Overview

The First Canine Behavior and Genetics Conference: Summary and recommendations for future directions in canine behavioral science

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ABSTRACT

This paper is a narrative descriptive review of the oral presentations from the first Canine Behavior and Genetics Conference and is a synthesis of the general themes from these messages to generate key conclusions on future directions for canine behavior science. The conference was set in London in June 2015 and had 91 attendees from 10 countries. There were 17 oral presentations supported by a poster schedule with 16 posters. Two rapporteurs were invited to attend the conference and to give their conclusions on routes forward for Canine Behavioral Science. The oral presentations covered diverse topics including behavioral genetics and genomics, phenotype assessment, neurobiology and sensory biology, evolution, and socialization. The rapporteurs concluded from these presentations that global consensus on standardized systems for behavioral nomenclature (definitions) and behavioral measurement were required for the improvement of scientific output from canine behavioral research. A multidisciplinary research model and the use of linked databases were also deemed critical for effective advancement of canine behavioral science. The first Canine Behavior and Genetics Conference acted as an incubator for many nascent ideas and collaborations in canine behavioral science. The coming years will judge whether these eggs hatch and generate real welfare improvements for dogs and increased respect of the dog as both a valued working animal and a model of important translational diseases worldwide.

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Introduction

The human species has both intentionally and unintentionally moulded the behavior of the now domesticated dog ever since man first formed a commensal relationship with their ancestors, the gray wolf. From these early domestication processes, through to what by comparison may be considered fine-tuning of behaviors in recent centuries, humans have endeavored to create a partner creature that can live, and in some cases, work harmoniously alongside themselves (Hare et al., 2002; Blaustein, 2015). In the UK, 31% of human households are shared with at least one dog (Murray et al., 2010), and an estimated 36% of US and Australian households are also shared with a dog (van Rooy et al., 2014). Consequently, dogs have been behaviorally specialized into diverse roles that include hunting, transport, guarding, sporting, herding, assistance, medical, companions, and objects of aesthetic appeal (Friedmann and Son, 2009). Desired suites of specific phenotypic and behavioral characteristics required for these novel roles have led to the development of over 400 recognizable breeds worldwide, paradoxically making the domestic dog both the most diverse mammalian species on the planet while also funneling individual breeds toward increasingly limited genetic diversity (Wayne et al., 2006; Leroy, 2011; Lewis et al., 2015). However, this partnership between man and dog is not necessarily without problematic consequences for either party. The transition from a primarily working role to a companion role for some domestic dog breeds over recent decades means that many dogs are now living lives that may be at odds with their natural proclivities, sometimes leading to the expression of what may be considered undesirable behaviors (Pierantoni et al., 2011). Such conflicts can place a major strain on dog-human relationships and also on the welfare of the individual dogs themselves (McGreevy and Bennett, 2010; O'Neill et al., 2013). Understanding the genetic basis of personality traits that support

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harmonious dog-human partnerships has the potential to improve selection toward the "ideal companion dog," with less emphasis being placed on the physical appearance of the dog, potentially enhancing both canine and human quality of life (Svartberg and Forkman, 2002). In addition, the importance of dogs in non-companion roles is becoming increasingly prominent worldwide, for example, with the acute olfactory abilities of the dog exploited in diverse roles, from explosive detection in military theatre to cancer detection in medical science (Gazit and Terkel, 2003). Discovering how to capture and enhance these abilities is of high importance for human health and security. It is clear that advances in canine behavioral science have never been so critical both for dogs and the humans with whom they share their lives (Overall, 2005).

With these great needs in mind, the first international Canine Behavior and Genetics Conference took place in London on June 25-28, 2015 and welcomed 91 delegates from 10 countries to 2 days of oral presentations supported by an exhibition of 16 posters and a busy social networking program. Attendees included clinical behaviorists, researchers in the field of canine behavior and genetics, working and service dog groups, kennel and breed clubs, journalists, veterinary clinicians, and epidemiologists. With such a diverse audience and range of presentations, this meeting recognized that showcasing emergent research and researchers across all areas of canine genetics and behavior and incubating potential collaborative research could have far-reaching impacts on canine behavioral welfare (Wilson and Wade, 2012), although only time will be the arbiter on the successful achievement of this particular target. However, the meeting organizers also aimed to harvest the overall conference content to generate ideas on key steps that could be used to improve future canine behavioral science. Their intention was to extract and condense key messages, both positive and negative, from across the presentations and the subsequent open discussion sessions and to synthesize some coherent conclusions from these that could inform the future direction canine behavioral science. To encourage fresh and open inference, the conference organizers invited 2 rapporteurs from outside the traditional inner core of canine behavior and genetics research to observe and report on the oral presentations. These rapporteurs were both full-time researchers at the Royal Veterinary College in London: Dr. Dan O'Neill who works within the VetCompass Programme (VetCompass, 2015) using primary-care veterinary clinical data for companion animal epidemiologic research and Dr. Rowena Packer, a canine health and welfare researcher, who currently studies canine idiopathic epilepsy and its impact on canine behavior and welfare. Their thoughts and conclusions form the basis of this article, and the recommendations presented herein represent their personal opinions derived from the essence of the conference.

