



Genetic Background of Cattle Temperament: A Short Review

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ABSTRACT

Animal temperament describes behavioural differences between individuals that are consistent over time and across different circumstances. Knowledge of the animal's temperament has a major effect on the safety of handling and caring for the animals as well as on the adaptation of the animals to changing rearing conditions. To understand animal temperament, we need to know not only the genetic basis of temperament, but also the influence of the environment on its expression. Similarly the temperament of dairy cows can be defined as the animal's response to environmental or social stimuli. In this review article, chromosomes with genomic regions containing QTLs, genes and candidate genes responsible for the expression of temperament traits in cattle are presented. Knowledge of the genetic background of temperament expression in cattle and its variability in these traits allows temperament to be included in the selection index.

Keywords: cattle, temperament genetics, QTL, SNP, heritability, serotonin, dopamine

MOLECULAR GENETICS AND TEMPERAMENT TRAITS

QTL studies

Temperament is defined as a stable individual traits (Grandin, 1989), and in cattle, can also be defined as the response of animals to human behavior (Burrow, 1997; Ferguson and Warner, 2008; Cafe et al., 2011). Most economically important traits in dairy cows are related to the function of a large number of genes, and their expression is influenced by the environment. These traits are longevity, fertility, calving ease, health, working ability and lactation performance. On the other hand, some genes play an important role in the inter-individual variability of aggressiveness, impulsive response and serotonergic responsiveness of the central nervous system, as well as in complex behavioral regulation. The dopamine and serotonin signaling systems are therefore central to

behavioral phenotypes such as temperament. Due to the influence of behavioural trait genes, the transporters and receptors of the serotonin and dopamine signalling pathways have been considered to harbour genetic variations that may be associated with variable behavioural responses (Momozawa et al., 2005).

Breeding programs for dairy cows focus on production traits, carcass conformation and functional traits. The genes coding for the proteins responsible for the above traits are attempted to be identified by the method of *marker assisted selection* (MAS). This method is particularly interesting for traits with low heritability (temperament, fertility, health) that cannot be effectively improved by existing selection (Schrooten et al., 2000; Ball, 2003). Use of MAS to determine genetic markers is associated with quantitative trait loci (QTL) (Kolbehdari et al., 2008). Genome-wide association studies (GWAS), which use international data to identify genomic regions and candidate genes and their biological mechanisms, can be used as a very convenient method to identify genetic factors that influence complex traits in an

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individual breed of cattle (Guo et al., 2012; Valente et al., 2016). Similarly, the study showed differences in temperament between and within breeds. Using molecular approaches, QTLs were found to influence behavioral traits in a number of breeds (Haskel et al., 2014).

Understanding the biological background of bovine behavior is a relatively new area of research. To gain insight into the genetic background of cattle behavior, the genome of cattle must first be sequenced. When more than one percent of the population has a different nucleotide at a specific location in the genome. This difference is called a single nucleotide polymorphisms (SNP). They are different alleles at the same location of the DNA. SNP are used as markers to study regions or loci on one or more chromosomes where the record for a particular trait, i.e. phenotype, is located. This region is called a quantitative trait locus (QTL) and is associated with the variability of a particular quantitative trait in the population (Lander et al., 2001). These are often economically important traits. The fundamental question is whether phenotypic differences are the result of the effect of a few loci with a major effect or a larger number of them with a minor effect (Miles and Wayne, 2008).

Friedrich et al. (2015) studied the association of SNP with milk yield (MY) and animal behavior. They found that of 41 SNP studied, nine were associated with both behavioral traits and MY in different lactation periods. Only SNP that affect behavioral traits assessed in the novel object test affect milk production traits. These SNP are located on chromosomes BTA7, BTA10, BTA14, BTA19, and BTA29. Of these SNP, six are associated with more than one milk production trait. The results show an association between the active and exploratory behavior of the dairy cow and its milk yield for SNP significantly associated with the behavior and traits of milk production. Genotypes associated with greater inactivity were associated with higher milk yield and less response to rehousing.

The identification of QTL for behavioral traits in cattle enables the identification of candidate genes located near genetic markers that have the greatest impact on a given trait. So far, this procedure has not been shown to be efficient and reliable enough due to the high complexity of the expression of an individual animal's behavior and its interaction with the environment (Schmutz et al., 2001; Gutierrez-Gil et al., 2008). Among the results of studies on the identification of QTL for behavioral traits in cattle, the study by Hiendlerer et al. (2003) is noteworthy. They investigated QTL related to conformation and behavior of dairy cows, especially those loci whose recording includes nervous/aggressive and "obedient" behavior during milking. A QTL for temperament was found on chromosome 29 (The Linkage mapping was performed with the Canadian Beef Reference Herd (<http://skyway.usask.ca/~sch-mutz/>)). As part of a larger QTL study of 162 microsatellites, four of these were

located on bovine chromosome 29 and were used to genotype all 18 parents and 136 progeny. Tyrosinase was mapped 9 cM from ILSTS015 (LOD score of a 5.65) and 15 cM from BMC8012 (LOD score of a 3.68). Microsatellites on chromosome 29 and tyrosinase were linked to CRI -MAP, resulting in the map ILSTS015 ± TYR ± BMC8012 ± BMC1206 ± BMC3224).

