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Recent progress in microbial cell surface display systems and their application on biosensors

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Abstract: Microbial cell surface display technology is a recombinant technology to express target proteins on the cell membrane, which can be used to redesign the cell surface with functional proteins and peptides. Bacterial and yeast surface display systems are the most common cell surface display systems of prokaryotic and eukaryotic proteins, that are widely applied as the core elements in the field of biosensors due to their advantages, including enhanced stability, high yield, good safety, expression of larger and more complex proteins. To further promote the performance of biosensors, the biomineralized microbial surface display technology was proposed. This review summarized the different microbial surface display systems and the biomineralized surface display systems, where the mechanisms of surface display and biomineralization were introduced. Then we described the recent progress of their applications on biosensors for different types of detection targets. Finally, the outlooks and tendencies were discussed and forecasted with the expectation to provide some general functions and enlightenments to this aspect of research.

Introduction

Microbial cell surface display technology is a molecular display technique that employs the gene recombination method to fuse the gene sequences of target proteins and carrier proteins into the microbial host cell (Ding *et al.*, 2019) so that the target proteins can be expressed and localized on the surface of microbial cells, and remain their independent spatial structure and biological activity (Pham and Polakovic, 2020). In the last decade, this ground-breaking technology has been broadly developed (Shibasaki and Ueda, 2014), and research in the field has shown a steady upward trend (Fig. 1a). So far, many proteins have been successfully expressed on cell surfaces of fungi, bacteria, mammals, and plants (Han *et al.*, 2018b; Wang *et al.*, 2021). Therefore, microbial cell display technology has become a helpful tool for displaying proteins on cell surfaces (Ding *et al.*, 2019).

Microbial cell surface display technology can realize the functionalization of foreign proteins through a section of carrier protein with secretory transport function and membrane localization (Yang *et al.*, 2019). So, the target foreign protein can be transported and anchored on the cell surface. Hence, the cell surface display system consists of three components: host (microbial cell), carrier (anchoring protein), and passenger (target foreign protein) (Han *et al.*, 2018b). (1) The host cell act as a substrate for fusion proteins and anchoring proteins. (2) The carrier proteins, also called anchoring proteins, are capable of secreting, transporting, and anchoring foreign proteins to the extracellular surface. (3) The passenger protein, also called the target foreign protein, has a specific function. Consequently, it is obligatory to closely coordinate the three mentioned above-mentioned components for the establishment of a proper surface display system. The fusion modes of the target protein sequence and carrier protein sequence mainly include C-terminal fusion and N-terminal fusion (Han *et al.*, 2018b). As the main microbial cell surface display systems, bacterial and yeast surface display systems have been widely used for the display of prokaryotic and eukaryotic proteins, respectively, which have the characteristics of vector diversity, high yield of recombinant proteins, and flexible genetic engineering (Huang *et al.*, 2018).

Up to now, microbial cell surface display technology has been successfully used in many fields, including the construction and high-throughput screening of peptide library, whole-cell adsorbents for heavy metal pollution, development of the live vaccine, recombinant whole-cell catalysis, biofuel cells, biosensors, etc. (Chen *et al.*, 2017;

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Ueda, 2016). Among them, there have been many advances in cell surface display systems-based biosensors (Fig. 1b). In particular, bacteria and yeast surface display systems have been widely applied in a variety of biosensors (Jahns and Rehm, 2012; Pham and Polakovic, 2020), involving various fields including medical diagnosis, environmental monitoring, food assay, biochemical analysis and so on (Chmielewski *et al.*, 2019; van Bloois *et al.*, 2011). So far, a large number of articles have been published on these aspects. This review mainly introduces bacterial and yeast surface display systems, and their biomineralized systems, the detection methods based on these systems.

Microbial Surface Display System

Bacterial surface display system

The bacterial surface display system takes advantage of the surface display technology to express target proteins on the surface of bacteria for precise functionalization (Chen *et al.*, 2019). This system has been generally used in recombinant bacterial vaccines, biofuel cells, whole-cell catalysts, and bioremediation (Xiang *et al.*, 2019). According to the source of carrier proteins, bacterial surface display systems can be categorized as Gram-negative bacterial surface display systems and Gram-positive bacterial surface display systems (Liu *et al.*, 2020). At present, the carrier proteins are commonly used in the surface display system of Gram-negative bacteria, such as outer membrane proteins (OMPs), lipoproteins, Lpp-OmpT (LOT), surface accessory structure subunits, ice nuclear proteins (INP), and autologous transporters and so on (Hui *et al.*, 2019; Song *et al.*, 2015; Wang *et al.*, 2021; Zhang *et al.*, 2018b). On the other hand, the development of surface display systems for Gram-positive bacteria is not as mature as that for Gram-negative bacteria (Kim *et al.*, 2021).