Oral presentations

Over the 2 days of conference, delegates were exposed to 17 excellent oral presentations from a spectrum of both established and promising early career researchers from 9 countries worldwide. The explored topics included genetics and genomics, sensory processing, evolution, phenotyping, and novel research possibilities (Table). Most of these presentations are planned to be published as full articles in the Journal of Veterinary Behavior: Clinical Applications and Research. Consequently, the purpose of this article is not to synopsize the talks but instead we aim to extract the key messages from each topic area and use these to suggest opportunities to enhance future canine behavior science.

Table
Oral presentations made at the First Canine Behavior and Genetics Conference in London 2015

Topic areas and specific presentations	Speaker and country of work
Genetics and genomics	
Dissecting genetic and nongenetic influences on dog personality	Pam Weiner, UK
The genetics of complex traits—applying theory to selection on behavior	Tom Lewis, UK
Genetic evaluation of behavior in dogs	Per Arvelius, Sweden
Complex genetics in the domestic dog	Heidi Parker, US
Using breed splits to explore the genomics of canine working behavior	Claire Wade, Australia
Canine opioid receptor gene polymorphism and behavior associations	Enikö Kubinyi, Hungary
Sensory processing	
Middle latency response testing for auditory cognition in canines	Peter Scheifele, US
The genetics of canine olfaction	Francis Galiber, France
Evolution	
Domestic dog evolution and genes under selection in the dog genome	Robert Wayne, US
Nature and nurture—how different environmental conditions interact with the behavior of the maturing dog	Erik Wilsson, Sweden
Phenotyping	
Measuring working dog performance	Nicola Rooney, UK
Performance assessments in dogs—determining "good" behavioral measures and phenotypes	Bjorn Forkman, Germany
Canine anxiety genetics: challenges of phenotyping complex traits	Katriina Tiira, Finland
Canine behavioral phenotypes: what makes a crisp phenotype and where does trouble lie?	Karen Overall, US
Novel research possibilities	
The contribution of nuclear medicine in the research of canine behavior disorders	Kathelijne Peremans, Belgium
Exploring future possibilities for studies in canine anxiety disorders	Niwako Ogata, US
Regional brain activity in awake unrestrained dogs	Peter Cook, US

Genetics and genomics

Not surprisingly, genetics and genomics contributed substantially to the conference program, covering 6 of the 17 presentations. In the period since the canine genome was first reported in 2005 (from a female Boxer dog called Tasha), canine genetics has become an ever expanding area of research and has promised huge advances for canine health (Lindblad-Toh et al., 2005). Because dogs have huge phenotypic diversity, well-characterized veterinary health metrics and over 400 known inherited diseases, it is also recognized that canine genetics also offers substantial potential benefits for mankind via translational research (Rowell et al., 2011). However, despite many inherited disorders having been identified in dogs (Farrell et al., 2015), few of these relate to behavioral attributes, and thus, exploration of established and novel approaches in behavioral genetics has huge potential to benefit both dogs and mankind (van Rooy et al., 2014).

Pam Weiner (UK), in a presentation entitled "Dissecting genetic and non-genetic influences on dog personality," proposed that the recognizable behavioral patterns of individual dog breeds suggested strong genetic components to canine personality, and that the clear evidence of within-breed variation in these traits offered significant opportunities for selection. Personality has been defined as a distinctive pattern of behaviors that are consistent across time and situations in an individual (Kubinyi et al., 2009). Using the Canine Behavior and Research Questionnaire (C-BARQ)

(van den Berg et al., 2010), the author explored associations between 12 discrete personality traits in Labrador Retrievers in the UK and a wide range of physical and environmental factors. The dog's role as a working, show, or pet animal had the strongest association with personality and was influenced by both genetic and nongenetic elements. Heritability estimates for the personality traits ranged from 0.00 to 0.38. Genome-wide association studies (Visscher et al., 2012) highlighted "trainability" as having the largest effect among specific regions significantly associated with behavioral traits.

Tom Lewis (UK) from the Kennel Club discussed "The genetics of complex traits—applying theory to selection on behavior" and explained that, according to quantitative genetic theory, effective selection can still be achieved without requiring specific knowledge of the location or variants of genes for complex traits with multiple genetic and environmental factors. Dr. Lewis postulated that as most behavioral traits are complex, they are ideally placed to be analyzed by quantitative genetic techniques such as estimated breeding values (EBV; Lewis et al., 2013) for either selection or removal of targeted behavioral traits. Because only genetic (and not environmental) effects are inherited, quantitative genetic analysis enables efficient use of phenotypic and pedigree data to estimate the genetic "liability" for traits in individual animals using data on both the animal itself and also its relatives. Although quantitative genetic technologies are already accepted methods in livestock production, Dr. Lewis believed that their potential was also high to improve canine selection and health.

