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Exogenous testosterone increases the audience effect in healthy males: evidence for the social status hypothesis

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Several studies have implicated testosterone in the modulation of altruistic behaviours instrumental to advancing social status. Independent studies have also shown that people tend to behave more altruistically when being watched (i.e. audience effect). To date, little is known about whether testosterone could modulate the audience effect. In the current study, we tested the effect of testosterone on altruistic behaviour using a donation task, wherein participants were asked to either accept or reject a monetary transfer to a charity organization accompanying a personal cost either in the presence or absence of an observer. We administered testosterone gel or placebo to healthy young men ($n = 140$) in a double-blind, placebo-controlled, mixed design. Our results showed that participants were more likely to accept the monetary transfer to the charity when being observed compared to when they completed the task alone. More importantly, this audience effect was amplified among people receiving testosterone versus placebo. Our findings suggest that testosterone administration increases the audience effect and further buttress the social status hypothesis, according to which testosterone promotes status-seeking behaviour in a context-dependent manner.

1. Introduction

Testosterone is one of the major sex steroids produced primarily by the gonads and plays a significant role in body growth and sexual differentiation [1]. Testosterone has been implicated in various social behaviours [2]. As theorized by the Challenge Hypothesis [3–5], testosterone levels rapidly adapt to mating and competitive challenges, and these adaptations are incorporated as feedback into social behaviours, particularly aggression, which in many species is the primary vehicle to gain and maintain social status. Complementary to the Challenge Hypothesis is the Biosocial Model of Status [6,7], according to which testosterone increases (decreases) experienced by winners (losers) should trigger a virtuous (vicious) cycle in terms of status achievement. Cross-species evidence, combined with early evidence from human studies, support the predictions of the Biosocial Model of Status by showing that testosterone advances social status by promoting anti-social behaviours (e.g. aggression, selfish behaviour, lack of empathy, rejection in the ultimatum game (UG)) [8,9].

Recent research [10–12], however, has revealed a more nuanced role of testosterone by showing that testosterone could also foster pro-social behaviours when such behaviours are contextually appropriate for gaining social status. For example, in their seminal study, Eisenegger *et al*. [11] found that participants receiving testosterone (versus placebo) were more likely to make generous offers in the UG. Because testosterone increased concerns for status, participants receiving testosterone made fairer offers to avoid rejections, which threatened participants' social status. A follow-up study by Dreher *et al*. [10] more directly

tested this hypothesis. In this study, a modified version of the UG was used in which the responder first accepted/rejected the proposer's offer and then had the opportunity to either reward or punish the proposer at his own expense [10]. Results showed that participants receiving testosterone (versus placebo) more severely punished proposers making unfair offers and more generously rewarded proposers making fair offers. Overall, these findings support the social status hypothesis [13], according to which testosterone flexibly promotes either pro-social or anti-social behaviours depending on their instrumental value to gain and maintain status in the context at hand.

Obtaining and maintaining a positive reputation can lead to high social status [14]. Reputation seeking explains why individuals tend to behave more altruistically when being watched by others (i.e. audience effect) [15,16]. For example, Bereczkei *et al*. [17] found that people were more willing to help others if their donation could be witnessed by an audience (versus concealed). Izuma *et al*. [18] replicated these findings in a group of healthy individuals. Although these studies have substantiated the link between the audience effect and status signalling, they leave open the question of whether testosterone, a major sex steroid associated with social status-seeking [13], could causally modulate altruistic behaviour when being observed.

To address this question, we adopted a novel task where participants were asked whether to accept or not a variable monetary transfer to a charity organization [19–21]. Monetary transfers were coupled with variable monetary costs that participants would incur if they accepted the transfer. Accordingly, in each trial, participants had to weight the benefit to the charity against the cost to themselves. Critically, we manipulated the audience effect such that, on half of the trials, participants' choices were observed by an unfamiliar observer sitting behind them (i.e. public condition), while, on the other half of the trials, participants' choices were made in private (i.e. private condition). Based on the social status hypothesis, we hypothesized that exogenous testosterone would magnify the effect of being watched on altruistic behaviour.

