

Imaging Social Motivation: Distinct Brain Mechanisms Drive Effort Production during Collaboration versus Competition

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Collaborative and competitive interactions have been investigated extensively so as to understand how the brain makes choices in the context of strategic games, yet such interactions are known to influence a more basic dimension of behavior: the energy invested in the task. The cognitive mechanisms that motivate effort production in social situations remain poorly understood, and their neural counterparts have not been explored so far. A dominant idea is that the motivation provided by the social context is reducible to the personal utility of effort production, which decreases in collaboration and increases in competition. Using functional magnetic resonance imaging, we scanned human participants while they produced a physical effort in a collaborative or competitive context. We found that motivation was indeed primarily driven by personal utility, which was reflected in brain regions devoted to reward processing (the ventral basal ganglia). However, subjects who departed from utility maximization, working more in collaborative situations, showed greater functional activation and anatomical volume in a brain region implicated previously in social cognition (the temporoparietal junction). Therefore, this region might mediate a purely pro-social motivation to produce greater effort in the context of collaboration. More generally, our findings suggest that the individual propensity to invest energy in collaborative work might have an identifiable counterpart in the brain functional architecture.

Introduction

When collaborating with others to achieve a common goal, people tend to decrease their effort in proportion to group size (Ringelmann, 1913). An economic explanation of this phenomenon, termed social loafing, involves a decrease in the personal utility of effort exertion (Karau and Williams, 1993). Indeed, as group size increases, the contribution of each individual will have a lesser impact on the outcome, which depends on the group performance. The decrease in personal utility translates into a higher cost/benefit ratio, which is assumed to diminish motivation and thereby to result in people spending less energy on the task.

The first aim of the present study was to assess whether effort production across social contexts is indeed driven by changes in personal utility and to identify the neural underpinnings of this putative utility-driven behavior. We extended this idea from cooperative to competitive contexts, in which personal utility increases because it pays not only to perform well but also to

perform better than the opponents. Thus, the utility theory predicts that effort production should increase across cooperative, individual, and competitive contexts. To test this prediction, we implemented a two-player task that involves subjects squeezing a handgrip to win money. The social context varied with the payoff equation, which was used to quantify variations of personal utility. This allowed distinguishing personal utility from the valence of social interaction (positive during collaboration and negative during competition). Personal utility was further dissociated from social valence by varying the monetary incentive and consequently the expected payoff. On the neural level, the utility theory predicts that the changes in effort production attributable to social contexts rely on circuits that also mediate the effects of monetary incentives, such as the ventral basal ganglia (Knutson et al., 2001; Pessiglione et al., 2007; Schmidt et al., 2012).

The second aim of this study was to examine whether social contexts have motivational properties, above and beyond the variations of personal utility, and to explore the underlying neural mechanisms. These putative social motivations (such as the desire to help or to defeat others) must not be confounded with the so-called social facilitation or audience effects, which refer to modulation of performance attributable to the mere presence of other people (Triplett, 1898; Zajonc, 1965; Guerin and Innes, 1993). To avoid this confound, our participants worked in the presence of their partner/opponent in all conditions. On the neural level, social motivation might recruit distinct brain regions, such as the medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ), two main components of the so-called social

