Testosterone reduces generosity through cortical and subcortical mechanisms

Jianxin Ou[a,b,1], Yin Wu[a,b,1,2], Yang Hu[c,d], Xiaoxue Gao (高晓雪)[c], Hong Li[e,f,2], and Philippe N. Tobler[g]

[a]School of Psychology, Shenzhen University, 518060 Shenzhen, China; [b]School of Psychology, Shanghai University of Sport, Shanghai 200438, China; [c]School of Psychological and Cognitive Sciences, Peking University, 100871 Beijing, China; [d]School of Business and Management, Shanghai International Studies University, Shanghai 201620, China; [e]School of Psychology, South China Normal University, 510631 Guangzhou, China; [f]Institute for Brain and Psychological Sciences, Sichuan Normal University, 610066 Chengdu, China; and [g]Zurich Center for Neuroeconomics, Department of Economics, University of Zurich, 8006 Zürich, Switzerland

Edited by Ernst Fehr, University of Zurich, Zurich, Switzerland, and accepted by Editorial Board Member Michael S. Gazzaniga February 4, 2021 (received for review October 17, 2020)

Recent evidence has linked testosterone, a major sex hormone, to selfishness in economic decision-making. Here, we aimed to investigate the neural mechanisms through which testosterone reduces generosity by combining functional MRI with pharmacological manipulation among healthy young males in a double-blind, placebo-controlled, between-subject design. After testosterone or placebo gel administration, participants performed a social discounting task in which they chose between selfish options (benefiting only the participant) and generous options (providing also some benefit to another person at a particular social distance). At the behavioral level, testosterone reduced generosity compared to the placebo. At the neural level ($n = 60$), the temporoparietal junction (TPJ) encoded the other-regarding value of the generous option during generous choices, and this effect was attenuated by testosterone, suggesting that testosterone reduced the consideration of other's welfare as underpinned by TPJ activity. Moreover, TPJ activity more strongly reflected individual differences in generosity in the placebo than the testosterone group. Furthermore, testosterone weakened the relation between the other-regarding value of generous decisions and connectivity between the TPJ and a region extending from the insula into the striatum. Together, these findings suggest that a network encompassing both cortical and subcortical components underpins the effects of testosterone on social preferences.

altruistic preferences | androgen | temporoparietal junction | prosocial behavior | social cognition

Altruistic acts characterize human societies. Individuals are willing to help others (even strangers) often at a cost to themselves, and these prosocial decisions benefit mankind (1). However, we are not equally generous to everyone alike. Instead, our generosity toward others critically depends on social and situational factors, such as the social distance between the decision maker and the person who benefits from a prosocial decision (2–4). Specifically, our generosity toward others declines with increasing social distance such that we usually behave more generously when interacting with close others compared to total strangers.

Behavioral neuroendocrinology has highlighted the central role of hormones in human social cognition and decision-making (5). For example, the sex steroid testosterone (6) has been shown to affect social interaction and economic choices involving others (7, 8). Moreover, testosterone administration in men reduces generosity in the Ultimatum Game (ref. 9, but see refs. 10 and 11) and trust in the Trust Game (12). In our own recent work, we revealed a causal link between exogenously increased levels of testosterone and reduced generosity in economic decision-making (13). Our social discounting task required participants to choose between selfish and generous options, and testosterone reduced generosity in particular when participants interacted with distant (versus close) others. However, the neural mechanisms through which testosterone influences social-distance–dependent generosity remained unclear.

It is well established that prosocial behavior is associated with theory-of-mind/mentalizing processes and empathy; in other words, taking the emotions, mental states, and preferences of others into account facilitates prosocial actions (14). The temporoparietal junction (TPJ) is activated consistently in theory-of-mind and perspective-taking tasks (15, 16). Noninvasive brain stimulation studies confirmed that the TPJ plays a critical role in perspective taking, self–other distinction, moral judgment, and intra/intergroup intention inference (17, 18). In the social discounting task, stronger TPJ activations were found for generous compared to selfish decisions (3). Indeed, TPJ activity is parametrically associated with altruism (19, 20) and with overcoming egocentric motives for generous choices (3, 21). Disrupting TPJ activity through transcranial magnetic stimulation leads to more selfish choices, providing causal evidence for the role of TPJ in prosocial behavior (22). Based on this mounting body of evidence, one may ask whether testosterone reduces generosity by affecting TPJ activity. Moreover, recent research implicates the striatum (23) and cross talk between the TPJ and the striatum (21) or ventromedial prefrontal cortex (3) in generous decisions.

Significance

Testosterone is associated with aggressive behavior in both animals and humans. Here, we establish a link between increased testosterone and selfishness in economic decision making and identify the neural mechanisms through which testosterone reduces generosity in a double-blind, placebo-controlled, between-participant study. We find that testosterone induces more selfish choices, particularly when distant others are concerned. Moreover, it disrupts the representation of other-regarding value in local activity and functional connectivity involving the temporoparietal junction and subcortical regions involved in reward processing. Our study provides causal evidence for a testosterone-mediated neurohormonal link between generosity and the valuation system.

Author contributions: J.O., Y.W., and P.N.T. designed research; J.O. and Y.W. performed research; J.O., Y.W., Y.H., X.G., H.L., and P.N.T. contributed new reagents/analytic tools; J.O., Y.W., and Y.H. analyzed data; and J.O., Y.W., Y.H., X.G., H.L., and P.N.T. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. E.F. is a guest editor invited by the Editorial Board.

[1]J.O. and Y.W. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: yinwu0407@gmail.com or lihongwrm@vip.sina.com.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2021745118/-/DCSupplemental.

Published March 15, 2021.