As for the biosensors, the bacterial surface display system can display the required enzymes on the surface of bacterial cells, making them react on the surface, thus enhancing the sensitivity, stability, and selectivity of biosensors (Han, 2020). For example, the surface display system based on *Escherichia coli* was applied to construct the acetaldehyde optical biosensor (Liang *et al.*, 2021). The technique mainly fixed the expressed fusion protein (acetaldehyde dehydrogenase, AldDH) onto the outer membrane of *E. coli* by LOT carrier. AldDH displayed on the surface can catalyze the production of NADH, which can be detected by the spectrometric method. Many relevant works demonstrate that the bacterial surface display system has many advantages (Fig. 2), including (1) bacterial surface is better suited for displaying large-sized proteins, (2) this system is highly productive. (3) This system can proliferate by binary fission because bacterial systems are prokaryotic cells (Park, 2020; van Bloois *et al.*, 2011).

Yeast surface display system

The yeast surface display system is an important eukaryotic protein surface display system (Teymennet-Ramirez *et al.*, 2021). The basic principle involves induction and expression of the exogenous target protein gene sequence fused with a carrier gene sequence in yeast cells (Chun *et al.*, 2020), then the fusion protein, guided by signal peptide, is secreted out of the cell. The fused protein can be anchored in the yeast cell wall, thereby immobilizing the foreign protein on the surface of the yeast cell (Fan *et al.*, 2020). The commonly used carriers in yeast cell surface display systems mainly include a-agglutinin, α-agglutinin, Flo1p, etc. (Han *et al.*, 2018b). In recent years, the yeast surface display system has attracted great attention for displaying eukaryotic proteins on the surface of cells (Gal *et al.*, 2016). The yeast surface display system has many advantages, such as superior safety, post-translational modifications, proper folding and glycosylation of proteins, disulfide isomerization of eukaryotic proteins, simplicity of the cell culture and genetic manipulation, and immobilization of protein (Hamilton and Gerngross, 2007; Han *et al.*, 2018b; Park, 2020; Teymennet-Ramirez *et al.*, 2021) (Fig. 2). As the most extensively used yeast on surface display systems, *Saccharomyces cerevisiae*, a unicellular eukaryote with a cell wall, has been widely applied for construction of the biosensor (Chun *et al.*, 2020; Gal *et al.*, 2016; Liang and Han, 2020a; Zhao *et al.*, 2020).

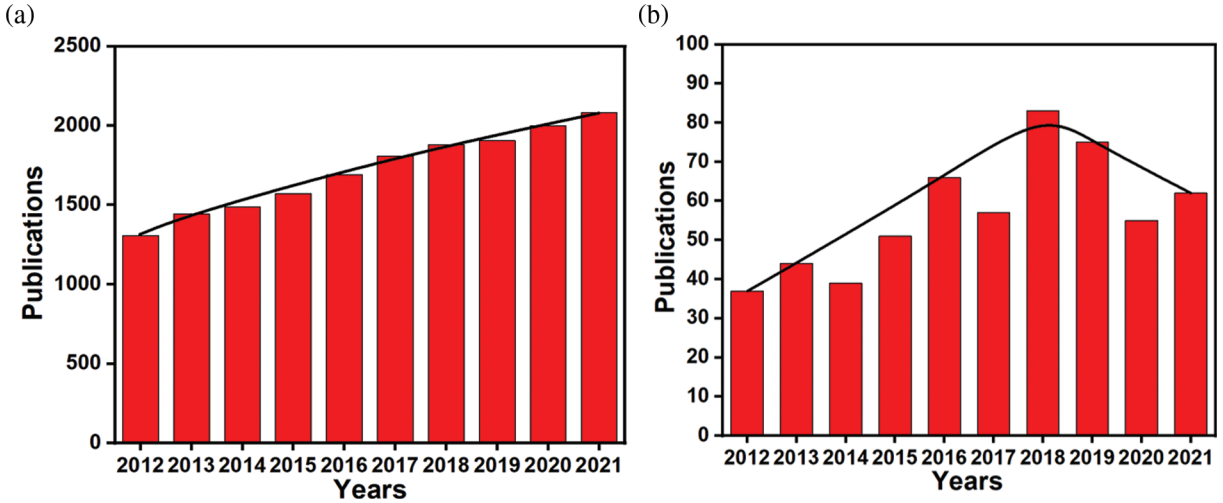

FIGURE 1. (a) Number of published papers on microbial cell surface display systems by the end of December 2021. Data are from the Web of Science. (b) Number of published papers on biosensors of microbial cell surface display systems by the end of December 2021. Data are from the Web of Science.