Per Arvelius (Sweden) discussed the "Genetic evaluation of behavior in dogs" and explained that behavioral traits should be an important component of any canine breeding goals because, while they impact on the welfare of the dog itself, they also affect the dog's owner and also society as a whole. However, effective behavioral selection requires effective behavioral measurement, and the author's previous work led him to recommend objective measures over subjective measures of behavior. Many different systems can be used to collect behavioral data and the ratings can describe individual behaviors in specific situations or overall expression of behaviors. From a breeding perspective, the data collection method can be expected to affect the usefulness of the measurements taken. Dr. Arvelius believed that EBV may be more useful for selecting general heritable behavior traits than for specific individual behaviors.

Heidi Parker (US) explored "Complex genetics in the domestic dog" and explained that dogs are useful models for human genetic research because of the commonality of environment and medical care between the species, their susceptibility to similar diseases and genetic × environmental interactions. An additional bonus for pedigree dogs was their discreet, known, and effectively closed populations. She went on to describe morphology and disease studies in her laboratory that used canine mapping methodologies, and demonstrated the power of this method. A study of body size identified 7 mutations that accounted for 86% of the variation in this trait. A study of squamous cell carcinoma identified KITLG as the first example of a deleterious gene being actively selected because of desired phenotype. Dr. Parker also highlighted the challenges of studying "breeds"; while 1 in 5 Bernese Mountain Dogs are reported to develop histiocytic sarcoma, different haplotypes exist between European and US populations. The caveat from this study is that when selecting a "breed" for genetic studies, researchers need to consider whether the group is genetically a single breed or whether there are multiple distinct genetic subtypes within the "breed."

Claire Wade (Australia) discussed "Using breed splits to explore the genomics of canine working behavior." The presentation explored concentrated analyses for selective sweeps within single dog breeds that had been subjected to either formalized breed splits or diverging selection pressures. Selective sweeps are long regions in the DNA that have little remaining variation in the cohort of animals under selection and are taken as genomic signatures of human or natural intervention in animal fitness. Chromosome 25 has not been well characterized previously for function in dogs but has been linked with obesity, cold sensitivity, reflexes, lethargy, coordination, and hypoactivity in the laboratory mouse. This study showed that chromosome 25 was associated with energy score in the Labrador Retriever, and the results were validated in a separate C-BARQ—characterized population. Chromosome 3 has been associated with cerebellar abiotrophy in the dog and with fear conditioning, nociception, gait, pupillary reflex, nystagmus, and anxiety response in the laboratory mouse. This study showed an association with chromosome 3 and reduced pain perception in Australian Kelpies. These dogs need to survive and run in an Australian outback that is covered in spiky plants, where individuals or breeds with lowered pain perception are more likely to function and thrive. Therefore, selection for reduced pain perception is a logical but potentially not explicitly realized selection pressure used by the breeder. These results highlighted that we are often coselecting for unknown adaptive traits during selection processes.

Enikö Kubinyi (Hungary) discussed "Canine opioid receptor gene polymorphism and behavior associations" and explained that her laboratory's research aimed to both use dogs as a model for human disease and also to improve canine welfare. The study she presented examined the mu-opioid receptor that responds specifically to endogenous and exogenous opioids. In humans, single nucleotide polymorphisms (The International SNP Map Working Group, 2001) in the protein-coding region of the mu-opioid receptor gene are involved in mediating complex behaviors including social bonds, addiction, and mood disorders. In the study described, a total of 120 purebred dogs and 24 wolves were genotyped, with questionnaire data available for 114 dogs and behavioral test data available for 118 dogs. Single nucleotide polymorphism associations were found for inattention factor and the dog's reaction to separation from their owner, offering potential insights into areas of the gene that may have some role in differences between individual dogs in behavior and response to opioid drugs.

Sensory processing

Peter Scheifele (US) explored "Middle Latency Response (MLR) testing for auditory cognition in canines." Brainstem auditory evoked response (BAER) testing measures auditory acuity and has been available for several years in dogs (Wilson, 2005). MLR testing, however, offers new ground for canine cognitive understanding by measuring changes in cognitive brain activity in direct response to auditory stimuli. The method can be used in combination with BAER testing for a more complete auditory assessment. Two systems were described in a study of 20 dogs of various breeds: mismatch negativity and auditory MLR. Mismatch negativity was useful to detect nonattentive response to a discordant "deviant" tone presented within a series of tones. In combination with BAER testing, MLR testing could identify dogs that were potentially noise reactive and could be useful for predicting distractibility in task performance or the ability to work with sounds in a noisy environment. Peter highlighted that reference ranges based on a large baseline population are required for auditory tests, which are not available at present. Understanding the perceptual abilities of an animal and detecting any deficits, for example, in hearing, may be important during the diagnosis of a behavioral problem.