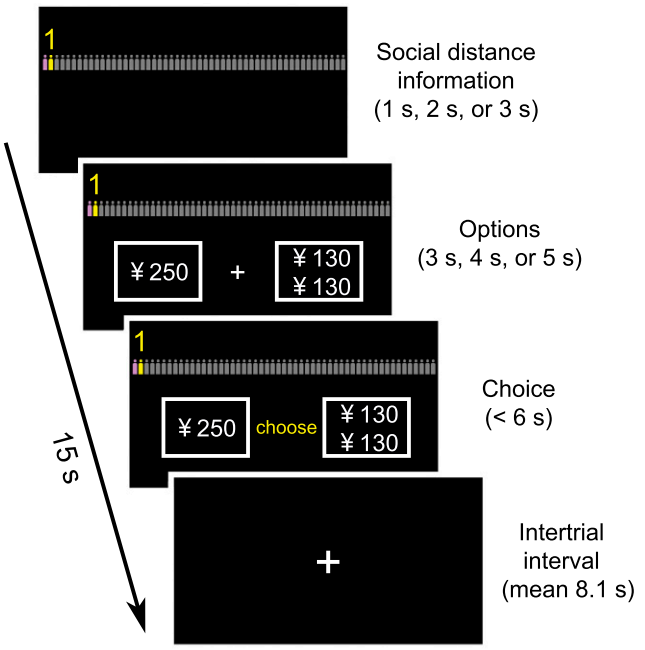

Fig. 1. Social discounting task. In each trial, participants viewed social distance information (8 levels, ranging from 1 to 100) regarding the other person, followed by two choice options. One option was generous (both the participant and the other person receive CNY 130), and the other option was selfish (the participant receives a typically larger amount of money alone; nine levels, ranging from CNY 130 to CNY 290).

Thus, here, we focused on the functional connectivity of the TPJ with the cortical and subcortical reward/valuation system.

The aims of the present study were twofold. First, we aimed to corroborate the effects of testosterone on generosity at the behavioral level. We administered a social discounting task (3) in which participants were required to choose between a selfish option (i.e., receiving a larger amount of money for themselves and nothing for the other person) and a generous option (i.e., receiving a smaller amount of money for themselves coupled with the same monetary reward to the other person). Participants made these decisions for interacting partners at different social distances. We have shown that testosterone reduces generosity in this task, particularly when interacting with distant others (13). Here, we aimed to corroborate these findings in the scanner environment. Second, we aimed to identify the neural mechanisms underlying the effects of testosterone on generous decisions. Given the central role of the TPJ (3, 22) in social, cognitive, and prosocial behavior, we focused on local activity and connectivity of the TPJ.

Results

Replication of Reduced Generosity by Testosterone Administration. To investigate how testosterone affected generosity, we used a social discounting task (Fig. 1), in which participants decided between a selfish option, which provided varying monetary amounts only for the participant, and a costly generous option, which provided money also for another person at a particular social distance. We first considered our model-free measure of generosity, that is, the area under the curve (AUC) of the costs participants incurred (amount forgone relative to the selfish option) by choosing the generous option. Model-free generosity in the testosterone group (median = 0.253 and mean rank = 29.75) was significantly smaller than in the placebo group (median = 0.314 and mean rank = 39.84; Mann–Whitney U test = 405, Z = 2.10, and P = 0.036; Fig. 2*A*). Thus, testosterone decreased overall generosity toward others.

For the model-based analyses (Fig. 2*B*), we observed a larger discount rate (k) in the testosterone group (median = 0.11 and mean rank = 39.78) than in the placebo group (median = 0.07 and mean rank = 28.56; Mann–Whitney U test = 386, Z = 2.33, and P = 0.020). In other words, participants receiving testosterone showed a steeper decline in generosity toward more remote others, suggesting an increased social discounting effect induced by testosterone. We did not find a significant difference on the V parameter, the intercept of the discount function representing other-regarding value at social distance D = 0 (Placebo: median = 149.91 and mean rank = 32.66; Testosterone: median = 153.41 and mean rank = 36.14; Mann–Whitney U test = 517, Z = 0.73, and P = 0.468), suggesting that the two groups did not differ in generosity at short social distances. Together, these findings replicate previous research indicating that testosterone reduces (model-free and model-based) generosity (13) and extend it by showing that the effect occurs also inside the scanner environment.

TPJ Encodes Value of Generous Options. For the functional MRI (fMRI) analyses, we focused on generous decisions and first aimed to identify brain regions that varied parametrically with the social-distance–dependent amount forgone. Across all participants, we observed a positive correlation between the other-regarding value of amount forgone and activity in the left TPJ (peak coordinate: [−60, −34, 20], Z = 4.29, and P = 0.011, whole-brain cluster-level family-wise error [FWE] corrected; Fig. 3*A*). Activity of the right TPJ showed a similar effect (peak coordinate: [57, −34, 26], Z = 4.31 and P = 0.050, whole-brain cluster-level FWE corrected, see Fig. 3*B* and Table 1). Thus, bilateral TPJ encoded the social-distance–dependent other-regarding value in generous decisions in the entire sample of participants. Moreover, in line with the role of social distance in generous choice, bilateral TPJ activity also parametrically covaried with social proximity, that is, the inverse of social distance (*SI Appendix*, Table S5).

Testosterone Reduces TPJ Signals Related to Value of Generous Options. Next, we tested whether testosterone played a role in coding the other-regarding value in the TPJ. Based on the group-level findings of the parametric effect in TPJ, we created an ROI (region of interest) which combined a 6 mm sphere centered at

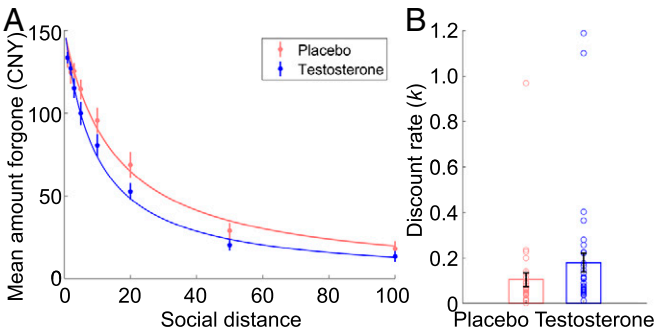

Fig. 2. Testosterone increases social discounting. (*A*) Generosity, as measured by the amount of money participants were willing to forgo to benefit the other person, decreased with social distance, both under placebo and testosterone. Amounts forgone were obtained separately for each participant by fitting a logistic function to the choices at each social distance. The mean amounts forgone were then fitted with a hyperbolic function capturing social discounting. (*B*) The discount rates (k, i.e., steepness of the individually determined social discounting function) were larger for the testosterone group than for the placebo group (Mann–Whitney U test = 386, Z = 2.33, and P = 0.020). All error bars are SEMs.

