly noticeable via the significant differences found in the performance and behavioural scores (e.g., Reward Responsiveness scores and DIAS subscale scores) across breed clades categorized under the Cooperative and Independent working groups. Results therefore suggest that potential differences might have also been present across breeds included within a certain clade but were not accounted or evaluated in the current study due to having small sample sizes. Therefore, future research may either benefit of studying different dog breeds without relying on the grouping approach or choosing one single breed from different clades to keep the within group and individual differences as small as possible. Although individuals within each dog breed can still exhibit significant and considerable variations due to varying life experiences[2,35].

Moreover, the limited sample size within each of the examined breed clades could have influenced the outcomes and the impact of predictors measured in the current study. As mentioned earlier, no adjustment for multiple comparisons was applied due to the exploratory nature of the study, which is also a considerable limitation. Therefore, it is imperative to interpret the results of the current study with caution, as some associations may have been over-interpreted due to a lack of correction for multiple comparisons within the entire dataset. Future research should therefore, implement corrections for multiple testing to provide more rigorous conclusions. These data, however, indicate potential correlations that would benefit from further experimental approaches to ascertain the causal factors affecting learning and behaviour in domestic dog breeds.

Different learning components were only measured and determined via one single task involving direct interaction with a human. Therefore, the task involved a highly heritable social component that may substantially vary across dog breeds[4,32,61]. As indicated by the results, the extensive involvement of human interaction likely played a significant role in influencing dogs' performance, as discussed within the framework of cooperativity working classification. Therefore, future research may benefit from evaluating the same learning components via different social and non-social cognitive tasks targeting various aspects of learning and behaviour to provide a more reliable and detailed conclusion.

Having previous experience with the hand-touch behaviour involved in the learning task did not significantly contribute into dogs' performance. However, the lack of variance in the sample regarding prior experience with this command may have contributed to the absence of significant effect from this experience on the measured learning and behavioural outcomes, as the majority of dogs had already acquired the skill, albeit to potentially varying degrees. It is also important to note that we do not have detailed information on how advanced or consistent the dogs' experience with this behavioural command was, even though their owners' reported familiarity with the behaviour. Some dogs might have learned the behaviour recently, while others could have practiced it regularly and for a long time, introducing further variability within the "familiar" group. Future studies should consider controlling for this factor by including only dogs who have been regularly practicing the hand-touch task for a certain amount of time or by ensuring a more balanced sample, with sufficient representation of both experienced and inexperienced dogs. This would allow for a more robust analysis of the potential impact of prior experience on learning and behavioural performance.

Another potential limitation of this study is the lack of control over whether the hand-touch command was consistently requested by the owner using the dominant hand only or if the dog was asked to generalize and respond to both hands regularly. If the owner alternated between hands, it might have facilitated the dog's ability to switch their responses between hands more easily during the RL phase, potentially affecting the RL outcome in this study. Thus, future studies should control for this factor to better assess the impact of prior experience with the hand-touch behaviour on dogs' ability to adapt during the reversal learning phase. The training context at which this behaviour was learnt (e.g., as a part of sport trainings) might also be important.

Despite this limitation, the high proportion of recruited dogs who already knew the hand-touch command suggests that this task could be a useful tool in future studies, particularly because many dogs nowadays are already familiar with this behaviour and consequently, the behaviour requires minimal time for acquisition and training before the test. The hand-touch task may therefore be suitable for large-scale studies, allowing researchers to focus on more advanced learning phases without dedicating extensive time to basic behavioural training. However, as discussed above, this may only feasible if an appropriate approach is used to balance and control for the effect of prior experience.

Utilizing a virtual task with dog owners performing the task as the main experimenter is another limitation. Having different individuals (owners) with different dog-related experiences performing the task might have impacted the dogs' performance. Lacking an experimenter (a research team member) guiding the owners throughout the experimental task was one of the main limitations of virtual experiments used in previous studies such as the Citizen Science approach[40,56], which was incorporated in the current study. A researcher was always available, guiding the owners throughout the task, and no significant errors from the owners directly influencing the participating dogs' behaviour in the current study was noted (except for the subject that was eliminated from the final study population). However, future studies should continue accounting for owners' procedural errors (e.g., recording and analyzing the impact of procedural integrity) if the goal is to study the dog's behaviour in their home and without involving a stranger in the task.