Francis Galibert (France) explored "The genetics of canine olfaction." Canines are well recognized for their exceptional olfactory abilities which natural selection has honed over millions of

years and supports their survival and behavioral traits (Quignon et al., 2012). Olfaction comprises 2 anatomic components: the nose (detector function) and the brain (analyzer function). The surface area of the canine olfactory epithelium is extensive: 200 cm^2 in German Shepherd dogs compared with just 5 cm^2 in humans. Genetically, the dog has 856 intact olfactory receptor genes compared with 391 in humans. However, in real life, most odors are mixtures of almost unlimited combinations, and the perceived smell is really a combinatorial code. Olfactory discriminant abilities are not just innate but can be learned, and this learning capability is related to both genotype and experiences. From a genetic perspective, high levels of polymorphisms were described that led to amino acid changes in olfactory proteins that may have affected function and that were clustered within breeds that had been subjected to differing selection pressures and showed differing olfactory abilities. The power of the study was limited by access to good transcriptomic data.

Evolution

Robert Wayne (US) explored "Domestic dog evolution and genes under selection in the dog genome" by summarizing published genetic studies of dog evolution to provide a context for behavioral studies. Wolves and dogs have a very complicated and admixed ancestry; it may be that dogs and modern wolves shared a common ancestor of archaic wolves that are now extinct. Genomics based on Clade A/grouping 1 suggest that most dog sequences have a single-point origin with first domestication about 36,000 years ago. Mitochondrial variation suggests that this may have been in East-Asia, whereas fossil and skull evidence suggests it may have been in Europe. Two models of breeding patterns were described: first, where "Like evolves Like," and second, where a single mutation gets passed around many breeds, for example, dwarfism. Genetic bottlenecks have had a large influence on the genetic diversity of the modern breeds that we now recognize. These bottlenecks were especially influential during early canine domestication and happened again during more recent breed creation and re-creation processes. Unfortunately, the genetic bottlenecks imposed by intense human selection for separated dog breeds over recent years have increased the expression of diseases caused by Mendelian recessive genes.

Phenotyping

Nicola Rooney (UK) discussed "Measuring working dog performance" and explained that meaningful and reliable measures of performance are essential for effective selection and breeding for optimal working ability. There are currently a vast array of systems for measuring dog performance but many lack standardization and validation. Dr. Rooney described her work using arms and explosives search dogs to develop a systematic and evidence-based approach to quantify working ability. Based on this work, she had derived an 8-point plan to improve the quality and usefulness of the measures of performance.

1. Identify the most important aspects of performance to measure
2. Standardize the vocabulary used for behavior
3. Optimize the measurement strategy
4. Consider the measurement context
5. Measurement validity and reliability
6. Choose the optimal rater
7. Optimize data collection tool
8. Implement some rater training

Bjorn Forkman (Germany) explored "Performance assessments in dogs - determining 'good' behavioral measures and phenotypes" and explained that we are really assessing the underlying motivational tendency of the dog when we try to predict the behavior of a dog in a specific situation. Because motivations can only be inferred and cannot be directly observed, it is important to assess multiple measures when trying to predict behaviors in specific situations. A number of types of measures for behavioral traits were described. Behavioral coding methods, such as counting the number of snaps (bite attempts) per minute, had the advantage of being more objective and giving higher inter-rater reliability but were quite restrictive in their application. Behavioral rating methods, such as evaluating for rejection of human contact attempts, offered more general application but were more subjective and thus inter-rater reliability is lower. Adjective rating methods were also available that measure traits such as courage or curiosity. The usefulness of questionnaire tools was explored, and it was emphasized that many still need to be validated both directly and also across populations and time, and needed to be demonstrated to have good interobserver reliability and repeatability. Questionnaires could also be compared to better understand their strengths and weaknesses, for example, comparing the Dog Mentality Assessment (Svartberg, 2005) with the C-BARQ (Hsu and Serpell, 2003). Understanding how the traits measured by tools such as the C-BARQ relate to the problem behaviors for which owners seek help in real life is of importance; for example, does C-BARQ measured "fear and/or anxiety" relate to owner-reported fear and/or anxiety behaviors, and if so which ones?

Katriina Tiira (Finland) discussed "Canine anxiety genetics: challenges of phenotyping complex traits" and explained that dogs offer promise as genetic animal models for human psychiatric disorders and that conversely, veterinary behavioral science can learn much from human psychiatry diagnosis, personality research, and genetic research. Study design features that heavily limit canine behavioral research include inadequate sample sizes (collaboration was critically useful here), difficulties in selection of appropriate controls, and poorly defined phenotypes and their dimensions (e.g., mild vs. severe). In addition, although different anxiety disorders are likely to share some affecting loci, little is known about behavioral phenotype comorbidity in dogs. Questionnaire and behavioral test results are often highly correlated, in which case it was advisable to use both. The choice of breed for study is also important as the heritability of behavioral disorders varies between breeds. It is also important to consider environmental effects during study design because these may act as confounding factors. For example, fearful dogs may have received poorer maternal care and less socialization in early life and may receive less daily exercise, whereas noise-phobic dogs are more likely to be older and sterilized and to receive less daily exercise. To achieve large sample sizes, multicentre studies are required; however, for such studies to be successful, consensus is required regarding what to measure and how to measure it. This should be seen as a positive challenge rather than a constraint because collaboration has the potential to unlock success.