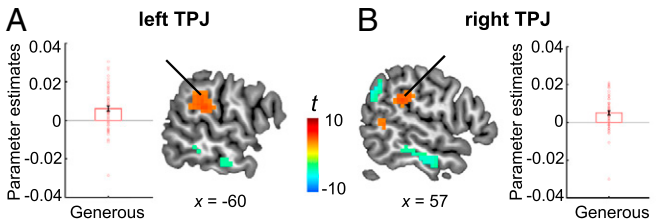

Fig. 3. TPJ activity processes generosity parametrically. (*A*) Left TPJ region (peak [−60, −34, 20]) coding degree of generosity ($Z = 4.29$ and $P = 0.011$, whole-brain cluster-level FWE corrected). The parameter estimates reflect parametric modulation of all participants from illustrated left TPJ region and show that activity encodes the amount forgone during generous choices. (*B*) Right TPJ region (peak [57, −34, 26]) showing trend-level relation to degree of generosity ($Z = 4.31$ and $P = 0.050$, whole-brain cluster-level FWE corrected). The parametric modulators of all participants from illustrated right TPJ region show that activity encodes the amount forgone during generous choices. Activations in *A* and *B* and similar figures throughout are displayed at $P < 0.001$ uncorrected.

Table 1. Activity: Regions showing significant parametric modulation by amount forgone for generous choices across all participants (Fig. 3)

				MNI coordinates		
Name	Side	Cluster size	*Z* value	*x*	*y*	*z*
Superior temporal pole	L	23	4.50	−42	5	−22
TPJ	R	82	4.31*	57	−34	26
Paracentral lobule	R	17	4.30	15	−31	47
TPJ	L	125	4.29*	−60	−34	20
Middle cingulate cortex	L	15	3.83	−15	−25	38
Middle temporal gyrus	R	12	3.40	57	−49	5

Threshold: uncorrected $P < 0.001$, cluster size ≥ 10.
*Cluster-level *P* (whole-brain FWE) < 0.05.

the peak coordinate in the left (−60, −34, 20; Fig. 4*A*) and right (57, −34, 26; Fig. 4*B*) TPJ (see above). Compared to the placebo group, TPJ activity was less sensitive to the amount forgone in the testosterone group (peak coordinates of left TPJ: [−57, −34, 23], $Z = 2.55$, and $P = 0.086$; peak coordinates of right TPJ: [57, −34, 29], $Z = 2.78$, and $P = 0.049$, small-volume peak-level FWE corrected; Fig. 4*C*). Thus, testosterone decreased the neural representation of other-regarding value in the TPJ during generous decisions.

Right Temporal-Parietal Junction (rTPJ) Activity Correlates with Individual Differences in Generosity More Strongly in the Placebo Group than in the Testosterone Group. As we observed that TPJ activity increased with the amount forgone in generous choice trials, one may ask whether TPJ activity also reflects individual differences in task-related generosity across all trials and whether and how testosterone affected this association. Thus, we performed regression analyses with generosity (i.e., log-transformed discounting rate or AUC) as dependent variables and with left and right TPJ activity as independent variables. A significant main effect of rTPJ was found (log *k*: $b = -45.04$, SE = 21.96, $t = -2.05$, and $P = 0.045$; AUC: $b = 17.86$, SE = 7.13, $t = 2.51$, and $P = 0.015$), suggesting that stronger rTPJ activity was associated with increasing generosity across individuals. The interaction between group and rTPJ activity was also significant (log *k*: $b = 74.19$, SE = 32.42, $t = 2.29$, and $P = 0.026$; AUC: $b = -26.06$, SE = 10.52, $t = -2.48$, and $P = 0.016$; see Fig. 5 and *SI Appendix*, Table S2), indicating that testosterone affected the relation between rTPJ activity and generosity. Specifically, rTPJ activity was associated with the amount forgone in the placebo group (log *k*: $b = -45.04$, SE = 24.83, $t = -1.81$, and $P = 0.081$; AUC: $b = 17.86$, SE = 7.47, $t = 2.39$, and $P = 0.024$) but not in the testosterone group (all $P > 0.1$, see Fig. 5 and *SI Appendix*, Table S2). Thus, the amount-forgone–related TPJ activity derived from generous choices reflected individual differences in overall generosity across the task, and testosterone administration weakened this association.

Testosterone Reduces Functional Connectivity between rTPJ and Insula/Striatum. Next, we asked whether and how testosterone affected coupling of the TPJ with other brain regions that contribute to the valuation of reward during generous decisions. Using the right TPJ as a seed region, we found a group difference in functional connectivity with the insula/striatum [Fig. 6*A*; peak coordinates: [−27, 17, −10], $Z = 4.20$, $P = 0.023$, small-volume FWE corrected within meta-analytically (24) derived valuation regions]. Compared to the testosterone group, participants receiving the placebo showed stronger functional coupling of the right TPJ with the insula/striatum as the amount forgone increased (Fig. 6*B* and Table 2; further details and additional analyses in *SI Appendix*, Supplementary Methods and Results and Fig. S2).

Discussion

Combining a pharmacological manipulation with fMRI, we tested the causal effects of testosterone on generosity and the corresponding neural basis in healthy young males. Both the model-free and model-based analyses showed that exogenous testosterone administration reduced generosity, particularly when interacting with more-distant others, corroborating our past findings (13) in the scanner environment. At the neural level, testosterone weakened the association between TPJ activity and amount forgone in generous decisions. Furthermore, the TPJ activity associated with amount forgone also correlated with individual differences in overall generosity in the placebo group and did so more strongly than in the testosterone group. Finally, testosterone disrupted the generosity-level–dependent connectivity between TPJ and insula/striatum.