On chromosome 29, the tyrosinase gene (*TYR*) was found to be associated with the QTL region for temperament and milking speed (Schmidt et al., 2001). *Tyrosinase* is a multifunctional enzyme involved in the metabolism of the neurotransmitter dopamine. It catalyzes the conversion of tyrosine to dihydroxyphenylalanine (DOPA is the catecholcontaining precursor of dopamine) and oxidizes DOPA to dopaquinone. Tyrosinase also oxidizes dopamine to form melanin via dopamine quinone, which has been shown to inactivate tyrosine hydroxylase, the rate-limiting enzyme for dopamine synthesis (Xu et al., 1998; Higashi et al., 2002). It follows that the tyrosinase gene QTL is a candidate for temperament in cattle. In addition, Gutiérrez-Gil et al. (2008) identified 29 QTL regions carrying a record for temperament traits distributed across 17 chromosomes in Holstein x Charolais (Table 2). Of them, 5 QTL were associated with FF traits (flight from feeder - animal moves away when approached by an observer), and 24 influenced SS test traits (social separation - activities the animal engages in when removed from its barn mates). No overlap of QTL markers was found for traits measured by two different tests (FF and SS). Wegenhoft (2005) reported QTL on 10 chromosomes and all but one QTL region carried candidate genes affecting behavior and temperament (Table 1). Boldt (2008) determined QTL for aggressiveness mapped to BTA3, BTA6, BTA12 and BTA29. QTL for nervousness and running speed were also identified at locations on BTA22 and BTA29. A QTL for sociability was detected on BTA22 and a QTL for running speed was detected on BTA12.

In cattle behavioral traits, researchers have generally focused on barn and milking parlor temperament and habituation ability. For example, Kolbehdari et al. (2008) studied temperaments during milking in 462 Canadian Holstein bulls. They found that 10 SNP significantly affected milking temperament. The chromosomes affecting milking temperament were BTA4, BTA13, BTA19, BTA22, BTA23, BTA26, and BTA29. Riley et al. (2016) also examined the associations of SNP on multiple chromosomes with temperament (nervousness and running speed with values ranging from 1 to 9). They found that five SNP on chromosomes BTA1, BTA24, and BTA29 had indirect associations with aggressiveness, nervousness, or flightiness at weaning. Aggressiveness was defined as the animal's willingness to intentionally attack the evaluator by hitting it with any part of the body, but especially with the head or foot. Nervousness and running speed were indicators of the calf's relaxation during the evaluation. Sociability was a measure of the animals'

willingness to separate from their group and feel comfortable in isolation from other cattle.

Table 1: Quantitative trait loci for temperament^a in cattle (according to Adamczyk et al., 2013)

BTA chromosome	Trait-associated marker	Chromosome position (cM)	Genotype	References
1	DIK70-PIT17B7	37	BT (Angus) × BI (Brahman, Nellore)	Wegenhoft (2005)
3	BM7225-ILSTS64	45	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
4	TEXAN17-MAF50	28–51	BT (Angus) × BI (Brahman, Nellore)	Wegenhoft (2005)
6	CSSM22-CSM34	1	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
8	BMS1864-BM3419	0	BT (Angus) × BI (Brahman, Nellore)	Wegenhoft (2005)
9	BM6436-BM4208	72	BT (Angus) × BI (Brahman, Nellore)	Wegenhoft (2005)
9	BM2504-UWCA9	30.92–49.99	CHA × HF	Gutierrez-Gil et al. (2008)
12	BMS2252-RM094	20 I 22	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
16	INRA013-BMS462	79	BT (Angus) × BI (Brahman, Nellore)	Wegenhoft (2005)
16	INRA48-BM3509	70	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
16	HUJ625	100.2	CHA × HF	Gutierrez-Gil et al. (2008)
16	ETH11-BM719	54.07–77.57	CHA × HF	Gutierrez-Gil et al. (2008)
18	BL1016-BM8151	18	BT (Angus) BI (Brahman, Nellore)	Wegenhoft (2005)
18	IDVGA-31-ABS013	0–15.75	Charolais × Holstein-Friesian	Gutierrez-Gil et al. (2008)
19	CSSM065-ETH3	69.83–90.04	Charolais × Holstein-Friesian	Gutierrez-Gil et al. (2008)
20	DIK015-BM5004	52.49–71.80	Charolais × Holstein-Friesian	Gutierrez-Gil et al. (2008)
25	BM737-INRA222	31.59–53.37	Charolais × Holstein-Friesian	Gutierrez-Gil et al. (2008)
26	ABS012-HEL11	9.9	Charolais × Holstein-Friesian	Gutierrez-Gil et al. (2008)
26	IDVGA59-HEL11	33	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
28	BP23	10,89	CHA × HF	Gutierrez-Gil et al. (2008)
29	BMS764-BMC8012	11.29–21.11	HF cows	Hiendleder et al. (2003)
29	DIK094-MNB101	40.16–69.73	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)
29	BMC3224-BMS764	21	BT (Angus) × BI (Brahman, Nellore)	Boldt (2008)

