Anodal Occipital Transcranial Direct Current Stimulation Enhances Perceived Visual Size Illusions

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Abstract

■ Human early visual cortex has long been suggested to play a crucial role in context-dependent visual size perception through either lateral interaction or feedback projections from higher to lower visual areas. We investigated the causal contribution of early visual cortex to context-dependent visual size perception using the technique of transcranial direct current stimulation and two well-known size illusions (i.e., the Ebbinghaus and Ponzo illusions) and further elucidated the underlying mechanism that mediates the effect of transcranial direct current stimulation over early visual cortex. The results showed that the magnitudes of both size illusions were significantly increased by anodal stimulation relative to sham stimulation but left unaltered by cathodal stimulation. Moreover, the anodal effect persisted even when the central target and surrounding inducers of the Ebbinghaus configuration were presented to different eyes, with the effect lasting no more than 15 min. These findings provide compelling evidence that anodal occipital stimulation enhances the perceived visual size illusions, which is possibly mediated by weakening the suppressive function of the feedback connections from higher to lower visual areas. Moreover, the current study provides further support for the causal role of early visual cortex in the neural processing of context-dependent visual size perception. ■

INTRODUCTION

Human visual size perception is not always a faithful representation of the physical world, but it heavily relies on the surrounding context. For instance, as illustrated in the Ebbinghaus illusion, an object appears larger when surrounded by small items relative to large items. Similarly, an object appears larger when placed at an apparently far location relative to at an apparently near location, which is known as the Ponzo illusion. Visual size illusions have been found to be correlated with the functional and structural features of the primary visual cortex (V1). Specifically, the spatial extent of V1 activity reflects the perceived size rather than the physical size of an object (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006). Similar V1 activation patterns have been observed for an afterimage whose apparent size varies with distance (Sperandio, Chouinard, & Goodale, 2012). Moreover, the magnitude of the Ebbinghaus illusion has been found to be negatively correlated with V1 surface area (Schwarzkopf & Rees, 2013; Schwarzkopf, Song, & Rees, 2011), and the Ponzo illusion correlates with the receptive field position shifts of V1 neurons (He, Mo, Wang, & Fang, 2015; Ni, Murray, & Horwitz, 2014).

If early visual cortex plays a pivotal role in context-dependent visual size perception, changes in its excitability should exhibit a causal effect on perceived visual size illusions. To examine this possibility, we directly manipulated occipital cortex excitability using transcranial direct current stimulation (tDCS), which is a noninvasive neurostimulation technique that uses constant, low-level intensity direct current to modulate cortical excitability in a polarity-dependent manner (Costa, Lapenta, Boggio, & Ventura, 2015). Anodal stimulation increases cortical excitability, whereas cathodal stimulation leads to cortical inhibition. Anodal stimulation of the occipital cortex can reduce surround suppression (Raveendran, Tsang, Tiwana, Chow, & Thompson, 2020; Spiegel, Hansen, Byblow, & Thompson, 2012), which is thought to originate within V1 (Osaki, Naito, Sadakane, Okamoto, & Sato, 2011; Akasaki, Sato, Yoshimura, Ozeki, & Shimegi, 2002; Walker, Ohzawa, & Freeman, 2000). Therefore, we expected that anodal occipital stimulation would weaken the suppression of the surrounding context in the illusory configuration, thereby leading to an increase in illusion magnitude.

Converging evidence suggests that the processing of visual size illusions relies on both early feedforward processing in V1 (Chen, Qiao, Wang, & Jiang, 2018; Nakashima & Sugita, 2018; Sherman & Chouinard, 2016; Jaeger & Klahs, 2015; Jaeger, Klahs, & Newton, 2014) and late feedback projections from higher visual cortex to V1 (King, Hodgekins, Chouinard, Chouinard, & Sperandio, 2017; Schmidt & Haberkamp, 2016; Schmidt, Weber, & Haberkamp, 2016;

