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REVIEW PAPER

Strain-to-strain differences within lactic and propionic acid bacteria species strongly impact the properties of cheese–A review

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Abstract Lactic acid bacteria (LAB) and propionic acid bacteria (PAB) are widely used in the manufacture of cheeses and other fermented dairy products. Bacterial species used as starters are mainly chosen according to their intrinsic properties: the milk acidifying capacity for LAB starters and the aromatizing properties of PAB, for example. Beyond the general characteristics of a bacterial species, many key phenotypic traits determining their interest for dairy applications depend on the strain within a given species. Through some examples, this review illustrates how the choice of a bacterial strain with specific technological characteristics, within a given species of LAB or PAB, can determine the final properties in the end product. This concerns the technological properties of cheeses, such as flavour, texture, and opening formation, and their functional properties, such as inhibition of undesirable microorganisms and health properties. When known, the genetic determinants of the diversity are presented. This review emphasizes the importance of preserving and exploring microbial resources at the intraspecific level, as an unending source of diversity for innovation in food fermentation.

Keywords Biodiversity · *Lactococcus* · *Lactobacillus* · *Propionibacterium* · Strain-dependency · Cheese · Organoleptic properties · Safety · Health properties

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1 Introduction

Microorganisms are key agents in the manufacture of fermented foods, where they generate a wide variety of flavours, textures, and appearances. Historically, milk fermentation was spontaneous and resulted from the presence of indigenous bacteria in milk and in the environment. Thanks to our increased knowledge of the fermentation process and of the bacterial groups involved in cheese manufacture, selected starters and ripening cultures are nowadays widely used to standardize the fermentation and reach the targeted properties for the final products. For this, bacterial species are chosen for their intrinsic species properties. For example, mesophilic or thermophilic species of lactic acid bacteria (LAB) are chosen according to their ability to acidify milk in the range of temperatures used in a given process. Likewise, some starter LAB species are chosen for their aromatizing or debittering properties, propionic acid bacteria (PAB) are used in Swiss-type cheeses to generate holes and specific flavour notes, and surface bacteria contribute to the characteristic flavour and colour of smear-rind cheeses. Many of these properties depend on the strain within a species, and the choice of a selected strain is thus a means to modulate the final cheese properties.

A bacterial species is defined on the basis of phenotypic properties and whole-genome DNA-DNA hybridization, which is a reference tool in microbial species delineation (Auch et al. 2010; Stackebrandt et al. 2002). In practice, the use of a polyphasic approach including an almost complete and high quality 16S rRNA gene sequence combined with a robust phenotypic description is widely accepted for strain identification up to the species level (Stackebrandt et al. 2002). Within a bacterial species, a strain is defined as "the descendant of a single isolation in pure culture and usually made up of a succession of cultures ultimately derived from an initial single colony" (Staley and Krieg 1984). Although the strains of a given species share many phenotypical and genomic properties, they also exhibit some marked differences due to the genomic plasticity. Bacterial genomic plasticity is provided by two mechanisms: vertical transfer, which is related to the transfer of genetic information from one generation to the next, and horizontal gene transfer (HGT), which occurs between even non taxonomically related organisms of the same generation (Rossi et al. 2014; Cavanagh et al. 2015). It is largely responsible for bacterial adaptation (Ryall et al. 2012).

The adaptation to diverse ecological niches is genetically determined by the acquisition of new genes by HGT, in parallel to the decay and loss of non-essential genes as highlighted by comparative genomic analysis in LAB and PAB (Cai et al. 2009; Cavanagh et al. 2015; Kelleher et al. 2015; Loux et al. 2015; Papadimitriou et al. 2015). Many examples of HGT in food-related LAB species have been reported (Rossi et al. 2014). For example, the extracellular protease PrtS and the glutamic acid decarboxylase GadB in *Streptococcus thermophilus* have both been acquired by HGT (Rossi et al. 2014). Many technologically important traits are plasmid-encoded in *Lactococcus lactis* (Kelleher et al. 2015). Most dairy-associated isolates of *L. lactis* carry extensive plasmid complements, which can constitute up to 9% of the genetic material (Ainsworth et al. 2014). Transposable elements are commonly found in the chromosome and plasmids of *L. lactis*, and insertion sequences (IS) are involved in mutations resulting in gene activation or deactivation (Cavanagh et al. 2015). An extensive gene decay is observed in food-related LAB, resulting in up to 10% of pseudogenes in the genome (Papadimitriou et al. 2015).

The intensive selection of LAB on properties for their dairy industrial use led to an increased specialization of so-called "domesticated" strains with an exacerbation of the targeted quality, such as fast acidification and a concomitant loss of other useless characteristics, compared to the "wild-type" ancestral strains. For example, the traditional division into dairy strains and non-dairy strains of *L. lactis* has recently been replaced by a new classification that distinguishes ecotypes corresponding to "domesticated" and "environmental" strains (Passerini et al. 2010). In *Lactobacillus rhamnosus*, the integration of genomic and phenotypic data of 100 strains isolated from various ecological niches revealed the presence of two prevailing geno-phenotypes, characterized by traits explaining their adaptation to dairy-like environments or to the intestinal tract, respectively (Douillard et al. 2013). Some pheno-genomic markers, such as carbohydrate metabolism, were proposed to characterize the ecology of *L. rhamnosus* strains. All the strains domesticated to the dairy environment share common properties, but they can also differ in the phenotypic traits of importance for their use in the dairy industry due, for example, to point gene mutations.

This review illustrates how the strain-dependent phenotypic variability can deeply impact the final properties of cheeses. This paper will preferably report on the results of studies that have demonstrated the impact of strains in situ in cheeses or in other dairy products including those in model dairy systems, when available, rather than in classical laboratory media. The mechanisms that explain the observed differences will also be presented whenever they are known. This paper provides some examples illustrating the extent of variations in the final properties of cheeses (e.g. organoleptic, techno-functional, safety, and health properties) that can result from the choice of selected strains within a LAB or PAB species.

2 Technological properties

This section gives examples of the strain-dependency of activities in LAB and PAB species that generate various metabolites involved in the formation of cheese flavour, texture, and techno-functional properties.

2.1 Flavour properties

The formation of flavour results from the conversion of milk lactose, citrate, caseins and lipids into taste and aroma compounds during the fermentation of dairy products. This section, through three examples, illustrates how the strain-to-strain variations in LAB and PAB species can strongly impact the formation of important flavour compounds in cheese. Some of the examples cited below are further detailed in Tables 1 and 2 illustrating the results of screening studies of LAB (Table 1) and PAB (Table 2).