^aTemperament was measured once by the degree of animal nervousness in changed/new environmental conditions for the animal, with the assessed animal being most often separated. BT – *Bos taurus*, BI – *Bos indicus*, CHA – Charolais, HF – Holstein-Friesian

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The temperament of cattle can also be evaluated as a result of the action of various metabolites. Such a complex study was carried out on 25 Charolais × Holstein cows based on the new object test (NO). Subsequently, the NO was replaced by an unknown person (Brand et al., 2015). The study showed that they can classify four temperaments of the tested cows, namely: fearful/neophobic-alert, interested-stressed, subdued/uninterested-calm, and outgoing/neophilic-alert temperament. These four types of temperament may also be due to the specific regulation of molecular signaling pathways that are activated in response to fear in stressful situations. Cows with a temperament characterized as fearful/neophobic-alert and interested-stressed have lower levels of glutamic acid, aspartic acid, and Gamma-Aminobutyric Acid (GABA), whereas cows with a temperament, of uninterested-calm, sociable, and indifferent, have higher levels of the aforementioned excitatory (glutamic- and aspartic acid) and higher levels of the inhibitory neurotransmitter GABA.

Common genomic regions

The considerable variation in the areas of cattle genetics associated with behavior can largely be attributed to the use of different research methods. Bailey et al. (2015) found associations between land use indices and genetic markers near candidate genes, demonstrating that grazing distribution is heritable and providing a new approach for linking genetic variation to grazing behavior in beef cattle. They identified QTL regions on chromosomes BTA17 and BTA29 that contain genes responsible for locomotion, motivation and spatial memory. In the study, 770,000 genetic

SNP markers were examined on 30 bovine chromosomes. They were used to genotype these cows to examine the genetic association with cattle distribution on pasture (selecting cattle with favorable phenotypes for pasture distribution can reduce the number of cattle in riparian areas and improve grazing uniformity in mountainous terrain). They concluded that associations between land use indices and genetic markers near candidate genes prove that it is possible to genetically determine the specific movement of cattle on pasture and that this is a heritable trait.

Table 2: Quantitative trait loci for habituation ability in cattle (Adamczyk et al., 2013)

Trait	BTA chromosome	Trait-associated marker	Chromosome position (cM)	Genotype	References
Habituation ^a	1	BM6438	1.78	CHA × HF	Gutierrez-Gil et al. (2008)
	1	BMS4044	141	CHA × HF	Gutierrez-Gil et al. (2008)
	4	MAF50-DIK026	51.21–86.23	CHA × HF	Gutierrez-Gil et al. (2008)
	6	DIK5076-BM1329	4.51–35.39	CHA × HF	Gutierrez-Gil et al. (2008)
	7	RM006-BM1853	25.39–85.32	CHA × HF	Gutierrez-Gil et al. (2008)
	8	CSSM047	115.2	CHA × HF	Gutierrez-Gil et al. (2008)
	9	BM888-CSRM60	59.98–77.81	CHA × HF	Gutierrez-Gil et al. (2008)
	10	BMS528-TGLA378	24.01–43.65	CHA × HF	Gutierrez-Gil et al. (2008)
	11	ILSTS100-IDVGA-3	59.11–81.8	CHA × HF	Gutierrez-Gil et al. (2008)
	16	BM121	26.4	CHA × HF	Gutierrez-Gil et al. (2008)
	19	BMS2142-CSSM065	43.31–69.83	CHA × HF	Gutierrez-Gil et al. (2008)
	21	HEL10-TGLA337	65	CHA × HF	Gutierrez-Gil et al. (2008)
	29	RM044-MNB166	24.48–33.51	CHA × HF	Gutierrez-Gil et al. (2008)
Habituation ^a + Temperament ^b	1	BMS574	15.42	BB cattle from ET	Schmutz et al. (2001)
	5	RM103	29.42	BB cattle from ET	Schmutz et al. (2001)
	9	ILSTS013	48.73	BB cattle from ET	Schmutz et al. (2001)
	11	LISTS036	61.57	BB cattle from ET	Schmutz et al. (2001)
	14	RM180-ILSTS008	33.31–50.91	BB cattle from ET	Schmutz et al. (2001)
	15	ADCY2	22.67	BB cattle from ET	Schmutz et al. (2001)

^aHabituation was defined by the authors as adaptability of animals to novel environmental conditions in a given time period.

