Effects of maternal investment, temperament, and cognition on guide dog success

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Contributed by Dorothy L. Cheney, June 21, 2017 (sent for review April 3, 2017; reviewed by Sarah Marshall-Pescini and Karen J. Parker)

A continuing debate in studies of social development in both humans and other animals is the extent to which early life experiences affect adult behavior. Also unclear are the relative contributions of cognitive skills ("intelligence") and temperament for successful outcomes. Guide dogs are particularly suited to research on these questions. To succeed as a guide dog, individuals must accomplish complex navigation and decision making without succumbing to distractions and unforeseen obstacles. Faced with these rigorous demands, only ∼70% of dogs that enter training ultimately achieve success. What predicts success as a guide dog? To address these questions, we followed 98 puppies from birth to adulthood. We found that high levels of overall maternal behavior were linked with a higher likelihood of program failure. Furthermore, mothers whose nursing style required greater effort by puppies were more likely to produce successful offspring, whereas mothers whose nursing style required less effort were more likely to produce offspring that failed. In young adults, an inability to solve a multistep task quickly, compounded with high levels of perseveration during the task, was associated with failure. Young adults that were released from the program also appeared more anxious, as indicated by a short latency to vocalize when faced with a novel object task. Our results suggest that both maternal nursing behavior and individual traits of cognition and temperament are associated with guide dog success.

guide dogs | nursing style | maternal style | temperament | cognition

It is often assumed that, in both human and nonhuman animals, variation in cognitive abilities contributes to variation in problem-solving skills. However, there remains little consensus about what attributes, exactly, comprise such abilities, because performance is affected not just by variation in general "intelligence" (1) or reasoning ability (e.g., refs. 2, 3) but also by variation in more affective attributes, such as impulse control, neophobia, motivation, and exploration (e.g., refs. 4–6).

Similarly, the long-term effects of early life experiences remain poorly understood. There is now considerable evidence that early exposure to stress has lasting effects on physiology [e.g., humans (refs. 7–9), rodents (refs. 10, 11), rhesus macaques (ref. 12 and reviewed in ref. 13)]. In rhesus macaques, mothering style is correlated with offspring cortisol and serotonin levels (14, 15), and in baboons, the male offspring of subordinate mothers exhibit higher glucocorticoid levels than the offspring of more dominant mothers (16). In rodents, experiences across the early weeks of life have lasting implications for later temperament measures, such as stress reactivity and fear (17, 18), and cognitive skills, such as spatial memory (19). Similar effects are observed in children, where negative life events in childhood are linked to later reductions in adolescent self-control (20).

Guide dogs are particularly suited to research on the long-term effects of early experience on adult outcomes. Over the first 5 wk of life, puppies remain with their mothers in the same facility, where they are housed in highly controlled conditions and available for systematic observation. By 2 y of age, a relatively quick period of maturation, their adult behavior can be assessed according to a discrete dependent measure: either success in or release from the training program. Achieving success, moreover, requires meeting stringent temperament and cognitive requirements. Guide dogs must follow the commands of their owners, respond appropriately to a rich array of environmental stimuli (e.g., revolving doors, escalators), ignore their impulses (e.g., to chase a squirrel), and react to the unexpected (e.g., barriers along their route). Indeed, many of the traits that we value in guide dogs, such as attention, inhibitory control, and problem solving, are also beneficial in other species, including our own. However, despite being bred and raised with the specific aim of becoming guide dogs, only ∼70% of dogs that enter training ultimately succeed in the program.

In dogs, high levels of maternal care have been linked to physical and social engagement, aggression, and lower levels of anxiety and fear (21–23). Furthermore, aspects of young adult temperament, as measured by behavioral observations and questionnaires after 6 mo of age, have routinely been found to affect working dog success (24–35). In military and police dogs, high levels of search focus, sharpness, prey drive, and aggression have been linked to success (25, 27, 34). In drug detection dogs, a desire for work, measured via obedience, activity, and concentration, leads to better outcomes (33). In guide dogs specifically,

Significance

A successful guide dog must navigate a complex world, avoid distractions, and respond adaptively to unpredictable events. What leads to success? We followed 98 puppies from birth to adulthood. Puppies were enrolled in a training program where only ∼70% achieved success as guide dogs. More intense mothering early in life was associated with program failure. In addition, mothers whose nursing style required greater effort by puppies produced more successful offspring. Among young adult dogs, poor problem-solving abilities, perseveration, and apparently greater anxiety when confronted with a novel object were also associated with program failure. Results mirror the results from rodents and humans, reaffirming the enduring effects on adult behavior of maternal style and individual differences in temperament and cognition.