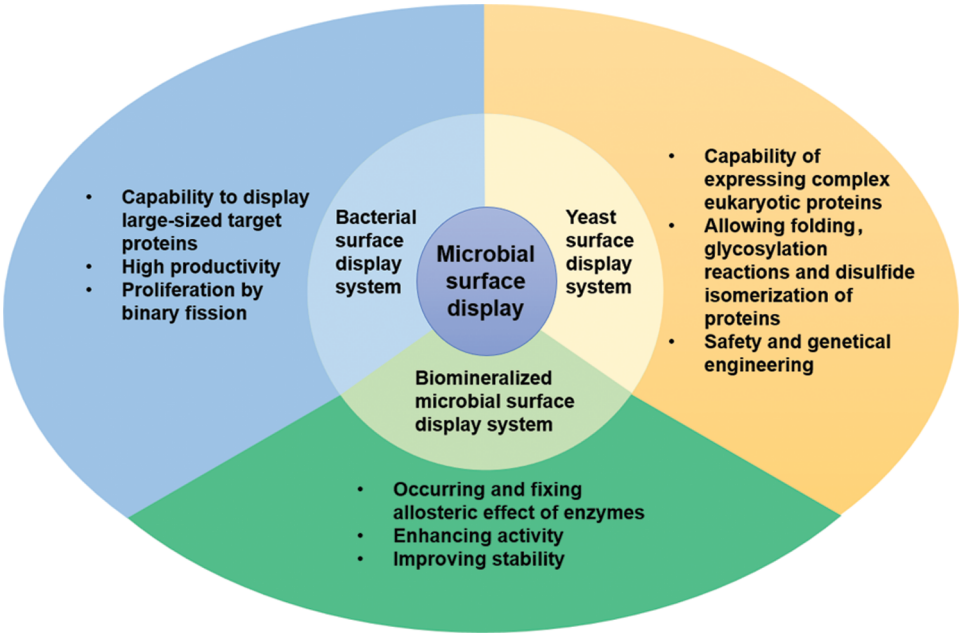

FIGURE 2. Three kinds of microbial cell surface display systems and their advantages.

Biomineralized microbial surface display system

Biomineralization refers to the formation process of inorganic minerals on organisms (Sang *et al.*, 2020). The biggest difference between biomineralization and general mineralization lies in the involvement of biomacromolecules, cells, and other organic substrates (Wei *et al.*, 2019). The characteristic of biological mineralization is the transformation of ions in solution into solid minerals under the control or influence of biological materials at certain physicochemical conditions (Mangano *et al.*, 2019). So, biomineralization is a complex and dynamic process regulated by organic matter, crystal growth mechanism, and external environment. With the increasing attention to biological mineralization, various biological substances (such as the phage, violet membrane, bovine serum albumin, and lysozyme) are used as templates (Liang and Han, 2020b; Zhao *et al.*, 2022) for the synthesis of bio-inorganic hybrid materials (Han and Liu, 2017). Inspired by the bio-templated mineralization described above, researchers have begun to introduce biomineralization into phage surface display systems (Han *et al.*, 2016, 2017). Whereafter, biomineralization was introduced into microbial cell surface display systems, which generated the biomineralized microbial surface display technology.

Biomineralized microbial cell surface display technology is a combination of biomineralization and microbial surface display technology, where the target proteins on the cell surface provide nucleation sites of inorganic crystals to form a bio-inorganic hybrid system. So far, there have been several types of research on the biomineralized microbial surface display system (Bian *et al.*, 2022; Han *et al.*, 2018a; Han and Liu, 2017). The biomineralization can increase the catalytic activity of enzymes on the surface of cells due to allosteric effects (Fig. 2), a phenomenon in which an allosteric effector binds to a site (allosteric site) on an enzyme molecule, causing conformational change, thereby indirectly managing the property of another particular site (active site) on the same enzyme molecule. The above positive performances are reflected in some studies. For example, after $Co_3(PO_4)_2{\cdot}8H_2O$ biomineralization on the cell surface, the displayed enzymes were transformed from the inactive state to the active state by allosteric effects, and the active state was "fixed" (Han and Liu, 2017) (Fig. 3a). The activity of the biomineralized system is increased by about three times, compared with the initial cells (Fig. 3b). In addition, the mineralized cells were also more stable than the original cells (Han and Liu, 2017). In contrast to the biomineralized microbial surface display system, conventional immobilization generally decreases the catalytic activity of enzymes (Sharifi *et al.*, 2018). Therefore, biomineralized microbial surface display systems would become ideal substitutes for conventional immobilized enzymes and whole-cell catalysts.