^bTemperament was measured once by the degree of animal nervousness in changed/new environmental conditions for the animal, with the assessed animal being most often separated. ET = embriotransfer; CHA – Charolais; HF – Holstein-Friesian; BB – beef breed

Most genes identified in cattle (*Bos taurus*), pigs (*Sus scrofa*), and sheep (*Ovis aries*) that are associated with a range of behavioral traits (e.g., temperament, indexes of terrain use, milking speed, tail biting, and suckling) likely control stimulus reception (e.g., olfaction), internal recognition of stimuli, and body response to stimuli. In a review article, Alvarenga et al. (2021) examined genomic regions associated with behavior in livestock such as cattle, pigs and sheep. In cattle, 383 such markers were identified. Six genes (*NR3C2*, *PITPNM3*, *RERG*, *SPNS3*, *U6*, and *ZFAT*) were identified in both cattle and pigs. About half of the genes associated with behavior in livestock (cattle, sheep, and pigs) are also responsible for various behavioral, psychological, and neurological disorders in humans. For example, *NCOA7*,

GAD2, *PDGFD*, *TMPRSS5*, *DRD2*, *IQSEC1*, *MAOB*, *PTPRF*, *SLC25A16*, *TMC05A*, and *SNRPB2*, which are associated with temperament in dairy cows, have already been linked to neuropsychiatric disorders in humans. Identifying the molecular mechanisms of behavior may contribute to a better understanding of behavioral problems that are widespread in many areas of animal husbandry, such as animal handling, susceptibility to stress, or adaptation to different production conditions. On the other hand, research has shown that the influence of genetic differences on behavior is not direct but manifests at other levels, including transcripts, proteins, metabolites, and through complex networks of neurophysiological and structural factors (Johnston and Edwards, 2002).

CANDIDATE GENES

Identification of candidate genes and functional analyses

The creation of genetic maps for various domestic animal species and efforts to improve animal welfare in different production systems have increased the number of studies on the genetic background of animal temperament. In the past, the selection of animals in livestock production was based mostly on their adaptability to the environment and their responsiveness to humans. However, differences between breeds of animals quickly appeared. For example, *Bos indicus* were found to be more restless than *Bos taurus* and heifers were found to have more lively temperaments than bulls (animals with a lively temperament pose a considerable risk to the stockperson and other animals). It has also been found that animals exhibiting calmer temperaments grow faster than those that are agitated during normal husbandry routines (Voisin et al., 1997).

In order to reveal the functional consequences of the discovered candidate genes, the researchers analyzed the biological processes, cellular components, and molecular functions of the genes in their study. Among other things, the researchers focused on the serotonergic and catecholaminergic systems and their interplay for the synthesis and metabolism of important neurotransmitters such as serotonin and dopamine. The gene encoding dopamine receptor D4 (*DRD4*) has been associated with behavioral traits such as finding new objects and curiosity in humans and various animals such as cattle (Bailey et al., 2007) and Great tits (Korsten et al., 2010). In cattle, *DRD4* is possibly located in the distal part of chromosome BTA29 (Glenske et al., 2011). The latter analyzed ten microsatellites in German Angus calves. The candidate gene for the D4 dopamine receptor was analyzed and included in a quantitative trait loci (QTL) study based on three different behavioral tests in cattle (score tethering test, weighing test, separation and restraint test). A *DRD4* fragment was mapped to the distal region of BTA29. The results showed that BTA29, with a putative QTL in the proximal part and a *DRD4* candidate gene in the distal part, plays an important role in regulating temperament (Glenske et al., 2011).

The next frequently discussed functional candidate gene is the monoamine oxidase A (*MAOA*) gene. The enzyme monoamine oxidase A (*MAOA*) breaks down monoamines such as the neurotransmitter serotonin. The *MAOA* gene is assigned to the X-chromosome in all mammals analyzed so far, including humans and cattle. The *MAOA* gene and its product play an important role in the complex regulation of behavior in cattle. The *MAOA* gene of humans, mice, and monkeys is thought to determine the trait aggressiveness. Lühken et al. (2010) also analyzed the coding region of the

MAOA gene with the aim of detecting the genetic variability of behavior using four tests (I, behavior after two minutes of enthering, IIa, behavior when entering the scale, IIb, behavior during weighing, III, behavior during the separation test which classifies the different activities carried out by cattle, when they are removed from their familiar environment). They identified five SNPs in the coding region, three of which were in the coding region of the gene (exons III and XV). One of the SNPs in exon XV (NC_007331.3:g.80340C>T) was a nonsynonymous mutation. In a nonsynonymous mutation, there is usually an insertion or deletion of a single nucleotide in the sequence during transcription when the mRNA copies the DNA. This single missing or added nucleotide results in codon shuffling and mutation of the amino acid sequence.

