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# Effect of a magnetic field on the activity of superoxide dismutase studied at the enzyme level

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Regulation of reactive oxygen species is essential for maintaining cellular homeostasis, and superoxide dismutase (SOD) is a key antioxidant enzyme responsible for the removal of superoxide. In this study, the effect of a static magnetic field on SOD activity was analyzed at the molecular level using a purified enzyme-based reaction system. Superoxide was generated through the xanthine oxidase (XOD)–xanthine reaction, and the magnetic field effect was evaluated using optical methods. Both superoxide generation and SOD-mediated superoxide removal were facilitated by the magnetic field. To further understand the enhanced scavenging activity, SOD was immobilized on an Au electrode surface, and electrochemical analyses confirmed that the electron transfer characteristics between the Cu center in SOD and the electrode were altered under the magnetic field. These results present, for a single-enzyme-level system, that a magnetic field can be involved in the electron transfer behavior of antioxidant enzymes and the resulting catalytic activity, and provide fundamental insight into the interaction between magnetic fields and biological redox reactions.

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## Introduction

Reactive oxygen species (ROS) are continuously generated during various metabolic processes, and cells maintain redox balance by eliminating them through antioxidant systems.<sup>1</sup> When this balance is disrupted, excessive ROS can cause damage to proteins, lipids, and nucleic acids, leading to impaired cellular function, inflammation, and the development of degenerative diseases.<sup>2</sup> Therefore, proper regulation between ROS generation and removal is essential for cellular homeostasis.<sup>3</sup> Among ROS, superoxide is considered a primary precursor from which multiple ROS are derived, and superoxide dismutase (SOD), an antioxidant enzyme that catalyzes the removal of superoxide, plays a critical role in this regulatory system.<sup>4,5</sup> Meanwhile, recent studies have reported that external physical stimuli, such as magnetic stimulation, can influence cellular redox balance.<sup>6</sup> In this study, we investigate whether a magnetic field can modulate the enzymatic activity of SOD.

Previous studies have primarily investigated magnetic-field-related changes in SOD activity at the cellular or organismal

level.<sup>7–9</sup> In those studies, cells or living systems were exposed to magnetic fields, and variation in SOD activity was evaluated alongside other oxidative-stress-related markers as part of a broader physiological response. Although such approaches provide valuable biological insight, they do not isolate the enzyme from confounding biological factors and therefore offer limited information on how magnetic field directly influence the catalytic activity of SOD at the molecular level. Studies using purified SOD in well-defined systems remain particularly limited.

Here, we report the effects of a static magnetic field on a simplified reaction system containing purified SOD (Fig. 1). Superoxide, the substrate of SOD, was generated using a xanthine oxidase (XOD)–xanthine reaction system.<sup>10</sup> Prior to evaluating the effect of magnetic fields on the superoxide scavenging activity of SOD, we first investigated their effect on the XOD–xanthine reaction system using a standard optical method. The same optical method was then used to quantify changes in SOD activity by the magnetic field. Finally, to directly verify how the magnetic fields affect the redox behavior of the Cu center in SOD, which is central to its catalytic activity, electrochemical measurements were performed. By avoiding the complexity of cellular or organismal systems, this molecular-level analysis provides a more fundamental basis for interpreting the effects of magnetic fields on antioxidant systems, and may help clarify mechanisms relevant to magnetic-stimulation-based clinical technologies.