2. Methods

(a) Participants

One hundred and forty healthy males (mean age = 20.48 years, s.d. = 1.68, age range = 18–25) were recruited through university advertisement. We screened participants through telephone interviews, and those individuals taking psychotropic medications or having any psychiatric/neurological disorders were considered ineligible to participate. We recruited males as the dosing and pharmacokinetics of single dose Androgel administration have only been established for men [22]. Participants were instructed to abstain from alcohol, caffeine intake, and smoking for 24 h before the testing session. Each participant received a single dose of Androgel or placebo gel in a double-blind, placebo-controlled, mixed design. Written informed consent was obtained from all participants. Participants were compensated with 170 Chinese yuan (approx. $24) as a participation fee. This study was conducted in accordance with the Declaration of Helsinki and approved by the Shenzhen University Medical Research Ethics Committee.

(b) Testosterone administration

All sessions started at 13.00 and lasted approximately 4 h. Participants in the testosterone group received a single dose of testosterone gel, containing 150 mg testosterone (Androgel®). Participants in the placebo group received a colourless hydroalcoholic gel. In both treatment groups, the gel was applied to shoulders and upper arms by a male research assistant, who was blind to both the experimental condition (i.e. the testosterone gel and placebo were packed identically) and purpose of the study. The donation task commenced 3 h post-dosing in accordance with previous pharmacokinetic data [22–25]. Participants also completed two additional tasks on social cognition that are not reported here. During the waiting period, participants were asked to stay in the testing rooms and were provided with newspapers and magazines that were not related to the present study.

(c) Donation task

In a pilot experiment, 50 participants from the same student population rated 20 real charity organizations in terms of their willingness to donate money to those organizations ('To what extent are you willing to donate to the charity', with 1 = 'least willing to donate' and 9 = 'most willing to donate'). Among them, the organization *Help the Orphan with Rare Diseases* was rated with the highest score ($M = 7.48$, s.d. = 1.10) and was thus selected as the charity organization for the donation task.

The task was a modified version of the dictator game (see also Izuma *et al*. [21]; Obeso *et al*. [19]; Park *et al*. [20]), in which we orthogonally manipulated the amount of money donated to the charity (range: renminbi (RMB) 4 to 40, in incremental steps of RMB 4) and the monetary cost incurred by the participants (range: RMB 1–10, in incremental steps of RMB 1) (figure 1*a*). Each matrix cell was presented twice in the public condition and twice in the private condition, respectively (see below), yielding a total of 400 trials. Within each condition, matrix cells were presented in a randomized order. Participants were endowed with 15 yuan and were told at the beginning of the study that at the end of the experiment one trial would be randomly selected, and their decision on that trial would be implemented. For example, in a trial in which the participant had incurred a 9 yuan cost for a 40 yuan benefit for the charity, the participant gained 6 (i.e. 15–9) yuan and the charity gained 40 yuan. At the end of the experiment, participants were asked to make the donation ($M = 18.31$, s.d. = 12.52, range = 0–40) in agreement with the selected trial to the *Help the Orphan with Rare Diseases* organization through a mobile App (i.e. Wechat Pay). Thus, the donation task was incentive-compatible.

On each trial, participants were presented with two options with white frames. One option presented the monetary cost to the participants and the monetary benefit to the charity organization in case participants decided to proceed with the transfer. The other showed the consequences (i.e. no cost for the participants and no benefit for the charity organization) in case participants decided not to proceed with the transfer. Participants were asked to choose one of the options within 5000 ms. After participants decided whether to accept or reject the proposed monetary transfer, their chosen option was highlighted by a red rectangle for 1.5 s. The position of the two options was counterbalanced across trials within each participant. An intertrial interval of 1000 ms was used (figure 1*b*). The task was programmed using E-Prime (v. 2.0; Psychology Software Tools, Inc., PA, USA).

(d) Manipulation of the audience effect

Crucially, participants needed to complete the above task in both public and private conditions (within-subject independent variable). In the public condition, participants' performance was watched by an unfamiliar male observer, while in the private condition, participants completed the task alone. Notably, half of the participants were randomly assigned to experience the