2.1.1 Formation of flavour compounds by L. lactis

"Wild" strains of *L. lactis* produce a larger number of compounds in comparison to industrial dairy strains and may generate an unusual flavour, either desirable or undesirable (Alemayehu et al. 2014; Ayad et al. 1999; Cavanagh et al. 2014; Cavanagh et al. 2015).

Many flavour compounds in cheese results from amino acid catabolism by LAB, generating a range of flavour notes in cheese (Yvon and Rijnen 2001). The amino acid-converting ability of LAB varies greatly from strain to strain (Smit et al. 2005). Two thirds of the wild strains of *L. lactis* grown in milk produced an unusual flavour compared to those produced by the industrial reference strains (Ayad et al. 1999). Tested in Gouda cheese manufacture in association with a reference industrial starter strain, some selected strains generated varied flavour notes, such as malty/chocolate, fruity and H_2S (Table 1). Some "wild" non-dairy strains of *L. lactis* have been shown to produce glutamate dehydrogenase (GDH), an enzyme that converts glutamate to α-ketogluturate, thus enhancing the first rate-limiting reaction of the amino acid conversion to flavour compounds, an aminotransferase reaction, which requires an amino group acceptor such as α-ketoglutarate (Tanous et al. 2002).

Lactococcus lactis subsp. *lactis* biovar *diacetylactis* strains are used in the dairy industry for generating acetoin and notably diacetyl, which imparts a buttery flavour note (Curioni and Bosset 2002). An elegant study recently highlighted the large strain-dependency in the production of acetoin and diacetyl in a collection of 35 *L. lactis* strains from diverse origins (Passerini et al. 2013). Dairy domesticated strains of the biovar *diacetylactis* harbour a *citP* plasmid gene encoding citrate permease and a chromosomal region *citM-citI-citCDEFXG* involved in citrate metabolism. These strains produce diacetyl or acetoin at a high level during early growth. Two out of the 11 environmental strains tested also produced a significant amount of these aroma compounds, although they do not use citrate (Passerini et al. 2013). In these strains, pyruvate flux was rerouted through the acetoin–diacetyl pathway and resulted in a production at a lower rate compared to citrate positive strains. Ten out of the 11 environmental strains were citrate-negative but produced acetoin or diacetyl through this pathway, in a highly strain-dependent manner, with final aroma concentrations varying from 2 to 20 mM (Passerini et al. 2013). In another study, the 15 *L. lactis* strains tested produced different profiles of flavour compounds in fermented milk, with a clear distinction between the 3 dairy strains and 12 plant-derived strains. For example, the production of diacetyl and acetoin varied by a factor >20 and 200, respectively (Alemayehu et al. 2014). Differences between the amounts of acetoin produced by wild strains of *L. lactis* were also observed in miniature Chihuahua-type cheese (Nájera-Domínguez et al. 2014).

2.1.2 Hydrolysis of caseins by LAB: a complex proteolytic and lytic system implied in the formation of sapid peptides

Proteolysis is a complex series of reactions which hydrolyses caseins, the main milk proteins, into peptides and free amino acids. It involves proteinases and peptidases from different origins: milk, coagulants added during process and microorganisms. The production of peptides by LAB cell envelope proteinases (CEP) is highly variable, both quantitatively and qualitatively, but gives fingerprints of overall proteolysis that are distinguishable among the various dairy fermented products. The size of peptides produced from casein hydrolysis ranges from 3 to more than 45 amino acid residues, due to the very broad specificity of the proteinases on caseins.

Either a unique or multiple CEP is present in LAB, depending on the species. For example, a unique CEP, PrtP, is present in *L. lactis* (Monnet et al. 1987), PrtS in

S. thermophilus (Fernandez-Espla et al. 2000), PrtB in *Lactobacillus delbrueckii* (Laloi et al. 1991), and PrtR in *L. rhamnosus* (Pastar et al. 2003), whereas up to four CEPs are present in *Lactobacillus helveticus*, referred to as PrtH to PrtH4 (Broadbent et al. 2011; Sadat-Mekmene et al. 2011b). Moreover, the activity and specificity of CEP can also vary within a given species. For example, the PrtP proteases of the two strains of *L. lactis* subsp. *cremoris* WG2 and SK11 possess distinct specificities towards the peptide αs1-casein (f1–23) and were classified as type PI and PIII, respectively (Exterkate 1990; Exterkate and Alting 1995). The PrtP of *L. lactis* subsp. *lactis* NCDO 763 was classified as intermediate type PI/PIII (Monnet et al. 1992). The strain-dependency of casein hydrolysis is still higher within the *L. helveticus* species. The specificity of cleavage of β- or α_{s1}-caseins varies from strain to strain and also depends on the substrate (purified caseins or casein micelles in milk) (Sadat-Mekmene et al. 2011b). The 15 strains studied in vitro rapidly hydrolysed pure β-casein, but differed in the hydrolysis kinetics of α_{s1}-casein, depending on their number of CEPs (Sadat-Mekmene et al. 2011a). Moreover, in cheese, the degree of proteolysis differed by a factor of 1.5 in Emmental cheeses manufactured using either *L. helveticus* ITGLH77 with only PrtH2 and a low level of lysis, or *L. helveticus* ITGLH1 having at least PrtH and PrtH2 encoding genes and a high lytic activity (Sadat-Mekmene et al. 2013). The kinetics of α_{s1}-casein hydrolysis in these cheeses was in agreement with the results observed in vitro.

