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Chapter 12

“Genetics and the Social Behavior of the Dog” Revisited: Searching for Genes Relating to Personality in Dogs

Enikő Kubinyi, Mária Sasvári-Székely, and Ádám Miklósi

12.1 New Concepts in Dog Research

Without a doubt, the scientific interest in dogs has grown tremendously. Previously, dogs were considered “artificial” animals and of little interest to biologists studying the causes of behavior. However, things have changed, partly due to parallel developments of thoughts and research efforts in ethology, genetics, and evolutionary biology. Many researchers have realized that if scientific questions are asked in the right way, the biological study of dogs could provide valuable (and even generalizable) answers. These new insights have put dogs in the forefront of biology, and this is particularly the case for medical and behavioral genetics.

Behavioral genetics researchers traditionally used rodent models, mainly because of the rodents’ short lifespans and tolerance of laboratory environments. However, the social structure of mice and rats differ greatly from that of the top predator, humans. Canids’ social systems show more similarities and therefore as a species are better models for humans in several aspects. Dogs’ genetic heritage from the ancient wolves includes the ability to maintain life-long relationships with their mates, food-sharing, context-dependent hierarchies, and complex communicative behavior – all of which are similar to the abilities of humans (Miklósi 2007). Domestication may have facilitated the emergence of different social cognitive skills in dogs, enhancing their chances of survival in human families. Exposure to the human social environment results in individual experiences that in many respects correspond to that of human children. Therefore, the comparison of human infants and dogs enables one to determine how two organisms with very different evolutionary paths behave after having been exposed to a similar social environment

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(Gomez 2005). Moreover, the genetic sequence information of dogs is considered a standard for comparison to the human genome system (Wayne and Ostrander 2004). Dog's phenotypic diversity and the large number of genetic diseases common to humans (Wayne and Ostrander 2007) provide a unique possibility to model biologically relevant questions of basically human interest.

12.1.1 Ethology: Human and Dog Behavioral Parallels

Wherever they live in the world, most dogs develop some ties with the local human populations. In some cases this could be very close (e.g., if dogs and humans share their resources in a family setting). These dogs are usually described as pets and are considered family members by humans (Kubinyi et al. 2009). For many years, researchers have argued that this co-habitation would not be possible without some genetically based changes that allow dogs to form complex social relationships with humans (see Miklósi 2007 for a review). Recent findings (some of which have been supported in independent laboratory investigations) reveal that dogs have the ability to rely on complex human visual and acoustic communicative cues, can obtain information by observing human companions, may understand some aspects of human intention, and engage in complex cooperative interactions (see Miklósi 2007 for a review). The corpus of data suggest that in a broader framework the behavioral changes in dogs could be viewed as convergent in relation to functionally similar human traits (Topál et al. 2009a). During their evolution, dogs adopted patterns of behavior that to some extent functionally matched those of their human partners. Based on this theory, we expect dogs to show behavioral differences from those of their ancestor, the wolf, which enhance their chances of survival in a human setting. At the same time, the behavior of dogs shares some similarity with that of their human counterparts (e.g., Topál et al. 2009b).

In 2000, Overall as well as Ostrander and her colleagues introduced the concept of the dog as a natural model of human behavior in respect to mental disorders (Ostrander et al. 2000; Overall 2000). It soon became obvious that this idea could be extended to personality traits of healthy individuals as well.

12.1.2 Domestication: Evolutionary Process

Although Darwin used many examples of domesticated animals for making plausible suggestions about the hypothesized evolutionary processes to the inexperienced readers of his time, it took some time to realize the truth in these arguments. For many years, domestication was considered artificial selection for animals living in captivity. Price (1984) was one of the first to define domestication as an adaptation to captive environments that is achieved through genetic changes that occur over generations, environmental stimulation, and experiences during an animal's lifetime.

In line with this concept, Coppinger and Coppinger (2001) suggested that the habitat overlap between wolves and humans facilitated the emergence of subpopulation(s) of wolves that, through their closer contact with humans, became slowly isolated from the “wild” wolf population. This early separation into two populations was followed by a diverse selection for different phenotypes, which became the ancestors of today’s dogs. This so-called two-stage process has recently gained support in the field of evolutionary biology. The statistical analysis and modeling of linkage disequilibrium in dogs suggested two population bottlenecks during the course of domestication (Lindblad-Toh et al. 2005). However, from an evolutionary point of view, there could be some differences. The first bottleneck might have been associated with directional selection for certain “general” dog-specific morphological and behavioral traits that are still characteristic for present-day dogs. The second bottleneck might have emerged during a diversifying selection process when some clades of dogs as well as the ancient genetic stock of modern breeds became established. A similar two-stage process has been suggested on the basis of behavioral differences between wolves and dogs (Hare and Tomasello 2005). Accordingly, the first-phase selection favored individuals who showed specific actions in a wide range of social behaviors (changes in emotional reactivity), and the second phase favored individuals expressing specific behavioral skills (e.g., hunting performance) (Brenoe et al. 2002).