Author contributions: E.E.B., D.L.C., J.A.S., and R.M.S. designed research; E.E.B. performed research; E.E.B., M.D.S., D.L.C., and R.M.S. analyzed data; and E.E.B., D.L.C., and R.M.S. wrote the paper.

Reviewers: S.M.-P., Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, and University of Vienna; and K.J.P., Stanford University.

The authors declare no conflict of interest.

Data deposition: The data reported in this paper have been deposited on Dryad Digital Repository, www.datadryad.org (http://dx.doi.org/10.5061/dryad.50fj0).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1704303114/-/DCSupplemental.

success is associated with high levels of obedience and trainability and low levels of reactivity, hyperactivity, aggression, distraction, and anxious behaviors (e.g., barking) (24, 26, 29, 32, 35). To date, however, no study has examined the direct effect of mother–puppy interactions on program success or failure; examined the direct effect of performance on cognitive tests on subsequent working dog success; or simultaneously explored maternal, cognitive, and temperament effects within the same model, thereby testing each variable while controlling for the others.

To examine these questions, we studied a population of German Shepherds, Labrador Retrievers, and Golden Retrievers bred to enter a guide dog training program at two life stages: puppyhood and adolescence. We began by observing mothers and their litters over the puppies' first 3 wk of life (36) (Table S1). We then tested the same individuals on 11 cognitive and temperament tasks as young adults, at 14–17 mo of age. Some tests examined variables previously shown to predict adult working dog performance: distractibility, interest in fetching, and other temperament measures (Table S2). Other tests examined variables presumed to be important for guide dogs: temperament factors, such as obedience and attentiveness to task and handler, and cognitive factors, such as flexibility, problem solving, and proficiency in navigating a detour (Table S2). These skills have been linked to variation in adult behavior among humans and other animals but never measured in guide dogs.

By 2.5 y of age, all dogs (n = 98) had received an outcome: either success [placed as a guide or breeder, n = 66 (67%)] or failure [released from the program, n = 32 (33%)] (Table S3). Our overall aim was to examine the relation between dogs' success in the program and both their mothers' behavior before weaning and their performance in subsequent cognitive and temperament tests as young adults.

Results

Maternal Style. From videotapes of mothers and puppies, we extracted seven variables of maternal behavior: time spent in a nursing box with puppies, contact, licking/grooming, lateral nursing (mother lying on side), vertical nursing (mother sitting/standing), ventral nursing (mother lying on stomach), and orienting away from puppies. These behaviors all loaded onto one principal component (PC), *Maternal behavior*, that explained a significant portion of the variance (54%), remained stable over time, and was correlated with concurrent experimental and hormonal measures of maternal care (36). Mothers that scored high on this component were vigilant, often in proximity to their litter, and regularly interacted with their puppies (further details are provided in *SI Materials and Methods*). These mothers also showed higher baseline cortisol levels and a greater stress response when briefly separated from their puppies.

Differences in *Maternal behavior* were associated with several measures of young adult performance (Table S4). Dogs that experienced more maternal care were more active when isolated (task 1b: estimate = 0.57, Wald = 7.35, P = 0.007), slower and more perseverative at multistep problem solving (task 5: estimate = 0.48, Wald = 4.21, P = 0.04), and quicker to vocalize during the novel object task (task 10b: estimate = –0.59, Wald = 5.62, P = 0.02). All other maternal behavior effects varied by breed (*SI Materials and Methods* and Table S4). Differences in *Maternal behavior* were also associated with outcome, whereby puppies that experienced lower levels of maternal behavior were more likely to succeed (*SI Materials and Methods* and Table S5).