As a consequence of CEP diversity, the peptide profile is highly dependent on the LAB species used as a starter. Some of the numerous peptides produced, rich in hydrophobic amino acid residues, confer bitterness to dairy products and notably in cheese, depending on their size, sequence and amount (Lemieux and Simard 1992; McSweeney 1997; Vassal and Gripon 1984). Proteolysis is a continuous process, and these hydrophobic bitter peptides can be further hydrolysed by bacterial intracellular peptidases released in cheese through LAB autolysis. The smaller peptides and free amino acids produced are associated with other taste compounds (sour, sweet, acid, brothy) and are precursors of flavour compounds (Yvon and Rijnen 2001). These peptidases are active throughout the ripening time in cheese, as shown in different cheeses (Emmental, Gagnaire et al. 1998; Valence et al. 2000, Cheddar, Sheehan et al. 2006, and semi-hard cheese, Boutrou et al. 1998). In semi-hard cheese manufactured using with five single strains of *L. lactis* with different lytic and proteolytic properties, good flavour scores and in particular non-bitter cheeses were only obtained with the strains both lytic and with a high proteolytic potential (Boutrou et al. 1998). It should be underlined that testing the in vitro proteolytic potential of LAB gives only a partial view of what can be expressed in situ in cheese. For example, the proteolytic potential of starter strains measured in vitro for cell-free extracts was not found to be correlated with the activity released in Cheddar cheese (Sheehan et al. 2006). The impact of strain-dependency due to the differences in *L. lactis* CEPs was shown in 50% reduced-fat Cheddar cheese manufactured using isogenic single strains of *L. lactis* that had CEP with different substrate specificities and a CEP-negative strain (Broadbent et al. 2002). Cheeses made with the CEP-negative strain did not develop bitterness, whereas the other cheeses developed slight to moderate bitterness depending on CEP specificity (Broadbent et al. 2002). This could be related to the starter peptidase activity that could be reinforced in a CEP-negative strain (Farkye et al. 1990) compared to a CEP-positive strain. Therefore, the higher production in CEP-negative strains in Cheddar cheese of

Table 1 Examples of results of screening studies of lactic acid bacteria related for their activities related to the organoleptic, techno-functional or safety or health properties of fermented dairy products

Property	Species	Number of strains tested and experimental conditions	Main conclusions	References
Lytic and proteolytic activities	*L. lactis*	Five strains with different lytic and proteolytic activities; Manufacture of Saint Paulin cheeses Sensorial tests to evaluate bitterness	Development of sensory properties of cheeses depends on cell lysis and proteolytic enzyme activity	Boutrou et al. (1998)
Lytic and proteolytic activities	*L. lactis*	Three strains Test of proteolytic activities in cell-free extracts (CFE) Comparison to the activities released into Cheddar cheese	Differences in autolysis influence proteolytic enzyme activities released into Cheddar cheese during ripening; No correlation between the proteolytic potential measured in CFE and the levels of activity released in cheese	Sheehan et al. (2006)
Lytic and proteolytic activities	*L. lactis*	Four isogenic strains with different CEP specificity: group a, e, h and l strain CEP-negative (all deleted in the gene encoding the major peptidoglycan hydrolase, AcmA to avoid lysis) Manufacture of single strain Cheddar cheese with 50% reduced-fat, flavour evaluation	CEP specificity influences the accumulation of some α_{S1}-casein (f1–23)-derived peptides in cheese; Cheese made with strains with CEP a, e, or h significantly more bitter than cheese made with the CEP-negative strain Bitterness was at the highest in cheeses with CEP h	Broadbent et al. (2002)
Production of flavour compounds from amino acid (AA) catabolism	*L. lactis*	99 strains (20 industrial, 47 dairy wild and 32 non-dairy wild strains) Growth in milk and cheese paste Flavour assessment and analysis of volatile compounds	Two thirds of wild strains (of both subsp. *lactis* and *cremoris*) grown in milk produced unusual flavour compared to those produced by the industrial reference strains Good correlation between the flavour produced in milk and in cheese paste shown for five selected wild strains High production of branched-chain alcohols and aldehydes (produced from the catabolism of branched-chain AA in three out of five wild strains associated with chocolate flavour)	Ayad et al. (1999)
Production of flavour compounds from amino acid (AA) catabolism	*L. lactis*	Eight wild strains tested in combination with a reference industrial cheese in Gouda manufacture compared to a control cheese with the reference industrial cheese alone	Similar or slightly lower levels of proteolysis in cheeses with added wild strains compared to the control cheese Particular features in some cheeses: malty/chocolate flavour associated with high levels of branched-chain alcohols and aldehydes (three strains); fruity and yeasty flavour associated with high	Ayad et al. (2000)

Table 1 (continued)

Property	Species	Number of strains tested and experimental conditions	Main conclusions	References
			levels of ethyl esters (two strains); H_2S flavour (two strains)	
Production of flavour compounds from amino acid (AA) catabolism	*L. lactis*	Eight dairy and eight non-dairy strains compared Growth in milk, analysis of volatile compounds Five non-dairy strains tested as adjuncts in mini Gouda cheeses, biochemical and sensory analyses	Four out of the eight non-dairy strains showed a clearly different volatile profile compared to classical starter strains Post-proline dipeptidyl aminopeptidase PEPX activity varied by factor of eight, respectively, in cheese extracts Sensory evaluation separated experimental cheeses with non-dairy strains from control cheese	Cavanagh et al. (2014)
Miscellaneous: galactose consumption	*S. thermophilus*	74 plant isolates Growth in lab broth with 1% galactose	6/74 positive for galactose fermentation pH decrease ranged from 0.61 to 2.73	Umamaheswari et al. (2014)
Lytic activity	*L. helveticus*	24 strains, highly diverse in terms of origin, biotope and autolytic activity; Evaluation of the clone diversity of the nine peptidoglycan hydrolases (PGHs) genes by zymography	The nine PGHs genes: ubiquitous and transcribed early during growth; Similar molecular size of the bands on zymograms Strain-to-strain variations in the number of bands: two to five lytic bands per strain	Jebava et al. (2011)
Lytic activity	*L. helveticus*	Three strains, two with a high and a low autolytic activity, and a strain particularly sensitive to lytic activity to other *L. helveticus* strains	The cell walls of the three strains contain different strain-specific polysaccharides	Vinogradov et al. (2013)
Stretchability	*L. helveticus*	Two strains of *L. helveticus* protease deficient or not Mozzarella cheese manufactured with single strain of *L. helveticus* or paired with *S. thermophilus*	Protease deficient *L. helveticus* strain led to higher stretchability	Oberg et al. (1991)
Stretchability	*L. helveticus* *L. delbrueckii* subsp. *lactis*	Three strains of each species Manufacture of Emmental cheese with single strains or mixed paired of lactobacilli species Stretching measured at three ripening times	Stronger stretchability being observed with *L. helveticus* cultures. Qualitative rather than quantitative aspects of proteolysis are determinants for the development of stretchability	Richoux et al. (2009)
Stretchability	*L. helveticus*	Two strains of *L. helveticus* having PrtH2 or at least PrtH and PrtH2 Manufacture of Swiss-type cheeses and measurement of stretching properties, of proteolysis and lysis, identification of peptides	Stretchability was correlated to a lower level of proteolysis obtained with the PrtH2 strain, and also accompanied by a lower release of intracellular peptidases into the cheese aqueous phase	Sadat-Mekmene et al. (2013)