Recent estimates of dog–wolf differences at the DNA level suggest a value of about 0.2% (Wayne 1993). Naturally, at present, it is difficult to judge the functional genetic nature of such a difference. The 25,000–50,000 years since their divergence might not have been enough for the emergence and spreading of novel mutations in dogs. However, there are some findings that counter such views. Recently, Parker et al. (2009) found that a second copy of an existing gene, *FGF4* (fibroblast growth factor 4), was inserted at the other end of the same chromosome (no. 18) and retarded the growth of short-limbed dogs. The trait is dominant, so it could have manifested relatively rapidly in the dog population. A second source for the difference could come from changes in allele frequencies. During domestication, dogs with some types of allele could have been selected for in the anthropogenic environment. In certain cases, some existing but rare alleles could become increasingly frequent in dog populations (see also below).

12.1.3 Genetics: Dog Genome

Two years after the publication of the first generation of dog DNA sequence (Kirkness et al. 2003) the high-quality draft genome sequence of the domestic dog was made public (Lindblad-Toh et al. 2005). This information on the genetic structure not only paved the way for studying the functional significance of genes in dogs but also allowed a comparison with the genomic structures of humans and mice.

These analyses revealed that despite the fact that the ancestors of dogs were separated much earlier from the joint primate–rodent clade in some respects,

compared to rodents, the genomic structure of dogs may be more similar to that of humans (see Haitina et al. 2009). Genes that are shared between dog and human, on average, show approximately twice the sequence similarity as is observed between human and mouse genes (Wayne and Ostrander 2004). This likely reflects the more rapid rate of sequence evolution in the mouse compared to human and dog (Kirkness et al. 2003). The dog sequence recovers slightly more human genes (18,473) than does that of the mouse (18,311).

In summary, it seems that in addition to the more recent convergent evolutionary process that affected the behavior and probably the genetics of the dog, the particular evolution of the Canidae clade (including the wolf and the dog) retained an increased similarity to the genome of primates (including humans). As a result, we should expect a mixture of both homologies and convergences at various levels of biological organizations such as genes and behavior traits.

12.2 In the Footsteps of Giants

Scott and Fuller's *Genetics and the Social Behavior of the Dog* (1965) became the bible of dog researchers. The work covered by the book was aimed at providing information about the genetic background of morphological and behavioral features of the dog. Scott, Fuller, and their colleagues applied a traditional Mendelian method for the genetic analysis, but they also carefully controlled for environmental influences. They worked with various breeds of dog that were similar in size and were maintained and socialized in similar ways. They were particularly careful when choosing the breeds for comparison. Basenjis represented the "ancient dogs," and Beagles, Shetland sheepdogs, Cocker Spaniels, and Fox Terriers represented groups of dog breeds that have been selected for various behaviors and forms. There are many lessons to be learned from these efforts. Taken together, this work did not differ much from laboratory studies of rodents. This approach constrained the chances of researchers to demonstrate the uniqueness of dogs. Without providing a full list, here are a few points for consideration.

Although all dogs were socialized to the human laboratory staff, no individual social relationships developed. Understandably, the large number of animals prohibited a more intensive social contact between humans and dogs; but, then, these subjects could not be considered to have experienced "normal" environmental input. Nevertheless, they missed simple, ethologically based behavioral traits assessing dog-human relationships (e.g., attachment and social cognition). Instead, they preferred to use laboratory learning tests established for testing rats or monkeys (e.g., T-mazes and string pulling). Although the biological parallels between dogs and humans was a fundamental issue for Scott and Fuller, their approach for testing behavioral phenotypes in dogs prevented direct comparative accounts due to the lack of complementary data on people.

Scott and Fuller reported considerable differences among breeds, but they also found remarkable variation in individual behavior in the tests. Notably, the authors

concluded that “it is impossible to generalize about any one breed from experience with one dog or even one strain of dogs” (Scott and Fuller 1965, p. 378). It seems that the morphological similarity of dog breeds may be deceptive, leading many researchers to assume a similarly homogeneous behavioral phenotype and physiology, which is clearly not the case.

Scott and Fuller also noted that there are relatively few general behavioral traits in dogs. Dog breeds could be considered as behavioral mosaics of special characteristics, many of which reflect their selection history.

The work and research strategy started by Scott and Fuller has been continued on rodents. Dog research should not and cannot compete with these efforts for theoretical, methodological, and practical reasons. However, for the very same reasons, research on privately owned family dogs could provide a valuable model for human behavior. First, as pointed out previously, one of the most unique additions of dogs to research is their specific evolutionary history with humans. This can be investigated only if dogs are observed (and reared) in their natural environment (see above). Second, if comparative behavioral work is envisaged (whether it concerns “normal” or “pathological” traits), observations and tests should be comparable to those of humans (e.g., Vas et al. 2005; Lakatos et al. 2009). Third, from both the welfare and financial points of view, it is problematic to keep a large number of dogs in a laboratory setting.

12.3 Dogs in Their Natural Environment

12.3.1 *Practicalities of Dog Research*

One of the most important reasons dogs have become a favorite animal for behavioral scientists is the practical aspect. The natural environment of dogs is the human social setting, which means that studies can be conducted anywhere – from the home with a family to an empty room of the laboratory. In the home, however, there is no need for animal housing, trained animal care staff, and so on. The natural environment of dogs varies greatly and can be manipulated more easily than that of humans. For example, it would be possible to conduct cross-fostering studies of dogs. The health care service for dogs is almost comparable to that of humans. The existence of breeds and the careful mapping of individual relatedness provide natural opportunities for studying gene–environment interactions. Moreover, the lifespan of dogs is notably shorter than that of humans: 1- to 2-year-old dogs are adults.