## Experimental methods

XOD, xanthine, water-soluble tetrazolium 8 (WST-8), SOD, and cysteine were purchased from Sigma-Aldrich and used as

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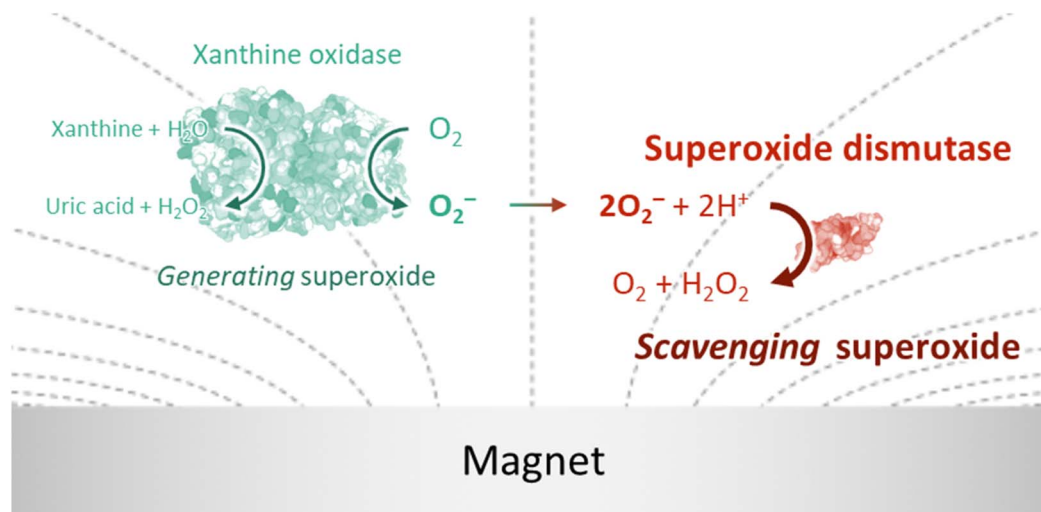


Fig. 1 Schematic representation of the experimental configuration for the study of the magnetic field effect on the activity of superoxide dismutase during the scavenging of superoxide generated by xanthine oxidase.

received without further purification. All solutions were prepared in phosphate buffer solutions (pH  $\sim$ 7.18, 0.1 M, in deionized water).

To apply the magnetic field, cylindrical permanent magnets were used. Three magnets were stacked and aligned in a vertical configuration. For absorbance measurements, the magnets were placed above and below the reaction solution, whereas for electrochemical measurements, they were positioned below the reaction solution. A home-built magnet holder was used to fix the magnet positions stably. The magnetic flux density applied to the system was measured using a Gauss meter (HGM09 s, MAGSYS Magnet Systeme, Germany). Approximately 700 mT was applied to the solution during absorbance experiments, whereas approximately 560 mT was applied during electrochemical measurements; these values were chosen based on safety considerations associated with each experimental setup. For direct comparison between optical and electrochemical results, additional absorbance measurements were performed at 560 mT, and the corresponding data are provided in the SI (see details below).

To evaluate the superoxide generation by the XOD–xanthine system and the superoxide scavenging by SOD, UV-vis absorption spectra were recorded in the range of 400–540 nm (SpectraMax M5, Molecular Devices, USA). To observe the redox behavior of SOD, cyclic voltammetry was performed (CHI 600E, CH Instruments, USA). A three-electrode configuration consisting of a Au working electrode, an Ag/AgCl (3 M KCl) reference electrode, and a Pt wire counter electrode was used, with a phosphate buffer solution as the supporting electrolyte. The potential was applied from +0.4 to  $-0.3$  V at a scan rate of  $100 \text{ mV s}^{-1}$ . To monitor the adsorption behavior of SOD on the Au working electrode, quartz crystal microbalance with dissipation monitoring (QCM-D, QSense OMNI, Biolin Scientific, Sweden) measurements were used. All experiments except QCM-D measurement were conducted in the presence and the absence of a magnetic field.

To form a self-assembled monolayer of cysteine on the Au electrode surface, the electrode surface was first mechanically and electrochemically polished.<sup>11</sup> A 10 mM cysteine solution was then drop-cast onto the Au electrode. The electrode was subsequently rinsed with deionized water to remove physically adsorbed cysteine.