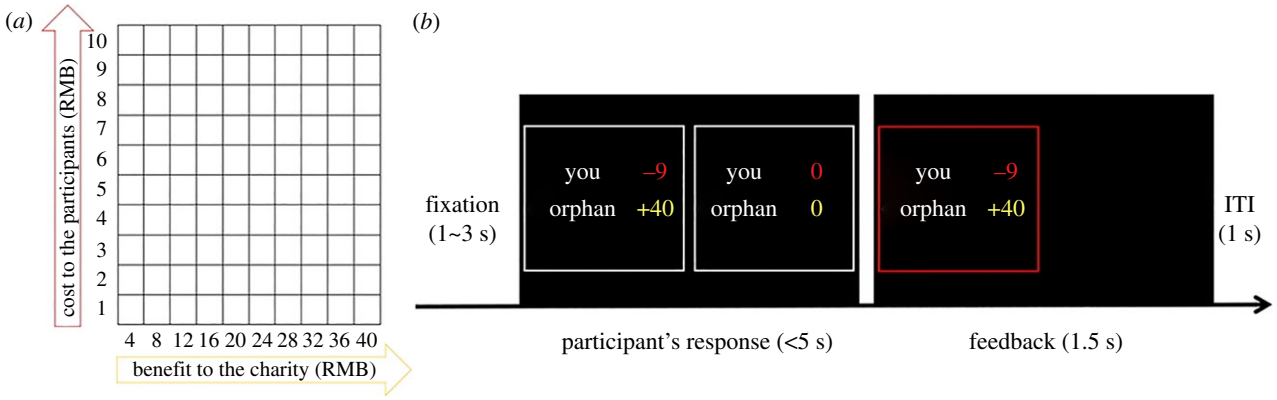

Figure 1. (*a*) The donation task matrix. Numbers on the *y*-axis indicate the amount of money participants could lose; numbers on the *y*-axis indicate the amount of money the charity could benefit. (*b*) Trial and trial timing example. In this trial, the participant would lose 9 RMB and the charity would gain 40 RMB, if the participant accepted the proposed monetary transfer. (Online version in colour.)

private condition first and the public condition second, whereas the opposite was true for the remaining half of the participants (counterbalancing). At the beginning of the experiment, a male experimenter gave a paper with instructions about the donation task and information about the *Help the Orphan with Rare Diseases* organization (e.g. mission, how the donated money will be used). Participants were given time to read the paper and ask any questions. For those participants experiencing the public condition first, the donation task was set up such that it would crash after the practice trial [21]. At that point, the experimenter entered the testing room and took out the laptop to repair it. After three minutes of waiting, the experimenter came back and told participants that the problem had not been fixed and a research assistant would stay in the room and record their choices to make sure that all data would be saved. The observer sat about 90 cm behind the participant throughout the session. After completing the first session, participants took a short break and then started the second session. At the beginning of the second session (private condition), the experimenter told participants that the problem had now been fixed and they could now complete the task alone in the room. For those participants experiencing the private condition first, the experimenter left the testing room after setting up the donation task, and participants performed the task alone in the room. After finishing the first session, the above-mentioned procedure was followed, and participants completed the task in the presence of an observer (public condition). No participants expressed suspicion about the study procedure.

(e) Measures of individual difference

Previous research has shown that personality characteristics such as impulsivity level, emphatic concern, autistic trait, and social value orientation could influence our prosocial decisions in daily life [26]. Thus, we also measured a series of personality traits that could confound the treatment effect on behaviour using the following questionnaires, including the Barratt impulsivity scale (BIS) [27], the interpersonal reactivity inventory (IRI) [28], the psychopathic personality inventory (PPI) [29], the autism quotient (AQ) [30], the Machiavellianism test (Mach-IV) [31], and the social interaction anxiety scale (SIAS) [32]. Participants completed these questionnaire measures before the pharmacological manipulation [19].

(f) Statistical analysis

We removed 105 trials (0.19% of the total trials) in which participants failed to respond within 5 s. We used R and lme4 [33] to perform a linear mixed-effects analysis on the choice behaviour. This model predicted the probability of accepting an offer (logit) and tested the effect of testosterone on the audience effect (see below).

$$\begin{aligned}\text{logit}(P(\text{accept})) = {} & \beta_0 + \beta_1 * \text{benefit} + \beta_2 * \text{cost} + \beta_3 * \text{treatment} \\ & + \beta_4 * \text{observation} + \beta_5 * \text{treatment} * \text{observation},\end{aligned}$$

Specifically, the logit parameters in the model tested the likelihood of acceptance as a function of the potential monetary value of the offer, with cost being the monetary cost for the participants and benefit being the benefit to the charity organization, treatment (testosterone versus placebo), and observation (public versus private). Treatment and observation were entered as categorical fixed-effect factors, while cost and benefit were treated as continuous fixed-effect predictors. The random-effects structure of the model was selected based on the maximal complexity rule, which was supported by our data [34]. For the order of observation variable (i.e. public or private condition first), no significance order effect was found, and this variable did not interact with any other variables. For these reasons, order of observation was omitted from further analyses.