In recent years, scientists from a variety of backgrounds have begun to study dogs. As a result, there has been some confusion with respect to the methods used and the interpretation of findings. There is therefore an urgent need for standardized testing and identification of the genetic and environmental variables that affect dog behavior (Diederich and Giffroy 2006; Miklósi 2007). The study of dogs is also complicated because of the many uncontrolled environmental variables. Researchers therefore need to assess the generalizability of their results via replication.

Instead, despite the fact that experiments are often conducted in a single country, region, or city, findings are often assumed to apply to dogs in general. However, one should not forget that dog-keeping practices, owners' perceptions of their dogs, and in fact the dogs themselves may vary around the world; and researchers might consider replicating behavioral research with dogs from different populations as well before firmly concluding that the findings are applicable to all dogs (Wan et al. 2009).

12.3.2 Niche of Dogs in Western Cultures

Presently, most dogs in Western societies live as family pets in a complicated, often uncertain environment while being highly dependent on their owner. In Western societies, only a small proportion of dogs are free-ranging; for example, in the United States, shelters admit approximately 4% of the total population as "strays" (Patronek and Glickman 1994). Research on dogs in cultures where dogs function mainly as food or pelt are underrepresented.

The percentage of dog-owning households varies across countries. Whereas approximately 40% of households in the Czech Republic and Australia include a dog (Marston and Bennett 2003; Houpt et al. 2007), only 14% of Austrian households do so (Kotrschal et al. 2004). The number of dogs kept per household depends on many factors (urbanization, economic situation). In a German-speaking sample with 14,004 individuals (Kubinyi et al. 2009) 33.1% of the owners reported to have more than one dog.

There are marked differences even among Western cultures in dog-keeping practices. For example, we found that German shepherd owners in the United States were more likely than those from Hungary to (1) keep their dogs indoors during the day and night, (2) report that their dogs were kept as pets, and (3) engage their dogs in a greater number of training exercises, such as conformation or agility training (Wan et al. 2009). It is also worth noting that more women have dogs than men; for example, in our German-speaking sample (Kubinyi et al. 2009) 79.6% of the respondents were women, and in an Australian population it was 85.0% (Bennett and Rohlf 2007).

12.3.3 Breeds As Genetically Isolated Populations

Having approximately 400 recognized breeds presents a major advantage in studying dogs. Selective breeding resulted in a great variety among dogs in terms of their appearance and behavior. Most current breeds are approximately 100–200 years old, but despite this fact, dogs can be correctly assigned to their respective breeds on the basis of their genotype (Parker et al. 2004; Sundqvist et al. 2006). According to Parker et al. (2004) variation among breeds accounts for more than 27% of the

total genetic variation. Therefore, breeds are inbred, genetically isolated units, with reduced genetic heterogeneity (Lindblad-Toh et al. 2005; Saetre et al. 2006). According to Ostrander and Comstock (2004), “The development of dog breeds by selection for rarefied traits represents one of the greatest experiments in biological variation ever done by man” (p. R99). There are over 350 inherited diseases in dogs, many associated with just a few breeds. By studying the affected breeds, genes underlying complex diseases can be mapped.

However, not only genetic diseases, but certain typical behavioral phenotypes are associated with breeds: personality trait differences among breeds were detected in several studies (e.g., aggressiveness: Bradshaw and Goodwin 1998; Svartberg 2006; Notari and Goodwin 2007; Duffy et al. 2008; playfulness: Svartberg 2006; sociability: Seksel et al. 1999; Svartberg 2006; trainability: Bradshaw and Goodwin 1998; Serpell and Hsu 2005; Ley et al. 2009; boldness: Svartberg and Forkman 2002; Svartberg 2006).

12.4 Personality Studies in Dogs

12.4.1 *Concept*

Personality is often defined as an individual's distinctive pattern of behavior (other than feeling and thinking) that is consistent across time and situations (e.g., Pervin and John 1997). An individual's personality is based on a set of traits. A personality trait has contributions from more than one quantifiable behavioral item or variable. For example, activity–impulsivity items can consist of lack of self-control, fidgeting, difficulty controlling the behavior, and strong motivation for playing and running (Vas et al. 2007).

Personality or temperament studies in dogs have become very popular during the last decade (Jones and Gosling 2005; Kubinyi et al. 2009). In addition to its theoretical interest, dog personality is a matter of public concern and has a wide range of practical applications, including significant influence on the dog–human bond. Despite the increased interest, at present there is neither standard methodology nor standard terminology in dog personality studies (Diederich and Giffroy 2006).