## Results and discussion

### Magnetic-field-responsive characteristics of the reaction system

The reaction system employed in this study consists of the superoxide generation through an enzymatic reaction of XOD with xanthine and O<sub>2</sub>, followed by SOD-mediated superoxide removal. XOD, O<sub>2</sub>, and SOD possess paramagnetic properties, indicating that they may respond to an external magnetic field. The SOD used in this study, SOD1, contains a Cu cation complex at its active center, where the Cu alternates between the +2 and +1 oxidation states to oxidize and reduce superoxide, respectively.<sup>12</sup> When the Cu is in +2 state (electronic configuration d<sup>9</sup>), it possesses one unpaired electron spin and thus exhibits paramagnetic character.<sup>13</sup> In the XOD reaction, electrons extracted from xanthine are transferred to O<sub>2</sub> via Mo centers, Fe–S clusters, and flavin adenine dinucleotide (FAD), and the radical intermediates formed in this process exhibit paramagnetic characteristics.<sup>14</sup> O<sub>2</sub> dissolved in a solution also exhibits paramagnetic character based on its triplet ground state.<sup>15,16</sup> Together, these attributes constitute the minimal conditions necessary for our experimental system to respond to a magnetic field.

### Magnetic field effect on superoxide generation

To investigate the effect of a magnetic field on SOD activity, it is necessary first to determine how the field affect the amount of its substrate, superoxide. Superoxide generation was examined in a buffer solution containing only XOD, xanthine, and water-



soluble tetrazolium 8 (WST-8), an optical probe for superoxide, without SOD. WST-8 is reduced by superoxide to form WST-8 formazan, changing the solution color from pink to orange.<sup>17</sup> First, xanthine and WST-8 were added to the buffer solution and exposed to a static magnetic field (700 mT) for 30 min. As a negative control, an identical solution was prepared without exposure to a magnetic field. Subsequently, XOD was added to both solutions simultaneously to initiate superoxide generation under conditions with and without the magnetic field.

Fig. 2A shows absorption spectra used to evaluate the magnetic field effect on superoxide generation. WST-8 present in a xanthine solution does not exhibit absorption in the range of 400–550 nm, while WST-8 formazan formed by the reaction of WST-8 with superoxide exhibits an absorption peak at approximately 460 nm. The spectra were collected 10 min after adding XOD to solutions containing xanthine and WST-8 in the presence and absence of a magnetic field. Under both conditions, absorption peaks corresponding to WST-8 formazan were observed, indicating that superoxide was generated *via* the XOD–xanthine reaction. In the presence of the magnetic field, the peak intensity was approximately 30% higher than that observed in the absence of the field. Statistical analysis for 10 samples per group using Student's *t*-test indicates a significant difference between the two groups ( $p < 0.01$ , Fig. 2B), suggesting that the magnetic field enhances the XOD–xanthine-based superoxide generation. To interpret this result, we focus on the reaction of FAD in XOD, which directly transfers electrons to O<sub>2</sub>. The reaction between FAD and O<sub>2</sub> branches into one-electron or two-electron pathways depending on the overall reduction state of XOD, which includes Mo center and Fe–S cluster in addition to FAD. When XOD is fully reduced, the reduced FAD (FADH<sub>2</sub>) reacts with O<sub>2</sub> to form FADH' and superoxide through one-electron pathway, whereas under partially reduced conditions of XOD, FADH<sub>2</sub>–O<sub>2</sub> becomes FADH'–superoxide and transforms to flavin peroxide, finally producing H<sub>2</sub>O<sub>2</sub> through two-electron pathway.<sup>18</sup> If the one-