To exclude the possibility that any treatment effect (testosterone versus placebo) on donation decisions was due to individual differences in personality traits, we also did a series of additional analyses to check the robustness of the findings in the main analyses. To this end, we first compared group difference on these trait measures, and next we included these scores as covariates in the regression model to test if the effects of interest (see above) remained significant.

We ran similar mixed-effect linear regression analyses to determine whether the predictors reported in the above equation predicted choice latency. Response time was skewed and log-transformed. More information about these analyses is reported in the Results section.

(g) Open practice

All the data and analysis scripts are available on the project's open science framework (OSF) page: https://osf.io/3n6q5/.

3. Results

(a) No group difference in personality traits

Participants in the testosterone and placebo group did not differ in terms of their personality traits related to donation decisions (table 1).

Table 1. Personality differences between testosterone and placebo groups. Note: BIS: Barratt impulsivity scale; IRI, interpersonal reactivity inventory; PPI, psychopathic personality inventory; AQ, autism quotient; Mach-IV, Machiavellianism test; SIAS, social interaction anxiety scale.

	placebo	testosterone	*t*	d.f.	*p*-value
BIS	65.63 (8.27)	63.33 (8.20)	1.65	138	0.10
IRI	93.76 (8.32)	94.17 (8.23)	−0.30	138	0.77
PPI	149.20 (19.86)	151.76 (21.12)	−0.74	138	0.46
AQ	22.63 (5.06)	21.59 (5.60)	1.16	138	0.25
Mach-IV	96.13 (8.86)	97.51 (7.95)	−0.97	138	0.33
SIAS	27.84 (11.76)	29.86 (11.58)	1.02	138	0.31

Table 2. Results of mixed-effect logistic regressions predicting donation decision. Note: reference levels were set as follows: treatment, placebo; observation, private. Table also shows goodness-of-fit statistics: AIC, Akaike information criterion; BIC, Bayesian information criterion. Significance: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

	all	placebo	testosterone
	b (SE)	*b* (SE)	*b* (SE)
intercept	2.338*** (0.445)	2.403*** (0.538)	2.618*** (0.383)
cost	−0.497*** (0.057)	−0.594*** (0.083)	−0.412*** (0.075)
benefit	0.430*** (0.039)	0.518*** (0.063)	0.346*** (0.045)
treatment	0.281 (0.606)		
observation	0.299*** (0.068)	0.303*** (0.069)	0.523*** (0.064)
treatment × observation	0.231* (0.093)		
AIC	12 997.4	6051.5	6941.2
BIC	13 104.6	6133.9	7023.6
N (observation)	55 895	27 957	27 938
N (participant)	140	70	70

(b) Testosterone administration enhances the audience effect

Using linear mixed-effects analysis, we predicted the likelihood of acceptance as a function of Cost and Benefit associated with the proposed monetary transfer, Treatment, Observation and their interaction term (see Methods). Results of these analyses are reported in table 2. We found a main effect of benefit ($b = 0.430$, s.e. = 0.039, $Z = 11.155$, $p < 0.001$) and cost ($b = -0.497$, s.e. = 0.057, $Z = -8.753$, $p < 0.001$), indicating that participants were more likely to donate as the benefits for the charity increased and less likely to donate as the cost for themselves increased. No significant main effect of treatment was found. However, a significant main effect of observation ($b = 0.299$, s.e. = 0.068, $Z = 4.386$, $p < 0.001$) emerged, such that participants were more likely to donate in the public (versus private) condition (audience effect). More importantly, this effect was qualified by a significant interaction with Treatment ($b = 0.231$, s.e. = 0.093, $Z = 2.479$, $p = 0.013$, figure 2). When the analyses were run separately within the testosterone and placebo group, we found a significant main effect of Observation; however, this effect was greater in magnitude in the testosterone group ($b = 0.523$, s.e. = 0.064, $Z = 8.234$, $p < 0.001$) than in the placebo group ($b = 0.303$, s.e. = 0.069, $Z = 4.424$, $p < 0.001$). The directionality of this interaction is also evident from figure 2.