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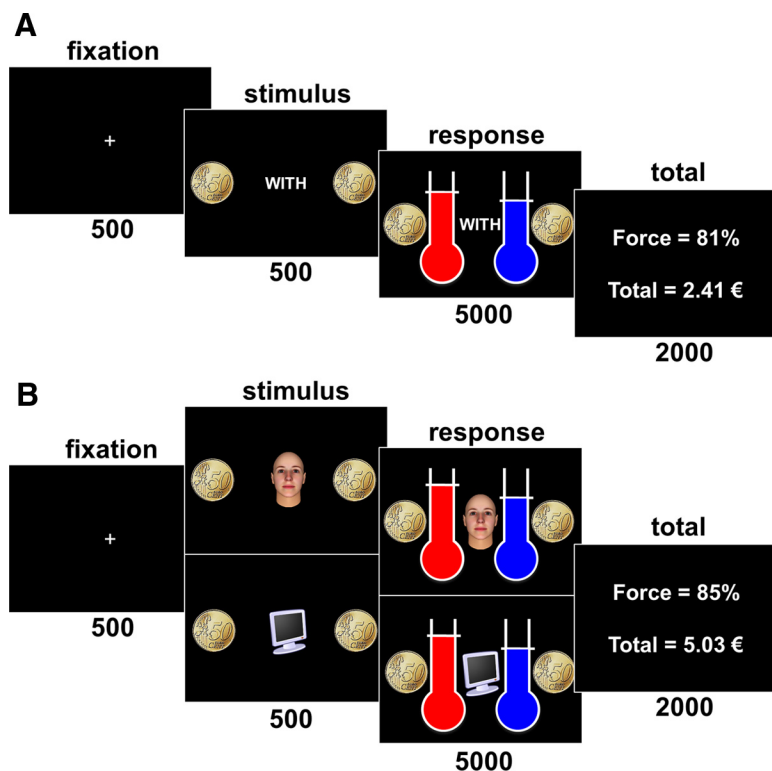


Figure 1. The social incentive force task. The successive screens displayed in a trial are illustrated from left to right, with duration in milliseconds. Subjects first saw the cues indicating the monetary incentive (10, 20, or 50c) and the social context. Then they started effort production when two thermometers appeared on screen, in which fluid level represented their own (in red) or the other's (in blue) cumulative force. Finally, a last screen indicated the level of force produced and the total of monetary earnings. **A**, Task 1. Subjects believed that they played with a person in all trials. Social context could be individual, collaborative, or competitive, depending on the condition tag (Alone, With, or Against, respectively). **B**, Tasks 2 and 3. Subjects believed that they played either with a person or a computer, depending on the context cue (computer or face image). All trials were collaborative in Task 2 and competitive in Task 3.

brain network (Van Overwalle, 2009; Rilling and Sanfey, 2011). Although the neural substrates that mediate the effects of pro-social factors (such as trust, reciprocity, fairness, and altruism) on decision-making have been well documented (Sanfey et al., 2003; King-Casas et al., 2005; Harbaugh et al., 2007; Hsu et al., 2008; Tricomi et al., 2010), little is known about how the brain translates social context into more or less effort production.

Materials and Methods

To summarize the procedure, we converted a paradigm that involved participants squeezing a handgrip to win monetary rewards (Pessiglione et al., 2007) into a two-player game (Task 1). In addition to the monetary incentive (0.1, 0.2, or 0.5€), we also varied the social context (with collaborative, individual, or competitive conditions) and the social position (with the subject performing better or worse than the other player). The three factors were manipulated on a trial-by-trial basis, while the same two individuals played the game throughout the experiment. Each subject believed he or she played with a human person, but in fact played with a computer simulation. The simulation was designed such that the temporal dynamics of force production was realistic, that final force levels matched those of the subject on average, and that the social position varied across trials (with the subject ending above or below the simulated player). The social context was manipulated by basing the payoff on the subject's force (individual condition), on the average with the other's force (collaboration condition), or on the individual force plus the difference with the other (competition condition). This ensured that, across social contexts, the personal utility of effort varied, whereas the expected payoff was kept constant. The incentive level and social context were explicitly cued at the beginning of trials, whereas the social

position was manipulated implicitly. Subjects were given real-time visual feedback on the two cumulative forces, represented as fluid levels rising in two thermometers (Fig. 1A).