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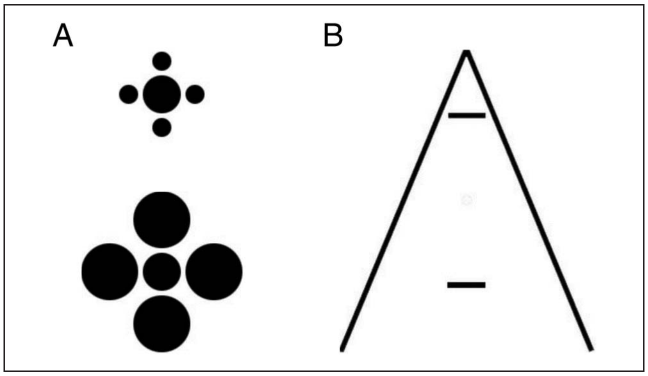

Figure 1. Schematic representation of the illusory configurations. (A) In the Ebbinghaus illusion, a central circle was surrounded by four small or large inducers, and (B) in the Ponzo illusion, a horizontal bar was presented either near or far from the apex of a pair of converging lines.

Schwarzkopf, 2015; Sperandio & Chouinard, 2015; Weidner et al., 2014; Schwarzkopf et al., 2011). Whether occipital tDCS affects the early or late processing stage remains to be determined. To probe this issue, we simultaneously presented the central target and surrounding inducers of the Ebbinghaus configuration to separate eyes during occipital tDCS. Binocular integration primarily occurs in V1 (Hubel & Wiesel, 1968), and almost all neurons beyond V1 are binocular (Peel, Sherman, Sperandio, Laycock, & Chouinard, 2019; Song, Schwarzkopf, & Rees, 2011; Zeki, 1978). If the enhancement of the Ebbinghaus illusion magnitude induced by anodal stimulation persists in this dichoptic condition, then the anodal effect would primarily affect the relatively late binocular processing stage. The Ebbinghaus illusion has been suggested to be mediated by both lateral interaction in the early processing stage (Sherman & Chouinard, 2016; Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013) and feedback projections from higher to lower visual areas (King et al., 2017; Schmidt et al., 2016; Schwarzkopf, 2015). Meanwhile, the Ponzo illusion largely relies on feedback projections from higher cortical areas to V1 (Zeng, Fink, & Weidner, 2020; He et al., 2015; Fang et al., 2008). The Ponzo illusion has been found to have an equivalent magnitude whether the target and surrounding contexts are presented to the same or different eyes (Song et al., 2011). Therefore, we did not include the dichoptic presentation of the Ponzo illusion. If occipital tDCS also modulates the perceived magnitude of the Ponzo illusion in a similar way as that of the Ebbinghaus illusion, then early visual cortex causally contributes to context-dependent visual size perception and tDCS primarily affects the late instead of the early processing stage.

METHODS

Participants

Seventy-two healthy right-handed participants (24 men; 21.3 ± 2.0 years old) gave their informed consent to participate in the study, with 18 participants for each of the four experiments (Experiment 1: eight men, 21.6 ± 2.0 years old; Experiment 2: five men, 21.6 ± 1.8 years old; Experiment 3: seven men, 21.5 ± 1.6 years old; Experiment 4: four men, 20.7 ± 2.3 years old). All participants had normal or corrected-to-normal vision, no metallic implants, and no history of any neurological or psychiatric illness. They were compensated for their time. The study was approved by the institutional review board of Liaoning Normal University and conducted in accordance with the tenets of the Declaration of Helsinki.

Stimuli and Procedures

Stimuli were displayed using MATLAB (The MathWorks, Inc.) together with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The Ebbinghaus configuration was composed of a central circle (1.1° × 1.1°) surrounded by four large (1.7° × 1.7°) or small (0.6° × 0.6°) circles (Figure 1A). The proximal distance between the central circle and the surrounding inducers was 0.14°. The Ponzo configuration consisted of a horizontal bar (1.1° × 0.2°) surrounded by a pair of converging lines (7.7° × 9.1°). The horizontal bar was presented either near or far from the apex of the two converging lines (2.6° from screen center; see Figure 1B). The initial size of a comparison circle and the initial length of a comparison bar were varied from trial to trial ranging from 0.86° to 1.43° in 0.06° steps. The central location of the illusory configurations was varied randomly between ±0.3° of the screen center in each trial. Participants were seated 57 cm from a gray computer screen (1440 × 900 at 60 Hz) with their head stabilized by a chin rest.