For decades, selection has exerted selection pressure on a specific phenotype of animal behavior, such as aggressiveness, thus altering the specific frequencies of alleles for this trait in the cattle population. Eusebi et al. (2019) studied the Lidia breed of cattle, which has been selected for aggressiveness, ferocity, and fast movements since the 18th century because it is used in bullfights. They focused on mapping selection markers associated with aggression on the X chromosome and compared samples of Lidia cattle with two Spanish breeds that show the opposite, calm behavior. The most important markers appeared in the vicinity of monoamine oxidase A (*MAOA*). A polymorphism consisting of a variable number of tandem repeats of nucleotide "C" was detected. The lower number of repeats in the Lidia breed compared to the other cattle breeds suggests that the lower number of these repeats is associated with aggressive behavior, rapid response and fast movement of the animal.

Among published research identifying novel genes for behavioral traits in cattle is the study by Garza-Brenner et al. (2016), which examined an interaction network approach to identifying novel genes (interacting genes) and evaluated their effects and the effects of 19 dopamine- and serotonin-related genes on temperament. Their potential to be associated with temperament was evaluated based on their reported biological activities, which included interactions with neuronal activity, receptor function, targeting or synthesis of neurotransmitters, and association with behavior. Results from Charolais cows in the Pen Score (PS) and Exit Velocity (EV) tests were used to calculate temperament. Results of single marker association analysis between genotypes and temperament measurements (EV, PS and/or TS Temperament Score) showed significant associations of six SNPs from four candidate genes. Markers rs109576799 and rs43696138, located in the *DRD3* and *HTR2A* genes, respectively, were significantly associated with EV and TS traits. Four markers, rs110365063 and rs137756569 from the *POMC* gene and rs110365063 and rs135155082, located in *SLC18A2* and *DRD2*, were associated with PS.

In addition, Garza-Brenner et al. (2020) studied a group of molecular markers previously associated with temperament and their influence on growth traits. Phenotypic data were sorted and used to determine correlations between birth weight (BW), weaning weight (WW), yearling weight (YW), and temperament traits measured as exit velocity (EV is defined as the rate (m/s) at which an animal traverses a specific distance after exiting a squeeze chute) and temperament score (TS values were calculated by averaging the PS and EV). Pen score (PS) is a subjective measure, based on individual visual assessments of animals behavior while confined to a pen in groups of five animals, where a score of 1 is calm and 5 is aggressive. Significant correlations between BW and WW and both temperament scores (EV and TS) were observed only in the young cow group. The study showed that markers rs109576799 (*DRD3*), rs134604468, rs137756569 (*POMC*), and rs43696138 (*HTR2A*), previously associated with temperament traits in cattle, were also associated with weight traits (BW and WW). Four markers located on candidate genes for temperament traits also influenced BW and WW in Charolais cows, suggesting that both traits may be influenced by the same genes.

The proopiomelanocortin (*POMC*) gene associated with temperament is located on chromosome BTA11. The *POMC* gene is a posttranslationally processed precursor of peptide hormones, some of which are involved in energy homeostasis, including α -melanocyte-stimulating hormone (MSH), adrenocorticotrophic hormone (ACTH), and β -endorphin. Another gene of interest is neuropeptide Y (*NPY*), which regulates appetite, feeding behavior, and hormonal function. Because of its role in feeding, some SNP of this gene have been associated with growth traits in cattle. Both the *POMC* and *NPY* genes are important regulatory factors in the leptin/melanocortin pathway, which is considered one of the most important pathways regulating energy metabolism. Both are involved in hypothalamic function – the pituitary-adrenal axis – which plays an important role in regulating numerous physiological processes, including reproduction, anxiety, stress response (fight-or-flight), learning and memory, and the cardiovascular system.

There are still no studies in the literature comparing the behavior of different breeds, especially animals raised under similar housing conditions. A study by Paredes-Sanchez et al. (2020) identified genomic regions and genes associated with temperament in Brahman cattle. In testing the cattle, they used three different tests: EV – exit velocity, PS – pen score, and TS – temperament score. Fourteen bovine temperament SNP were associated with the above tests, all with EV and few with PS and TS. They identified about 21 candidate genes for temperament in Brahman breed of cattle. Studies on the influence of breed on temperament specificity in cattle were also conducted on a sample of Nellore breed cattle, where they also investigated which candidate genes shape temperament in cattle. Valente et al.

(2016) conducted a study to uncover genomic regions, potential candidate genes, and their biological mechanisms underlying temperament as measured by the running speed test (FS). In this study, nine regions associated with temperament were identified. Among them were six known genes *NCKAP5*, *PARK2*, *ANTXR1*, *GUCY1A2*, *CPE* and *DOCK1*. Of these genes, *PARK2*, *GUCY1A2*, *CPE* and *DOCK1* are related to the dopaminergic system, memory formation, biosynthesis of peptide hormones and neurotransmitters, or brain development.