In a meta-analysis, Jones and Gosling (2005) identified seven main personality dimensions that characterizes dogs: reactivity, fearfulness, sociability, responsiveness to training, aggression, dominance, and activity. As a result of different methods used, researchers suggested different numbers of potential personality traits for dogs (e.g., 11 personality traits by Hsu and Serpell (2003); 2 personality traits – shyness–boldness and aggressiveness – by Svartberg and Forkman (2002)). Recently, based on the human Big Five questionnaire, we found four traits, all but one of which can be related to the human counterparts (Kubinyi et al. 2009). There was no evidence for conscientiousness in dogs, in line with Gosling and John (1999), who noted that conscientiousness appears only in chimpanzees and humans.

So far, dog personality research has focused on (1) developing tools for characterizing behavior (e.g., Sheppard and Mills 2002; Hsu and Serpell 2003; Ley et al. 2008); (2) investigating breed-related genetic differences (e.g., Wilsson and Sundgren 1997a, b; Svartberg and Forkman 2002; Strandberg et al. 2005; van Oers et al. 2005; Svartberg 2006); and (3) studying the effect of development or stability of the behavioral characteristics over an extended time. In the latter case, individuals are repeatedly tested during early puppyhood, at a juvenile age (time of sexual maturation), and later in adulthood with the aim of evaluating the predictability of certain early behavioral characteristics (e.g., Wilsson and Sundgren 1998; Slabbert and Odendaal 1999).

12.4.2 Methods in Personality Studies

Two methods are typically used for recording information about the behavior of individual animals: behavioral coding and subjective ratings (Gosling 2001). These methods reflect different resolutions to the supposed trade-off between quantifying behavior in terms of objective acts and using humans to record and collate information more subjectively (Kubinyi et al. 2010).

Behavioral coding is rooted in the tradition of ethology and aims to capture as faithfully as possible what an animal does on a particular occasion. For example, researchers might count the number of times an animal performs an act (e.g., charges at another), the latency to do something (e.g., time taken to approaching a novel object), or the duration of a behavior (e.g., time spent looking at another animal). Coding approaches are widely believed to not be influenced by observer biases. In dog personality studies, breed clubs' or working dogs' character tests or working field trials provide large sample sizes and support the investigation of dogs over a long period of time (Goddard and Beilharz 1986; Wilsson and Sundgren 1997b; Ruefenacht et al. 2002; Strandberg et al. 2005; Saetre et al. 2006). In these studies, because of the standard circumstances and the large number of dogs, evaluation of behavior is based on the subjective judgment of several observers or judges. Although the judges are mostly well trained, there could be significant differences in their assessments (e.g., Murphy 1995; Ruefenacht et al. 2002; Lindberg et al. 2004).

Rating approaches are rooted in the tradition of psychology and aim to capture what an animal does at a higher level of abstraction. For example, rather than record the number of times an individual engages in specific acts of aggression, raters use their judgment to rate the general frequency of aggressive acts (e.g., a rating from "rarely" to "often") or to rate an animal's standing on a trait (e.g., a rating from "unaggressive" to "aggressive"). Rating approaches, which intrinsically rely on the experience and judgment of observers, are widely considered less objective than coding approaches; indeed, they are often referred to as "subjective ratings" (e.g., Stevenson-Hinde and Zunz 1978). This is based on the assumption that each owner assesses or interprets the dogs' behavior differently depending on their age, sex, experience level, and so on. As a result, ratings are sometimes thought to be an inappropriate method for scientific measurement (Vazire et al. 2007; Uher et al. 2008). However, several researchers argue that aggregated observations of multiple

observers are reliable and independent of the peculiarities of individual observers. Many studies have argued that owners' ratings are a reliable information source about dogs' behavior and could be useful in ethological surveys (Gosling et al. 2003; Kwan et al. 2008; Meagher 2009). For intrinsically broad constructs such as personality, collating information about animals from experienced observers via broad ratings is more efficient than the relatively time-consuming behavioral coding.

Questionnaire-based personality surveys are frequently used in psychology, so there are elaborated criteria and judgment procedures (Gosling and Vazire 2002). In the case of dogs, owners are generally considered experienced observers. Owners have multiple experiences with their dog; thus, by involving owners, researchers have the possibility to collect information about the dog's behavior outside the testing situations. By means of questionnaires, researchers can survey aspects of the character that are difficult to assess via behavioral tests (e.g., dogs often fail to show certain types of aggressive behavior in staged tests) (Duffy et al. 2008). Additionally, by using questionnaires, we can investigate sample sizes that far exceed those obtained with traditional testing methods. Finally, the owners observe the dog's behavior continuously, so they can assess the dog on the basis of many similar situations and conduct a "mental factor analysis" (Miklósi 2007). These features make questionnaires a useful tool for measuring traits (e.g., personality) that are stable and consistent across time and situations (Pervin and John 1997).

There is evidence on the relations between owners' ratings and behavioral observations (Gosling and Bonnenburg 1998; Gosling et al. 2003; Hsu and Serpell 2003; Svartberg 2005; Vas et al. 2007; Kubinyi et al. 2010). These correlations are usually relatively weak (0.2–0.3) but not weaker than in human studies (Gosling et al. 2003). In any case, the questionnaires used should be checked for criteria of reliability and validity (Gosling 2001; Taylor and Mills 2006; Kubinyi et al. 2010; Meagher 2009). Personality traits or factors are usually identified from factor analysis or principal component analysis (or other data reduction method) by examining the correlation pattern between narrow behavioral variables (test variables or questionnaire items).