In Experiment 1, the Ebbinghaus configuration was presented at the screen center, and a comparison circle was simultaneously presented below it (8.6° from the screen center). Participants were required to adjust the size of the comparison circle to match that of the central target without time limit. There were 132 trials with 22 repetitions for each condition (size of inducers: large or small; stimulation condition: anodal, cathodal, or sham).

In Experiment 2, the central target and the surrounding inducers of the Ebbinghaus configuration were simultaneously presented to different eyes. Participants viewed the stimuli through a mirror stereoscope with a chin and forehead rest and were required to adjust the size of the comparison circle to match that of the central target without time limit. There were 132 trials with 22 repetitions for each condition (size of inducers: large or small; stimulation condition: anodal, cathodal, or sham).

In Experiment 3, the Ponzo configuration was presented at the screen center, and a comparison bar was simultaneously presented at the right side of the screen (8.6° from the screen center). Participants had to adjust the length of the comparison bar to match that of the target bar without time limit. There were 132 trials with 22 repetitions for each condition (location of the target: upper or lower; stimulation condition: anodal, cathodal, or sham).

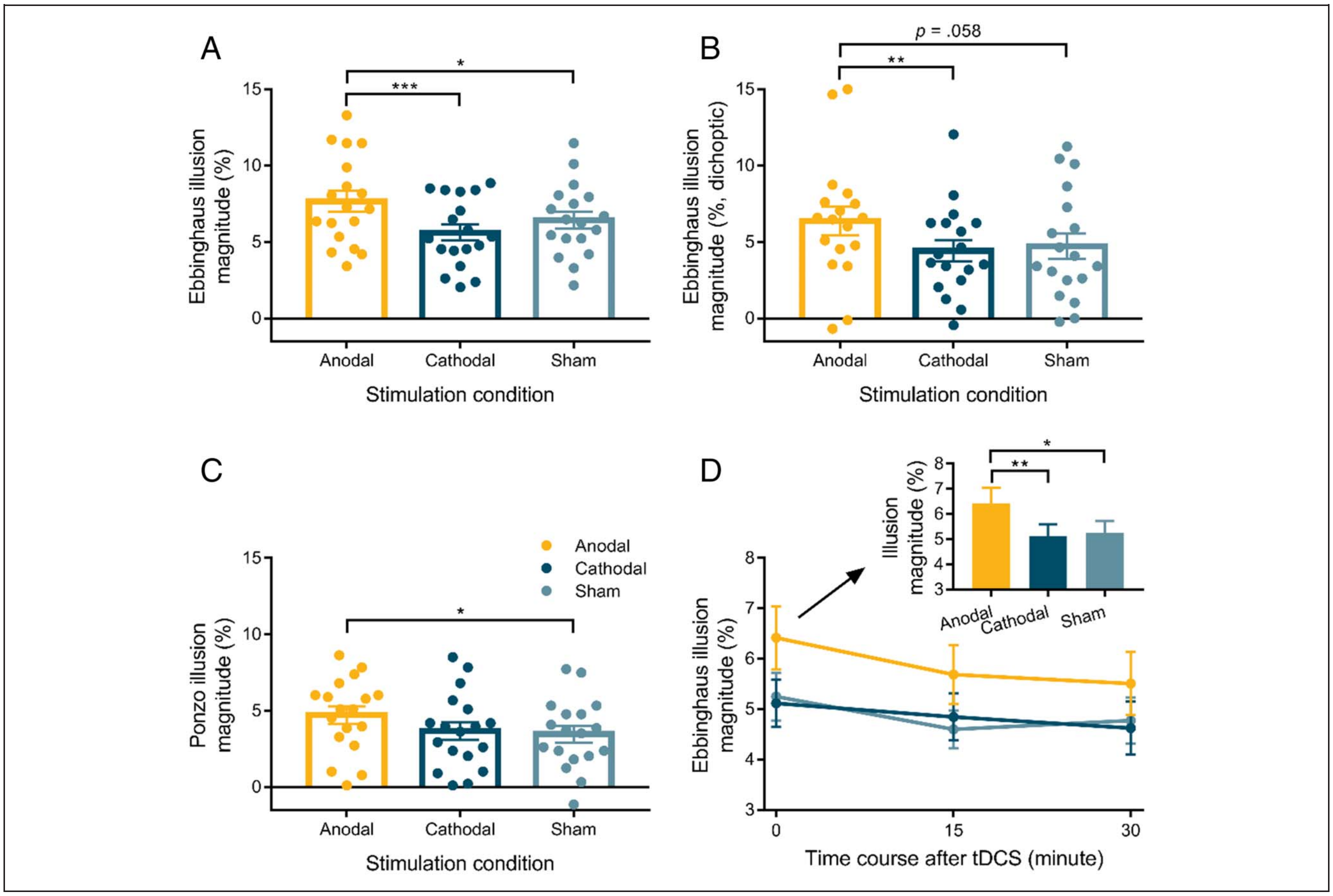

Figure 2. Results of Experiments 1–4. The Ebbinghaus illusion magnitude with (A) binocular and (B) dichoptic presentations as a function of stimulation condition in Experiments 1 and 2, (C) the Ponzo illusion magnitude under the three stimulation conditions in Experiment 3, and (D) the Ebbinghaus illusion magnitude as a function of time course after tDCS in Experiment 4, with the top subpanel illustrating the illusion magnitude measured during the stimulation (i.e., 0 min). Error bars denote 1 *SEM*. $^{*}p < .05$, $^{**}p < .01$, and $^{***}p < .001$.

In Experiment 4, the stimuli and procedure were identical to those of Experiment 1, with the exception that the illusion magnitude was also measured 15 and 30 min after the end of stimulation. There were 396 trials with 22 repetitions for each condition (size of inducers: large or small; stimulation condition: anodal, cathodal, or sham; time course: during stimulation, 15 or 30 min after the end of stimulation).

tDCS