Hiendleder et al. (2003) performed a genome scan for quantitative trait loci (QTL) in Holstein animals. They found 60 QTL that were significant at the 5% chromosome level for 22 body shape and behavior traits, with estimated heritabilities of 0.07–0.41, indicating that a substantial number of loci influence body conformation and behavior. Mapping QTL for body conformation and behavior in cattle on multiple chromosomes revealed that QTL for correlated traits are present in the same chromosomal regions. An example is a QTL for temperament and milking speed ($rG = 0.53$) on chromosome 5 at 136/136 cM, on chromosome 18 at 105/109 cM, on chromosome 29 at 20/20 cM, and on chromosome X/Y at 9/9 cM.

On the other hand, researchers have not detected any biological functions of the *DRD3* gene in cattle. However, in humans, genetic variants of dopamine receptor D3 (*DRD3*) have been linked to schizophrenia and autism. The gene has also been associated with emotional reactivity, executive functions, and stress responses. The bovine rs109576799 *DRD3* marker, located in the intron of the *DRD3* gene, suggests that this variation has no obvious functional effects on gene expression. However, its effect on temperament traits could be explained by the gene's role in emotional reactivity and the sensitivity of the dopamine system to environmental stressors, which in turn could be explained by its association with behavior (National Library of Medicine, 2024).

The results of previous studies have proven the genetic orientation of behavior and, moreover, have confirmed the assumption that certain behavioral traits are influenced by different genomic regions. Research by Dos Santos et al. (2017) examined genome-wide association studies for reactivity assessed by the REATEST® (this test uses an electronic device with an accelerometer positioned under the chute record of Guzarat (*Bos indicus*) cow movement for 20 seconds during routine weighing) (Table 3). They examined reactivity to humans, which is mainly influenced by past experience. They identified QTL for bovine reactivity on chromosomes BTA1, BTA5, BTA14, and BTA25. The candidate gene on the first chromosome is *ZBTB20* (zinc finger and *BTB* domain containing 20). The *ZBTB20* directly affects the development of different parts of the hippocampus and influences behavioral traits such as memory and anxiety. A candidate gene *KIAA1429* was identified on chromosome BTA14. Two associated genes were discovered on chromosome BTA25.

The first is the *ABCC1* gene, a membrane-associated protein belonging to the ATP superfamily, and the von Willebrand factor domain-containing gene 3A (*vWA3A*). Proteins containing von Willebrand domains are involved in basement membrane formation, cell migration, cell differentiation, adhesion, hemostasis, signal transduction, chromosome stability, malignant transformation, and immune defense. Although *vWA3A* is differentially expressed in blood, brain, lung, ovary, and testis, there is still no evidence for the function of this gene in cattle.

Bos indicus cattle often have a reputation for poor or dangerous temperament. For example, Riley et al. (2016) studied subjective temperament scores (1 to 9; higher scores indicate less favorable temperament) for aggressiveness, nervousness, flight, sociability and overall temperament in one-year-old *Bos indicus* crossbred cattle and weaned calves. *Bos indicus* cattle are characterized by a more stress response temperament and are also more aggressive than *Bos taurus* cattle. Therefore, they are of particular interest for the study of aggressiveness. Chen et al. (2020) found a total of five SNP on BTA1, BTA24, and BTA29 that we believe are associated with aggression, nervousness, or run/run speed when assessed after weaning, and 13 SNP on 11 chromosomes that are likely associated with aggression, nervousness, run or total temperament score of bulls at 1 year of age.

Milking speed (MS is mainly associated with the required milking time in relation to milk yield) and milking temperament (MT reflects behavioral responses to human or equipment during the milking process and can be subjectively scored on a linear scale of 1–5 points from very nervous to very calm animals) are important traits in

breeding dairy cows. These two traits are of global importance because the intensification of farming, the introduction of modern devices that reduces contact with humans, e.g. automatic milking machines require properly adapted animals. This is important both from a breeding point of view and from the point of view of introducing both hereditary traits into selection. Genomic selection represents a potential method to increase the genetic progress of both traits. From this point of view, Chen et al. (2020) studied the associations of >5.7 million whole genome sequence variants with MT and MS in 4,381 and milk flow rate in 4,219 Holstein cattle. They found 40 and 35 significant SNP independently associated with MT and MS, respectively, distributed across 26 chromosomes (Table 3). Eight candidate genes *GRIN3A*, *KCNJ3*, *BOSTAUV1R417*, *BOSTAUV1R419*, *MAP2K5*, *KCTD3*, *GAP43*, and *LSAMP* are thought to play an important role in the expression of MT traits because they are involved in biologically important signaling pathways such as the glutamatergic synapse, vomeronasal receptor, and oxytocin signaling. Since production traits in animal breeding are usually polygenic, this is also true in our case. MT and MS are traits regulated by a large number of genes. The SNP for both traits were located on 19 chromosomes. Important biological pathways have also been identified in relation to the expression of this trait, such as glutamatergic synapse function and oxytocin signaling. Knowledge of the biological mechanisms underlying the phenotypic expression of MT and MS in dairy cows is useful for optimizing genomic prediction of breeding value.