Table 1 (continued)

Property	Species	Number of strains tested and experimental conditions	Main conclusions	References
Genetic diversity in proteolysis and amino acid (AA) catabolism	*L. helveticus*	38 strains from different origins Comparative genome hybridizations to a CNRZ 32 microarray	*L. helveticus* CNRZ 32 genome encodes many proteolytic enzymes: four CEP paralogs, seven oligo-endopeptidases, three general aminopeptidases, five proline-specific peptidases, five di- or tri-peptidases, and at least six other peptidases. Peptidase genes: almost universally conserved; peptidase activity can vary considerably in different strains CEP genes: one to four CEP present per strain AA catabolism-related genes: highly conserved, except two: several Italian whey isolates did not contain cystathionine-β-lyase, an enzyme that converts Met into methanethiol, a volatile sulphur compound associated with desirable cheese flavour and aroma; absence of *serC*, which encodes phosphoserine transaminase, in eight strains	Broadbent et al. (2011)
Production of bioactive peptides	Various species of LAB	26 strains: 10 *L. helveticus*, 11 *Lactococcus lactis*, 1 *L. acidophilus*, 1 *L. casei*, 1 *L. plantarum*, 1 *L. rhamnosus*, 1 *L. delbrueckii* subsp. *bulgaricus*. Tests in vivo in rats: ingestion of fermented milks by gastric intubation, measurement of blood pressure after injection of angiotensin I and bradykinin	*L. helveticus* strains produced more in vitro inhibitory peptides than *L. lactis* strains Under in vivo conditions only *L. helveticus* strains produced antihypertensive peptides in sufficient amount to efficiently decrease blood pressure. Two out of the ten *L. helveticus* strains had highly antihypertensive activity	Fuglsang et al. (2003)

Table 2 Examples of results of screening studies of *P. freudenreichii* related for their activities related to the organoleptic, techno-functional or safety or health properties of cheese

Property	Number of strains tested and experimental conditions	Main conclusions	References
Formation of flavour compounds: free fatty acids (FFA) from lipolysis	21 strains Cheese-like medium added with an emulsion of milk fat	Activity of strains comparable in cheese and laboratory conditions Variation by a factor >40 between strains	Abeijon Mukdsi et al. (2014)
	Five strains tested in Emmental cheese	1.8 to 5.2 mg FFA.kg^{-1} cheese	Chamba and Perreard (2002)
Formation of flavour compounds: volatile fatty acids from amino acid catabolism	40 strains Cheese-like medium: lactate broth, pH 5.4, 21 g.L^{-1}, NaCl, at 24 °C	Activity of strains comparable in cheese and laboratory conditions Variation by a factor ~10 between strains (methylbutanoic acid 6 to 57 mg.L^{-1})	Dherbécourt et al. (2008)
	Eight strains Inoculated in Emmental cheeses made from the same milk with the same lactic starters	Variation by a factor ~6 between strains (methylbutanoic acid 19 to 114 mg.kg^{-1} cheese)	Thierry et al. (2004b)
Formation of holes: CO_2 production	12 strains Incubation of cell-free extract in the presence of aspartate; quantification of the fumarate produced	Aspartase activity: 0.5 to 35 mmol.min^{-1}.mg^{-1} protein	Turgay et al. (2011)
	97 strains Incubation of cell-free extract in the presence of aspartate. Quantification of NH_3 produced	Aspartase activity (one unit of activity is the quantity of enzyme producing 0.01 nmol NH_3.min^{-1}.mg^{-1} of bacterial proteins): <100 units for 50% of strains from <150 to >1500 units for the other strains	Blasco et al. (2011)

small peptides and amino acids that are precursor of in flavour compounds in cheese during ripening could have explained the different development of flavour in both types of strains having or not having CEP.

Bacterial lysis mainly concerns the LAB species used as starters, such as *L. lactis*, *S. thermophilus*, *L. helveticus*, and *L. delbrueckii* and, to a lesser extent, non-starter lactobacilli, such as *Lactobacillus casei*, *Lactobacillus paracasei* and *Lactobacillus plantarum*, and PAB. The molecular mechanisms responsible for different abilities to lyse are diverse and not all elucidated. Lysis results from the activity of peptidoglycan hydrolases (PGH) on the bacterial cell wall. It can also result from the induction of a prophage in *L. lactis* and *L. helveticus* but this is not a general mechanism (Lortal and Chapot-Chartier 2005; Deutsch et al. 2002, 2003). In *L. helveticus*, which exhibits a large range of autolytic abilities (Valence et al. 1998), the nine PGH genes are ubiquitous and transcribed early during growth in all the strains (Jebava et al. 2011). The differences of autolytic properties of strains would result from differences in cell wall composition (Vinogradov et al. 2013) (see Table 1 for further details).

2.1.3 Formation of flavour compounds by propionibacteria

Propionibacterium freudenreichii is used in the manufacture of Swiss-type cheeses, in which it is responsible for the formation of the typical flavour. It grows during the ripening, with lactic acid as the main carbon source, which is converted into propionic acid, acetic acid and CO_2, responsible for hole formation (Fröhlich-Wyder and Bachmann 2004; Langsrud and Reinbold 1973). This ability is present in all propionibacteria strains. However, their growth and fermentation rates in cheese depend on the conditions, in particular, the NaCl content of the cheese (Richoux et al. 1998).