tDCS was delivered by the ActivaDose II controller (Activa Tek, Inc.) using a pair of electrodes placed inside saline-soaked sponges (5 × 5 cm). Anodal or cathodal electrode was positioned at Oz, and the reference electrode was placed over Cz, according to previous studies (Raveendran et al., 2020; Spiegel, Byblow, Hess, & Thompson, 2013; Spiegel et al., 2012; Antal, Kincses, Nitsche, Bartfai, & Paulus, 2004; Antal, Kincses, Nitsche, & Paulus, 2003a, 2003b). A constant current of 2-mA intensity with a duration of 8 min was applied for both anodal and cathodal stimulation and was initiated 4 min before the measure of illusion magnitude. The current density was 0.08 mA/cm^2, which has been applied and considered safe in humans (Iyer et al., 2005). The setup of sham stimulation was identical to that of anodal stimulation, with the exception that the stimulator was turned on for 60 sec. The current was ramped up or down over the first and last 10 sec of stimulation, respectively. Participants were naive to the stimulation conditions, and they completed the anodal, cathodal, and sham sessions on separate days, with the order randomized across participants.

Data Analysis

The magnitude of the Ebbinghaus illusion was measured as the difference of the perceived size of the central target surrounded by small and large inducers relative to its physical size (%). The magnitude of the Ponzo illusion was calculated as the difference of the perceived length of the target bar presented at the upper and lower locations relative to its physical length (%). The illusion magnitude was entered into a repeated-measures ANOVA with Stimulation condition (anodal, cathodal, or sham) as a within-subject factor for Experiments 1–3 and with Stimulation condition and Time course (during stimulation, 15 or 30 min after the end of stimulation) as within-subject factors for Experiment 4. Post hoc multiple comparisons were Bonferroni corrected (two-tailed).

RESULTS

In Experiment 1, the main effect of Stimulation condition was significant, $F(2, 34) = 11.34, p < .001, \eta_p^2 = .40$. Post hoc comparisons showed that the illusion magnitude for anodal stimulation was significantly larger than that for cathodal stimulation, $t(17) = 4.55, p < .001, d = 1.07$, and sham stimulation, $t(17) = 2.77, p = .040, d = 0.65$ (Figure 2A). However, the illusion magnitude for cathodal stimulation was comparable to that for sham stimulation, $t(17) = -2.04, p = .173, d = 0.48$.