Research in other species has shown that specific maternal behaviors, particularly nursing styles, can have long-term effects on offspring development (Introduction), and our *Maternal behavior* PC included three nursing types that loaded at varying strengths and recalled some differences in nursing styles in other species. Therefore, we analyzed which of the behaviors that loaded strongly onto *Maternal behavior* were associated with outcome (36). We standardized each variable and entered it singly as a predictor variable. Upon determining which variables were significantly associated with outcome in individual models, we combined those variables into a single logistic regression model. We built a generalized estimating equation (GEE) general linear model (GLM) with outcome as the dependent variable; time in the nursing box, licking/grooming per puppy, vertical nursing per puppy, and ventral nursing per puppy were entered as predictors with breed, maternal parity, sex of puppy, and age at return entered as covariates. Litter identification (ID) was a random effect. Results (Table S6) revealed a main effect of ventral nursing (Wald = 10.20, P = 0.001): Puppies exposed to high levels of ventral nursing were more likely to be released from the program [odds ratio (OR) = 4.22, odds of program release 4.22-fold higher]. There was also a main effect of vertical nursing (Wald = 34.57, P < 0.001), but in the opposite direction: Puppies exposed to more vertical nursing were less likely to be released (OR = 0.25, 75% lower odds of program release).

Young Adult Test Performance. Dogs participated in 11 tasks of temperament and cognition as young adults, just before entering The Seeing Eye training program (5, 6, 22, 26, 27, 31, 37–51) (*SI Materials and Methods* and Table S2). The 11 tasks yielded scores that could be summarized by 13 PCs and two standardized/z-scored variables (*SI Materials and Methods* and Table S7).

To determine which of the young adult performance tests best predicted program outcome (52, 53) (*SI Materials and Methods*), we included data from both our primary dataset (n = 98; 66 successes and 32 behavioral releases) and from an additional 32 subjects that had entered the training program but were subsequently released for medical reasons (imputed dataset; Table S8). Three young adult test scores were associated with program outcome in both the observed and the observed plus imputed datasets (Table S8, tasks 5, 10b, and 11a): poor performance on the multistep problem-solving task, latency to vocalize when presented with a novel object, and umbrella-opening reactivity. We therefore selected these three tests for inclusion into a final multivariate logistic regression model (Table S9) that used program outcome from only the observed (nonimputed) dataset as the dependent variable. All three tests remained associated with program outcome (*SI Materials and Methods*).

Maternal Style and Young Adult Performance Combined. To compare the predictive strength of maternal style and young adult test performance, we built a single model that incorporated both classes of variables as predictors. Program outcome was the dependent variable, and predictors were the *Maternal behavior* PC and the three young adult test performance variables listed above. We included as covariates breed, maternal parity, sex of puppy, and age at return. Litter ID was entered as a random effect. Results are summarized in Table 1.

As in earlier tests, we found a main effect of *Maternal behavior* (Wald = 4.62, P = 0.03), indicating that puppies raised by mothers with high scores on *Maternal behavior* were more likely to be released (OR = 2.61, odds of program release 2.61-fold higher). We also found an association with performance on the multistep problem-solving task (Wald = 4.52, P = 0.03), indicating that dogs performing poorly on this task were more likely to be released (OR = 1.67, odds of program release 1.67-fold higher; Movie S1). In addition, young adults of all breeds that were slow to vocalize during the novel object task were less likely to be released (Wald = 4.39, P = 0.04, OR = 0.50, odds of program release 50% lower; Movie S2). Finally, we found an interaction between breed and reactivity to the umbrella-opening task (Wald = 11.00, OR = 0.27, P < 0.001): Labrador Retrievers that showed stronger behavioral responses had higher rates of release from the program (Wald = 4.89, P = 0.03, OR = 1.80, odds of program release 1.80-fold higher), whereas Golden

Table 1. Model exploring the combined effect of *Maternal behavior* and young adult performance on outcome

Predictor variables	OR	Estimate	SE	Wald	*P* value
Maternal behavior	2.61	0.96	0.44	4.62	0.032*
Multistep problem-solving poor performance	1.67	0.51	0.24	4.52	0.034*
Novel object quiet	0.50	−0.69	0.33	4.39	0.036*
Golden score	0.59	−0.53	0.31	2.89	0.089
Labrador score	0.72	−0.33	0.45	0.54	0.461
Maternal parity	1.04	0.04	0.14	0.07	0.792
Sex of puppy	0.42	−0.86	0.57	2.27	0.132
Age at return	0.57	−0.57	0.24	5.94	0.015*
Interaction	0.27	−1.32	0.40	11.00	<0.001***
Umbrella-opening reactivity × German Shepherd	0.75	−0.29	0.52	0.30	0.584
Umbrella-opening reactivity × Labrador Retriever	1.80	0.59	0.27	4.89	0.027*
Umbrella-opening reactivity × Golden Retriever	0.48	−0.73	0.32	5.28	0.022*