Another constraint in the present study pertains to the measurement approach employed for dogs engaging in the task over multiple days. Since the cumulative performance of dogs was assessed for each phase, it is plausible that, for example, a dog ceasing to respond due to the lack of motivation after only two sessions of DL could receive a more favorable DL component score compared to a dog persisting through the maximum six DL sessions, with this favorable score being possibly due to achieving a higher percentage of correct trials. Nevertheless, as the measure for the component scores also accounted for the percentage of No-response trials and session terminations, it is unlikely that a dog's lack of response would result in a lower learning difficulty score merely due to a smaller number of sessions and potentially a higher percentage of correct trials, as the same dog would also have a higher percentage of session terminations and No-response trials.

The Emotionality score in the current study was evaluated via recording the frequency of certain frustration-like behaviours such as vocalization and owner-directed responses (e.g., pawing or jumping at the owner), however, due to the virtual setting of the experiment, some important behaviours such as lip licking or tail position (as monitored in previous research[42]) could not be evaluated. Furthermore, due to the noise cancelation feature of Zoom that was originally activated on some owner's Zoom account, some vocalizations (e.g., whining) might have been missed throughout the video coding process. Future studies using virtual experimentation may benefit from using more than one camera to record the experiments and a virtual communication program that does not have an active noise cancellation feature to be able to record frustration-like behaviours more precisely.

Furthermore, in examining dogs' training history, the designation of sport dogs was limited to those engaged in Rally/obedience or Agility, chosen for their resemblance to the hand-touch learning task in terms of following human cues. However, we did not ask whether these sport dogs are actively participating, retired, or withdrawn from training, nor the extent of their advanced training.

Furthermore, previous research found that clicker training can be particularly useful in maintaining established behaviours when the primary reinforcement is unavailable[53]. This is because the clicker may act as a conditioned or secondary reinforcer, signaling to the dog that a reward is forthcoming, which can prolong their engagement in a task. In the current study, dogs with prior experience using a clicker might have continued to engage in the task for a longer period of time during the extinction phase. However, the effect of this experience was not specifically accounted in the current study. Future studies should consider controlling for prior clicker training experience to better understand its potential impact on extinction performance and other learning outcomes.

Lastly, some questions regarding the dogs' training history, the owners' experience with dogs, and their dog training knowledge might have had a very general nature. Thus, these questions might not have provided precise information to help with a more reliable discussion and conclusion regarding the contribution of owner-related factors on dogs' behavioural performance. For example, the questions focusing on owners' dog ownership experience and their dog training knowledge did not precisely provide information regarding the type of training course owners have passed and how many of the dogs they have owned in the past were actually from the same breed clade of their current dog. Future studies may benefit from more detailed questions providing more reliable and precise information for analyzing the impact of training history on behaviour and learning performance.

Conclusion

Results of the current study revealed both between and within-breed clade differences in the learning performance, depending on the type of learning feature being evaluated, and in frustration-like behaviours following difficulty to adjust with the rewarding schedule. The Cooperative working breed clades experienced more difficulty in the reversal learning phase, but still exhibiting a significantly higher perseverance during the extinction phase, which might be significantly associated with the context of testing and their historical function. Thus, it is crucial to carefully consider the working context created in the experimental settings, and to account for potential breed effects on dogs' reward motivation and behavioural performance.

The owner-reported measures including Reward Responsiveness and Impulsivity scales predicted more within-breed clade rather than between-breed clade variations in the current study. Thus, different breed clades may have different learning profiles, which can further be influenced by factors such as age, food or Ball/Toy Responsiveness, impulsivity, or training history. However, the extent to which these factors contribute into learning performance is different across breeds and are not always in the same direction.

Data availability

The dataset used in this study is available at https://doi.org/10.5683/SP3/WSKH1N.

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Author contributions
Conceptualization and study design, A.A. and A.P.; data collection, A.A.; writing—original draft, A.A.; writing—review and editing, A.A. and A.P.; statistical analysis and data visualization, A.A.; supervision and funding acquisition, A.P.; all authors have read and agreed to the submitted version of the manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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