electron pathway is favored, the superoxide formation can increase.<sup>19</sup> From a thermodynamic perspective, it is considered unlikely that the magnetic field used in this study significantly alters the intrinsic redox properties of XOD, as the Zeeman energy under sub-tesla fields is more than two orders of magnitude smaller than thermal energy at room temperature. Instead, it is possible that the magnetic field modulates reaction kinetics by influencing O<sub>2</sub> accessibility near the flavin site. As O<sub>2</sub> is paramagnetic, magnetic fields may influence its local accessibility in solution without significantly altering equilibrium solubility under the conditions used in this study.<sup>20</sup> This could alter the encounter dynamics at the flavin reaction interface. Under conditions of enhanced O<sub>2</sub> accessibility, the initial one-electron transfer from FADH<sub>2</sub> to O<sub>2</sub> is expected to occur more frequently. In contrast, completion of the two-electron pathway requires that the intermediate persists long enough for a second electron transfer step, which depends on intramolecular electron redistribution within XOD. If O<sub>2</sub> encounters become more frequent but shorter-lived, the reaction is more likely to terminate after the first electron transfer step, leading to enhanced superoxide formation. Within this framework, the magnetic field is interpreted to subtly enhance superoxide formation through kinetic modulation of pathway branching in XOD.

#### Magnetic field effect on superoxide scavenging by SOD

After confirming that a magnetic field enhanced superoxide generation, we investigated its effect on the superoxide scavenging activity of SOD. A buffer solution containing xanthine, SOD, and WST-8 was first prepared and exposed to a magnetic field (560 mT) for 30 min. As a negative control, an identical solution that was prepared without the exposure to the field. Subsequently, XOD was added to both solutions simultaneously to initiate the superoxide-generating reaction under conditions with and without the magnetic field.

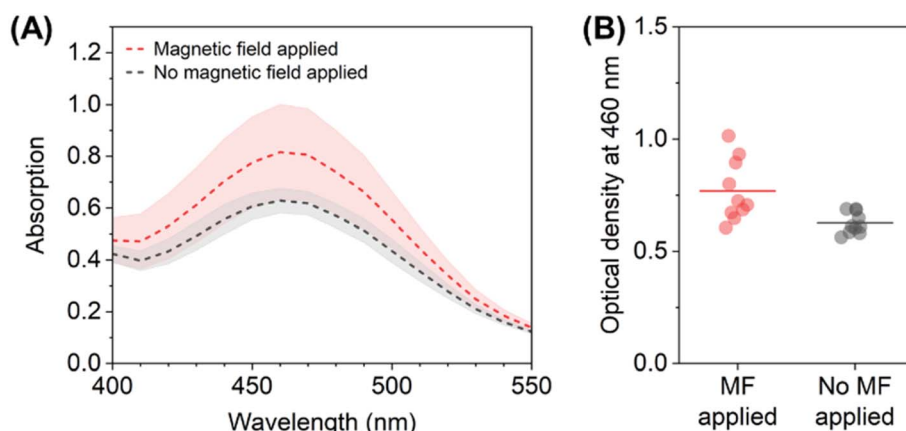


Fig. 2 Effect of magnetic field on superoxide formation. (A) Absorption spectra of solutions containing xanthine oxidase (XOD), xanthine, and water-soluble tetrazolium 8 (WST-8) in the presence (red) and the absence (black) of a magnetic field. The spectra were obtained 10 minutes after adding XOD to the solution containing xanthine and WST-8. Dashed lines and shaded areas denote average and standard deviation, respectively ( $N = 10$  per group). (B) Optical density at 460 nm observed from (A). Horizontal bars indicate the average values. Statistical significance was assessed using the Student's *t*-test ( $p < 0.01$ ). MF: magnetic field.



Fig. 3 shows that SOD-mediated suppression of WST-8 formazan formation, which reflects superoxide scavenging, depends on the presence a magnetic field. Superoxide generated *via* the XOD–xanthine reaction either reduces WST-8 to form WST-8 formazan or reacts with SOD (Fig. 3A). When superoxide is scavenged by SOD, WST-8 formazan formation is suppressed and the absorption signal decreases. In the presence of a magnetic field, SOD suppressed the WST-8 formazan peak intensity by 69.0% (Fig. 3B), whereas the suppression was 57.8% in the absence of the field (Fig. 3C). Fig. 3D shows that the suppression ratio increased by approximately 11.2% by the magnetic field. A *t*-test comparing the suppression ratios between the two groups ( $N = 10$  per group) revealed a statistically significant difference ( $p < 0.05$ ). Thus, we conclude that the superoxide-scavenging activity of SOD increases in the presence of a magnetic field. To further investigate the magnetic field effects on the behavior of SOD, we performed electrochemical analyses as described below.