The dependent variable was outcome in the program, 1/0 (released from program or successfully placed as guide or breeder). Predictor variables retained were as follows: *Maternal behavior*; multistep problem-solving poor performance; long latency to vocalize when presented with a novel object; an interaction between umbrella-opening reactivity and breed (German Shepherd, Labrador Retriever, and Golden Retriever); Golden score, Golden Retriever compared with German Shepherd; Labrador score, Labrador Retriever compared with German Shepherd; maternal parity, 1–5; sex of puppy, 1/0 (male or female); and age at return, 14–17 mo. Litter ID was entered as a random effect. $n = 98$ (32 release dogs, 66 successes). Statistical tests of significance used GEE (***$P < 0.001$; *$P < 0.05$).

Retrievers with stronger responses had lower rates (Wald = 5.28, $P = 0.02$, OR = 0.48, odds of program release 52% lower).

Finally, age at return, a demographic factor, was also found to be important. Dogs that returned to headquarters at a younger age had higher rates of program release (Wald = 5.94, $P = 0.02$, OR = 0.57, odds of program release 43% lower with each additional month remaining with puppy-raising family).

Model Comparisons. Several measures of maternal behavior and young adult performance were significantly associated with outcome. The associations remained significant even when the predictors were combined into a single model. To determine which combination of measures best predicted outcome, we tested the discrimination, or performance, of each model by calculating the area under the curve (AUC), which quantified each model's ability to classify a dog correctly as an eventual program release or success (higher AUCs indicate better predictive power) (54, 55) (*SI Materials and Methods*). The AUCs and 95% confidence intervals for all models are listed in Table S10. Values for all models were above 0.5, indicating that all combinations of maternal and young adult measures were predictive of outcome at above chance levels (56). When we compared models, we found that the *Maternal behavior*-only model was significantly different from the young adult-only model (the latter was better: Z = –1.99, $P = 0.05$) and the combined *Maternal behavior* and young adult model (the combination model was better: Z = –2.24, $P = 0.03$). We therefore concluded that both maternal style and young adult behavior are important, but the young adult measures were more powerful from a predictive standpoint.

For illustrative purposes, we summarize in Fig. 1 the main effects of *Maternal behavior* and young adult performance on outcome and illustrate the likelihood of success when dogs were ranked according to their performance on these measures.

Discussion

Like Foyer et al. (21) and Guardini et al. (22), we found an association between maternal behavior and young adult behavior in tests of temperament. However, contrary to their results, we found that increased maternal behavior was positively associated with undesirable anxiety-related behaviors and performance in young adult dogs, including high activity when isolated, a short latency to vocalize when presented with a novel object, and perseverative errors and poor performance during a problem-solving task.

In our final model, the only nonbehavioral covariate related to outcome was the age at which dogs were returned for training. Dogs that returned from their puppy-raising families at a younger age (14 mo) were less likely to succeed than older dogs (17 mo). These results are consistent with the results obtained in one previous study (57), where dogs entering training at 17 mo were more likely to succeed than older individuals (up to 27 mo). Given that personality traits in dogs, such as calmness and boldness, have been linked to age (58), it seems possible that returning for training at a specific age leads to better acclimation to a kennel setting. Additionally, the accrual of more "real-world" experiences before training may lead to better outcomes, but only up to a point.

Even when controlling for the effect of age on outcome, however, behavioral differences in mothers and puppies had significant consequences for success in the program.

First, variation in *Maternal behavior* was significantly associated with dogs' later success in guide dog training. Contrary to our expectations, however, puppies that received higher levels of maternal behavior were less likely to succeed in the program. This finding may not be an isolated result. Parker and Maestripieri (59) point out that the influence of stress on outcome has long focused on extreme disruptions of the parent–offspring relationship, and thus been treated in the literature as a linear function, in which the more early life stress an individual faces, the worse the outcome. They argue, however, that the relationship is actually quadratic: Too much stress is certainly a bad thing, but so is too little, because young animals then lack the experience of learning to deal independently with stress. Rather, facing an intermediate amount of stress in early life can have an inoculating effect on subsequent behavior (60). Several studies support this view. Although long maternal separations are universally acknowledged to have deleterious consequences (e.g., refs. 61–64), studies in squirrel monkeys show that repeated short-term separations give young animals a chance to respond to temporary aversive events, which is adaptive over the long term (65). These benefits may also extend to cognitive performance and response inhibition.