Our results revealed that the TPJ represents a parametric generosity signal, which supports the idea that the TPJ contributes to encoding other-regarding benefits and promoting generous choices. Previous research linked structural gray-matter volume and functional activity of the TPJ to individual differences in altruistic behavior (20, 21). Moreover, the TPJ has been associated with attention reorientation (25), theory of mind/mentalizing (16), overcoming egocentricity bias (3, 22), and trust behavior (26). For instance, suppressed TPJ activity is associated

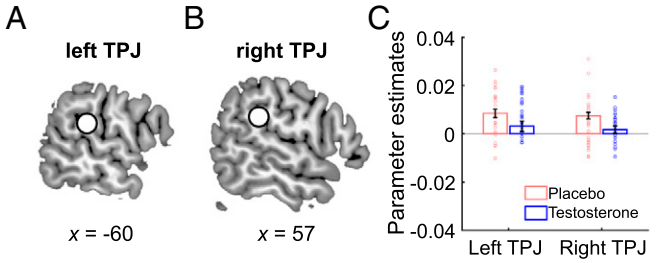

Fig. 4. Testosterone reduces neural coding of parametric generosity. Regions of interest in (*A*) left TPJ (based on Fig. 3*A*; 6 mm sphere at [−60, −34, 20]) and (*B*) right TPJ (based on Fig. 3*B*; 6 mm sphere at [57, −34, 26]). (*C*) During generous choices, the TPJ of participants receiving placebo coded the amount forgone more strongly than the TPJ of participants receiving testosterone (left TPJ: $Z = 2.55$ and $P = 0.086$; right TPJ: $Z = 2.78$ and $P = 0.049$, small-volume FWE corrected in ROI shown in *A* and *B*, respectively).

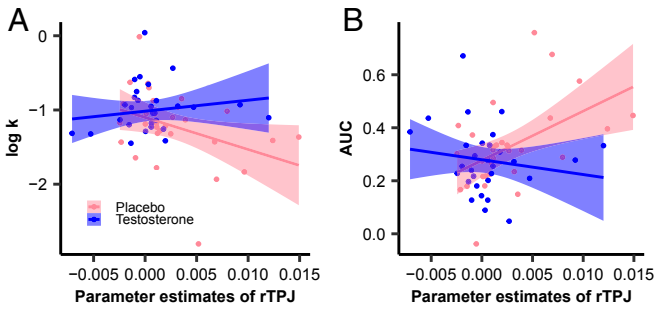

Fig. 5. Testosterone disrupts the association between individual generosity and rTPJ activity. When explaining individual differences in generosity, a significant interaction effect of group × rTPJ was found: log *k*: $b = 74.19$, SE = 32.42, $t = 2.29$, and $P = 0.026$; AUC: $b = -26.06$, SE = 10.52, $t = -2.48$, and $P = 0.016$. The right TPJ activity correlated with individual differences in task-related generosity (log-transformed discounting rate in *A* and AUC in *B*) in the placebo group (log *k*: $b = -45.04$, SE = 24.83, $t = -1.81$, and $P = 0.081$; AUC: $b = 17.86$, SE = 7.47, $t = 2.39$, and $P = 0.024$) but not in the testosterone group ($P > 0.1$, also *SI Appendix*, Table S2). Outlier-resistant rank-based correlation analyses confirmed the findings in the placebo group (Spearman's-$\rho = -0.41$, $P = 0.026$ for log *k* and $\rho = 0.52$, $P = 0.004$ for AUC) and the testosterone group (Spearman's-$\rho = 0.19$, $P = 0.324$ for log *k* and $\rho = -0.14$, $P = 0.474$ for AUC). Moreover, the correlation coefficients differed significantly between groups (Fisher's $z = -2.31$, $P = 0.021$ for log *k* and Fisher's $z = 2.64$, $P = 0.008$ for AUC). The shaded regions indicate the CI.

with reduced transfers to others in the trust game (26), indicating a crucial role of TPJ in social interaction. By revealing parametric generosity signals, the present study informs the existing understanding of the role of the TPJ in social cognition in general and prosocial preferences independent of social distance more specifically (19). Indeed, our data suggest that TPJ activity encodes generosity across multiple levels of social distance.

Our finding that testosterone reduces the association between social-distance–dependent generosity and bilateral TPJ activity is compatible with the notion that testosterone reduces considerations of the needs and desires of others, which leads to more selfish behavior. Indeed, higher levels of testosterone have been associated with reduced empathy and theory of mind (e.g., inference of others' mental states in the Reading the Mind in the Eyes task) (27–29). Moreover, testosterone administration has been associated with reduced TPJ activity during moral judgments (30). The present findings extend the inhibitory role of testosterone in social cognition to the domain of social decision-making (i.e., other-regarding valuation) and suggest that testosterone implements this role through actions on TPJ activity. Moreover, activity in the right TPJ region that increased with amount forgone in generous choice trials correlated also with individual differences in generosity as determined in all trials. This finding extends a previous report that established a link of TPJ gray-matter density and blood-oxygen-level–dependent (BOLD) activity with individual differences in altruistic behavior (20). Importantly, this link was weakened after testosterone administration, which further substantiated the neuropharmacological mechanism relating prosocial decision-making with testosterone and TPJ activity.

Our results demonstrate stronger generosity-related functional connectivity between the right TPJ and insula/striatum under placebo than testosterone, suggesting that testosterone reduces cross talk between other-regarding value processing (i.e., TPJ) and structures processing motivation and general value signals. Indeed, the striatum has been consistently involved in processing subjective value, both in social and nonsocial situations (24, 31), including the valuation of future rewards (32), generosity to friends (versus foes) (33, 34), and happiness induced by sharing with others (21). Thus, in our experiment, cross talk between the TPJ and striatum may facilitate generous choice under placebo, and testosterone could suppress the incorporation of other-regarding value into the subjective value of the generous choice alternatives. This interpretation converges with the notion that TPJ causally regulates striatal activity during shifts of attention to social information or when taking the perspective of others during reward processing (32). Moreover, the anatomical connection between the TPJ and putamen also strengthens the possibility of a modulatory role of the TPJ as a "social brain" region for the reward valuation system (35). Our findings suggest that testosterone partly controls this connection during generous decisions.