Karen Overall (US) discussed "Canine behavioral phenotypes: what makes a crisp phenotype and where does trouble lie?" Although the reliability and validity of behavioral phenotyping, especially for pathologic behaviors, have been questioned, there are options to improve the quality of behavioral data collected in canine behavioral research. Application of objective criteria may set a lower bound, but the false negative rate is high if behaviors are episodic and/or infrequent. Rating scales are subjective and usually lack validated assessment criteria, making them less reliable. Direct observation and standardized testing can characterize quantitative behavioral response surfaces to create good behavioral phenotypes.

These can be compared across individuals, time, and context to assess for patterns indicating true biological consistency. The use of well-defined terminology in diagnosis and research has the potential to improve the quality of scientific investigation of neurochemical, neuromolecular, and genomic mechanisms of action in behavior.

Novel research possibilities

Kathelijne Peremans (Belgium) spoke about "The contribution of nuclear medicine in the research of canine behavior disorders." Molecular imaging modalities that can evaluate canine neuronal function include brain single photon emission computed tomography, positron emission tomography, and brain perfusion and metabolism (based on glucose consumption). These tools are useful both as diagnostic tools and also to investigate the neurobiological base of brain (dys)function and to evaluate psychopharmaceuticals. Pathophysiologies that can be imaged include impulsive aggression (reduced frontal cortex but increased limbic activity), anxiety (reduced serotonin receptors), the aging brain, and psychopharmaceuticals (e.g., cipramil or selective serotonin re-uptake inhibitor studies). However, the requirement for anesthesia with an understanding of its effects on the brain and the dedicated licensed infrastructure required for the use of radioactive compounds are limitations to the wider application of nuclear medicine. If these constraints can be overcome and more facilities to carry out these methods become available, then these techniques can offer fascinating insights into the function and dysfunction of the canine brain.

Niwako Ogata (US) discussed "Exploring future possibilities for studies in canine anxiety disorders." Anxiety disorders in dogs are believed to cover a spectrum of clinical behavioral problems such as aggression, canine compulsive disorders (CCD), and separation anxiety. However, unlike human research, epidemiologic data in veterinary behavior medicine are scarce. In humans, anxiety is reported to comprise 83%-91% of clinical behavior cases and to have an 18.8% prevalence with 22.8% of cases classified as severe. In dogs, separation anxiety is estimated to affect 29%-50% of animals, whereas CCD is estimated to affect 20%-28%. This presentation described a study of CCD in genetically predisposed breeds. Based on cases of flank and/or blanket sucking in Dobermans, a susceptibility locus to CCD on chromosome 7 was described. To thoroughly investigate these cases, Dr. Ogata advised to explore beyond clinical signs and define the endophenotype based on physical and/or medical, neuroanatomical (e.g., total brain and gray matter higher in CCD), neurochemistry (e.g., serotonin receptor abnormality in OCD), and neurocircuitry assessment.

Peter Cook (US) explored "Regional brain activity in awake unrestrained dogs." Although functional magnetic resonance imaging (MRI) has been a foundational tool of human cognitive neuroscience, its application in dogs has been limited because of the requirement for anesthesia and restraint. Despite the MRI environment being novel, enclosed, elevated, and loud, and that the dogs are not allowed to move, this research group found that dogs can readily be trained to remain awake, relaxed, and unrestrained in the MRI environment using positive reinforcement during a 2-4 months training period. Using functional MRI techniques in these dogs, Dr. Cook reported multiple tests showing associations between stimuli and regional brain activation. These included validation (simple reward prediction task using a reward; a hotdog), odors (olfactory bulb and caudate activation indicative of reward associated with familiar human scent), facial recognition (fusiform part of brain), and impulse control (Go/No go decisions showing the premotor cortex and frontal cortex were associated with successful inhibit). The researchers aim to develop a brain map: a functional atlas describing the regional activation associated with both positive, negative, and neutral stimuli. This groundbreaking research, although incredibly time and labor intensive, offers novel insights into the functioning of the canine brain, striving to achieve the level of understanding already seen in human medical research but in a relatively noninvasive environment.