12.5 Genetic Association Studies in Dogs

We have provided an overview on the benefits of using dogs as the functional model of some aspects of human behavior and personality. In the following, we show how this approach can be turned into action when one is interested in the underlying genetic factors that influence personality traits in dogs.

12.5.1 What Genes and Why

Quantitative studies (e.g., Wilsson and Sundgren 1998; Ruefenacht et al. 2002) are able to assess the heritability of certain behavioral traits and may provide estimates

of the number of underlying genes. However, these studies cannot reveal the genetic background of the traits. Candidate gene analysis assumes that the phenotypic trait is determined to some extent by genes that have detectable effects. Candidate genes are usually related to the neurotransmitter and hormonal systems, and the aim is to find a significant association between variation in the phenotype and the allele polymorphism. In recent years this approach has become widespread in research on humans (Reif and Lesch 2003).

In research on dogs, the strategy has been to find allelic variation in dog candidate genes for which some effect can be hypothesized based on human studies. Although several polymorphisms have been found in dogs, it is important to note that the genetic nature of the polymorphism in dogs might differ from that of humans. For example, variability could affect different exons or introns, the length, and/or the number of repeats; moreover, single nucleotide polymorphisms (SNPs) likely have a different position in the DNA sequence (see below for the case of the *DRD4* gene). Even if the variability is present in similar regions (e.g., exon 3 in the *DRD4* gene), it does not ensure a similar effect on the phenotype (Héjjas et al. 2007b).

Importantly, genetic association studies have some pitfalls. Principally, there is a high chance of getting false-positive results. Also, individuals from genetically isolated populations (e.g., breeds) are more likely to show behavioral differences due to their population-specific background, not due to the presence of a single gene (Hamer and Sirota 2000). Thus, candidate gene analysis should be carried out within single breeds and include unrelated individuals.

Another pitfall is identification of the phenotype. A widely used method includes relying on breed stereotypes provided by experts such as dog trainers – not direct phenotypic measures of the individuals (Jones et al. 2008; Chase et al. 2009). To reveal a valid association between genetic factors in the association studies, precise behavioral phenotyping at the individual level is definitely as important as accurate genotyping.

12.5.2 Behavioral Associations with the *DRD4* Gene

Some personality traits are supposed to be homologous in vertebrates, including humans; and therefore the underlying neurobiological and neuroendocrine factors should be similar. A significant association in the animal (dog) model supports the external validity of human findings and offers the multiple advantages associated with animal models.

The *DRD4* gene was the first candidate gene for which it was implied that allelic differences are associated with different patterns of human behavior (Ebstein et al. 1996). The dopamine D4 receptor is highly abundant in the limbic system, which is responsible for emotions and cognitive functions. Since 1996, the *DRD4* exon 3 has been one of the most studied candidate gene polymorphisms. The most thoroughly investigated polymorphism of the gene is located on exon 3, where the repeat number of a 48-base pair (bp) long segment varies from 2 to 10. A large number of studies deal with this variable number of tandem repeats as a possible

risk factor for several psychiatric disorders (Ebstein 2006). Importantly, several independent laboratories found associations between attention deficit and hyperactivity disorder (ADHD) and the *DRD4* gene (Faraone and Mick 2010).

12.5.2.1 Looking for a “Good” Phenotype: Activity/Impulsivity Trait

Our research group successfully adapted a human parental ADHD questionnaire (DuPaul 1998) for measuring activity–impulsivity and attention deficit traits in dogs (Vas et al. 2007). This activity–impulsivity and inattention questionnaire (Dog-AIA-Q) is short and simple: owners are asked to rate the frequency of 13 behavioral traits of their dog, such as, “My dog fidgets all the time” and “My dog’s attention can be easily distracted.” The Dog-AIA-Q showed satisfactory test–retest and interobserver reliability, internal consistency, and external validity on a sample of 220 individuals drawn from 69 breeds. Thus the phenotype obtained by the questionnaire seemed to be suitable for a genetic study. Based on human data, we chose to investigate the possibility of an association between polymorphism of the dopamine receptor *D4* gene and activity–impulsivity traits in dogs.

12.5.2.2 Looking for a Polymorphism: *DRD4* Exon 3 in Dogs

In 1999, a Japanese research group found seven length-variant polymorphisms in *DRD4* exon 3 in dogs (Niimi et al. 1999, 2001). Similar polymorphisms do not exist in rodents (e.g., O’Malley et al. 1992) but are present in nonhuman primates (Bailey et al. 2007). Furthermore, an SNP polymorphism was found in horses (Momozawa et al. 2005).

Niimi et al. (1999) and Ito et al. (2004) suggested that *DRD4* gene variations are related to behavioral traits such as excitability, aggression, and reactivity. In Ito et al.’s study (2004), allele frequencies of 23 dog breeds were determined and correlated with behavioral differences. The breeds were divided into two main groups based on the allele frequencies of the *DRD4* exon 3 polymorphism. Dogs belonging to group A had a higher frequency of alleles named 2 and 3a, whereas the alleles 3b, 5, and 6 were more frequent among the animals of group B. Phenotypes of the dogs were analyzed by means of a questionnaire for dog professionals. They found that dogs in group B obtained a higher average score of aggressiveness and a lower value of reactivity compared with individuals in group A.