Although the main optical absorbance data were obtained under a magnetic field of 700 mT, the optical absorbance response was also examined at 560 mT (see Fig. S1 in the SI), which corresponds to the magnetic flux density used in the electrochemical measurements, to allow direct comparison between the optical and electrochemical results. The same overall trend was observed at 560 mT, although the magnitude of the magnetic-field-induced effect was slightly smaller.

### Electrochemical investigation of the redox behavior of SOD under magnetic fields

The optical experiments described above indicate that a magnetic field enhances SOD activity in a chromogenic assay. To analyze this phenomenon from a redox behavior perspective, electrochemical measurements were employed.<sup>21</sup> Because the Cu center in SOD must be electrically accessible to the Au electrode, SOD was immobilized on the electrode surface. We attempted to observe the redox signal of freely diffusing SOD using an unmodified Au electrode; however, no characteristic redox peaks were observed under our experimental conditions (see details below). Therefore, SOD immobilization was used to enable electrochemical access to the Cu redox center. Although this configuration does not fully reproduce freely diffusing SOD in biological fluids, it provides a controlled interfacial model for examining magnetic-field-dependent SOD redox behavior.

To immobilize SOD on a Au electrode surface, a self-assembled monolayer (SAM) was first formed on the Au surface using cysteine.<sup>22</sup> In a neutral buffer solution, the carboxyl and amine groups of cysteine carry negative and positive charges, respectively, enabling electrostatic interactions with amino acid residues of SOD, while hydrogen bonding and hydrophobic interaction may also contribute to adsorption, thereby facilitating the immobilization of SOD on the electrode surface. This immobilization *via* cysteine is known to help SOD retain its activity for the dismutation of superoxide.<sup>22</sup> Using the cysteine-modified Au electrode, cyclic voltammograms (CVs)