Future directions

The role of the rapporteurs was to absorb and digest the content of the presentations and any subsequent general discussions over the entire conference period and to synthesize these threads into formalized action points that could be used to direct future endeavors in canine behavioral science. These recommendations were presented to the attendees at the closing session of the conference. This article presents an ordered list beginning with the most urgent needs as perceived by the rapporteurs based on their personal opinions and also the responses from the audience of the conference. These recommendations are given in the spirit of "thought provokers" that require attention and discussion, rather than an absolute set of "12 Behavioral Commandments."

Single accepted standard nomenclature

There is a clear need for a comprehensive, and common-sense nomenclature on companion animal behavior that is universally accepted among veterinary behavioral experts. Since behavioral terms are often complexly interlinked, such a system would need to be hierarchical, offering the options of parent-child relationships between terms (for example, "fear-aggression-conspecific" might be a child term to "fear-aggression" as a parent term, and "aggression" as a grandparent term). Extensive discussions may be required to reach consensus on terminology and hierarchies; however, this system does not have to be static and can be routinely reviewed and updated based on new evidence. The proposed behavioral nomenclature could be stand-alone and modeled on existing veterinary systems or could be built as an extension of a current veterinary system such as the VeNom Coding group (The VeNom Coding Group, 2015). Term names could be supplemented with agreed case definitions to standardize the output of disparate behavioral research projects across the globe and over time.

Agreed on, validated measurement systems

Specifications for reliable and well-defined behavioral measurement systems and for reference ranges describing both normal and abnormal results across a wide variety of breeds and locations were identified as a current deficit in canine behavioral science. Such systems need to be extensively peer reviewed and published, and to be thoroughly validated across locations, breeds and contexts. An open-access repository could be built to store these methodologies, their validation credentials, and details of their use in both the clinical and research setting, along with contact information for previous users who were willing to share their experiences. Once a system was deemed trustworthy, this could then be used consistently across studies to facilitate comparison between studies and to assist with meta-analyses and systematic review. An online forum could be established to share and build on experiences with extant measurement systems and reduce the trend toward creation of numerous novel but poorly validated systems which is time and resource wasteful.

Multidisciplinary: Experts from many fields

The diversity of backgrounds, specialisms, and nationalities of the attendees at this conference is testament to the breadth of

interests that already exist in canine behavioral science. Building formal links between these various groups for genuine collaborative research is likely to substantially accelerate the pace and quality of scientific understanding in this field. Dogs are potentially excellent models for human behavioral and psychiatric states, are naturally occurring in contrast to genetically induced rodent models, and may greatly enhance translational medicine. Research funding is becoming increasingly difficult to secure, but financial and intellectual economies of scale make collaborative projects more attractive to funding bodies. Small sample size has frequently limited the power of previous behavioral studies and collaborative, and multicentre research efforts are a potential solution to this problem. Finally, no one person or research group can necessarily hold all the skills required for effectively executing a multidisciplinary canine behavior project: sharing the responsibilities across groups has the potential to bring out the best from each group and ensure higher quality and timelier research results.

When a breed is not a breed

Breeds are not always a single standard entity but in reality may be split across space, time, and function. Different subpopulations exist within breeds across different countries and even across different areas within countries; the Labrador Retriever that exists in Australia is not necessarily the same as that which exist in the US. Breeds change over time in response to changing public demands, breeds standards, and selection pressures so that the results of a breed behavioral study completed some years ago may no longer apply to individuals of the current breed. Even breeds that are close in space and time are likely to have subgroups that are bred, socialized, and used very differently with consequently highly disparate behavioral attributes. For example, pedigree dogs that are retained in the breeding and/or show world may differ behaviorally to those released into the pet population. The message here is that such variation needs to recognized and taken into account in study design and interpretation.

Why we are doing the research?

It was apparent from the wide range of speakers at the conference that there are often very different reasons for conducting canine behavioral research. Although these differences should in theory not affect the essence of the study results, in reality they may impact greatly on the study design, sample selection, data collected, and direction of data analysis. Research can be primarily directed toward improving dog welfare but can also be focused on therapy, basic science, or translational medicine. Because of differing target impact areas (e.g., for the dog, for man, for science, for personal gain), studies ostensibly covering similar topics and samples can report quite differently and lead to confusion. It is important to clearly define and state the motivation behind behavioral research and emphasize that the findings should be viewed in this light. The same data may be useful for multiple purposes, and if a study is well designed with these multigoals in mind, it may be able to increase the number of research questions that can be answered.

What's in a diagnosis?

High-quality clinical behavioral research generally emphasizes the importance of acquiring "definitive" diagnoses in canine behavioral cases before proceeding to explore other dimensions within these animals, for example, genetics or biomarkers to be linked with diagnosis. The "diagnosis" in some cases may be perceived as a subjective label applied by the canine behaviorist, and the underlying emotional state that leads to the behaviors in question (e.g., aggression toward unfamiliar dogs) may vary between dogs. As it is the emotional state, and not the individually exhibited behaviors, that require treatment, diagnoses based on these emotional states are preferable. Further discussion is required to agree on what constitutes a diagnosis, and whether research based on individual behaviors is appropriate, or whether moves towards "endophenotypes" are more appropriate.