Table 3: Chromosomes and genes responsible for temperament traits in cattle

Chromosome	Temperament characteristic	Peak markers	Gen	Reference
1	Reactivity	rs41965198		Dos Santos et al. (2017)
1	Reactivity	rs109007595	POU1F1 (POU class 1 homeobox 1)	Dos Santos et al. (2017)
1	Milking temperament	rs109576799	<i>DRD3</i> (dopamine receptor D3)	Garza-Brenner et al. (2016)
1	Milking temperament	rs211042818		Chen et al. (2020)
1	Milking temperament	rs42810614		Chen et al. (2020)
1	Milking temperament Reactivity	rs108944043	<i>ZBTB20</i> (zinc finger and BTB domain containing 20)	Dos Santos et al. (2017)
2	Milking temperament	rs383768960		Chen et al. (2020)
3	Temperament	rs110572929	<i>OR6P1</i> (olfactory receptor, family 6, subfamily P, member 1)	Riley et al. (2016)
3	Temperament	rs110358340		Riley et al. (2016)

Chromosome	Temperament characteristic	Peak markers	Gen	Reference
3	Milking temperament	rs208423467		Chen et al. (2020)
3	Milking temperament	rs132650029		Chen et al. (2020)
3	Milking temperament	rs446551565		Chen et al. (2020)
3	Milking temperament	rs110358340		Chen et al. (2020)
4	Milking temperament	rs41587635	<i>NRCAM</i> (neuronal cell adhesion molecule)	Kolbehdari et al. (2008)
5	Reactivity	rs29002595		Dos Santos et al. (2017)
6	Milking temperament	rs211661579		Chen et al. (2020)
6	Milking temperament	rs381423005		Chen et al. (2020)
8	Milking temperament	rs43695372		Chen et al. (2020)
8	Milking temperament	rs382298735		Chen et al. (2020)
9	Milking temperament	rs210732867		Chen et al. (2020)
9	Milking temperament	rs109147749	<i>SFT2D1</i> (SFT2 domain containing 1)	Chen et al. (2020)
9	Milking temperament	rs377930383	<i>TBC1D32</i> (TBC1 domain family member 32)	Chen et al. (2020)
9	Milking temperament	rs110768750		Chen et al. (2020)
9	Milking temperament	rs383164349	CFAP206 (cilia and flagella associated protein 206)	Chen et al. (2020)
9	Milking temperament	rs385265013	<i>TBC1D32</i> (TBC1 domain family member 32)	Chen et al. (2020)
10	Milking temperament	rs385815295	<i>MAP2K5</i> (mitogen-activated protein kinase kinase 5)	Chen et al. (2020)
10	Milking temperament	rs442437054	<i>REC114</i> (REC114 meiotic recombination protein)	Chen et al. (2020)
11	Pen score	rs134604486	<i>POMC</i> (proopiomelanocortin)	Garza-Brenner et al. (2016)
11	Pen score	rs137756569	<i>POMC</i> (proopiomelanocortin)	Garza-Brenner et al. (2016)
11	Milking temperament	rs461599895		Chen et al. (2020)
12	Temperament	rs43696138	<i>HTR2A</i> (5-hydroxytryptamine receptor 2A)	Garza-Brenner in sod. (2016)
12	Milking temperament	rs207744310		Chen et al. (2020)
12	Milking temperament	rs133939404		Chen et al. (2020)
13	Milking temperament	rs41601522	<i>CSTFI</i> (cleavage stimulation factor subunit 1)	Kolbehdari et al. (2008)

