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Research Paper

Nature and nurture—How different conditions affect the behavior of dogs

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ABSTRACT

Temperament tests for working dogs can provide substantial information about a particular dog's behavioral phenotype. When a larger proportion of the population is tested, the test results can also provide information about the effects of different environmental conditions on the phenotype because if the population is large, the social and physical environments to which the dogs are exposed differ. This means that we need to include in our evaluations the perspective that uses information about the environment in relation to the individual dog's level of development. There is substantial evidence that basic temperament traits in dogs are moderately heritable. There is also evidence that postweaning conditions have a huge effect on development, and this effect is often not assayed. Selective breeding for desired traits in combination with optimal environmental conditions, adapted to the individual dog's level of maturation, is a key point when producing outstanding working dogs.

Introduction

Information from behavior tests of dogs can be used in different ways. It can be used when selecting dogs for training and breeding and when deciding what type of training a particular dog is best suited for, and within a breeding program, such information can be used for progeny testing.

Tests of behavioral responses can also provide information on different factors affecting behavior. Pedigree information makes it possible to calculate heritabilities of the tested traits, that is, the proportion of the phenotypic variance that has an additive genetic component. We can also estimate effects from the common litter environment, including litter size, parity, age of the mother, and season of birth with respect to the test result or training outcome.

Weight data from birth to weaning may suggest effects of factors related to growth during puppyhood. When information on how the dogs were cared for after weaning is available, the effects from the postweaning condition can be analyzed. The effects of being raised in a rural or urban environment, with children in the family or being raised without children, the prior experience of raising or training dogs by the caregiver, and so on all matter are seldom evaluated with any consistency.

The purpose of this article is to present information on relevant factors that affect the adult working dog phenotype, from birth to adult age.

Information from temperament test

Most temperament tests have been conducted on adult dogs, that is, dogs older than 12 months (Diederich and Giffroy, 2006; Jones and Gosling, 2005). When tests are performed on a large number of dogs, the effect of the genetics on behavior can be calculated. Wilsson and Sundgren (1997b) evaluated a temperament test performed at the former Swedish Dog Training Center on 1310 German Shepherds (GS) and 797 Labrador Retrievers (LR). For GS, heritabilities varied from 0.37 (affability) to 0.13 (sharpness). For LR, the estimations ranged from 0.35 (ability to cooperate) to 0.05 (prey drive). The comparison of variance components based on sire and dam indicated small effects due to the preweaning conditions/maternal environment (common litter environment) on the test result. A similar result was found by Van der Waaij et al. (2008), who also analyzed data from the former Swedish Dog Training Centre, using a somewhat different statistical approach. Strandberg et al. (2005) studied the genetic effects on the temperament test on 5959 GS in Sweden. Heritabilities for the broader temperament

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profiles extracted from the factor analysis ranged from 0.09 to 0.23. Again, the effects of the common litter environment were small. Arvelius et al. (2014a) analyzed the results from the same test on 1738 rough collies. Heritabilities ranged from 0.14 to 0.25 for the traits extracted from the factor analysis. Once again, the effects of the common litter environment were small. Arvelius et al. (2014b) also analyzed the test results on 873 GS from the Swedish Armed Forces breeding program. Heritabilities were low to moderate, ranging from 0.12 to 0.28 on the aggregated traits from the PCA, which were higher than for the individual traits evaluated by the test. All analyses discussed thus far are for dogs older than 1 year.

The fact that there have been no maternal effects found for tests on adult dogs does not mean that the maternal environment does not affect puppies. When studying maternal effects based on pedigree data, it is assumed that any maternal effect is evenly distributed within the litter, across puppies. Differences between mothers then would have a similar effect on all puppies in a litter and increase the intralitter variation. However, if the maternal effort is not evenly distributed across the litter, the effect of the mother may increase interlitter variation without appearing as a maternal effect when comparing heritabilities based on sire and dam. Wilsson (1997) found that female puppies were punished 75% more often than male puppies during weaning, clearly indicating that the maternal effort does not have to be evenly distributed.

Heritabilities ranging from 0.1 to 0.3 means that 70%-90% of the recorded variation in the adult dog is caused by environmental factors or variance components related to the testing procedure. The question becomes “How and when do these environmental effects arise?” It should be noted that identification of a large variance component associated with testing does not mean that genetics can be neglected. Effects from selection on heritable traits will accumulate over time, from generation to generation, whereas environmental factors (if not epigenetic) do not.