Application of Microbial Cell Surface Display Systems on Biosensors

The biosensor is an assay device that detects various analytes (such as biomacromolecules and small organic molecules) by the biological recognition elements (such as proteins, DNA, and cells) (Park, 2019; Pyun *et al.*, 2005). A biosensor generally consists of three main parts (Fig. 4): receiver, transducer, and other auxiliary equipment (Chen *et al.*, 2023). Among them, the core of the receiver is a molecular recognition element, specifically surface-displayed enzymes. The transducer can capture electrical or optical signals from the enzymatic product by an electrode or optical probe (Hou *et al.*, 2015).

Microbial cell surface display technology is a powerful tool to express and produce proteins on the cell surface and has been widely applied to biosensors. As shown in Table 1, biosensors employing surface-displayed enzymes are superior to those employing traditional microbial whole-cells. For traditional whole-cells, the substrate needs to enter

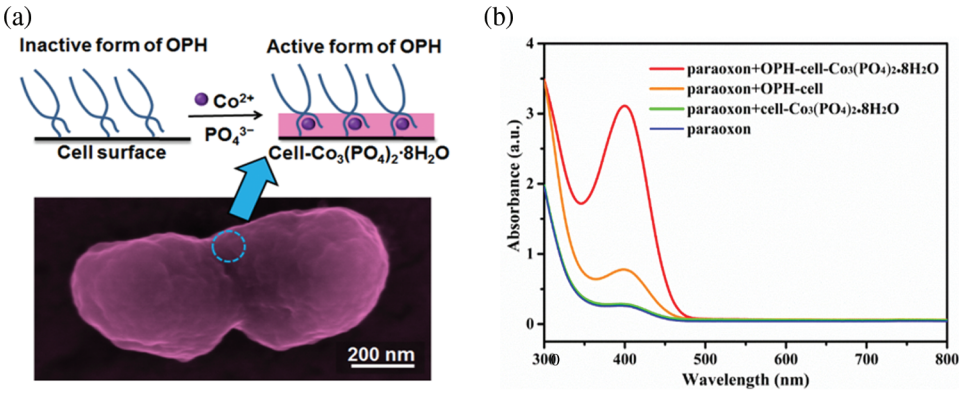

FIGURE 3. An example of biomineralized microbial surface display systems. (a) Biomineralized organophosphorus hydrolase (OPH)-fused cells exhibit enhanced catalytic activity due to the allosteric effects from "inactive" form to "active" form, where OPH is embedded in inorganic crystal ($Co_3(PO_4)_2{\cdot}8H_2O$) (Han and Liu, 2017). (b) The obtained bio-inorganic hybrid whole-cell catalyst shows three times higher activity than the original whole-cell catalyst. Reprinted (adapted) with permission from (Han and Liu, 2017). Copyright (2023) American Chemical Society.

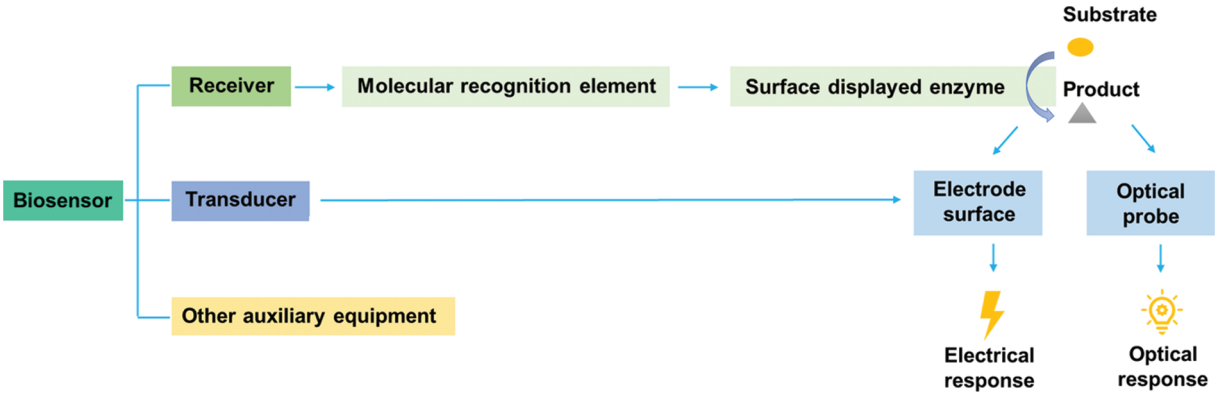

FIGURE 4. Constituents of biosensors based on microbial surface displayed enzymes.