Some limitations should be noted. First, we recruited only healthy young males in the present study. Baseline testosterone and the corresponding physiological functions differ strongly between males and females. Future research should investigate the role of testosterone in generosity for both genders and ask whether the present findings generalize to women. Second, previous research has shown that the effects of testosterone administration on social behavior critically depend on other factors, such as personality traits (36), self-construal (37), and context [e.g., time pressure (38)]. For instance, men with stronger dominance, impulsivity, and independent self-construal traits are more likely to behave aggressively following testosterone administration (38). Therefore, individual and contextual variables could be included to better understand the causal role of testosterone administration in social decision-making. Third, we administered the behavioral task in the scanner environment 3 h after testosterone gel administration, in line with published pharmacokinetic (39) and our own data (40). Other experiments using testosterone gel administration reported peak serum testosterone levels after 1 h (36). We encourage future research to characterize the pharmacological and behavioral effects of testosterone gel administration over time. Finally, in the current design, it is difficult to separate reduced consideration of the needs of others from increased attention/concern for one's own outcomes because a loss for other is a gain for self (and vice versa). Our findings appear more compatible with the notion that testosterone reduced concern for the profits of others. On the one hand, we did not observe significant group differences in the neural representation of self-gains during the decision phase, providing no evidence to support the hypothesis that testosterone elevated the valuation and attention toward one's own earnings. On the other hand, we found a significant between-group difference in the strength with which TPJ encoded social-distance–dependent generosity. This difference mirrored the behavioral effects of testosterone, suggesting its effects on

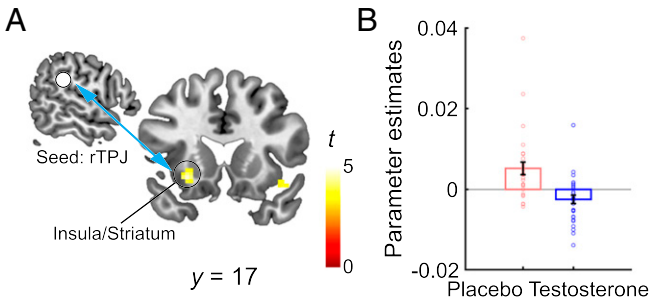

Fig. 6. Testosterone affects parametric generosity-related coupling of TPJ with insula/striatum. (*A*) Functional connectivity between the seed region of the right TPJ (peak coordinates: [57, −34, 26], from Fig. 3*B*) and insula/striatum (peak coordinates: [−27, 17, −10]). (*B*) The insula/striatum region was more strongly coupled with the amount-forgone coding region in the right TPJ in the placebo than the testosterone group ($Z = 4.20$ and $P = 0.023$, small-volume FWE corrected).

Table 2. PPI: Regions showing stronger functional connectivity with the right TPJ as amount forgone parametrically increased during generous choices in the placebo group more than the testosterone group (Fig. 6*A*)

Name	Side	Cluster size	*Z* value	MNI coordinates		
				x	*y*	*z*
Placebo versus testosterone						
Insula/striatum	L	36	4.20*	−27	17	−10
Inferior temporal gyrus	R	13	3.85	48	−7	−34
Inferior frontal gyrus	L	26	3.81	−36	41	2
Medial orbitofrontal cortex	R	21	3.75	12	56	−10
Middle frontal gyrus	R	18	3.69	42	32	35
Medial frontal cortex	L/R	19	3.68	0	38	47
Precuneus	R	21	3.64	12	−58	41
Inferior orbitofrontal cortex	R	37	3.57	48	41	−10
Precentral gyrus	L	15	3.56	−33	8	38
Superior temporal gyrus	R	11	3.51	45	17	−16
Precentral gyrus	L	10	3.47	−51	−1	17
Middle frontal gyrus	R	10	3.43	45	47	8
Angular gyrus	R	12	3.39	54	−58	32

Threshold: uncorrected $P < 0.001$, cluster size ≥ 10.
*Peak-level P (small-volume FWE corrected) < 0.05.

generous choices may have at least partly reflected considerations of other's benefits (i.e., other-regarding utility). Still, to better understand the specific role of testosterone in valuation and attention processes during social decision-making, future studies may want to use paradigms that break the reciprocal link between gains and losses. Moreover, it may be interesting to study eye movements to more closely investigate attention.

In conclusion, by combining pharmacological manipulation with approaches from neuroeconomics, the present study extends the current understanding of the neural mechanism by which testosterone affects social decision-making. We find testosterone to be associated with more selfish choices and to disrupt the representation of other-regarding value in local activity and functional connectivity involving temporoparietal and subcortical regions involved in reward processing. Thus, the present study provides causal evidence for a testosterone-mediated neurohormonal link between generosity and the valuation system.

Materials and Methods

Participants. A total of 70 healthy males (mean age = 20.39 y, SD = 1.78, and age range = 18–25) participated in this study. Two participants were excluded, one because it was impossible to fit a model to their behavior (see below) and one because of current depressive symptoms (Placebo: $n = 32$, mean age = 20.81 y, SD = 1.71, and age range = 18–25; Testosterone: $n = 36$, mean age = 20.00 y, SD = 1.71, and age range = 18–24). Participants were asked to abstain from alcohol, caffeine, and smoking for 24 h before the testing session. This study was conducted in accordance with the Declaration of Helsinki and was approved by Shenzhen University Medical Research Ethics Committee. All participants provided written informed consent before the start of the experiment. They were paid CNY (Chinese Yuan) 200 (~$30) as a show-up fee plus a variable amount depending on the decisions they made in the social discounting task (see below).

General Procedure. All sessions started between 11:00 AM and 1:00 PM and lasted about 4 h. The present study employed a double-blind, placebo-controlled, between-participant design. Participants in the testosterone group received a single dose of 150 mg testosterone gel (Androgel), while those in the placebo group received a colorless hydroalcoholic gel. For both groups, a male research assistant, who was blind to both the experimental conditions and the purpose of the study, applied the gel to the participants' shoulders and upper arms. We only tested males because the dosing and pharmacokinetics of a single dose of Androgel has been established for men only (39). We administered the decision-making task in the fMRI scanner 3 h after gel administration, as in our previously described protocol (13, 40, 41). During the 3-h waiting period, participants rested and were provided with newspapers and magazines unrelated to the study.

Social Discounting Task. We used a modified version of the social discounting task (3, 13). Before the fMRI session, participants were asked to familiarize themselves with the concept of social distance by rating their closeness to the following individuals: mother, father, sibling, partner, child, grandparent, family member, kin, best friend, member of circle of friends, colleague, neighbor, acquaintance, and stranger (1 = very close to 20 = not close, on a 20-point Likert scale). The corresponding trial was skipped if a particular individual did not exist in the participant's social environment. Then, participants were asked to parse their social environment and identify individuals to whom they had positive or neutral attitudes at the following social distances: 1, 2, 3, 5, 10, 20, 50, and 100. Except for social distances 50 and 100 (mere acquaintance and complete stranger), participants reported on a paper the names of the person at each social distance, their relationship with him/her, and the contact information for payment purpose. Next, participants performed the social discounting task in the scanner.