In Experiment 2, the main effect of Stimulation condition was significant, $F(2, 34) = 6.32, p = .005, \eta_p^2 = .27$. Post hoc comparisons showed that the illusion magnitude for anodal stimulation was significantly larger than that for cathodal stimulation, $t(17) = 3.44, p = .009, d = 0.81$ (see Figure 2B) and was marginally larger than that for sham stimulation, $t(17) = 2.58, p = .058, d = 0.61$. The illusion magnitude for cathodal stimulation was comparable to that for sham stimulation, $t(17) = -0.53, p = 1.000, d = 0.12$.

In Experiment 3, the main effect of Stimulation condition was significant, $F(2, 34) = 4.34, p = .021, \eta_p^2 = .20$. Post hoc comparisons showed that the illusion magnitude was significantly larger for anodal stimulation than that for sham stimulation, $t(17) = 3.06, p = .021, d = 0.72$ (see Figure 2C). However, the illusion magnitude for cathodal stimulation was comparable to that for anodal stimulation, $t(17) = -2.10, p = .153, d = 0.50$, and sham stimulation, $t(17) = 0.47, p = 1.000, d = 0.11$.

In Experiment 4, the main effects of both Stimulation condition, $F(2, 34) = 5.31, p = 0.010, \eta_p^2 = .24$, and Time course, $F(2, 34) = 4.29, p = .022, \eta_p^2 = .20$, were significant, but their interaction failed to reach significance, $F(4, 68) = 0.51, p = .730, \eta_p^2 = .03$. When the illusion magnitude was measured during the stimulation, the main effect of Stimulation condition was significant, $F(2, 34) = 7.54, p = .002, \eta_p^2 = .31$, confirming the results of Experiment 1. Post hoc comparisons showed that the illusion magnitude for anodal stimulation was significantly larger than that for cathodal stimulation, $t(17) = 3.75, p = .005, d = 0.89$, and sham stimulation, $t(17) = 2.81, p = .036, d = 0.66$ (Figure 2D). However, the illusion magnitude for cathodal stimulation was comparable to that for sham stimulation, $t(17) = -0.39, p = 1.000, d = 0.09$. When the illusion effect was measured 15 and 30 min after the end of stimulation, the main effect of Stimulation condition failed to reach significance (15 min: $F(2, 34) = 2.90, p = .069, \eta_p^2 = .15$; 30 min: $F(2, 34) = 1.86, p = .171, \eta_p^2 = .10$).

DISCUSSION

In a series of experiments, we found that anodal occipital stimulation transiently increased the magnitudes of both the Ebbinghaus and Ponzo illusions relative to sham stimulation, whereas cathodal stimulation showed a comparable effect to sham stimulation. Moreover, similar patterns of results were observed when the central target and surrounding inducers of the Ebbinghaus configuration were presented to separate eyes.