However, as mentioned above, to avoid false positives in single gene–behavior trait associations it is advisable to use within-breed comparisons instead of between-breed comparisons to avoid the effect of population stratification (Hamer and Sirota 2000).

Although the associations of Niimi et al. (1999) and Ito et al. (2004) might be spurious, the frequency data are valuable and facilitate cross-country comparisons. After genotyping 655 individuals from three dog breeds and 44 European wolves, we found that the allele frequencies of the *DRD4* exon 3 in German shepherds and

Table 12.1 Frequency of *DRD4* exon 3 genotypes in domestic dogs and wolves

Genotype	Belgian Tervueren (<i>n</i> = 100)	Belgian Groenendael (<i>n</i> = 105)	Belgian Malinois (<i>n</i> = 50)	German Shepherd Dog (<i>n</i> = 308)	Siberian Husky (<i>n</i> = 91)	European wolf (<i>n</i> = 44)
<i>DRD4</i> exon 3						
2/2	14.00	29.52	18.00	41.56	3.30	15.91
2/3a	47.00	43.81	36.00	42.53	5.50	2.27
3a/3a	39.00	26.67	46.00	15.91	5.50	4.55
2/5	0	0	0	0	1.10	13.64
3a/5	0	0	0	0	18.70	0
5/5	0	0	0	0	40.60	15.91
8/8	0	0	0	0	11.00	22.73
3a/8	0	0	0	0	14.30	4.55
2/8	0	0	0	0	0	18.18
5/8	0	0	0	0	0	2.27

The results are expressed in percents

Data from Héjjas et al. (2007a, b, 2009) and unpublished results

Siberian huskies were similar in Japanese and Hungarian samples (Ito et al. 2004). These frequencies are reported in Table 12.1, and for comparison we also report frequencies for Belgian shepherds (Tervueren, Groenendael, Malinois). In a recent study, we found a new allele in Siberian huskies and European wolves that was not identified by the Japanese researchers. According to gel electrophoresis, this allele is the longest variant of all; therefore we labeled it as the “eighth” allele (Héjjas et al. 2008).

By using a single breed to avoid population stratification, we found that police German shepherds having at least one 3a allele showed significantly higher scores on the activity–impulsivity dimension of the Dog-AIA-Q (Vas et al. 2007) than dogs lacking this allele (Héjjas et al. 2007b) (Fig. 12.1). The same genotype–phenotype association could not be demonstrated in pet German shepherds living with their owners. It was hypothesized that various environmental effects (e.g., the attitude of the owners, the quality of training) overshadow the subtle genetic effects of the *DRD4* polymorphism. In contrast, the police dogs lived and were trained in a homogeneous environment in that they all went through the same special training, are kept in similar environmental conditions, and experience similar stressors. Similar findings in humans were described by Lahti et al. (2005). They found that childhood sociodemographic characteristics (e.g., the mother’s education) moderated the association between certain *DRD4* variants and novelty-seeking during adulthood. Importantly, another animal model, rhesus macaque (*Macaca mulatta*) demonstrated gene–environment interactions repeatedly that translated to the human condition (Schwandt et al. 2010). According to a recent finding, early adversity in males (but not females) carrying the short allele of the serotonin transporter gene (*5-HTTLPR*) was associated with higher frequencies of contact aggression toward a conspecific intruder (Schwandt et al. 2010). These findings suggest that gene–environment interactions are an important factor in behavioral genetic studies (Caspi and Moffitt 2006).

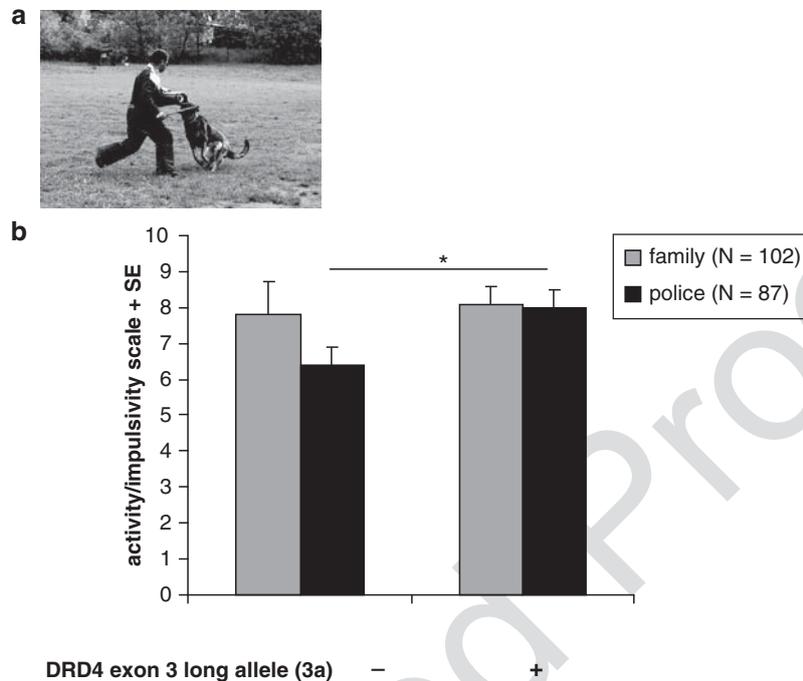


Fig. 12.1 (a) Activity–impulsivity in police and family German Shepherds according to their *DRD4* exon 3 genotypes. (b) The phenotype measure was derived from the Dog-AIA-Q filled in by the owner of the dog. The mean scores are plotted in the genotype categories. Groups were defined based on the presence (+) or absence (–) of the long allele. (Based on the results of Héjjas et al. 2007a)