Estimated breeding value

Historically, canine behavioral research projects have largely focused on individual disorders in individual animals. However, these results are then often applied to populations which are complex composites of genetics and the environment. Such complexity is an essential part of biological existence and should be embraced in study design. The application of EBV can assist in overcoming some of the limitations of missing data on individuals within a study group by proportionally taking information from related individuals into account. EBV additionally can investigate many different attributes simultaneously. This optimizes breeding selection based on multiple characteristics, and hence, reduces the risk of unintentionally selecting for other problems when trying to ameliorate the target condition.

Use appropriate techniques: Genetic, statistical

Modern scientific method uses an ever-widening array of techniques and tools to better understand the world around us. Although canine behavioral science is a relatively new science, it is important to develop solid scientific foundations for the methods used. We can learn much from our medical counterparts who are expert in human psychiatric and neurologic disease and may have insights into methods and concepts that will enhance our canine scientific endeavors. It is also important to "borrow" knowledge from other specialties that may not necessarily be behaviorally focused by building collegiate links and sharing ideas. These specialities can include geneticists, neurologists, statisticians, epidemiologists, and information technologists.

Beware behavioral indices

Many behavioral studies collect comprehensive data across a spectrum of clinical features. These data are then subjected to sophisticated data reduction techniques (e.g., principal components analysis and factor analysis) that identify combinations of variables which tend to co-occur within a data set, and derive indices from these behaviors. Although these "index" behavioral measures may be statistically sound, given sufficient sample sizes, they often describe contrived behavioral composites that make limited biological "real-life" sense, relate expressly to the originating study and are difficult to evaluate in clinical practice. We should avoid taking these indices on face value, based on the interpretation of the study authors; new indices should be critically appraised for their content, and compared across populations and to existing measures.

The power of linking data and databases

Aristotle has been quoted as saying that "the whole is greater than the sum of its parts," and he could just as well have been talking about modern databases. Although individual datasets may hold substantial depths of information on their caseloads, cross-referencing between datasets enables the power of matrices to multiply rather than just to sum the data. Such linking of databases

vastly increases the power of research to understand complex topics. However, successful database linking requires careful planning during study design and a collaborative mind-set between research groups. Collection of unique identifiers that are used consistently across studies is essential for linkage; microchip codes may be the most useful here, although tattoo codes or kennel club registration numbers are other possibilities.

Need good epidemiology and statistical principles integrated into behavior research programs

Behavioral research offers huge potential for veterinary behaviorists to improve the quality of lives of their patients, but effective research projects must also encompass high-quality epidemiologic and statistical principles. Veterinary epidemiology has progressed enormously over the past 20 years, and an experienced epidemiologist and/or statistician should now be a key team member in all behavioral research programs, and play an active role from the project conception onwards to ensure that the research question, study design, and planned statistical analysis are appropriate. Seeking epidemiologic or statistical assistance for the first time at the point of data analysis may result in missed opportunities at best, or failure of the study at worst.

Second Canine Behavior and Genetics Conference?

The First Canine Behavior and Genetics Conference brought together wide-ranging opinions, groups, and current research and provided a forum for mapping out the future of veterinary behavioral science. After a requisite period (perhaps 2 years) for the various actors to assimilate and act on the novel ideas presented at the conference, a Second Canine Behavior and Genetics Conference to share the results of these novel projects would be highly beneficial. Such a meeting would galvanize collaborations born at the first conference while also giving opportunity to forge new unions.

Conclusions

The First Canine Behavior and Genetics Conference brought together wide-ranging opinion and stakeholders in the world of canine behavioral science. It is hoped that this will result in productive collaboration and more effective scientific method and discovery. This article represents one achieved outcome whereby the conference content was condensed to identify 12 routes toward improving future canine behavioral science and understanding.

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Ethical considerations

This article did not require ethical approval.

Conflict of interest

References

Blaustein, R., 2015. Unraveling the mysteries of animal domestication: Whole-genome sequencing challenges old assumptions. BioScience 65 (1), 7—13.

Farrell, L., Schoenebeck, J., Wiener, P., Clements, D., Summers, K., 2015. The challenges of pedigree dog health: Approaches to combating inherited disease. Canine Genet. Epidemiol. 2 (1), 3.

Friedmann, E., Son, H., 2009. The human—companion animal bond: How humans benefit. Vet. Clin. North Am. Small Anim. Pract. 39 (2), 293—326.

Gazit, I., Terkel, J., 2003. Domination of olfaction over vision in explosives detection by dogs. Appl. Anim. Behav. Sci. 82 (1), 65—73.

Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of cognition in dogs. Science 298, 1634—1636.

Hsu, Y., Serpell, J.A., 2003. Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J. Am. Vet. Med. Assoc. 223 (9), 1293—1300.