P. freudenreichii produces flavour compounds in cheese from three main pathways: lactate fermentation, amino acid catabolism, and fat hydrolysis (Thierry et al. 2011a). Regarding amino acid catabolism, *P. freudenreichii* mainly produces branched-chain (BC) volatile fatty acids from BC precursors. These BC volatile fatty acids are flavour-active compounds in many cheeses where they bring typical flavour notes of old cheese (Urbach 1997; Yvon and Rijnen 2001). Since the biosynthesis of BC volatile fatty acids is closely related to that of membrane fatty acids, this activity is constitutive and observed in all strains. However, the amounts of BC volatile fatty acids produced are highly strain-dependent. For example, the concentrations of BC volatile fatty acids ranged from 6 to over 50 $mg.mL^{-1}$ in the cultures of 40 strains of *P. freudenreichii* grown in cheese-like conditions (Dherbécourt et al. 2008). They ranged from 19 to 114 $mg.kg^{-1}$ at the end of ripening in eight experimental Swiss cheese manufactured using a single strain culture of *P. freudenreichii* (Thierry et al. 2004a). The formation of many other amino acid-derived aroma compounds varied significantly depending on the PAB strain, in *P. freudenreichii* as well as in the three other dairy PAB species (Yee et al. 2014). The ability to produce aroma compounds was not correlated with the subspecies of *P. freudenreichii* (De Freitas et al. 2015). The mechanism responsible for this strain-dependency is still unknown.

Fat hydrolysis during cheese ripening is another important aspect for flavour formation, because the free fatty acids (FFA) released are important flavour compounds in most cheeses. In Swiss-type cheeses, *P. freudenreichii* is the main agent of lipolysis

(Chamba and Perreard 2002; Dherbécourt et al. 2010). However, the intensity of lipolytic activity of *P. freudenreichii*, again, is highly strain-dependent. In experimental Swiss cheeses manufactured using five different strains of *P. freudenreichii*, the net increases in FFA concentrations ranged from 0.2 to 3–4 $mg.g^{-1}$ cheese, compared to the control cheeses manufactured without propionibacteria (Chamba and Perreard 2002; Dherbécourt et al. 2010; Thierry et al. 2005). In a model medium supplemented with an emulsion of milk fat, 19 strains out of the 21 tested strains released FFA, with a net production of FFA ranging from 0.137 to 1915 $mg.g^{-1}$, whereas two strains did not display any detectable lipolytic activity (Abeijon Mukdsi et al. 2014). Interestingly, the intensities of lipolysis by *P. freudenreichii* were similar in this model medium and in cheese. In both non-lipolytic strains, the lipase gene responsible for lipolysis possesses a non-sense mutation leading to non-functional enzyme (Abeijon Mukdsi et al. 2014).

2.2 Texture and exopolysaccharide production

The production of exopolysaccharide (EPS) within LAB has been widely studied as a way to improve the texture of dairy products, such as low fat cheeses, and to reduce syneresis in fermented milks. The relationships between the amount and molecular characteristics of EPS and their functionality in the dairy products remain difficult to establish. However it clearly appears that the strain has a great impact on the final characteristic of the dairy products, since the production of EPS differs from strain to strain. Hence, some strains do not produce EPS, while other strains within the same species produce different molecules.

In fermented milks, it has been demonstrated that a reduced syneresis can be obtained by a discerning choice of the LAB strains implemented. Five EPS-producing or non-EPS-producing LAB (*S. thermophilus*, *L. delbrueckii* subsp. *bulgaricus* and *L. lactis*) were studied by Purohit et al. (2009). All the EPS-producing strains reduced the syneresis of fermented milks, whereas only some of these strains reduced the syneresis after cutting the products, indicating that the effectiveness of EPS-producing cultures depends on the type of EPS produced.

Fermented milks manufactured using 28 EPS-producing strains of *Lactobacillus* (14 *L. plantarum* strains, 9 *L. kefiranofaciens* strains and 5 *L. paracasei* strains) differed in their rheological properties (Hamet et al. 2015). The analysis of the EPS produced highlighted large variations between strains in terms of concentration and molecular weight of the molecules produced.

The relationship between the EPS structure and its function in situ has been investigated. The rheological properties of fermented milks made with strains of LAB producing EPS with known properties of charge, flexibility and degree of branching were affected. This indicates that the rheological properties of dairy products are affected by the structural characteristic of the molecules, especially the anionic charges (Gentès et al. 2011). These examples highlight that, with a careful selection of the strain, it is possible to improve the rheological and textural characteristics of dairy products.

2.3 Opening and gas formation

Propionibacterium freudenreichii has a key role in the formation of the typical round holes (eyes) in Swiss-type cheeses. The correct formation of holes depends on physico-chemical factors, such as the presence of nucleation sites for hole development, an

appropriate cheese structure, a massive production of carbon dioxide (CO_2) that induces a local saturation of gas leading to the formation of holes. During the ripening in the warm room, *P. freudenreichii* produces CO_2 from lactate fermentation, thus producing the main part of the CO_2 formed in cheese, the remaining part being formed by facultative heterofermentative lactobacilli from citrate fermentation and amino acid catabolism (Thierry et al. 2010).

Some *P. freudenreichii* strains express an aspartase activity, responsible for aspartate deamination. These strains co-ferment lactate and aspartate into propionate, acetate, succinate and CO_2, which result in a higher ratio of CO_2 produced per mole of fermented lactate (Wyder et al. 2001; Fröhlich-Wyder and Bachmann 2004). The screening of aspartase activity of *P. freudenreichii* strains isolated from cheese showed a very large strain-dependency (Table 2). The activity of cell-free extracts of eight wild strains of *P. freudenreichii* was shown to vary by a factor >200. In another study, half of the 100 strains tested exhibited <100 units (quantity of enzyme producing 0.01 nmol of NH_3. min^{-1}.mg^{-1} of protein), while the activity of the other strains ranged from <150 to >1500 units (Blasco et al. 2011). The molecular bases of these strain-to-strain variations have not been investigated. Emmental cheeses manufactured using two multi-strain PAB cultures with high and low aspartase activity, respectively, were compared (Wyder et al. 2001). The PAB cultures with a high aspartate activity generated cheeses with no residual aspartate and aspargine, a higher content in succinate (×3), and a greater number and size of holes. These types of strains induced an accelerated ripening of cheese, but also an increased risk of late fermentation associated with "split defect" in Swiss-type cheeses (Daly et al. 2010; Fröhlich-Wyder and Bachmann 2004).

2.4 Techno-functional properties

2.4.1 Stretchability

Some techno-functional properties of cheese, such as stretching after the culinary preparation of Mozzarella or Swiss-type cheese is related to proteolysis.

In the case of Mozzarella cheeses, LAB starters are *S. thermophilus* and *L. helveticus* or *L. delbrueckii* subsp. *bulgaricus*. Oberg et al. (1991) used two strains of *L. helveticus* highly (Prt^+) or weakly (Prt^-) proteolytic as a single starter strain or in combination with *S. thermophilus* and evaluated the consequences on stretching, melting and browning. Melting properties did not significantly differ depending on the starters used (Oberg et al. 1991). In contrast, stretching properties were higher in cheeses made with *L. helveticus* Prt^- strain, compared to the Prt^+ strain.