Subjects

The study was approved by the Ethics Committee of the Pitié-Salpêtrière Hospital (Paris, France). Subjects were recruited via the Relais d'Information en Sciences Cognitives website and screened for exclusion criteria: left-handedness, age younger than 18 or older than 39, regular taking of drug or medication, history of psychiatric or neurological illnesses, and contra-indications to MRI scanning. A total of 32 subjects were scanned (20 males, 24.7 ± 0.9 years old). All gave informed consent before taking part.

Behavioral tasks

fMRI study (Task 1). Subjects were informed that they would be tested in pairs, playing together the same game displayed on two connected computers, one in the scanner and one in the control room. In reality, the player sitting in the control room was a fictive subject, whose performance was simulated by the computer program. A male actor was used for male participants and female for female participants to avoid any cross-gender effect. The two individuals had the opportunity to talk to each other for a few minutes before the experiment began. Then they were given written instructions and were allowed to perform practice trials.

The experimental manipulation followed a $3 \times 3 \times 2$ factorial design: three explicit monetary incentives (0.1, 0.2, or 0.5€), three explicit social contexts (individual, collaborative, or competitive), and two implicit social positions (stronger or weaker partner, from +15 to –15%). The different cells of the factorial design were randomly distributed over the series of trials. Subjects performed six sessions of the social incentive force task, each containing five repetitions of the nine cells combining the explicit factors (3 monetary incentives \times 3 social contexts), for a total of 45 trials. The implicit factor (social position) was only counterbalanced with the others after the first repetition, for the last 36 trials (see below, Fictive player simulation).

In every trial (Fig. 1A), subjects had to fixate a central cross and then pay attention to a central word symbolizing social conditions ("Alone," "With," or "Against") and to coin images indicating the amount of money at stake (10, 20, or 50 eurocents). Two thermometers then appeared on the screen: one on the left with red fluid for the subject and one on the right with blue fluid for the second player. This was the trigger signal for subjects to squeeze the power grip to move the fluid level up as high as possible, within a 5000 ms interval. The movement speed was adjusted online in proportion to the force produced on the grip. Subjects knew that the top of the thermometer corresponded to their maximal cumulative force exerted in 5 s.

Subjects were informed that, on each trial, they would win the monetary incentive (I) multiplied by a performance measure that was defined as their individual force level (F_1) in the Alone condition, as the mean of the two players' forces ($(F_1/2 + F_2/2)$) in the With condition, and as their individual force minus the difference with the other player ($F_1 + F_1 - F_2$) in the Against condition. Force was expressed in percentage of the maximal force measured before each session.

The personal utility of effort production was defined as the money won for each unit of force exerted by the subject, i.e., as the payoff derivative ($\partial \text{Payoff} / \partial F_1$). Personal utility was thus experimentally con-

trolled by both monetary incentives and social contexts. It was calculated as the incentive multiplied by 0.5, 1, and 2 in the With, Alone, and Against conditions, respectively. These coefficients form a parametric modulation that we call “context-related,” as opposed to “incentive-related,” variation in personal utility. On the contrary, the expected payoff was only modulated by monetary incentives: it was kept constant across social contexts, because F_2 was matched to F_1 on average in each condition.

Random time intervals (jitters of 500–2000 ms) were inserted before the feedback screen to ensure better sampling of the hemodynamic response. Then the feedback screen displayed for 2000 ms the force level reached in the current trial and the cumulative total of monetary earnings.

Subjects believed they were playing for real money, but in the end, their payoff was rounded up to a fixed amount (100€). Before leaving, they were debriefed on their beliefs about the task. Importantly, none of the subjects expressed any doubt about playing with another real subject.

Pilot study (Task 1). A total of 12 subjects were tested (six males, mean age of 21.8 ± 0.5 years). Two unacquainted subjects were tested simultaneously. They had the opportunity to meet and chat for a few minutes before the experiment. They were tested in the same room, placed back to back. They were told that they would play with each other, but in reality they played with the same computer simulation as implemented for the fMRI study. In other words, subjects believed that the blue fluid level on their screen indicated the other subject's performance, but it was in fact simulated. The task was similar to that used for the fMRI study, with the same $3 \times 3 \times 2$ factorial design (three monetary incentives, three social conditions, and two social positions). It comprised four sessions, each containing seven repetitions of the nine explicit cells, for a total of 63 trials.