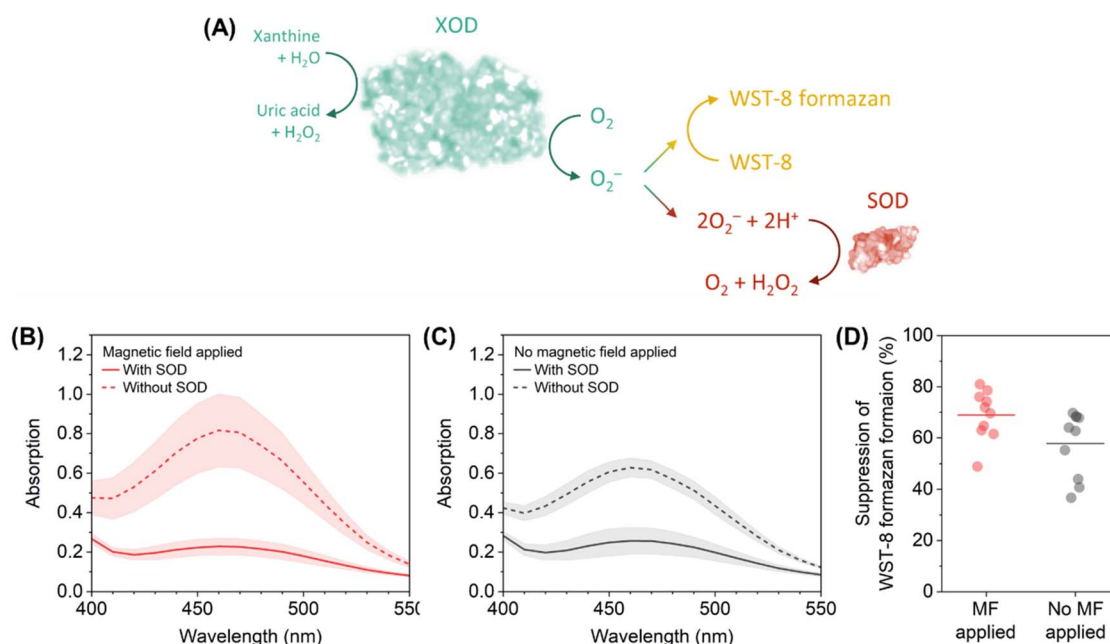


Fig. 3 Effect of magnetic field on the activity of superoxide dismutase (SOD). (A) Schematic illustration of the reaction pathways of superoxide generated by xanthine oxidase (XOD). Superoxide reacts with either SOD or water-soluble tetrazolium 8 (WST-8). As a result of superoxide–WST-8 reaction, WST-8 formazan is formed, which exhibits strong absorption at 460 nm. (B and C) Absorption spectra of solutions containing xanthine, XOD, and WST-8 (dashed lines) and of solutions additionally containing SOD (solid lines), recorded in the presence (B) and the absence (C) of a magnetic field (flux density: 700 mT). All spectra were obtained 10 minutes after adding XOD to the solution containing xanthine and WST-8 with or without SOD. Lines and shaded areas denote average and standard deviation, respectively ( $N = 10$  per group). (D) Suppression of the absorptions at 460 nm observed in B (red) and C (black). Statistical significance was assessed using the Student's *t*-test ( $p < 0.05$ ). MF: magnetic field.



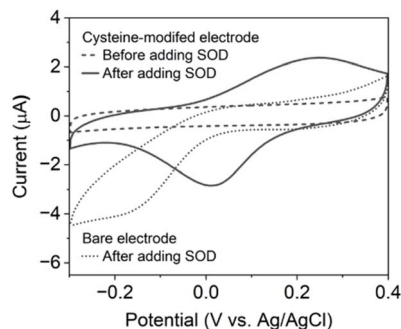


Fig. 4 Cyclic voltammograms of superoxide dismutase (SOD) recorded using cysteine-modified and bare Au electrodes.

were first obtained in a blank buffer solution, followed by the measurements after adding SOD to the same solution. Fig. 4 shows CVs presenting the differences in SOD signals in the presence and the absence of the cysteine SAM. On a bare Au electrode, only currents originating from the oxygen reduction reaction (ORR, onset potential:  $\sim 0$  V vs. Ag/AgCl) of dissolved  $\text{O}_2$  were observed in both blank and SOD-containing buffer solutions. In contrast, CVs recorded with a cysteine-coated Au electrode in a blank buffer showed no ORR, indicating that the SAM formed a compact coating that hindered the ORR.<sup>23</sup> When SOD was added to this solution and the potential was scanned in the negative direction, a reduction peak appeared at approximately  $-0.0$  V. Upon reversing the scan direction, an oxidation peak appeared near  $0.2$  V. These peaks are attributed

to the reduction and oxidation of the Cu center in SOD.<sup>22</sup> By coating the electrode with cysteine, stable measurement of the SOD redox signal was enabled, and all subsequent electrochemical experiments were performed using cysteine-coated electrodes.

The influence of a magnetic field on the redox behavior of the Cu center in SOD was examined. Fig. 5A shows time-dependent CVs recorded after immersing a cysteine-coated electrode in a buffer containing only SOD in the presence of a magnetic field. In this experiment, neither XOD nor xanthine was present in the solution; therefore, no superoxide was generated. The measured current is attributed exclusively to electron exchange between the Cu center in SOD and the electrode, for which electron tunneling is considered the dominant pathway. Measurements were conducted for 120 min at 10 min intervals. An increase in current over time was observed (Fig. 5C). QCM-D measurements (performed in the absence of a magnetic field, see Fig. S2 in the SI) confirmed progressive adsorption of SOD onto the cysteine-coated Au surface. Thus, the current increase is attributed, at least in part, to gradual SOD adsorption. However, the accompanying increase in peak separation (Fig. 5D) suggests that the adsorbed SOD population does not contribute uniformly to the electron transfer, likely reflecting a distribution of coupling states, including weakly coupled species with slower apparent electron transfer kinetics.<sup>24</sup>