Consistent with this view, we found that high levels of ventral nursing were associated with program release, whereas high

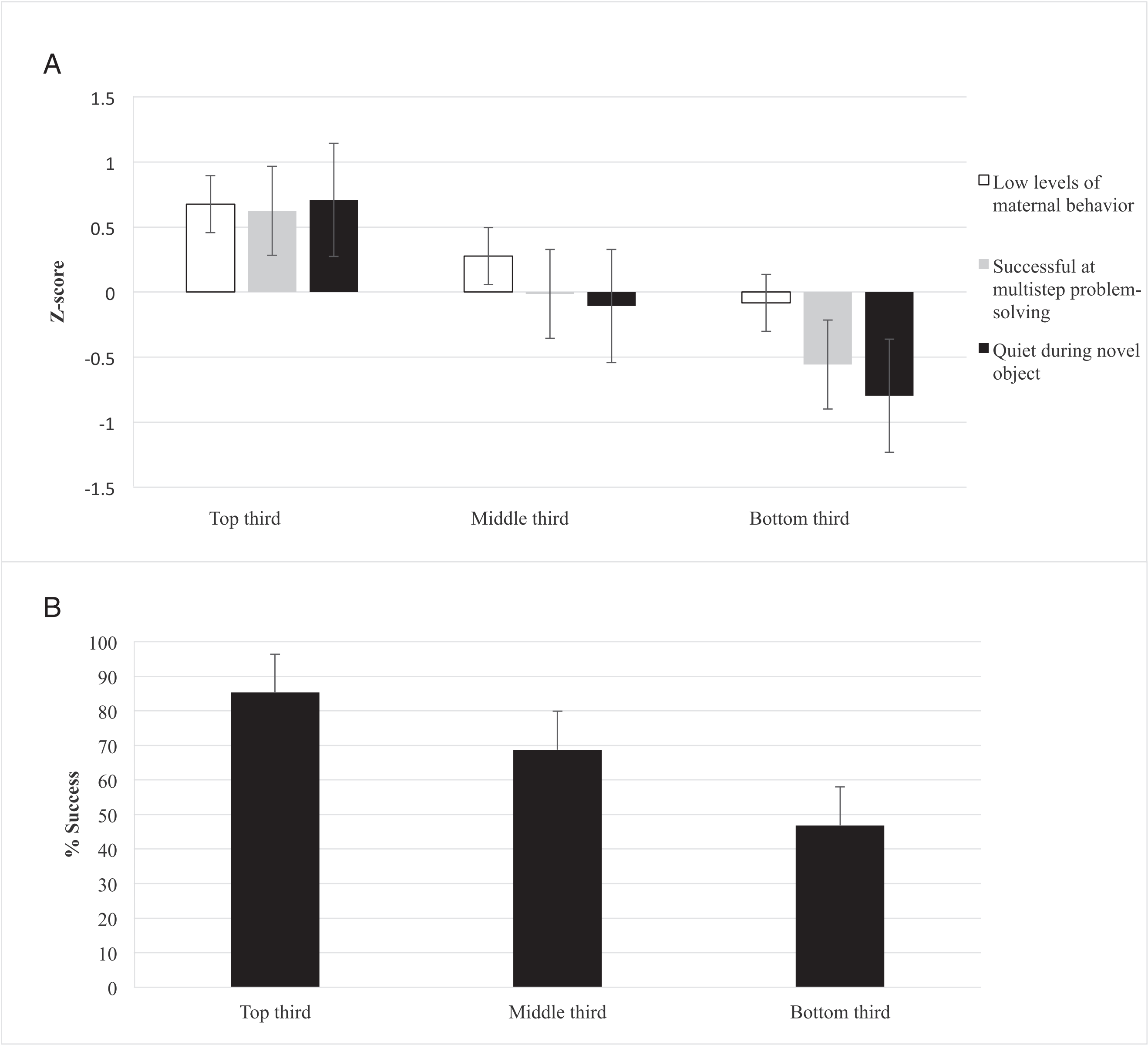

Fig. 1. Relation between dogs' scores on three behavioral measures (*A*) and their success in the program (*B*). (*A*) Dogs were ranked according to their scores on the three behavioral measures that most strongly predicted outcome (low levels of maternal behavior, good performance on young adult multistep problem solving, and slow latency to vocalize to a novel object as a young adult) and then divided into thirds (top third, $n = 34$; middle third, $n = 32$; and bottom third, $n = 32$) based on the sum of their ranks. (*B*) Same dogs' mean percentage of success in The Seeing Eye program, calculated by group, is depicted. Error bars represent the SEMs.