Control studies (Tasks 2 and 3). Task 2 is a variant of the social incentive force task that is restricted to collaborative trials (Fig. 1B). Subjects were again tested in pairs and were instructed that they would alternately collaborate with each other or with a computer. As done in the previous task, the second (blue) thermometer was in fact always simulated by a computer. A total of 13 subjects were included (six males, mean age of 22.5 ± 0.8 years). Three additional subjects were tested but were excluded after debriefing, because they noticed the simulated force. The task followed a $3 \times 2 \times 2$ factorial design: three explicit monetary incentives (10, 20, or 50¢), two explicit collaborators (“Human” or “Computer”), and two implicit social positions (below or above the other). At the trial start, a central cue indicated the identity of the collaborator: a neutral face for the human collaborator (borrowed from Oosterhof and Todorov, 2008) or a computer image for the control condition. Payoff was calculated on every trial as the incentive times the mean of the two players' forces [$\text{Payoff} = I \times (F_1 + F_2)/2$]. Subjects performed six sessions, each containing seven repetitions of the six explicitly different trial types, for a total of 42 trials. The third factor (social position) was counterbalanced for the last six repetitions (36 trials), as was done in Task 1.

Task 3 had the same structure as Task 2, except that it only included competitive trials (Fig. 1B, which also applies to Task 3). A total of 12 subjects were included (six males, mean age of 23.5 ± 0.9 years). Payoff was calculated on each trial as the incentive times the subject's force plus the difference with the other player [$\text{Payoff} = I \times (F_1 + F_1 - F_2)$]. All subjects declared during debriefing that they really thought they were playing alternately with a computer and the other player.

After the experiment, subjects participating in the two control studies also completed the 24-items ring measure of social value orientation (SVO), which provided an independent measure of their social preferences (Liebrand and McClintock, 1988). In this task, participants were asked to make 24 two-option choices for allocating money to themselves and to another person. Together, the amount of money allocated to oneself and the amount allocated to the other determined a vector. The angle of this vector characterized a person's SVO. After a previously published cutoff (Liebrand and McClintock, 1988), subjects were categorized as pro-social when the angle was above 22.5° and non-pro-social otherwise.

Fictive player simulation. The false subject's force production was simulated on a trial-by-trial basis as follows. To make the dynamics plausi-

ble, the temporal pattern was matched to that produced by the true subject in the immediately preceding trial (or during calibration for the first trial). The amplitude (cumulative force) was derived from the level previously reached by the true subject in the last instance of the same social/incentive condition (except for the first nine trials in which it was predefined from pilot studies). A modulation factor corresponding to the social position, either positive (from +5 to +15%) or negative (from -5 to -15%), was also applied to calculate the final level reached by the simulated subject. Social position was not explicitly cued at trial start but was revealed in the course of effort production, during which participants could compare their force level with that of the other player. This factor was not applied in the first repetition of explicit conditions (first nine trials) and was counterbalanced with respect to monetary incentive and social context in the four remaining repetitions (36 last trials). Thus, to recapitulate, the simulation was adjusted for each trial such that the rise in fluid level for the fictive subject (1) followed the same dynamics as that of the true subject in the preceding trial and (2) ended at a level that was between -15 and +15% of the level reached by the true subject in the preceding occurrence of the same incentive/social condition.

A fatigue function was also integrated in the simulated force level to anticipate the decay in the true subject's performance. This function ($3.6e^{-5} \times T^2 - 1.4e^{-3} \times T + 0.97$), with T standing for trial number, was estimated from the pilot study. This procedure ensured that average produced (F_1) and simulated forces (F_2) were similar. In fact, the observed average was 67.9 and 69.4% of maximal force for F_1 and F_2 , respectively. The small difference between F_1 and F_2 is unlikely to account for any behavioral effect, because 1.5% of force represented 6.2 pixels on the screen, which was below the width of the horizontal bar indicating fluid level (10 pixels).