Kubinyi, E., Turcsán, B., Miklósi, Á., 2009. Dog and owner demographic characteristics and dog personality trait associations. Behav. Processes 81 (3), 392—401.

Leroy, G., 2011. Genetic diversity, inbreeding and breeding practices in dogs: Results from pedigree analyses. Vet. J. 189 (2), 177—182.

Lewis, T., Abhayaratne, B.M., Blott, S., 2015. Trends in genetic diversity for all Kennel Club registered pedigree dog breeds. Canine Genet. Epidemiol. 2 (1), 13.

Lewis, T., Blott, S., Woolliams, J., 2013. Comparative analyses of genetic trends and prospects for selection against hip and elbow dysplasia in 15 UK dog breeds. BMC Genet. 14 (1), 16.

Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas, E.J., Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E.A., Ponting, C.P., Galibert, F., Smith, D.R., deJong, P.J., Kirkness, E., Alvarez, P., Biagi, T., Brockman, W., Butler, J., Chin, C.W., Cook, A., Cuff, J., Daly, M.J., DeCaprio, D., Gnerre, S., Grabherr, M., Kellis, M., Kleber, M., Bardeleben, C., Goodstadt, L., Heger, A., Hitte, C., Kim, L., Koepfli, K.P., Parker, H.G., Pollinger, J.P., Searle, S.M.J., Sutter, N.B., Thomas, R., Webber, C., Lander, E.S., 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature 438, 803—819.

McGreevy, P.D., Bennett, P.C., 2010. Challenges and paradoxes in the companion-animal niche. Anim. Welf. 19, 11—16.

Murray, J.K., Browne, W.J., Roberts, M.A., Whitmarsh, A., Gruffydd-Jones, T.J., 2010. Number and ownership profiles of cats and dogs in the UK. Vet. Rec. 166 (6), 163—168.

O'Neill, D.G., Church, D.B., McGreevy, P.D., Thomson, P.C., Brodbelt, D.C., 2013. Longevity and mortality of owned dogs in England. Vet. J. 198 (3), 638—643.

Overall, K.L., 2005. Proceedings of the Dogs Trust Meeting on Advances in Veterinary Behavioural Medicine London; 4th—7th November 2004: Veterinary behavioural medicine: A roadmap for the 21st century. Vet. J. 169 (1), 130—143.

Pierantoni, L., Albertini, M., Pirrone, F., 2011. Prevalence of owner-reported behaviours in dogs separated from the litter at two different ages. Vet. Rec. 169, 468.

Quignon, P., Rimbault, M., Robin, S., Galibert, F., 2012. Genetics of canine olfaction and receptor diversity. Mamm. Genome 23 (1-2), 132—143.

Rowell, J.L., McCarthy, D.O., Alvarez, C.E., 2011. Dog models of naturally occurring cancer. Trends Mol. Med. 17 (7), 380—388.

Svartberg, K., 2005. A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. Appl. Anim. Behav. Sci. 91 (1—2), 103—128.

Svartberg, K., Forkman, B., 2002. Personality traits in the domestic dog (Canis familiaris). Appl. Anim. Behav. Sci. 79 (2), 133—155.

The International SNP Map Working Group, 2001. A map of human genome sequence variation containing 1.42 million single nucleotide polymorphisms. Nature 409 (6822), 928—933.

The VeNom Coding Group, 2015. 'VeNom Veterinary Nomenclature' [online], available at: http://www.venomcoding.org [Accessed August 11, 2015].

van den Berg, S.M., Heuven, H.C.M., van den Berg, L., Duffy, D.L., Serpell, J.A., 2010. Evaluation of the C-BARQ as a measure of stranger-directed aggression in three common dog breeds. Appl. Anim. Behav. Sci. 124 (3—4), 136—141.

van Rooy, D., Arnott, E.R., Early, J.B., McGreevy, P., Wade, C.M., 2014. Holding back the genes: Limitations of research into canine behavioural genetics. Canine Genet. Epidemiol. 1 (1), 7.

VetCompass, 2015. 'VetCompass: Health Surveillance for UK Companion Animals' [online], available at: http://www.rvc.ac.uk/VetCOMPASS/ [Accessed August 11, 2015].

Visscher, Peter M., Brown, Matthew A., McCarthy, Mark I., Yang, J., 2012. Five years of GWAS discovery. Am. J. Hum. Genet. 90 (1), 7—24.

Wayne, R.K., Leonard, J.A., Vila, C., 2006. 'Genetic analysis of dog domestication'. In: Zeder, M.A. (Ed.), Documenting Domestication: New Genetic and Archaeological Paradigms. University of California Press, Berkeley, California, pp. 279—293.

Wilson, B.J., Wade, C.M., 2012. Five years of GWAS discovery. Am. J. Hum. Genet. 23, 195—202.

Wilson, W.J., 2005. Brainstem auditory-evoked response in dogs. Am. J. Vet. Res. 66 (2), 2177—2187.