In each trial, social distance information was presented with both numbers and icons (Fig. 1). The numbers (1, 2, 3, 5, 10, 20, 50, or 100) indicated the social distance levels of the other person. Two icons on a scale were used, with the leftmost purple icon representing the participant and the yellow icon representing the other person involved in that trial. The distance between the purple and yellow icons corresponded to the social distance level. Then, two options were presented alphanumerically, inducing participants to choose either a larger amount for themselves (i.e., selfish option) or a smaller amount for themselves coupled with a benefit to the particular other person (i.e., generous option). Participants had to respond within 6 s, otherwise the trial was aborted (mean number of missing trials: mean = 1.54 [mean proportion: 1.07%], SD = 4.10), and the task proceeded to the next trial after displaying "Pay attention" for 2 s.

The selfish option varied from CNY 130 to CNY 290 with increments of CNY 20. The generous option was fixed at CNY 130 for both the participant and the other person. Each combination of social distance and selfish amount was presented twice in two separate runs, resulting in a total of 144 trials (8 distance levels × 9 selfish amounts × 2 runs). Each run comprised eight blocks, with each block concerning one person at a specified social distance level. Within each block, the order of the selfish amounts was randomized. Moreover, the order of the blocks was randomized across participants.

The task was incentive compatible such that one trial was randomly selected and implemented at the end of the task. With generous choices for partners at social distances 50 or 100, a random person in the same building or on campus received the payment. All payments were implemented via "Alipay," a popular smartphone payment platform in China.

Behavioral Analyses. We followed previously established methodology in analyzing the behavioral data (3, 4, 13). In particular, we first determined subjective indifference points at each social distance using logistic regression. These indifference points correspond to the selfish reward amount at which a participant chooses the selfish and generous option equally often (50%).

When participants exclusively chose one option at a particular social distance level, the indifference point was set at half of an increment below or above the range of the selfish option (i.e., CNY 120 if the participant always chose the selfish option and CNY 300 if the participant always chose the generous option). We then subtracted CNY 130 (the amount participants would have earned if they had chosen the generous option) from the indifference point, resulting in the net amount forgone as the actual cost of choosing generously. Accordingly, we used amount forgone as a measure of generosity and investigated whether and how it declined with increasing social distance level.

First, we imposed no model on the relationship between generosity and social distance, thereby making no assumptions about the shape of the discounting curve. In particular, we determined the AUC of the amounts forgone at each social distance for each group. We calculated AUC for each participant by normalizing amount forgone v as a percentage of maximum v, normalizing social distance D as a percentage of maximum D, connecting the amount forgone points by straight lines and then summing the trapezoids formed (42). Following standardization, AUC can vary from 1 (no discounting) to 0 (maximal discounting). AUC can be interpreted as a model-free measure of generosity. We tested for group differences in AUC by using a Mann–Whitney U test, as the data were not normally distributed.

Second, we investigated generosity as a function of social distance with a social discounting model (4). We fitted the amount forgone at each social distance to the standard hyperbolic model:

$$v = V/(1 + kD),$$

where v corresponds to the amount forgone at each social distance and D to the social distance level, and V and k are free parameters representing the intercept (subjective value of generosity at $D = 0$) and slope of the function (steepness by which the subjective value of generosity decreases as a function of social distance). Therefore, V represents generosity at close social distance, with large values corresponding to increased generosity toward close others, while k represents the degree of decline in generosity at increasing social distance, with larger values reflecting steeper declines. We used the nonlinear least-squares methods (nls function) with initial values of $V = 130$ and $k = 0.01$ for parameter estimations in R.

fMRI Image Acquisition. Scans were performed on a 3T Siemens Trio MRI scanner at Shenzhen Institutes of Advanced Technology at the Chinese Academy of Sciences. Functional images were acquired using a T2*-weighted echo planar imaging sequence with the following parameters: repetition time (TR) = 2,000 ms; echo time (TE) = 25 ms; flip angle (FA) = 90°; field of view (FOV) = 192 mm × 192 mm; and slice thickness = 3 mm, 41 slices covering the whole brain. Moreover, structural data were acquired using a T1-weighted magnetization-prepared rapid acquisition gradient echo sequence with the following parameters: TR = 2,530 ms; TE = 2.96 ms; TI = 1,100 ms; FA = 7°; 1.0 mm isotropic voxels; and FOV = 256 × 256.

fMRI Image Preprocessing. The fMRI data were preprocessed in SPM12 (Wellcome Centre for Human Neuroimaging, University College London, https://www.fil.ion.ucl.ac.uk/spm). Images were slice-time corrected, motion corrected, and normalized to Montreal Neurological Institute (MNI) space for each individual with a spatial resolution of $3 \times 3 \times 3$ mm^3. Images were then smoothed using an 8-mm Gaussian kernel and high-pass filtered at a cutoff of 128 s. Eight participants were removed from fMRI analyses due to excessive head movements (>4 mm in translational and >4° in rotational parameters). Thus, the final fMRI sample comprised 60 participants (Placebo: $n = 30$, mean age = 20.87 y, SD = 1.74, and age range = 18–25; Testosterone: $n = 30$, mean age = 19.93 y, SD = 1.68, and age range = 18–24).

General Linear Model. To identify the brain regions that encode the subjective value of generosity (i.e., amount forgone, see *Behavioral Analyses*), we aimed to explain each voxel's time series in a general linear model (GLM). Specifically, we defined four onset regressors with which we modeled BOLD responses as stick functions: onset of the social distance information (R1), onset of options in trials in which the participant made a selfish (R2) or generous (R5) choice (from option onset until button press), and onset of the button press (R8). Parametric modulators (i.e., the trial-by-trial self-gain of the selfish option and social-distance–dependent amount forgone) were used to track the neural representation of gains for the participant and generosity, both for selfish choices (R3 and R4, respectively) and generous choices (R6 and R7). Additionally, the missing trials (R9) and six movement parameters (i.e., three translational movements and three rotation movements) were also modeled in the GLM as regressors of no interest.