Behavioral data acquisition

The handgrip was made of two molded plastic cylinders compressing an air tube, which was connected to a transducer able to convert air pressure into voltage. Thus, compression by an isometric handgrip resulted in the generation of a differential voltage signal, linearly proportional to the force exerted. The signal was fed into the stimuli presentation personal computer via a signal conditioner (CED 1401; Cambridge Electronic Design). Stimuli presentation was programmed with Cogent 2000 (Wellcome Trust Center for Neuroimaging, London, UK). The dynamic changes of recorded signal were used to provide subjects with a real-time visual feedback about the force being exerted on the grip, as a fluid level moving up within a thermometer (Fig. 1). We calibrated the baseline (while the grip was not squeezed at all) and measured the maximal 5 s cumulative force (while the subject squeezed the grip as hard as possible) before starting every session. To limit muscular fatigue, subjects were asked to change hands between task sessions.

Behavioral data analyses

Grip force was extracted as the cumulative force reached after 5 s and expressed as a percentage of the maximal force (measured before the current session). Although we kept raw percentages for illustration purposes, grip force was converted into z-score for statistical analysis. A global repeated-measures ANOVA using Greenhouse–Geisser correction for nonsphericity was first conducted, with grip force as the dependent variable, to test main effects of incentive-related personal utility (coded 1, 2, and 3 for 10, 20, and 50¢), context-related personal utility (coded $\frac{1}{2}$, 1, and 2 for collaborative, individual, and competitive conditions), and social position (1/–1 for ahead/behind), as well as interactions. We pooled all the data obtained using Task 1, because results were similar in the pilot and fMRI studies. Taking cardinal parameters (10, 20, and 50) for incentives yielded similar results as taking their ordinal position (1, 2, and 3). *Post hoc* comparisons between incentive and social categories were performed using two-tailed paired *t* tests across subjects. To globally capture personal utility, we took the product of incentive- and context-related utility. We then conducted a multiple regression of grip force against personal utility (incentive-related \times context-related utility), collaboration (1 or 0), competition (1 or 0), social position (1 or -1), and fatigue (indexed as the trial number). Two-tailed one-sample *t* tests across subjects were used to test the significance of regression coef-