(c) Personality characteristics do not account for the testosterone effect

To rule out the possibility that individual difference in impulsivity, empathy, autistic trait, psychopathy, and mood could confound the behavioural effects observed, we included these variables as covariates. The pattern of results of the variables of interest was the same as our original model, as the interaction between social observation and testosterone treatment remained significant ($b = 0.232$, s.e. = 0.093, $Z = 2.374$, $p = 0.018$). Therefore, the effects of testosterone on donation decisions could not be attributed to group difference on individual personality traits that are relevant to prosocial decisions (see electronic supplementary material, table S1 for details of regression outputs).

(d) Social observation shortens choice latency

A last set of analyses was run to predict choice latency. This model contained the same predictors reported in the equation above (see Methods), with response time (log-transformed) introduced as the dependent variable (see electronic

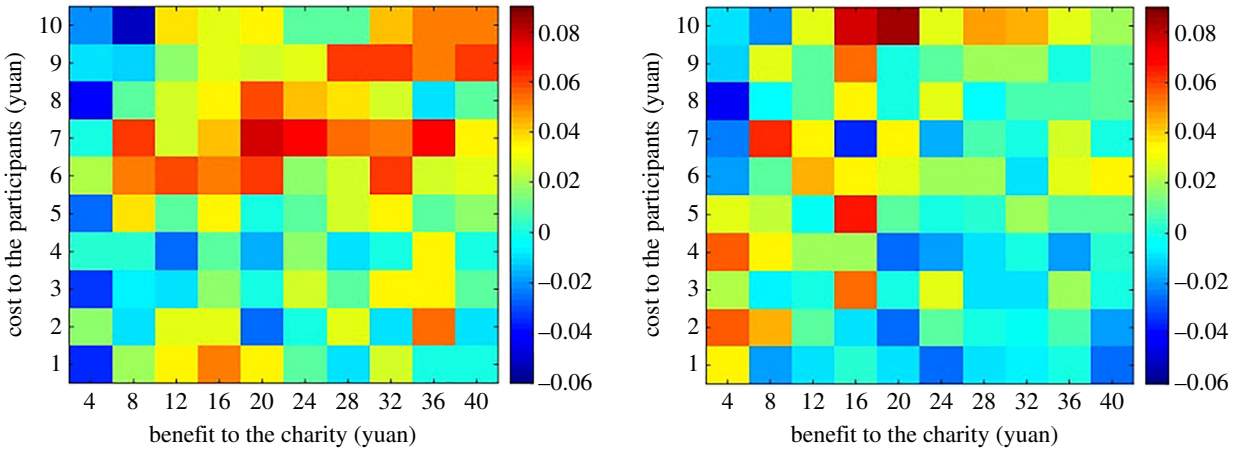

Figure 2. Heatmap of the probability of acceptance to donate, with warmer colours indicating greater probability of acceptance in the public versus private condition (i.e. greater audience effect). Heatmap on the left refers to the testosterone group, while heatmap on the right refers to the placebo group. (Online version in colour.)

supplementary material, table S2 for details of the results). Participants made faster decisions as the benefits to the charity increased ($b = -0.003$, s.e. = 0.0004, $t = -9.338$, $p < 0.001$) and made slower decisions as the cost to themselves increased ($b = 0.009$, s.e. = 0.001, $t = 8.334$, $p < 0.001$). Moreover, participants responded faster in the public ($M \pm$ s.d. 899 ± 440 ms) compared to the private condition (950 ± 491 ms), $b = -0.044$, s.e. = 0.004, $Z = -11.426$, $p < 0.001$, corroborating the social facilitation effect shown in past research using a similar paradigm [21]. These effects held after including personality traits as covariates in the regression model.

4. Discussion

In the current study, we tested the effects of testosterone (versus placebo) on altruistic behaviour using an incentive-compatible donation task, wherein participants were asked to either accept or reject a monetary transfer to a real charity organization both in the presence and absence of an observer. Trials varied in terms of benefits to the charity and costs to the participants. First, corroborating previous findings in the human prosocial decision-making literature [19,21,35], participants' altruistic behaviour increased with increasing benefits to the charity and decreased with increasing costs to themselves. Second, in support of the audience effect [15,16,21], we found that participants donated more money when in the presence of an unfamiliar observer compared to when they completed the donation task alone. More importantly, we demonstrated that testosterone magnified this audience effect, and this effect held after controlling personality characteristics related to prosocial decisions. Furthermore, participants responded faster in the presence of an observer rather than its absence, corroborating past research on the social facilitation effect [21].