Regressors R1 through R9 were convolved with the canonical hemodynamic response function. We interrogated the amount forgone parametric modulator by putting a 1 on it at the single subject level. The generated contrast images were used to perform a second-level analysis with a one-sample t test for all participants combined. We used whole-brain FWE correction at the cluster level ($P_{FWE} < 0.05$) with a cluster-inducing voxel threshold of $P < 0.001$ uncorrected. This analysis identified the left and right TPJ (see *Results*). Next, we performed a two-sample t test to assess whether the neural representations of amount forgone differed between the placebo and the testosterone groups using small volume correction on the TPJ (i.e., 6 mm sphere around the peak coordinates of the TPJ cluster in the GLM analyses from all participants). For all second-level models, individual proportions of generous choice (Placebo: mean = 0.55 and SD = 0.15; Testosterone: mean = 0.50 and SD = 0.09; $t(66) = 1.88$ and $P = 0.065$) and the variance of amount forgone in generous choices (Placebo: median = 1115.76 and mean rank = 28.50; Testosterone: median = 1321.92 and mean rank = 39.83; Mann–Whitney U test = 384 and $P = 0.018$) were included as covariates to account for the possibility that they explain generosity-related activation. The results were similar without these covariates. All small-volume analyses were FWE corrected at the voxel level $P_{FWE} < 0.05$. All whole-brain contrast images reported in the figures were set to $P < 0.001$ with a cluster size of $k \geq 10$ voxels. The results are reported using the MNI coordinate system.

Individual Difference Analyses in Generosity. To test how TPJ activity (i.e., 6 mm ROI of the peak of bilateral TPJ in Fig. 4 *A* and *B*, respectively) related to individual and group differences in task-related generosity, two regression models were performed. The dependent variable was log-transformed discounting rate (log k) or AUC. The independent regressor in both models was group, the left and right TPJ activity, and their interaction terms. The ROI signals were extracted from a variant of a GLM in which the trials were not conditioned by choice (see GLM in *SI Appendix*, Fig. S1).

Psychophysiological Interaction Analysis. To examine how testosterone influenced the functional connectivity between TPJ (or the dopaminergic midbrain, *SI Appendix*) and other brain regions, we performed the generalized form of psychophysiological interaction (gPPI) analyses via the gPPI toolbox (https://www.nitrc.org/projects/gppi) (43). In particular, we established two psychophysiological interaction analysis (PPI) GLMs using the left and right TPJ [and one PPI GLM using substantia nigra/ventral tegmental area (SN/VTA)] as seed region. We extracted the time series of the seed regions from the parametric amount forgone contrast in generous choices (R7). The location of the left TPJ was selected based on a 6 mm sphere around the peak of the significant cluster of left TPJ (coordinates: [−60, −34, 20]; Fig. 3*A*) that survived in the GLM. Similarly, the ROI of right TPJ was a 6 mm sphere around the peak of the right TPJ cluster (coordinates: [57, −34, 26]; Fig. 3*B*). To test the functional connectivity associated with the representation of generosity, we assessed regions of the valuation system [as described by Table 1 and Fig. 3A of Bartra et al. (24)] following previous reports of generosity-related TPJ connectivity with the value system (3, 21).

For all PPI GLMs, we included the following regressors: time course of the seed region, task regressors (onset regressors and the corresponding parametric modulators in the GLM), PPI for task regressors, nuisance regressors of button press, missing trials, and head-movement parameters. With the exception of the movement parameters, these regressors were convolved with the canonical hemodynamic response function. We focus on the PPI contrast of the parametric modulator of amount forgone among generous choices. Single-subject beta estimates were interrogated with a one-sample t test. A two-sample t test was adopted to explore the group difference (i.e., placebo versus testosterone) using the mask that involved the region's coding subjective value for small volume correction. We also added the proportion of trials in which participants made a generous choice and the corresponding variance of amount forgone as covariates in all second-level PPI GLMs. Again, the results were similar without these covariates.

Data Availability. Behavioral data with the analyzed code are available on the Open Science Framework at https://osf.io/mw3tj/.

ACKNOWLEDGMENTS. We are grateful to Mr. Jiajun Liao for his help with the study. This work was supported by the National Natural Science Foundation of China (31600923, 31872784), Guangdong Educational Science Research Fund (2018GXJK150), Shenzhen University Research Fund (SZUGS2020JG07, 860/000002110601), and the Shenzhen Peacock Plan (827-000233) to Y.W. Y.H. was supported by China Postdoctoral Science Foundation (2019M660007). P.N.T. was supported by the Swiss National Science Foundation (Grants 100019_176016 and 100014_165884). X.G. was supported by Natural Science Foundation of China (31900798) and China Postdoctoral Science Foundation (2019M650008). The funding sources had no further role in the study design, data collection, analysis, interpretation, and decision to submit this manuscript for publication.

1. E. Fehr, K. M. Schmidt, A theory of fairness, competition, and cooperation. *Q. J. Econ.* **114**, 817–868 (1999).
2. T. Strombach *et al*., Charity begins at home: Cultural differences in social discounting and generosity. *J. Behav. Decis. Making* **27**, 235–245 (2014).
3. T. Strombach *et al*., Social discounting involves modulation of neural value signals by temporoparietal junction. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1619–1624 (2015).
4. B. Jones, H. Rachlin, Social discounting. *Psychol. Sci.* **17**, 283–286 (2006).
5. C. McCall, T. Singer, The animal and human neuroendocrinology of social cognition, motivation and behavior. *Nat. Neurosci.* **15**, 681–688 (2012).
6. A. D. Mooradian, J. E. Morley, S. G. Korenman, Biological actions of androgens. *Endocr. Rev.* **8**, 1–28 (1987).
7. C. Eisenegger, J. Haushofer, E. Fehr, The role of testosterone in social interaction. *Trends Cogn. Sci.* **15**, 263–271 (2011).
8. C. L. Apicella, J. M. Carré, A. Dreber, Testosterone and economic risk taking: A review. *Adapt. Human Behav. Physiol.* **1**, 358–385 (2015).