The time-dependent SOD redox signals differ between measurements performed in the presence (Fig. 5A) and the absence (Fig. 5B) of a magnetic field. Fig. 5C and D summarize

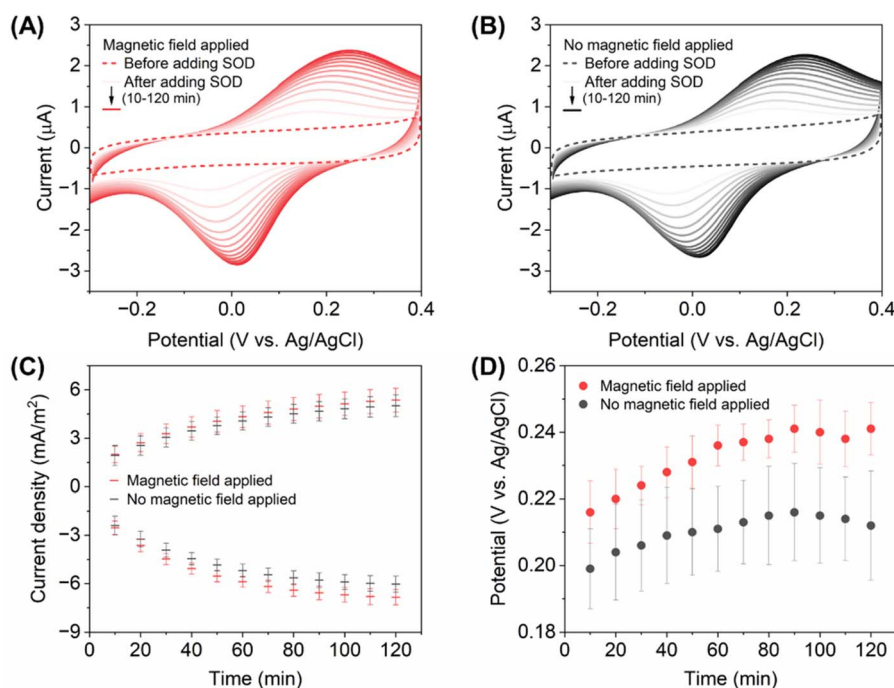


Fig. 5 Effect of a magnetic field on the redox properties of superoxide dismutase (SOD). (A and B) Cyclic voltammograms (CVs) of SOD recorded in the presence (A) and the absence (B) of a magnetic field ( $N = 5$  per group, magnetic flux density: 560 mT). CVs were recorded before and after adding SOD to the electrolyte solution at 10 min intervals. (C and D) Time-dependent changes in the current density (C) and the peak-to-peak separation (D) for the reduction and oxidation peaks of SOD observed in A and B.

the peak current density and the peak potential separation averaged from five electrodes per group. Higher peak current density and wider peak separation were observed under the magnetic field. In the context of the time-dependent evolution of the SOD signal discussed above, these results suggest that the magnetic field increases the apparent surface density of electrochemically addressable SOD, rather than simply accelerating the intrinsic Cu-centered electron transfer kinetics. A possible origin of this behavior is perturbation of the interfacial electrochemical environment. Previous magnetoelectrochemical studies have shown that static magnetic fields can modify the electrochemical double layer and shift the outer Helmholtz plane in systems containing interfacial paramagnetic species, thereby altering the apparent electrochemical response without necessarily changing intrinsic redox kinetics.<sup>25</sup> In our SOD-cysteine-modified Au system, such changes in the interfacial potential distribution may allow previously weakly electroactive SOD species to contribute to the measured current. This interpretation explains the increase in peak current density, while the wider peak separation reflects less efficient or more heterogeneous coupling of this additional SOD population to the electrode.