TABLE 1

A simple comparison between biosensors employing surface-displayed enzymes and biosensors employing traditional microbial whole-cells

	Surface-displayed enzymes biosensors	Traditional microbial whole-cell biosensors
Reaction position	Extracellular	Intracellular
Substrate sensing path	Extracellular-sensing	Intracellular-cell-membrane-extracellular-sensing
Catalytic efficiency	High	Low
Reaction substrate	Anything theoretically	Substrates crossing cell membranes and walls

the cell in order to achieve enzyme-based catalytic reactions. By contrast, the enzymes displayed on the cell surface can directly come in contact with the reaction substrate, which greatly improves the catalytic efficiency (Han and Liu, 2017). For the biosensors employing surface-displayed enzymes, the reaction substrate (target) can be anything theoretically. For the traditional microbial whole-cells, the substrate must be able to cross the cell membrane and wall (Ye *et al.*, 2021). Accordingly, by applying microbial cell surface display technology, biosensors can detect various target substances. So far, reported biosensors employing surface-displayed enzymes mainly involve four categories of target substances: organophosphorus pesticides, phenolic compounds, glucose, and L-glutamate. According to the targets, different types of enzymes are used in surface display systems, such as the laccase (Li *et al.*, 2021; Park *et al.*, 2019; Wu *et al.*, 2020; Zhang *et al.*, 2018a), organophosphorus hydrolase (Liang *et al.*, 2019), xylanase (Chen *et al.*, 2012), exoglycanase (Chen *et al.*, 2012), and carbonic anhydrase (Fan *et al.*, 2011).

Detection of organophosphorus pesticides

Organophosphorus pesticides (OPP) are phosphorus-based organic compound pesticides that have been widely used in agricultural production (Hassani *et al.*, 2017). In addition, as a strong neurotoxic cholinesterase inhibitor (Tang *et al.*,

2014a), OPP can inhibit hydrolysis of acetylcholine (central nervous system neurotransmitter), causing health problems for animals and humans (Xu *et al.*, 2018). Therefore, it is necessary and urgent to search and employ the detection methods of OPP residue. To overcome the above-mentioned problem, many surface display systems and biomineralized systems are actively studied and applied in biosensors for the detection of OPP (Bian *et al.*, 2022; Han *et al.*, 2018a; Liu *et al.*, 2013; Tang *et al.*, 2014a). In this section, we discuss and provide some recent examples of the OPP biosensor based on display systems.

Direct detection method based on organophosphorus hydrolase

Given that organophosphorus hydrolase (OPH) can hydrolyze a wide range of organophosphorus ester bonds (such as P—S, P—O, and P—F bonds) (Pundir *et al.*, 2019; Tang *et al.*, 2014a), it has been developed as a key element in OPP degradation and biosensing. For example, Tang *et al.* (2014a) successfully constructed a mutated OPH displayed on the surface of an *E. coli* strain, using INP as the anchoring motif. Fortunately, the recombinant strain was more robust and stable than the purified OPH, promising for detecting OPP sensitively. Further, they immobilized the fused-OPH on the surface of the ordered mesopore carbons-modified glass carbon electrode to develop a novel microbial biosensor for detecting p-nitrophenyl OPP (Tang *et al.*, 2014b). In addition, the relationship between time and current was observed at different OPP concentrations, then the experimental conditions were optimized. Therefore, a fast and accurate biosensor for detecting OPP was established by applying the microbial cell surface display.

Our team synthesized a suitable composite material, combined with biomineralization and microbial cell surface display, and then constructed an ultra-sensitive electrochemical biosensor to detect OPP residues (Han *et al.*, 2018a). The carbon nanotube@amino acid ionic liquid (CNT@AAIL) composites were introduced into the electrochemical biosensor based on mineralized OPH-fused cells. Considering three reasons for this design: (1) OPH could specifically hydrolyze organophosphorus compounds, (2) to make up for the poor solubility of CNT during electrode modification, AAIL with good fluidity, stability, biocompatibility, and biodegradation was combined for the first time, (3) electrochemical biosensor had the advantage of high sensitivity, fast response speed, and positive real-time detection. Particularly, we used AAIL as a stabilizer and modifier to greatly improve the dispersion and biocompatibility of CNT in the aqueous phase. The obtained CNT@AAIL composite improved the electrical conductivity and electrochemical activity of mineralized OPH-fused cell (M-Cell). Surprisingly, the as-fabricated biosensor was more accurate and had 2–8 orders of magnitude lower detection limit than the OPP analytic method reported. Thus, the anti-interference ability of the OPP biosensor has also been proven to a certain extent.