In Emmental cheese, Richoux et al. (2009) compared the stretchability of three strains of *L. helveticus* or *L. delbrueckii* subsp. *lactis*. Cheeses were manufactured with a single strain of *L. helveticus* or *L. delbrueckii* subsp. *lactis*, or a combination of one strain of each species. Only the cheeses manufactured with *L. helveticus* were able to make long strands (>350 mm). In cheeses manufactured with *L. delbrueckii* subsp. *lactis* alone or in combination with *L. helveticus,* the ability to stretch was at least decreased by a factor of two. It was not correlated to the total amount of peptides but to a balance between hydrophobic and hydrophilic peptides (Richoux et al. 2009). The relation with the number and/or activities of *L. helveticus* CEP and the ability of strains to lyse and to release their intracellular peptidases was a determinant in the

stretchability, and differences in strand length between strains of more than 100 mm were observed (Sadat-Mekmene et al. 2013). Such a difference was correlated with a peculiar type of peptides, i.e. hydrophobic ones and with a size over 20 amino acid residues (Sadat-Mekmene et al. 2013).

2.4.2 Cheese quality and galactose catabolism

Galactose accumulation in cheese can favour the growth and CO_2 production by undesirable non-starter bacteria capable of galactose utilization (Wu et al. 2015). It can also induce the browning of Mozzarella cheese (Johnson and Olson 1985). LAB such as *L. delbrueckii* subsp. *bulgaricus* and most *S. thermophilus* strains are unable to metabolize galactose (Gal−), whereas *L. helveticus* strains are Gal+. Gal− strains release in the medium or cheese the galactose moiety after cleavage of lactose by a β-galactosidase. However, some *S. thermophilus* strains able to catabolise galactose have been identified. The use of both Gal+ strains of *Streptococcus* spp. in combination with *L. helveticus* strains in the starter culture was probably responsible for the low residual galactose in Mozzarella cheese (Mukhurjee and Hutkins 1994). Gal+ strains of *S. thermophilus* were also utilized to reduce the quantity of residual galactose in yogurt (Umamaheswari et al. 2014). A yogurt prepared using a Gal+ *S. thermophilus* strain (NCDC 659) associated with *L. delbrueckii* subsp. *bulgaricus* contained 0.37% galactose compared to 0.98% in a reference yogurt inoculated with a Gal− *S. thermophilus* strain (Anbukkarasi et al. 2014). Galactose catabolism by LAB mainly relies on chromosome located-genes encoding the tagatose-6P and/or Leloir pathways (Wu et al. 2015), but the genetic basis for strain-dependency of this trait is still unclear.

3 Functional properties

In this section, we will consider the strain-dependency of functional properties of LAB and PAB, considering the inhibition of deleterious microorganisms, with the example of bacteriocin production by PAB, the inhibition of pathogenic bacteria, through the production of inhibitory compounds, the inhibition of virulence expression through the perturbation of quorum sensing systems and the probiotic effect regarding the immunomodulation related to surface proteins of PAB and antihypertensive peptides.

3.1 Inhibition of spoilage and pathogenic microorganism growth

Beyond their direct implication in the fermentation process of fermented dairy products, LAB and PAB are also used for their protective potential against spoilage and pathogenic microorganisms. Although this inhibitory potential is one important criterion for the selection of LAB and PAB starters, only a few studies addressed the intraspecific variations in the inhibitory potential. In a study on the antibacterial activity of *L. plantarum*, 347 food-derived isolates were tested against five foodborne pathogens. About 3–6% of isolates exerted a high antibacterial activity against at least one indicator bacterium (Li et al. 2015). The effect was observed for seven out of the nine selected *L. plantarum* strains tested in fermented milk co-inoculated with a commercial yogurt starter (Li et al. 2015). In this section, we will consider the strain-dependency of

such properties, considering the inhibition of deleterious microorganisms, with the example of fungi in milk products, the inhibition of pathogenic bacteria, through the production of inhibitory compounds, and the inhibition of virulence expression through the perturbation of quorum sensing systems. Each of these potentials can be associated with the ability of the strains to produce a given compound, such as bacteriocins, organic acids, hydrogen peroxide, or must be considered as the combinatorial effect of several factors.

3.1.1 Bacteriocin production

Bacteriocins are ribosomally encoded peptides or proteins produced by bacteria to limit or totally inhibit the growth of competitor bacteria that are most often phylogenetically closely related. LABs have been screened for bacteriocin production for decades and several bacteriocins were discovered in LAB originating from various ecosystems and foodstuffs. Production and potential utilization of LAB-produced bacteriocins were recently reviewed in detail (see Bali et al. 2014; Perez et al. 2014).

PAB strains also produce bacteriocins (reviewed by Jan et al. 2007; Thierry et al. 2011b), including three antimicrobial peptides that display some quite unique traits compared with bacteriocins from LAB, propionicin T1, protease-activated antimicrobial peptide (PAMP) and propionicin F (Faye et al. 2011). The propionicin T1 peptide is produced by some strains of *Propionibacterium thoenii* and *Propionibacterium jensenii*, and is bactericidal towards all tested species of propionibacteria except *P. freudenreichii*. The encoding gene (*pctA*) is widely distributed within *P. jensenii* and *P. thoenii* (Faye et al. 2004). However, only 5 of 13 *pctA*-positive *P jensenii* strains produced antimicrobial activity corresponding to propionicin T1. The PAMP antimicrobial peptide is secreted in large amounts as an inactive precursor pro-PAMP protein, which is converted into PAMP upon proteolytic processing. The Pro-PAMP protein is produced by most strains of *P. jensenii* and *P. thoenii* but their sensitivity to PAMP varies quite extensively (Faye et al. 2004). Propionicin F is a hydrophobic and negatively charged bacteriocin produced by *P. freudenreichii*. It displays an intraspecies bactericidal inhibition spectrum, killing only strains of *P. freudenreichii* (Brede et al. 2004).