9. P. J. Zak *et al*., Testosterone administration decreases generosity in the ultimatum game. *PLoS One* **4**, e8330 (2009).
10. C. Eisenegger, M. Naef, R. Snozzi, M. Heinrichs, E. Fehr, Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature* **463**, 356–359 (2010).
11. C. Cueva *et al*., Testosterone administration does not affect men's rejections of low ultimatum game offers or aggressive mood. *Horm. Behav.* **87**, 1–7 (2017).
12. M. A. S. Boksem *et al*., Testosterone inhibits trust but promotes reciprocity. *Psychol. Sci.* **24**, 2306–2314 (2013).
13. Y. Wu *et al*., Testosterone administration increases social discounting in healthy males. *Psychoneuroendocrinology* **108**, 127–134 (2019).
14. G. Bellucci, J. A. Camilleri, S. B. Eickhoff, F. Krueger, Neural signatures of prosocial behaviors. *Neurosci. Biobehav. Rev.* **118**, 186–195 (2020).
15. R. Saxe, N. Kanwisher, People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *Neuroimage* **19**, 1835–1842 (2003).
16. M. Schurz, J. Radua, M. Aichhorn, F. Richlan, J. Perner, Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neurosci. Biobehav. Rev.* **42**, 9–34 (2014).
17. P. H. Donaldson, N. J. Rinehart, P. G. Enticott, Noninvasive stimulation of the temporoparietal junction: A systematic review. *Neurosci. Biobehav. Rev.* **55**, 547–572 (2015).
18. I. Santiesteban, M. J. Banissy, C. Catmur, G. Bird, Enhancing social ability by stimulating right temporoparietal junction. *Curr. Biol.* **22**, 2274–2277 (2012).
19. C. A. Hutcherson, B. Bushong, A. Rangel, A neurocomputational model of altruistic choice and its implications. *Neuron* **87**, 451–462 (2015).
20. Y. Morishima, D. Schunk, A. Bruhin, C. C. Ruff, E. Fehr, Linking brain structure and activation in temporoparietal junction to explain the neurobiology of human altruism. *Neuron* **75**, 73–79 (2012).
21. S. Q. Park *et al*., A neural link between generosity and happiness. *Nat. Commun.* **8**, 15964 (2017).
22. A. Soutschek, C. C. Ruff, T. Strombach, T. Kalenscher, P. N. Tobler, Brain stimulation reveals crucial role of overcoming self-centeredness in self-control. *Sci. Adv.* **2**, e1600992 (2016).
23. A. Soutschek *et al*., The dopaminergic reward system underpins gender differences in social preferences. *Nat. Hum. Behav.* **1**, 819–827 (2017).
24. O. Bartra, J. T. McGuire, J. W. Kable, The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage* **76**, 412–427 (2013).
25. J. J. Geng, S. Vossel, Re-evaluating the role of TPJ in attentional control: Contextual updating? *Neurosci. Biobehav. Rev.* **37**, 2608–2620 (2013).
26. J. B. Engelmann, F. Meyer, C. C. Ruff, E. Fehr, The neural circuitry of affect-induced distortions of trust. *Sci. Adv.* **5**, eaau3413 (2019).
27. J. M. Carré *et al*., Digit ratio (2D:4D) and psychopathic traits moderate the effect of exogenous testosterone on socio-cognitive processes in men. *Psychoneuroendocrinology* **62**, 319–326 (2015).
28. J. van Honk *et al*., Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3448–3452 (2011).
29. A. Olsson, E. Kopsida, K. Sorjonen, I. Savic, Testosterone and estrogen impact social evaluations and vicarious emotions: A double-blind placebo-controlled study. *Emotion* **16**, 515–523 (2016).
30. C. Chen, J. Decety, P. C. Huang, C. Y. Chen, Y. Cheng, Testosterone administration in females modulates moral judgment and patterns of brain activation and functional connectivity. *Hum. Brain Mapp.* **37**, 3417–3430 (2016).
31. R. Gu *et al*., Love is analogous to money in human brain: Coordinate-based and functional connectivity meta-analyses of social and monetary reward anticipation. *Neurosci. Biobehav. Rev.* **100**, 108–128 (2019).
32. A. Soutschek, M. Moisa, C. C. Ruff, P. N. Tobler, The right temporoparietal junction enables delay of gratification by allowing decision makers to focus on future events. *PLoS Biol.* **18**, e3000800 (2020).
33. E. Schreuders, E. T. Klapwijk, G. J. Will, B. Güroğlu, Friend versus foe: Neural correlates of prosocial decisions for liked and disliked peers. *Cogn. Affect. Behav. Neurosci.* **18**, 127–142 (2018).
34. E. Schreuders, S. Smeekens, A. H. N. Cillessen, B. Güroğlu, Friends and foes: Neural correlates of prosocial decisions with peers in adolescence. *Neuropsychologia* **129**, 153–163 (2019).
35. A. Kucyi, M. Moayedi, I. Weissman-Fogel, M. Hodaie, K. D. Davis, Hemispheric asymmetry in white matter connectivity of the temporoparietal junction with the insula and prefrontal cortex. *PLoS One* **7**, e35589 (2012).
36. J. M. Carré *et al*., Exogenous testosterone rapidly increases aggressive behavior in dominant and impulsive men. *Biol. Psychiatry* **82**, 249–256 (2017).
37. K. M. Welker *et al*., Preliminary evidence that testosterone's association with aggression depends on self-construal. *Horm. Behav.* **92**, 117–127 (2017).
38. B. M. Bird *et al*., Effect of exogenous testosterone on cooperation depends on personality and time pressure. *Neuropsychopharmacology* **44**, 538–545 (2019).
39. C. Eisenegger, A. von Eckardstein, E. Fehr, S. von Eckardstein, Pharmacokinetics of testosterone and estradiol gel preparations in healthy young men. *Psychoneuroendocrinology* **38**, 171–178 (2013).
40. Y. Wu *et al*., Single dose testosterone administration modulates emotional reactivity and counterfactual choice in healthy males. *Psychoneuroendocrinology* **90**, 127–133 (2018).
41. Y. Wu, Y. Zhang, J. Ou, Y. Hu, S. Zilioli, Exogenous testosterone increases the audience effect in healthy males: Evidence for the social status hypothesis. *Proc. Biol. Sci.* **287**, 20200976 (2020).
42. K. M. Vekaria, K. M. Brethel-Haurwitz, E. M. Cardinale, S. A. Stoycos, A. A. Marsh, Social discounting and distance perceptions in costly altruism. *Nat. Hum. Behav.* **1**, 0100 (2017).
43. D. G. McLaren, M. L. Ries, G. Xu, S. C. Johnson, A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *Neuroimage* **61**, 1277–1286 (2012).