In previous work, the mineralized OPH-fused cells were prepared by embedding OPH into cobalt phosphate. The synthetic bioinorganic hybrid material was applied to the sensitive paraoxon biosensor. In the sensor, allosteric effects, biomineralization techniques, and cell surface display techniques were combined to enhance OPH activity (Han and Liu, 2017). Therefore, the biomineralized microbial surface display system was promising in the future, especially for the establishment of ultra-sensitive and highly selective biosensors (Han *et al.*, 2018b). After continuous in-depth research, we constructed a portable detecting OPP device (Bian *et al.*, 2022). We took full advantage of structures, enzymes, and mineralized layers of displayed cells as well. To detect pesticides quickly and conveniently, we successfully prepared phosphate-mineralized organophosphorus hydrolase-fused cells (M-OPH) through the combination of biomineralization and microbial surface display techniques. In brief, the portable detection device was constructed by simply precipitating M-OPH on a syringe filter. Small colored impurities of real samples could be filtered out by M-OPH layer-modified filter membrane. In this device, the catalytic activity of OPH was enhanced by the allosteric effect caused by biomineralization; the stability of OPH was also enhanced by the protective effect of inorganic phosphate. With the tandem catalysis of the copper phosphate and OPH, hydrolysates of OPP were further reduced or oxidized to low-toxicity products.

Enzyme inhibition method based on acetylcholinesterase

Acetylcholinesterase (AChE) has been successfully used in OPP detection because organophosphorus is an effective inhibitor of AChE (Qi *et al.*, 2020). For example, Liang's team developed a fluorescence OPP detection method by combining AChE mutants displayed on the yeast surface and protein-directed electronegative fluorescent gold nanoclusters (Au NCs), which improved the sensitivity of AChE to OPP (Liang and Han, 2020a). Concretely, AChE mutants and wild-type from *Drosophila* were wonderfully displayed on the surface of *S. cerevisiae* cells, employing a-agglutinin-mediated cell surface display technology. In addition, the displayed AChE could catalyze the hydrolysis of acetylthiocholine, to produce thiocholine, which could not only bind to Au NCs through Au-S bonds but also absorb Au NCs, resulting in Au NCs aggregation and fluorescence quenching. More importantly, fluorescence detection based on the yeast surface displayed AChE and Au NCs was highly sensitive to minute amounts of OPP, and the detection limit was 2–6 orders of magnitude lower than previously reported methods. Therefore, combined with the enzyme-modified microbial cell surface display system and functional biological nanomaterials, the method had good reliability for the measurement of real samples.

Detection of phenolic compounds based on surface-displayed laccases

Phenolic compounds have a broad range of applications, including production areas, such as energy, food additives, and fine chemicals (Alcazar-Ruiz *et al.*, 2023). Therefore, some phenolic compounds are familiar to us, such as phenol, cresol, thymol, eugenol, aminophenol, nitrophenol, naphthol, carvacrol, chlorophenol, etc. (da Silveira *et al.*, 2015). However, phenolics have different toxicities. Due to their existence in air, water, and food matrices, they pose a significant risk of toxicity to the environment and humans

(Govindhan *et al*., 2015). Therefore, the detection of phenolic compounds is crucial to open up a path for ecological and environmental protection.

Laccases are blue multicopper oxidases, which can oxidize multitudinous aromatic compounds, including the oxidation of phenolic compounds (Akram *et al*., 2022). They are broadly distributed in bacteria, fungi, plants, and insects (Agarwal *et al*., 2022). In continuous laccase-based experiments, the immobilized laccase has been inevitably employed (Saoudi and Ghaouar, 2019). Compared to the free laccase, the immobilized laccase has more prominent advantages: (1) increased thermal stability of enzymes, (2) resistance to chemical reagents and extreme conditions, and (3) easy separation from reactants and ability to perform continuous bioreactor operation (Fernandez-Fernandez *et al*., 2013). Therefore, microbial cell surface display techniques are often used for preparing immobilized laccases. Accordingly, more attention has been paid to biosensors based on laccases displayed in recent years (Ricklefs *et al*., 2014). For example, Zhang *et al*. (2018b) developed an electrochemical microbial biosensor. Mechanistically, the sensor could immobilize the bacterial laccase on the *E. coli* cells and then adsorb modified living cells on the glassy-carbon electrode by combining microbial cell surface display and modified electrodes. In previous work, the live bacterial laccase was directly adsorbed onto the electrode surface and demonstrated the feasibility. However, the live cell activity was not maintained (Zhang *et al*., 2017). Therefore, Zhang *et al*. (2017) later designed a laccase-immobilized biosensor by the surface display, and it had been shown to maintain the adsorbed cells' activity for weeks or even months. Moreover, the electrochemical response of detecting catechol employing the electrochemical microbial biosensor kept a linear relationship within the concentration scope of 5.0 to 300.0 μM under optimum pH. In addition, the proposed biosensor presented certain anti-interference. In another work (Acquaviva *et al*., 2018), when employed to detect phenolics in real samples, the biosensor showed high accuracy, almost comparable to the results obtained by high-performance liquid chromatography; besides, high reproducibility and stability were also reflected.