3.1.2 Organic acid production

Organic acids have deleterious effects on many neutrophilic bacteria and can significantly reduce their growth and threaten their viability (Lund et al. 2014). The production of organic acids, and the resulting acidification, is a major parameter in the inhibitory potential of starter LAB. For instance, *Staphylococcus aureus* growth is completely stopped in milk acidified at pH 4.4–4.5 by lactic acid (Charlier et al. 2008). Only a few studies investigated the strain-dependency of this potential. In a panel of 75 *L. lactis* strains, 93% (n=70) presented a strong inhibition against the growth of the Gram positive pathogen *S. aureus* in milk, whereas 7% (n=5) were poor inhibitors, demonstrating that the inhibitory potential among *L. lactis* strains was not homogenous (Charlier et al. 2008). These results contrast with previous studies, which concluded that such a potential was homogenous (Haines and Harmon 1973a, b). Of note, these studies were based on a smaller panel of strains (n=5) and tested the inhibitory potential in laboratory conditions.

PAB also produced organic acids. In addition to their main fermentation end-products, propionic, acetic and succinic acids, they also produce other organic acids with antifungal activities, 2-pyrrolidone-5-carboxylic, 3-phenyllactic, and hydroxyphenyllactic acids (Thierry et al. 2011a).

3.1.3 Other compounds and combination of several compounds

Hydrogen peroxide (H_2O_2) is often cited as one of the inhibitory molecules produced by LAB. The ability of LAB to produce H_2O_2 appears to be strain-dependent. Ito et al. (2003) evaluated the ability of 193 LAB strains isolated from various food products to produce H_2O_2 and found strong variations between strains. The scarce studies on H_2O_2 production by LAB in a food context report the ability of LAB isolated from food products, including dairy products, to produce H_2O_2. However, H_2O_2 production assays are generally performed in laboratory conditions (Ito et al. 2003; Enitan et al. 2011) rather than in situ in dairy products, probably because of the difficulty to quantify this unstable metabolite.

H_2O_2 production by a *Lactococcus garvieae* strain was recently demonstrated in a cheese matrix and this was in part responsible for *S. aureus* growth inhibition (Delbes-Paus et al. 2010).

Diacetyl is a volatile compound produced by some LAB. It was shown to have an inhibitory activity against foodborne pathogens (Jay 1982; Kang and Fung 1999). Combinations of diacetyl with other antimicrobials such as nisin, an *L. lactis* bacteriocin, have shown a synergistic antimicrobial effect against foodborne pathogens (O'Bryan et al. 2009; Lee and Jin 2008). Only citrate-utilizing LAB can produce diacetyl and, in *L. lactis*, the citrate permease gene is plasmid-encoded. Likewise, a nisin operon is transposon-borne and thus, is not present in all *L. lactis* strains. Both diacetyl and nisin production are thus highly strain-dependent in this species. Such a synergistic effect of diacetyl and reuterin, a bacteriocin produced by some *Lactobacillus reuteri* strains, was recently demonstrated against several foodborne pathogens (*E. coli* O157:H7, *Listeria monocytogenes*, and *Salmonella enterica* subsp. *enterica* serovar Enteritidis (Langa et al. 2014)).

3.1.4 Phenomena related to competition for nutrients

While the inhibitory properties of LAB are frequently related to the production of inhibitory molecules, the involvement of nutrient-related phenomena should also be considered. Screening of 75 *L. lactis* strains revealed that strains exhibiting strong inhibitory properties, with regard to *S. aureus* growth in milk, included strains with both high and low acidifying properties, and a residual inhibition occurred when pH was regulated at neutral pH (Charlier et al. 2008). This remaining inhibition strongly depended on the medium used. Whether these nutrient-related phenomena were a direct nutritional competition or limitation, or an indirect inhibitory effect remains unknown.

3.1.5 Antifungal properties

The ability of LAB and PAB to exert antifungal activities is now well established. These properties are most of the time multifactorial and result from the production of

different metabolites by bacteria, such as organic acids, H_2O_2, CO_2, ethanol, and proteinaceous compounds (peptides, cyclic dipeptides) (Crowley et al. 2013; Dalié et al. 2010). The production of most of these compounds is strain-dependent as illustrated later in this section. *L. plantarum* is the LAB species that is the most documented for antifungal properties, as well as, to a lesser extent, other lactobacilli, e.g. *L. brevis*, *L. casei*, *L. pentosus*, *L. reuteri*, and species of the genus *Pediococcus* (Schnürer and Magnusson 2005). There is abundant literature on in vitro screening studies in order to find specific LAB strains with antifungal properties and even if the number of strains tested within a species is generally low, strain-dependency has been reported. Up to 75% of variation was observed, for example, between the five strains of *L. casei* tested for their potential to inhibit the growth of four spoilage moulds (Cortés-Zavaleta et al. 2014). Both the level of the antifungal activity and the spectrum of the fungal targets inhibited varied from strain to strain in LAB and PAB species tested in dairy models (Valence and Mounier, unpublished results).

3.2 Inhibition of virulence expression of pathogens by LAB strains

From a regulatory point of view among foodborne pathogens, toxin-producers like *S. aureus* can be tolerated in some foodstuffs (e.g. in raw milk cheeses) as long as it does not exceed a population level favouring the production of toxins (Cretenet et al. 2011a). The latter may indeed remain active in the end product even though the producer strain has disappeared. Besides inhibiting the pathogen growth, controlling the toxin production can thus be of special interest. The example of *S. aureus* enterotoxin production is of particular interest in a food context. It was shown that, when co-cultured with *S. aureus*, *L. lactis* strains are able to inhibit virulence expression in various *S. aureus* strains. The phenomenon is observed in laboratory conditions and in a model cheese where both species can grow at high levels (Even et al. 2009; Cretenet et al. 2011b). It is now known that *L. lactis* presence dramatically inhibits the accessory gene regulator (*agr*) system in *S. aureus*. This system tightly controls virulence expression in *S. aureus* and, notably, the expression of *agr*-dependent staphylococcal enterotoxins (SEs), such as SEC. This feature is of great interest to control SE, although some SEs like SEA, whose expression is *agr*-independent, do not respond to this inhibitory activity. The mechanism involved in the inhibition is multifactorial and involves both the acidification and reducing properties of *L. lactis* (Nouaille et al. 2014). Although the strain-dependency of this inhibitory activity has not been investigated in depth, one might consider that it is not highly strain-dependent. Indeed, when considered individually, the properties involved in the inhibition (reducing capacities and acidification) reportedly vary with the strains (Charlier et al. 2008; Charlier et al. 2009; Michelon et al. 2013), but they clearly overlap here in the virulence inhibition exerted by *L. lactis*. In this system, a low reducing capacity might likely be compensated by the acidification of the medium and thus might not result in a complete alleviation of the inhibition.