12.5.2.3 Other Behavioral Associations with Genes

The serotonin transporter (*5HTT*) genes play a role in anxiety through the signal transduction of serotonin (Reif and Lesch 2003). Maejima et al. (2007) reported a weak association between distractibility trait and a *5HTT* haplotype in Labrador Retrievers trained to detect drugs. Distractibility was derived from ratings by trainers on the traits “obedience training” (negative), “affection demand,” and “aggression toward dogs.” Similar studies might clarify factors related to the aptitude of working dogs to assess whether candidate dogs are suitable for the specific training programs.

Tyrosine hydroxylase (TH) is the rate-limiting enzyme in the synthesis of dopamine, which is a precursor of norepinephrine and epinephrine (Reif and Lesch 2003). Héjjas et al. (2007a) reported that there is a 36 bp long sequence in the intron 4 region of the *TH* gene that is present either as a single copy (short allele 1) or in a duplicated form (long allele 2). Allele 1 was rare in German Shepherds, Malinois, and gray wolves; but it was fairly frequent in Tervuerens and Groenendaels.

Recently, we have found a significant association between a *TH* intron 4 polymorphism and the activity–impulsivity trait in German Shepherds living in human

families (Vas et al. 2009). Activity–impulsivity and a related trait, Liveliness, were assessed based on two validated owner-questionnaire scales (Vas et al. 2007; Wan et al. 2009) combined with a novel test battery consisting of seven subtests. The results of the three instruments correlated with each other, suggesting that they measure the same trait. Importantly, the *TH* genotype was significantly associated with all scales. Heterozygote dogs had higher owner-rated scores on the questionnaire and higher codings in the behavioral test battery by independent observers. We concluded that the *TH* and activity–impulsivity association is consistent with the human data, and that the test battery is a reliable and valid instrument for measuring activity–impulsivity in German Shepherds kept by families. At present, we can only speculate on the molecular pathway involved. Any difference in the activity of the TH enzyme may influence the availability of dopamine at particular places of the brain.

Behavioral analysis of 96 unrelated German shepherds showed that polymorphisms at the exon 3 and intron 2 variable number of tandem repeats (VNTR) of the *DRD4* gene contributed to the social interest of German shepherds (Fig. 12.2), which manifests in approaching and following behavior while encountering a friendly but unfamiliar experimenter. This behavior could be an important aspect of a dog's personality, especially if it plays a role in adjusting social behavior to the demands of human society where such contacts with strangers frequently occur (Héjjas et al. 2009).

The *DRD4* intron 2 VNTR in the dog *DRD4* gene was described by Nara et al. (2005). It is an insertion/deletion of a 17 bp long region; however, the detailed structure of the polymorphism was not reported. Based on a thorough sequence analysis, we found that the 17-bp region was present in triplicate in the longer (Q) allele, and the middle module was deleted in the shorter (P) variant. Both long and short alleles were detected in Belgian and German Shepherds and Siberian Huskies. Interestingly, in the 22 European gray wolves tested, no Q allele was found (Héjjas et al. 2009).

12.5.3 Molecular Functional Analysis of *DRD4* Intron 2

In association studies, it is essential to demonstrate by independent methods that there is a difference in the functional aspects of the polymorphic alleles. Therefore, we decided to conduct a functional analysis on the *DRD4* intron 2.

It is obvious that the nonexonic regions of the genome are exposed to a lower rate of selection and therefore show higher variability among species. Nevertheless, intronic sequences might have an important regulatory role in gene expression, as was shown for a VNTR in intron 2 of the human serotonin transporter gene (Fiskerstrand et al. 1999).

As mentioned above, a short and long forms of the intronic variation were identified in 678 unrelated dogs from five breeds and in 22 wolves. For molecular analysis, the intron 2 region was cloned into a promoterless luciferase reporter vector that led to an elevation in transcriptional activity. Moreover, an allelic difference in promoter activity was detected, as was a repressive effect of the long allele