levels of vertical nursing were related to program success. These differences in nursing styles may provide different opportunities for puppies to "prevail over small challenges" (65). When mothers nursed ventrally, while lying on their stomachs, they were relatively immobile and their nipples were at the puppies' face level, making it easy for puppies to stay attached. In contrast, when mothers nursed vertically, while sitting or standing, nursing was a more difficult, active, and effortful endeavor for puppies. Vertical nursing in dogs is most similar to arched-back nursing in rodents, which has been linked to positive outcomes in adulthood, including better spatial memory (19) and lower anxiety (66). Some of these effects in rodents might be explained by the nipple switching facilitated by arched-back nursing, which results in increased tactile stimulation (19). Interestingly, in our population, as in rats (e.g., Fig. 1 in ref. 67), vertical nursing was the rarest of the nursing styles. Therefore, one possible explanation for our results is that a moderate amount of maternal care is beneficial but higher levels of maternal care are not challenging enough, and thereby have a negative effect on later performance. Perhaps in this population of dogs, where all puppies obtain sufficient maternal care and nutrition, receiving comparatively less (or an average amount of) maternal attention fosters resilience, whereas more maternal attention increases vulnerability.

One limitation of the current study is the potential confound of genetic effects. Because all mothers were related to the puppies they were rearing, we are unable to determine a precise causal link between maternal style and later puppy behavior and outcome. The mother's behavior could potentially be an artifact of the dog's genetic makeup contributing to a specific temperament, which is then inherited by the puppy. Cross-fostering studies similar to the studies conducted on rodents (e.g., refs. 19, 68) might help to disentangle the genetic vs. behavioral effects of maternal style on program outcome.

Some measures of temperament and problem-solving abilities were also linked to dogs' later success in the guide dog program. In a multistep problem-solving task, dogs that perseverated less and were quickest to solve the problem were more likely to succeed. This result supports our prediction that problem solving and impulse control are central to success. Similarly, dogs with shorter latencies to vocalize during the novel object task, a likely sign of higher anxiety (69), were more likely to be released from the program. This result is consistent with the findings of Harvey et al. (26), who found that the guide dogs predicted to be successful had lower scores on a fear/anxiety PC at 5 mo of age. The component was partially based on vocalizing during tasks.

Both the combined model and the young adult-only model had significantly higher AUCs than the *Maternal behavior*-only model. The fact that young adult temperament and cognitive measures had more predictive power is not entirely surprising, because they were collected much closer to the time of actual outcome. Importantly, however, the AUCs of the maternal style, young adult performance, and combination models were all greater than chance, indicating that data from both the maternal environment and young adult time period can be useful in predicting program outcome.

Additionally, we now know that maternal style affects both young adult behavior and outcome. We also know from our combination model that maternal style has a significant effect on outcome, even when controlling for young adult behavior. Thus, it remains for future research to examine whether the association between maternal behavior and program outcome is partially mediated by the association between maternal behavior and young adult performance.

In sum, what predicts a successful guide dog? Our results support previous studies on other animals in reaffirming the enduring benefits of maternal care—in moderation. Furthermore, they suggest that a few targeted tests associated with temperament, perseveration, and cognition may capture individual differences in ability that continue throughout adulthood.

Materials and Methods

Subjects (Table S1) were 21 mothers (nine German Shepherds, eight Labrador Retrievers, and four Golden Retrievers) and their 21 litters (n = 138 puppies) belonging to The Seeing Eye, Inc. (Morristown, NJ), a philanthropic organization that breeds, raises, and trains guide dogs for the blind and visually impaired. The Seeing Eye granted informed consent to the study. All mothers lived at the breeding station, where the puppies were whelped and weaned. The young adult testing took place at headquarters, where puppies returned for training and placement. All testing procedures adhered to regulations set forth by the University of Pennsylvania Institutional Animal Care and Use Committee (protocol 805210).