One possible factor that may be considered is magnetohydrodynamic (MHD) convection under a magnetic field.<sup>26</sup> Although MHD convection can, in principle, arise from the Lorentz force ( $\mathbf{j} \times \mathbf{B}$ , where  $\mathbf{j}$  is current density and  $\mathbf{B}$  is magnetic flux density), its effect is expected to be minimal in our system, where both the magnetic field and the current are largely aligned along the surface normal, greatly reducing the Lorentz force. In addition, the current density is only on the order of several mA m<sup>-2</sup> and the magnetic flux density is below 1 T, further limiting the magnitude of the Lorentz force per unit volume. Using an approximate estimate with a diffusion-layer thickness of  $\sim 100$   $\mu\text{m}$ , the resulting flow velocity (estimated as  $JBL^2/\mu$ , where  $L$  is the characteristic length scale near the electrode and  $\mu$  is the dynamic viscosity of the solution) is expected to be on the order of  $10^{-2}$   $\mu\text{m s}^{-1}$ . This value is significantly smaller than that of diffusion-dominated transport. Therefore, MHD-driven enhancement of mass transport is unlikely to significantly influence the observed electrochemical response.

Another possible factor to consider is the magnetic-field-induced reorientation of SOD at the electrode surface. Although the Cu center in SOD is paramagnetic, the associated magnetic energy scale (estimated as  $g\mu_{\text{B}}B$ , on the order of  $10^{-23}$  J at 0.5 T, where  $g$  is the Landé  $g$ -factor and  $\mu_{\text{B}}$  is the Bohr magneton) is much smaller than thermal energy ( $k_{\text{B}}T \approx 10^{-21}$  J at room temperature, where  $k_{\text{B}}$  is the Boltzmann constant and  $T$  is the temperature), indicating that any magnetic-field-induced orientational bias is very weak. In addition, the enzyme is adsorbed on the electrode surface *via* electrostatic, hydrogen-bonding, and hydrophobic interactions, corresponding to interfacial binding energies, often reaching  $10 k_{\text{B}}T$  and more.<sup>27</sup> Reorientation would therefore require overcoming both thermal fluctuations and interfacial binding interactions, and is unlikely to significantly influence the observed response.

## Conclusion

In this study, the effect of a static magnetic field on SOD activity was analyzed at the molecular level using a purified enzyme reaction system. Optical quantification of superoxide generated through the XOD-xanthine system revealed that the magnetic field enhanced superoxide generation and, more importantly, the SOD-mediated superoxide removal. Electrochemical analyses further revealed that the electron transfer characteristics between the Cu center in SOD and the electrode were altered under the magnetic field, demonstrating that SOD redox behavior is magnetically responsive in this controlled interfacial system. These findings suggest that magnetic fields can influence the catalysis of antioxidant enzymes. Overall, this single-enzyme-level study provides fundamental insight into the interaction between magnetic fields and biological redox reactions.

## Author contributions

Conceptualization, K. K. and M. K.; methodology, S. Y. and M. K.; formal analysis, S. Y., S. L. and M. K.; investigation, S. Y.; resources, S.-G. P. and M. K.; writing—original draft preparation, S. Y. and M. K.; writing—review and editing, all authors; visualization, S. Y. and M. K.; supervision, M. K.; project administration, M. K.; funding acquisition, K. K. and M. K. All authors have read and agreed to the published version of the manuscript.

## Conflicts of interest

There are no conflicts to declare.

## Data availability

The data supporting the findings of this study are available within the article. Additional data that support the findings of this study are available from the corresponding author upon reasonable request.

Supplementary information (SI) is available. See DOI: <https://doi.org/10.1039/d5ra10059c>.

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