Chromosome	Temperament characteristic	Peak markers	Gen	Reference
14	Reactivity	rs110729726	<i>KIAA1429</i> (KIAA1429 ortholog)	Dos Santos et al. (2017)
14	Milking temperament	rs433044051		Chen et al. (2020)
15	Pen score	rs135155082	<i>DRD2</i> (dopamine receptor D2)	Garza-Brenner et al. (2016)
16	Milking temperament	rs381220479		Chen et al. (2020)
16	Milking temperament	rs385094052		Chen et al. (2020)
16	Milking temperament	rs380118891		Chen et al. (2020)
17	Milking temperament	rs457419900		Chen et al. (2020)
18	Milking temperament	rs209543233		Chen et al. (2020)
21	Milking temperament	rs109756761	<i>ADAMTS7</i> (ADAM metallopeptidase with thrombospondin type 1 motif 7)	Chen et al. (2020)
22	Milking temperament	rs29024274	<i>CACNA1D</i> (calcium channel, voltage-dependent, L type, alpha 1D subunit)	Kolbehdari et al. (2008)
22	Milking temperament	rs134284583	EEFSEC (eukaryotic elongation factor, selenocysteine-tRNA specific)	Chen et al. (2020)
22	Milking temperament	rs383977582	<i>KBTBD12</i> (<i>kelch repeat and BTB domain containing 12</i>)	Chen et al. (2020)
23	Milking temperament	rs41667511	<i>BYSL</i> (bystin like)	Kolbehdari et al. (2008)
23	Temperament	rs42037482	<i>RREB1</i> (ras responsive element binding protein 1)	Riley et al. (2016)
23	Milking temperament	rs383925248		Chen et al. (2020)
24	Milking temperament	rs208988018		Chen et al. (2020)
25	Reactivity	rs42063418	<i>ABCC1</i> (ATP binding cassette subfamily C member 1)	Dos Santos et al. (2017)
25	Reactivity	rs109589165	<i>VWA3A</i> (von Willebrand factor A domain containing 3A)	Dos Santos et al. (2017)
26	Milking temperament	rs1606777	SLC18A2 (solute carrier family 18 (vesicular monoamine transporter), member 2) <i>SLC18A2</i> (solute carrier family 18 (vesicular monoamine transporter), member 2)	Kolbehdari et al. (2008)
26	Pen score	rs110365063	SLC18A2 (solute carrier family 18 (vesicular monoamine transporter), member 2)	Garza-Brenner et al. (2016)
27	Milking temperament	rs207974554	<i>ZMAT4</i> (zinc finger matrin-type 4)	Chen et al. (2020)
27	Milking temperament	rs211354263		Chen et al. (2020)
27	Milking temperament	rs433573094	<i>ZMAT4</i> (zinc finger matrin-type 4)	
27	Milking temperament	rs109526335		Chen et al. (2020)
27	Milking temperament	rs109475419	<i>ZNF385D</i> (zinc finger protein 385D)	Chen et al. (2020)

Chromosome	Temperament characteristic	Peak markers	Gen	Reference
27	Milking temperament	rs385056921	ZMAT4 (zinc finger matrin-type 4)	Chen et al. (2020)
27	Milking temperament	rs42891178		Chen et al. (2020)
29	Milking temperament	rs466626658		Chen et al. (2020)
29	Temperament	Up:BMS764 Low:BMC8012		Hiendleder et al. (2003)
29	Temperament	BMS764		Glenske et al. (2011)
29	Milking temperament	rs41652321	CCDC88B (coiled-coil domain containing 88B)	Kolbehdari et al. (2008)
29	Milking temperament	rs41584970		Kolbehdari et al. (2008)
29	Milking temperament	rs43706181	DPP3 (dipeptidyl peptidase 3)	Kolbehdari et al. (2008)
29	Milking temperament	rs29024010	NTM (neurotrimin)	Kolbehdari et al. (2008)

CONCLUSIONS

To date, there have been many findings on behavioral genetics, from candidate genes to the effects of SNPs and QTLs to research on associations between SNPs and QTLs. Research confirms that phenotypic differences are the result of the influence of a few loci with a strong effect or a larger number of them with a small effect. The influence of genetic variants on behavior is not direct, but results from a complex feedback network of neurophysiological and structural factors such as hormones and proteins, which in turn are products of indirect genetic effects. Due to environmental influences, genes that influence temperament in cattle are less heritable compared to genetic loci associated with production traits. Future research on behavioral traits in cattle will likely focus on further exploring the genetic background and how variations in genes influence the expression of temperament in individual animals. This will make it possible to include temperament traits in selection indices. The main challenges for a more comprehensive integration of temperament in dairy cattle breeding programs are the definition of individual traits and large-scale monitoring of temperament. On the other hand, there is still a lack of understanding of the genetic background of traits and the availability of economic values for temperament.

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Genetsko ozadje temperamenta goveda: kratek pregled

IZVLEČEK

Temperament živali opisuje vedenjske razlike med posamezniki, ki so stalne skozi čas in v različnih okoliščinah. Poznavanje temperamenta živali pomembno vpliva na varnost pri ravnanju z živalmi in skrbi zanje ter na prilagajanje živali spreminjajočim se pogojem reje. Da bi razumeli temperament živali, moramo poleg genetske osnove temperamenta poznati tudi vpliv okolja na njegovo izražanje. Podobno lahko temperament krav molznic opredelimo kot odziv živali na okoljske ali socialne dražljaje. V tem preglednem članku so predstavljeni kromosomi z genomskimi območji, ki vsebujejo QTL, gene in kandidatne gene, odgovorne za izražanje lastnosti temperamenta pri govedu. Poznavanje genetskega ozadja izražanja temperamenta pri govedu in njegove spremenljivosti pri teh lastnostih omogoča vključitev temperamenta v selekcijske indekse.

Ključne besede: govedo, genetika temperamenta, QTL, SNP, dednost, serotonin, dopamin