Mothers and litters were videotaped (n = 328 min per litter on average) over the puppies' first 3 wk of life (36). Puppies were weaned at 5 wk and then sent at 7 wk to "puppy-raising" families who fostered, trained basic obedience, and exposed the puppies to a variety of experiences. Subjects returned to The Seeing Eye at the age of 13–17 mo (n = 133) for training. Before their formal entrance into the training program, we tested subjects individually on 11 cognitive and temperament tasks (Table S2).

Before 3 y of age, all dogs were either successfully placed as a guide or breeder or released from the program. Breeders completed 2 mo of guide dog training and then were selected for the breeding program based on health and behavior. Dogs could be released at any point, although only 4% of our sample was released before returning for training. The primary reasons that dogs were released were behavioral, such as lack of confidence, excitability, and inability to focus. Because we were only interested in program release for behavioral reasons, dogs released for medical reasons were excluded from analyses (e.g., ref. 29). Of the original 138 observed dogs, 29% (n = 40) were excluded from analysis due to release for medical concerns (n = 27), transfer to another organization (n = 1), or missing data on the young adult tasks (n = 12) (Table S3).

Maternal Style. Complete methods used to study maternal style can be found in a study by Bray et al. (36) (*SI Materials and Methods*).

Young Adult Performance. All testing took place at The Seeing Eye headquarters (*SI Materials and Methods*). Each dog first completed an hour-long session involving seven tasks (Table S2, tasks 1–7), was given at least an hour-long break, and then completed a 30-min second session (Table S2, tasks 8–11) (70). The main experimenter and dog handler were present at each session. These roles were always filled by two of five females of similar age, with the first author (E.E.B.) as the main experimenter in 87% of sessions.

Data Processing and Statistical Analysis. All statistical analyses were carried out in R version 3.3.0 (71). To test for associations between maternal behavior, young adult test performance, and outcome, we built logistic regression models. Variance estimates for the statistical tests on the regression coefficients were adjusted for clustering due to litter effects using GEE-GLM (72). Models were fit using "geepack" in R (73). To assess the calibration of each model, we performed Hosmer–Lemeshow goodness-of-fit tests (74). Nonsignificant P values (P > 0.05) for all models indicated there was no evidence of poor fit and all models were therefore correctly specified. Following previous studies (e.g., refs. 21, 36, 37), breed, maternal parity (1–5), sex of puppy (1/0, male vs. female), litter size (2–10 puppies), and age in months (14–17) when the dog returned for training were included as covariates in all models. Birth season (1/0, winter vs. spring) was not included because it was highly correlated with age when dogs returned for training. Covariates were then removed using a backward-selection strategy, with the final model retaining confounders that influenced any association of interest by greater than 15%.

We first built models to examine the effect of the PC, *Maternal behavior*, on young adult performance. These GEE-GLMs used a Gaussian error distribution with litter as the unit of analysis.

We next built models to examine how outcome was affected by *Maternal behavior*, the variables that comprised *Maternal behavior*, performance on cognitive and temperament tasks as a young adult, and *Maternal behavior* combined with young adult performance. These GEE-GLMs were conducted with the "logit" link and a binomial error distribution. In these models, litter size could be excluded as a covariate due to lack of confounding.

Finally, we evaluated the predictive ability of these models to discriminate correctly between dogs that were successful and dogs that were released from the program (*SI Materials and Methods*).

ACKNOWLEDGMENTS. We thank S. Bartner, L. Cohen, S. Frommer, N. Gay, A. Gersick, M. Ream, R. Schwartz, A. Seely, and M. Torres for assistance with data collection, dog testing, and coding. We also thank S. Hasan for his enormous help with Datavyu export code. We are grateful to Dr. Dolores Holle for coordinating our work at The Seeing Eye, as well as the leadership team of The Seeing Eye, Breeding Station Manager Maria Hevner, and Director of Canine Development Peggy Gibbon. We also thank the breeding station and training kennel staff for giving us access to the kennels at both the breeding station and headquarters, and allowing us to work with their dogs. This work was supported, in part, by the University of Pennsylvania Department of Psychology's Norman Anderson Graduate Student Fund, a University of Pennsylvania University Research Fund award, the Class of 1971 Robert J. Holtz Endowed Fund for Undergraduate Research, the University of Pennsylvania's University Scholars program, and a National Science Foundation Graduate Research Fellowship (DGE-1321851 to E.E.B.).

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