Detection of glucose

Glucose plays an essential role in cell homeostasis and metabolism (Choi and Kim, 2022). It is the energy source and the main energy-supplying substance of living organisms (Zheng *et al*., 2016). More importantly, glucose levels are closely linked to blood glucose levels (French *et al*., 2022). Glucose testing is crucial for people as high blood sugar levels can cause a variety of complications, such as diabetes.

About the above problem, Liang's team gave us appropriate answers using genetically engineered techniques; Liang *et al*. (2013b) first constructed an *E. coli* strain displaying glucose dehydrogenase (GDH) from *Pseudomonas borealis* on its surface with INP as an anchoring motif. In addition, by combining the constructed nanocomposite electrode, a novel glucose electrochemical biosensor was developed. The low detection limit of the prepared biosensor was 4 μM D-glucose. Later, they discovered that by using GDH from *Bacillus subtilis* for surface display, they could establish GDH mutants with better substrate specificity, stability, and activity (Liang *et al*., 2013a). In the same year, applying the same combination of the surface display and carbon nanotube-modified electrode, another biosensor for glucose detection was developed (Wang *et al*., 2013). The difference was that glucose oxidase (GOx) was displayed on the yeast surface with a-agglutinin as the anchoring motif, and the electrode was also changed. The low detection limit was 0.05 mM of D-glucose. This was the first report on yeast surface displaying GOx for glucose detection. More importantly, the GOx-displaying yeast system had high specificity to glucose and good stability over a broad pH range (3.5–11.5), as well as at higher temperatures (56°C). Almost four years later, they made more progress in biosensors for glucose detection. Liu *et al*. (2017) prepared bi-enzyme-based biosensors by collectively immobilizing GDH-displaying-bacteria and glucoamylase-displaying bacteria. Further, they constructed an electrochemical biosensor sensitive to maltose and glucose and insensitive to other monosaccharides and disaccharides. Interestingly, the sensitivity to detect glucose was 3.75 times higher than maltose at the same concentration. Compared with the biosensor based on free enzymes, the dual-strain modified electrodes showed better performance. The proposed biosensor had a broad dynamic range (0.2–10 mM) and a low detection limit (0.1 mM maltose). Biosensors designed in triplicate had different specific mechanisms but employed the same microbial cell surface display technology, from which the widespread use and great importance of surface display were proved. Later, Zhao *et al*. (2020) displayed microbial GDH and cholesterol oxidase on the surface of yeast cells and then prepared two biosensors for blood biochemical indicators detection. The yeast cells were immobilized on electrodes to construct electrochemical biosensors for glucose and cholesterol detection. The glucose biosensor efficiently responded at a wide concentration range of 20–600 $mg{\cdot}dL^{-1}$.

Detection of L-glutamate

L-glutamate is a non-essential amino acid that occurs naturally in protein-rich food (Liu *et al*., 2021). As a functional amino acid, it plays a role in cell metabolism and signaling (Lin *et al*., 2014). L-glutamate is also a significant excitatory neurotransmitter in the human body. However, excitotoxic processes mediated by glutamate are a major cause of neuropathology (such as stroke) (Hazell, 2007; Sheldon and Robinson, 2007). L-glutamate is also widely served as food flavor enhancers, such as soy sauce, chicken essence, monosodium glutamate (MSG), and some snack flavorings (Kurihara, 2009). Nevertheless, MSG has been associated with negative side effects, especially in animals, including diabetes, obesity, neurotoxic, and hepatotoxic (Kazmi *et al*., 2017). Therefore, neurodegenerative diseases

caused by L-glutamate and the consumption of L-glutamate should be taken seriously. So, an effective and convenient technique for L-glutamate detection is urgently required.