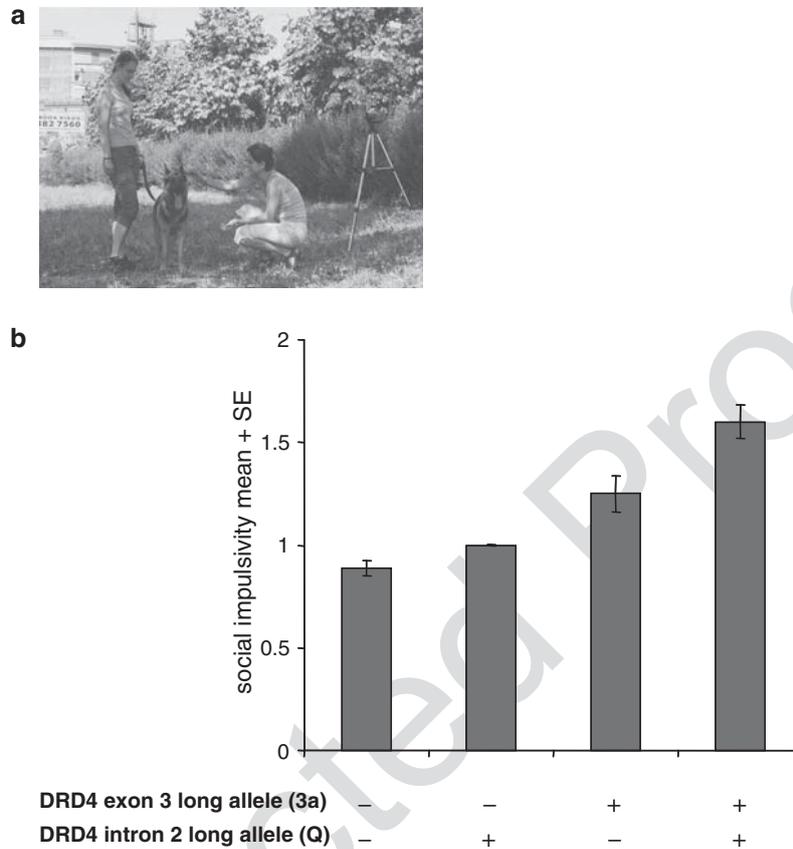


Fig. 12.2 Social interest in German Shepherds in a family setting according to their *DRD4* exon 3 and intron 2 genotypes. Dogs participating in the Greeting Test (**a**) had a score of 1 if they approached the experimenter plus another score of 1 if they followed the experimenter when she stepped away. The mean scores are plotted by the genotype categories. (**b**) Groups were defined based on the presence (+) or absence (-) of the long allele at the intron 2 and exon 3 VNTRs, respectively. (Based on the results of Héjjas et al. 2009)

(Héjjas et al. 2009). Although these findings suggest that the two intron variants of this gene may also have a different effect in vivo, more studies are needed to establish the functional significance of the nonexonic polymorphisms of the dopaminergic genes of the dog genome.

12.6 Conclusions

The chapter presented the most recent candidate gene studies in dogs. The results indicate that dogs can be a useful model species for the study of genetic effects on behavior and personality. Thus, we share the opinion of Scott and Fuller (1965, p. 4):

“The dog is a veritable genetic gold mine.... Anyone who wishes to understand a human behavior trait or hereditary disease can usually find a corresponding condition in dogs.” Although these association studies are still in their early stages, it is already obvious that these methods can offer outstanding possibilities for those who are looking for the genes’ underlying behavior. Researchers should never forget, however, that molecular genetic methods and detailed behavioral assessment should go hand in hand.

We have to underline here that as a result of the significant health care and social impact of dogs on human life, genetic studies of dogs have an applied aspect as well. Revealing the genetic background of complex traits could have important consequences for dog breeding or selecting which dogs are suitable for certain training programs. For example, attention skills are relevant to trainability and the communicative behavior of dogs, both of which contribute to the everyday challenges of dog–human interaction. Our results suggest that in the future the process of selecting a dog for a definite purpose (e.g., therapy, sports, police work) may be based partly on the animal’s genetic composition and that a large investment could be safe-guarded if individuals with appropriate genotypes are chosen.

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Chapter 14

Evolutionary Genetics of Coloration in Primates and Other Vertebrates

Nicholas I. Mundy

14.1 Introduction

Coloration is a fundamental trait of vertebrates and important in the lives of most species.¹ Coloration can have many functions, but in the context of behaviour it is particularly important for predator–prey interactions between species and social and sexual interactions within species. There are a number of properties of vertebrate coloration that make it an attractive system to study the evolutionary genetics of adaptation, including its evolutionary lability, ease of quantification, and, at least for some forms of coloration, knowledge of the underlying genetic networks. Coloration provides an excellent opportunity to obtain a detailed understanding of the mechanisms of phenotypic evolution from genetics to development and physiology through to behaviour and adaptation (Hoekstra 2006).

This chapter briefly introduces the proximate basis of coloration and types of colour variation before discussing progress in identifying the molecular basis of colour variation in wild vertebrates. It then considers the progress that has been made to date in primates. Functional explanations of coloration largely lie beyond the scope of this chapter. For recent reviews of the function of coloration in mammals, birds, and primates, respectively, see (Caro 2005; Hill and McGraw 2006b; Bradley and Mundy 2008).

¹Note for the nonspecialist reader: The vertebrates show an astonishing diversity of coloration, from the showy display of the peacock's tail to the bright red and blue face of a male mandrill monkey. Current research is now beginning to uncover the genes responsible for this diversity. This chapter explains the current progress in this research field. A notable finding is that the same genes can be responsible for mutations causing similar coloration from species as diverse as mammals, birds, and fish.

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