According to the social status hypothesis [13], testosterone promotes behaviours that are contextually appropriate to achieve and maintain social status. For example, using a modified version of the UG, Dreher and colleagues found that receiving testosterone increased aggressive behaviour (i.e. punishment) in status-threatening situations (i.e. being provoked via unfair offers), but increased altruistic behaviour (i.e. generosity) in the absence of status threats (i.e. receiving large offers) [10]. In our study, testosterone increased prosocial behaviour (i.e. donations to a charity organization) when participants' reputation was at stake (i.e. public condition). Reputation gained from displaying prosocial behaviour makes individuals more attractive as coalitional partners and thus more likely to enjoy high levels of influence, social respect, and valued resources (prestige-based social status). For example, individuals who are willing to help are more likely to be helped in return [36] and be chosen as allies, and less likely to have competitors [37]. In a series of studies using economic games, Barclay showed that individuals who generously contributed to a common fund were entrusted with more money in subsequent trust games [38], and individuals punishing free riders at their own expense in a cooperative group game were more likely to gain respect, trust, and money [14]. Other laboratory studies complemented these findings by showing that altruistic behaviour leads people to gain leadership [39], romantic interest [40], and high-status attributions [41].

Our findings also spark new research questions regarding the neural mechanism by which testosterone influences the audience effect. Neuroimaging studies showed that donating to a charity in the presence of observers recruited brain activity in the striatum, a brain region associated with reward processing [18]. The reward system is heavily populated by androgen receptors [42], and social behaviours modulate expressions of androgen receptors in this area [43]. Not surprisingly, human studies show that exogenous testosterone heightened activity in the reward system in response to various social stimuli [44,45]. For example, Herman *et al*. [44] found that exogenous testosterone increased ventral striatal responses during reward anticipation in a monetary incentive delay task and suggested that these effects were likely mediated by dopamine activity. Recent work by Wagels *et al*. [45] showed that testosterone administration increased brain activity in the default brain network, which is active when individuals process social information [46]. In addition to the reward system, the default brain network might also be involved in explaining the behavioural findings reported here; however, this hypothesis awaits empirical testing.

Some issues warrant further discussion. First, a large body of literature suggests that women are more prosocial than men across different cultural contexts [47,48].

As argued elsewhere [4], we do not anticipate the effects of acute testosterone pulses on social behaviours to be different between the sexes; however, it remains interesting to corroborate this prediction by replicating the current study in a sample of both men and women. Second, it is possible that the staged program crash used in our experiment to induce the public condition might have influenced participants' decisions. For example, some participants might have felt sorry for the experimenter and that could have influenced their decision in the task. Future research employing alternative ways to induce the public condition are needed to rule out this possibility and corroborate our findings. Third, in our task, one could speculate that keeping more money for oneself in the private condition might have been a way to achieve status through resource (i.e. money) acquisition. However, when we decomposed the interaction effect found in the main statistical model, we found no evidence that the donation rate in the private condition was reduced in the testosterone condition compared to the placebo condition ($b = 0.727$, s.e. = 0.673, $Z = 1.081$, $p = 0.28$). More studies are needed to address the boundary conditions under which testosterone promotes generous and selfish behaviour. Fourth, on each trial, participants were asked to make a decision within 5 s. Recent research suggests that testosterone administration interacts with time pressure in predicting cooperative behaviour [49]. Future studies could test whether the results found here are generalizable to conditions in which time constraints are absent.

In conclusion, our findings demonstrate that testosterone administration increases sensitivity to social reputation in a donation task. These data provide direct causal evidence for the social status hypothesis.

Ethics. All procedures were approved by the Shenzhen University Medical Research Ethics Committee and in accordance with the Declaration of Helsinki.

Data accessibility. All the data and analysis scripts are available on the project's Open Science Framework (OSF) page: https://osf.io/3n6q5/.

Authors' contributions. Y.W. and S.Z. conceived and designed the study, Y.Z. and J.O. collected the data. Y.W., J.O., and Y.H. analysed the data. Y.W. wrote the first version of the paper, Y.H. and S.Z. provided critical revisions. All authors approved the final version for submission.

Competing interests. We declare we have no competing interests.

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