3.3 Immunomodulation by dairy bacteria

Some dairy-related bacterial species are “2-in-1” bacteria that can be involved in both the elaboration of fermented dairy products such as cheeses and in beneficial health (so-called probiotic) effects on the host. As an example, the most used PAB species, *P. freudenreichii*, was shown to display anti-inflammatory properties, in a very strain-

dependent manner (Foligné et al. 2010). Out of a selection of 23 strains of *P. freudenreichii*, a continuum from strains having no immunomodulatory effect to strains with a very marked anti-inflammatory one was observed ex vivo on fresh human peripheral blood mononuclear cells (PBMCs) using Il-10 induction as a marker (Foligné et al. 2013). Accordingly, the strain inducing the highest level of IL-10 ex vivo protected mice from induced colitis in vivo, either consumed as a pure culture (Le Marechal et al. 2015) or as an experimental semi-hard cheese (Plé et al. 2015). In contrast, strains which failed to induce IL-10 ex vivo also failed to protect from colitis in vivo (Jan, unpublished results, ANR project ANR-2010-ALIA-016 "SURFING"). The surface compounds involved in this immunomodulation are strain-specific surface proteins of the S-layer-type (Le Marechal et al. 2015). By contrast, some *P. freudenreichii* strains produce a surface beta-glucan exopolysaccharide after growth in a dairy-based medium and display no immunomodulatory properties, while the mutational inactivation of this exopolysaccharide capsule leads to anti-inflammatory properties of the mutant strains (Deutsch et al. 2010, 2012). Accordingly, pure cultures of *P. freudenreichii* ET-3 in whey exerted protective effects in experimental colitis in mice (Okada et al. 2006; Uchida and Mogami 2005). A pilot clinical study on ulcerative colitis also suggests a beneficial effect of this strain in humans (Suzuki et al. 2006). The development of an experimental cheese, fermented by a selected anti-inflammatory strain of *P. freudenreichii* exclusively, and protective against colitis, recently evidenced that the choice of the starter strain(s) determines the probiotic effect of the cheese (Plé et al. 2015).

Similar strain-dependent immunomodulation was also reported for lactic acid dairy starters including *Lactobacillus debrueckii* (Santos-Rocha et al. 2012), *S. thermophilus* (Del Carmen et al. 2015), and *L. helveticus* (Hosoya et al. 2014; Yamashita et al. 2014). A yogurt containing anti-inflammatory *L. debrueckii* and *S. thermophilus* accordingly exerted preventive effect in ulcerative colitis patients (Magee et al. 2005). Furthermore, cheese made with *L. helveticus* LH2171 alleviated symptoms of experimental colitis (Hosoya et al. 2012), while another strain MIMLh5 displayed pro-inflammatory properties (Taverniti et al. 2013).

3.4 Production of antihypertensive peptides by lactic acid bacteria

Peptides have numerous bioactivities and among them, antihypertensive activity has been more particularly studied in milk and cheeses according to strain-dependency. Thus, Fuglsang et al. (2003) showed that among the 10 strains of *L. helveticus* and 11 strains of *L. lactis* that have antihypertensive activity after milk fermentation, two strains of *L. helveticus* were able to decrease blood pressure in rats after feeding with fermented milk, in contrast to *L. lactis* strains. Another predominant action of *L. helveticus* and *L. delbrueckii* was also shown in Swiss-type cheeses, in which the levels and dynamics of the ACE inhibitory activity varied according to the combination of lactobacilli strains used, up to sixfold at the end of the ripening time (Gagnaire et al. 2012). Among the 18 combinations of starters strains used, only one containing one strain of *L. helveticus* and one of *L. delbrueckii*, both with a moderate proteolytic activity, led to a high ACE inhibitory activity. The latter was not predictable from the intensity of proteolysis observed, showing that the quality of the proteolysis prevails on the quantity of the peptide produced (Gagnaire et al. 2012).

As a conclusion, the choice of dairy starters, taking into account their bioactive profile, may orientate a fermented food product towards probiotic effects, depending on the targeted specific population.

4 Conclusions and perspectives

This review illustrates how the choice of a bacterial strain within a given species can induce a great extent of differences for important properties of fermented dairy products. On one hand, and for some peculiar characteristics, the technological, probiotic, or inhibitory potential towards undesirable microorganisms of LAB or PAB is clearly strain-dependent, especially when it is based on the presence of a gene (or an operon) as it is for bacteriocin or diacetyl production. On the other hand, when the potential of interest relies on metabolic activities and overlapping properties (e.g. antifungal activity, inhibition of virulence expression in *S. aureus* by *L. lactis*), the strain-dependency may be lower, even though each of the features involved can be strain-dependent. However, only a few studies have tested large numbers of strains of the same species, preventing any definitive conclusion.

Some properties that were initially considered as constant features for a given species based on screening of a few strains can later appear to be highly variable and strain-dependent when a higher number of strains are investigated. Therefore, general conclusions on the compared properties of different species should not be drawn until a sufficient number of strains of each species are tested. The great impact of the intraspecific diversity on the final quality of fermented dairy products also stress the importance of an adequate preservation of microbial resources, which should be made accessible to the scientific community to facilitate their screening and valorisation. The Organization for Economic Cooperation and Development (OECD) has established the concept of Biological Resource Centre (BRC) and edited specific guidelines (OECD 2007). Microbial BRC, in particular, have been described as a factor in economic development (Smith et al. 2014). Microorganisms have both a patrimonial value and a potential for innovation. The larger the number of strains for a specific species, the greater the possibility of discovering strains with a specific potential for innovation. Interestingly, 79% of new microbial species described in 2009 are based on one unique strain, the type strain (Stackebrandt 2011). This underlines the role of food-related microbial BRCs, who continuously enlarge collections of microbial resources and are a major actor for innovation in the dairy industry. The concomitant development of high-through sequencing and screening facilities will help in linking phenotypic properties of interest with genomic and molecular features. Once established, these links will greatly enhance our understanding of strain-dependency as well as our screening procedures for the rational selection of LAB or PAB strains with a property of interest for the dairy industry.

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