It has been broadly demonstrated that tDCS modulates cognitive performance in a polarity-specific manner. For instance, anodal tDCS applied over V1 decreases phosphene threshold and increases the N70 amplitude evoked by gratings, whereas cathodal tDCS has the opposite effect (Antal et al., 2004; Antal et al., 2003a, 2003b). Anodal tDCS of V1 significantly improves contrast sensitivity, orientation sensitivity, and visual discrimination learning, whereas cathodal tDCS has no effect (Sczesny-Kaiser et al., 2016; Olma, Kraft, Roehmel, Irlbacher, & Brandt, 2011; Kraft et al., 2010). Similarly, anodal tDCS of the early visual cortex transiently improves contrast sensitivity in individuals with amblyopia, which is associated with the suppression of inputs from the amblyopic eye to the visual cortex (Li et al., 2011), whereas cathodal tDCS does not affect contrast sensitivity of the amblyopic eye (Spiegel et al., 2013). In line with and extending the aforementioned findings, the current study showed that anodal occipital stimulation significantly increased context sensitivity, as demonstrated by the increased illusion magnitudes, whereas cathodal stimulation had a negligible effect. Anodal stimulation has been found to reduce gamma aminobutyric acid (GABA) concentration in the motor cortex (Kim, Stephenson, Morris, & Jackson, 2014; Stagg et al., 2009) and increase glutamate concentration in the parietal cortex (Clark, Coffman, Trumbo, & Gasparovic, 2011), whereas cathodal stimulation inhibits glutamate concentration (Stagg et al., 2009) and has no effect on GABA levels (Antonenko et al., 2017). Moreover, anodal occipital stimulation significantly reduces surround suppression (Spiegel et al., 2012), which is thought to originate within V1 (Osaki et al., 2011; Akasaki et al., 2002; Walker et al., 2000) and involves GABA-mediated inhibition (Fu et al., 2010; Yoon et al., 2009, 2010). Therefore, in the current study, the enhancement of context sensitivity induced by anodal stimulation was likely caused by the reduction of GABA concentration in early visual cortex, which weakened the suppression of the surrounding inducers and resulted in the enhancement of context sensitivity. Moreover, this enhancement was transient, lasting no more than 15 min, consistent with previous findings (Molero-Chamizo et al., 2018; Kuo et al., 2013; Merzagora et al., 2010; Lang, Nitsche, Paulus, Rothwell, & Lemon, 2004). The functional effects of tDCS on cognitive tasks weaken with time, which agrees with the fact that the enhancement of cortical excitability is max immediately after anodal stimulation and then declines gradually (Muthalib, Besson, Dutta, Hayashibe, & Perrey, 2019; Molero-Chamizo et al., 2018; Zheng, Alsop, & Schlaug, 2011). The absence of a cathodal effect on context sensitivity in the current study may be attributed to a putative ceiling effect; that is, the surrounding context has been optimally suppressed by the visual system, and cathodal stimulation cannot strengthen the suppression further.

Converging evidence has indicated that the processing of the Ebbinghaus illusion emerges at a relatively early processing stage compared with the Ponzo illusion (Chen et al., 2018; Shen et al., 2015; Song et al., 2011; Jaeger & Pollack, 1977; Cooper & Weintraub, 1970). Two cognitive mechanisms have been proposed to account for the production of the Ebbinghaus illusion. One is low-level contour interaction (Todorović & Jovanović, 2018; Jaeger & Klahs, 2015; Jaeger et al., 2014; Jaeger, 1978), which is linked to lateral interaction in the early processing stage (Sherman & Chouinard, 2016; Salva et al., 2013), and the other is high-level size contrast (de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; Coren & Miller, 1974; Massaro & Anderson, 1971), which largely relies on feedback connections from higher to lower visual areas (King et al., 2017; Schmidt et al., 2016; Schwarzkopf, 2015). For the Ponzo illusion, feedback projections from higher visual areas to V1 have been suggested (Zeng et al., 2020; He et al., 2015; Fang et al., 2008). These feedback connections have been found to boost the response of V1 neurons to a central stimulus and meanwhile suppress the response to its surrounding context (Maniglia, Trotter, & Aedo-Jury, 2019; Vangeneugden et al., 2019; Nurminen, Merlin, Bijanzadeh, Federer, & Angelucci, 2018; Chen et al., 2014; Nassi, Lomber, & Born, 2013; Wang, Huang, Bardy, FitzGibbon, & Dreher, 2010; Bardy, Huang, Wang, FitzGibbon, & Dreher, 2009; Bullier, Hupé, James, & Girard, 2001; Hupé et al., 1998, 2001). In the current study, anodal stimulation significantly increased the magnitude of both the Ponzo illusion and the Ebbinghaus illusion, which was dichoptic presented, suggesting that anodal stimulation primarily influences the feedback projections from higher to lower visual areas. In particular, anodal stimulation might reduce the suppressive effect of the feedback projections on the surrounding context and further led to an increase in the magnitude of both size illusions.

Taken together, the increase in early visual cortex excitability induced by anodal stimulation can transiently enhance the context sensitivity of visual size perception, possibly by reducing cortical GABA levels, which weakens the suppressive function of feedback connections from higher to lower visual cortex. These findings provide further support for the causal role of early visual cortex in the neural processing of context-dependent visual size perception.

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Author Contributions

Anqi Wang: Data curation; Investigation; Software; Writing—original draft. Lihong Chen: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Writing—original draft; Writing—review & editing. Yi Jiang: Conceptualization; Funding acquisition; Project administration; Writing—review & editing.

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