Wilsson and Sundgren (1998a) analyzed the effect of genetic variation found in a puppy test of 630 eight-week-old GS puppies tested at the age of 56 days were all retested at the age of 15-18 months. Heritabilities for the 10 different scored groups in the puppy test ranged from 0.20 to 0.53 for the combined values (sire and dam combined). However, the heritability based on dam exceeded those based on sire for 6 of 10 scored groups. This result implies that there is a great effect on puppy behavior of the common litter environment. There was little or no correspondence between the puppy and the adult test results, suggesting that phenotypic variation seen in puppies does not predict the adult phenotype, perhaps because the desired traits have not yet matured and/or because the effect of the postweaning condition is large.

Although most studies have shown low predictive power in testing puppies, there are some studies indicating puppy tests might predict the adult phenotype (Slabbert and Odendaal, 1999; Svobodová et al., 2008). As we shall see, the postweaning environment is very important for the growing dog, and even the slightest change in rearing conditions caused by the puppy test result will give a confounding effect on the test result at the adult age.

We can conclude that the adult phenotype is largely affected by environmental condition and that the genetic effect is low to moderate but high enough to be used for selective breeding. The information also suggests that the maternal environment affects the puppy phenotype, but these maternal environment effects are less pronounced in the adult phenotype. Because growing dogs undergo a dramatic change from birth to adult age, we will now try to look at the effects of the environment on and during different stages in development.

The neonatal period (first to second week)

Puppies are born immature. As part of the altricial state, they are blind, deaf, poikilothermic, and their behavior is restricted to reflexes that help them to achieve their basic needs of food, warmth, and basic physiology. Tactile stimulation elicits eliminative behavior (Fox 1971). The hippocampus and front cortex are still developing, limiting the extent of learning through associative processes.

The needs of the neonatal puppy are primarily related to the mother who provides warmth, anogenital (AG) stimulation, and milk. The mean time for nursing and AG licking in 14 GS mothers is presented in Table 1. During the first 2 weeks, most mothers spent more than half the time allowing puppies to suckle. During the first week, the percentage of time mothers engaged in AG licking differed from 3% to 18%. During the second week, the amount of licking varied from 1% to 13%. These data represent large differences among mothers in their maternal behavior.

AG licking is of special interest. It not only stimulates eliminative behavior in puppies but also initiates activity in puppies, which in turn elicits more maternal attention (Figure 1). The amount of AG licking by the mothers, in particular during the first weeks, significantly corresponded to less “emotionality”, that is, mothers showing more AG licking during weeks 1-4 had puppies with longer latency times to shrieking when isolated (Table 2). Time to first shriek when isolated and explorative behavior (more active, less contact II, and more objects visited) in an arena test were measured in 75 puppies from 14 litters. These were also the groups showing the largest maternal effect in the puppy test (Wilsson & Sundgren 1998a).

The fact that puppies are undeveloped during the neonatal period does not mean they are not affected by external conditions but that we can expect their sensitivity to external factors to be different than later in life. Denenberg and Kline (1964) showed that rat pups, who, similar to dogs, are also altricial when subjected to handling (i.e., exposed individually to mechanical and acoustic stimulation, exposure to cold, especially during the days 6-8 of life), were superior to nonhandled puppies in avoidance conditioning. The handled rats showed lower defecation rates, increased activity, and lower levels of plasma corticosterone compared to nonhandled rats when exposed to novel conditions (Denenberg and Zarrow, 1968). Denenberg and Whimpey (1963) found that these early effects were transferred from one generation to the next. Fox and Stelzner (1966) showed that dogs that were handled from birth to 5 weeks had heavier adrenal glands, were more explorative, were superior in problem-solving, and were more social compared to nonhandled dogs. Gazzano et al. (2008) report similar results comparing puppies being daily gentled between 3 days and 3 weeks of age compared to those not being gentled. Puppies being

Table 1
Percent of time during daytime (7:00 AM to 4:00 PM) that mothers spent nursing and licking puppies (N = 15 litters for weeks 2-4; N = 14 for weeks 1, 5, 6; N=12 for week 7; adapted from Wilsson, 1997)

Week	Nursing			Anogenital licking		
	Mean	Max	Min	Mean	Max	Min
1	69	90	50	9	19	3
2	40	62	19	7	13	1
3	23	43	4	4	11	0
4	15	40	0	2	8	0
5	8	20	0	1	2	0
6	3	11	0	0	1	0
7	3	8	0	0	0	0