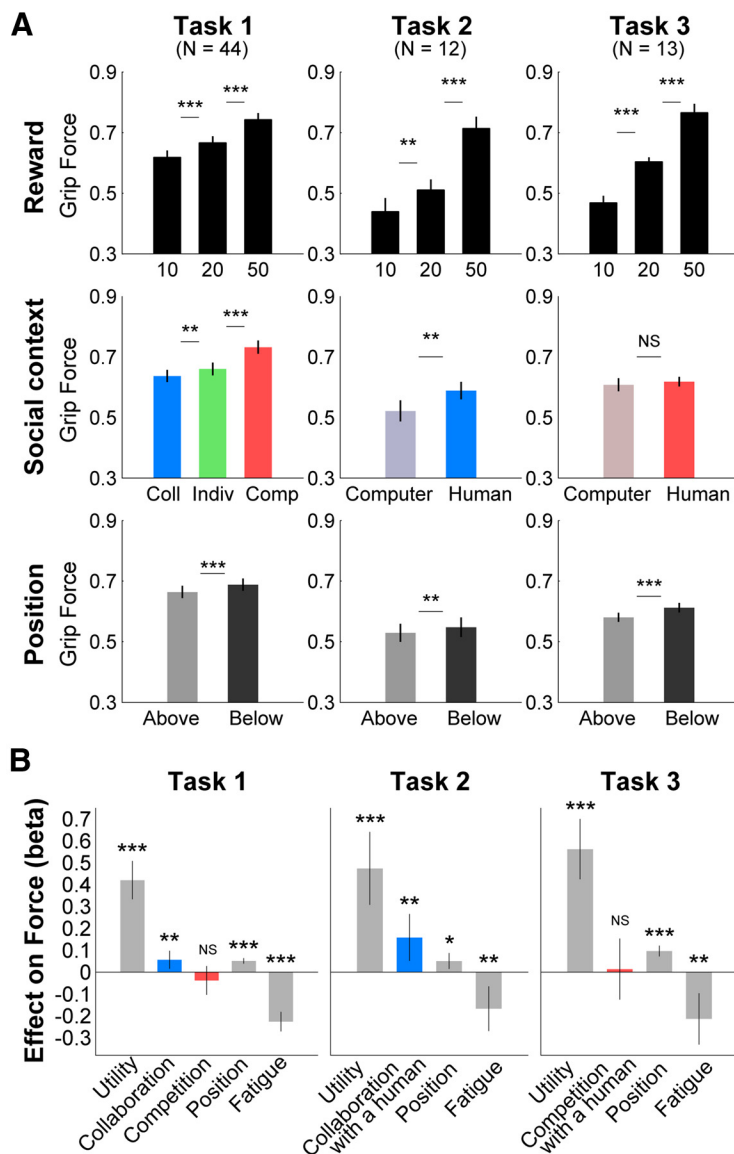


Figure 2. Behavioral results. **A**, Effects of monetary incentive (top), social context (middle), and social position (bottom) on grip force, expressed as a proportion of the subject's maximal force. Error bars indicate intersubject standard error of the mean (SEM). Coll, Collaborative; Indiv, individual; Comp, competitive. **B**, Linear regression of grip force against personal utility, collaboration, competition, position, and fatigue (trial number). Histograms represent regression coefficients (β values). Error bars indicate 95% confidence intervals. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS, nonsignificant.

ficients (β values). The social position factor was assigned a 0 value in the first repetition of explicit conditions, in which it was not applied. The same multiple regression model was fitted to data obtained with Task 2 and Task 3, except that one regressor was missing (competition for Task 2 and collaboration for Task 3). We defined the collaboration bias as the change in force production that is induced when collaborating with a human and that is not reducible to modulation of personal utility. This bias was thus captured by the β value of the collaboration regressor in the models fitted to Task 1 and Task 2. The repeated-measures ANOVAs were performed using R software (www.r-project.org). All other statistical tests, including regressions, were conducted with the MATLAB Statistical Toolbox (MATLAB R2011b; MathWorks).

Functional neuroimaging data acquisition

T2*-weighted echo planar images (EPIs) were acquired with blood oxygen level-dependent contrast on a 3.0 Tesla magnetic resonance scanner (Siemens Trio). A tilted plane acquisition sequence was used to optimize functional sensitivity in the orbitofrontal cortex. To cover the whole

brain with a repetition time of 1.98 s, we used the following parameters: 35 slices; 2.1 mm slice thickness; and 1.6 mm interslice gap. T1-weighted structural images were also acquired, coregistered with the mean EPI, segmented and normalized to a standard T1 template, and averaged across all subjects to allow group-level anatomical localization. EPIs were analyzed in an event-related manner, within a general linear model (GLM), using the statistical parametric mapping (SPM) software SPM8 (Wellcome Trust Center for Neuroimaging). The first five volumes of each session were discarded to allow for T1 equilibration effects. Preprocessing consisted of spatial realignment, normalization using the same transformation as structural images, and spatial smoothing using a Gaussian kernel with a full-width at half-maximum (FWHM) of 8 mm.

fMRI analyses

We used a single GLM to generate SPMs as follows. All trials were modeled with a single boxcar function covering periods when cues (coin images and condition tags) were present, hence covering periods of effort production. The GLM also contained five parametric modulations: screen luminance, collaboration, competition, social position, and personal utility. All regressors of interest were convolved with a canonical hemodynamic response function. To correct for motion artifact, subject-specific realignment parameters were modeled as covariates of no interest.