Glutamate oxidase (GluOx) and glutamate dehydrogenase (Gldh) are two enzymes commonly used to detect L-glutamate (Hughes *et al.*, 2016; Mruga *et al.*, 2021). We have learned that Ozel *et al.* (2014) and Wang *et al.* (2020) prepared biosensors for detecting L-glutamate based on the fixation of GluOx and nanocomposite materials. However, immobilized enzymes have certain advantages over free enzymes (such as higher activity, greater stability, ability to operate continuously, and more suitable for industrialization) (Fernandez-Fernandez *et al.*, 2013; Ranimol and Sunkar, 2022), but compared with surface display enzymes, immobilization is only a part of microbial cell surface display. Microbial cell surface display techniques can redesign cell surfaces using functional peptides or proteins immobilized on the cell surface to endow cells with some special features (Han *et al.*, 2018b). Therefore, we mainly introduce the employment of surface display technology to detect L-glutamate. In this regard, Liu's team conducted relevant experiments. First, they reported that Gldh is displayed on the surface of *E. coli* with the N-terminal region of INP as an anchoring motif (Song *et al.*, 2015). This was the first report on the optical detection of L-glutamate displayed on the bacterial surface. Additionally, the optimal pH value and temperature for the Gldh-displayed-bacterial cell surface were respectively 9.0°C and 70°C. The fused protein maintained almost 100% initial enzyme activity after incubation for 1 month at 4°C. Clearly, the Gldh-fused cell showed high cell activity. Then, based on previous experiments, multiwalled carbon nanotubes, and Gldh-displaying bacteria were modified onto glassy carbon electrodes to prepare L-glutamate biosensors (Liang *et al.*, 2015). The biosensor had a low detection limit (2 μM) and two linear sections of 10 μM–1 mM and 2–10 mM. Thus, the above-discussed L-glutamate biosensor had good selectivity, stability, and anti-interference to accurately detect real samples.

Conclusion and Prospects

The bacterial surface display system, yeast surface display system, and biomineralized microbial surface display system are reviewed here. The bacterial surface display technology makes full use of the principle of enzyme engineering and opens promising potential. So far, many varieties of anchoring motifs can be used to mediate the bacterial surface display of heterologous proteins. The yeast cell surface display technology has the advantages of display of complex eukaryotic proteins with post-translational modification or larger protein molecules. Both display systems have many merits. For example, cell surface-displayed enzymes can be facilely purified and reused, which is more convenient and economical. The display of enzymes on the surface of the cell can directly react with related substrates, which can dramatically raise catalytic efficiency and expand the types of targets. The cell surface supplies a biologically compatible microenvironment that maintains the stability of enzymes. However, some mechanisms of both systems are still unknown. For example, not much is known about the relationship between the quantity and activity of the enzyme displayed on the cell surface. How are enzymes displayed on the cell surface distributed to the progeny microorganism after the cell division? These issues still need to be explored.

Compared with the above two systems, the seldom-researched biomineralized microbial surface display system is more advanced and efficient and will be the research hotspot with great development potential in the future. By fusing cell surface display with multifunctional inorganic nanomaterials, the biosensor will have higher sensitivity and stability, which will trigger various assay strategies. Theoretically, any enzymes can be displayed after the optimization of the codon. In general, prokaryotic enzymes are displayed on the surface of prokaryotic bacteria (such as *E. coli*), and eukaryotic enzymes are displayed on the surface of eukaryotic microorganisms (such as *S. cerevisiae*). So, the enzyme to be displayed depends on the target analyte. The enzyme can be selected according to the target to catalyze the reaction of the target and produce the signal. For example, OPH and AChE were used for surface display to prepare biosensors for organophosphorus detection. Laccases were used to prepare biosensors based on surface display technologies for detecting phenols. Biosensors using GDH, Gox, and glucoamylase displayed on the microbial cell surface were developed to detect glucose. Gldh was used for surface display to prepare biosensors for L-glutamate detection. Therefore, more enzymes are expected to be displayed for more assay targets.

Although the displayed cells are more stable and have better catalytic efficiency than the untreated ones, the present assay methods based on cell surface display systems are still limited to several kinds of assay methods, including electrochemical biosensing, fluorescence, and spectrophotometry. More analytical methods should be combined with cell-surface display techniques. The biomineralized microbial surface display systems will have enormous potential in self-powered sensors, flexible sensors, single-molecule sensors, and *in vivo* non-invasive microsensors. To some extent, this review provides some information and insights for the research in the field of biosensors based on the microbial surface display system.

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H. Chen and L. Han; preparation of figures: Y. Wu and H. Chen; manuscript checking and approval: B. Huang and L. Han. Both authors reviewed the results and approved the final version of the manuscript.

Availability of Data and Materials: The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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