Linear contrasts of regression coefficients were computed at the individual subject level and then taken to a group-level random effect analysis (using one-sample t test). All reported significant activations, unless otherwise mentioned, contained a minimum of 150 voxels surviving a threshold of $p < 0.001$ (uncorrected), which corresponded to a threshold of $p < 0.05$ after clusterwise familywise error (FWE) correction for multiple comparisons at the cluster level.

For *post hoc* correlation with behavioral measures, parameter estimates (β values) were extracted from an 8-mm-diameter sphere centered on group-level activation peak (e.g., in the left TPJ for parametric modulation by collaboration).

We also examined whether the magnitude of activation in the left TPJ would explain intertrial variability in force production during collaboration. A GLM was built to this aim, with every trial modeled in a separate regressor that contained a single boxcar covering the effort period. This GLM also contained realignment parameters and session means. The β values obtained for regressors of interest were taken as trial-by-trial estimates of the response magnitude. These β values were extracted from the left TPJ and mPFC 8 mm spheres and normalized to the mean response magnitude over the brain, which was extracted from the entire SPM brain mask. The normalized β values were then regressed against the residuals of force production (after removing the variance predicted by personal utility), for collaborative trials only. Regression coefficients were tested for significance at the group level using one-sample t test.

Structural neuroimaging data acquisition

T1-weighted anatomical whole-brain scans were acquired (TE, 4.18 ms; TR, 2300 ms; voxel size, 1 mm isotropic) for voxel-based morphometry (VBM) analyses, which were conducted using SPM8 (Wellcome Trust Center for Neuroimaging). Anatomical images were corrected for inten-

sity bias and segmented into gray matter (GM), white matter (WM), and CSF in native space, using SPM8 “new segment” module. To increase the accuracy of intersubject alignment, GM and WM images were then simultaneously coregistered to an iteratively improved template using DARTEL nonlinear registration algorithm. The generated images were then registered to Montreal Neurological Institute (MNI) space by an affine registration, modulated using the Jacobian determinants, and smoothed with a 12-mm FWHM Gaussian filter. The modulation step scales GM images by the amount of contraction required to warp the image and hence preserves the local tissue volumes.

VBM analyses

Subjects were divided into two equal groups (highly or weakly collaborating) after median-split based on their behavioral regression coefficients. The GLM used to fit smoothed, modulated, normalized GM images included one variable of interest (group) and two regressors of no interest: age and total intracranial volume (calculated by summing across the GM, WM, and CSF images). SPMs showing significance of regression coefficients were thresholded at $p < 0.001$ (uncorrected) over the whole brain for illustration purposes. We also applied a threshold of $p < 0.05$, FWE corrected for multiple comparisons within an a priori region of interest (ROI) in the left TPJ. This ROI included the left angular gyrus and supramarginal gyrus, as defined in the Talairach Daemon atlas (Lancaster et al., 1997, 2000). It was delineated using the Wake Forest University PickAtlas toolbox (Maldjian et al., 2003, 2004) and registered to the MNI space.

Results

Behavior

The dependent variable was the cumulative force produced, which represented the energy invested in the task and hence the output of the motivation process. We found a main effect for all manipulated factors in both the behavioral pilot and neuroimaging studies, which were pooled for the subsequent analyses (Fig. 2A, left column). First, in replication of previous findings (Pessiglione et al., 2007), grip force increased with monetary incentive ($F_{(2,84)} = 85.2$, $p < 0.001$). Second, force production varied across social contexts in proportion to personal utility, i.e., decreased during collaboration and increased during competition, relative to the individual condition ($F_{(2,84)} = 61.5$, $p < 0.001$). Moreover, there was a significant interaction between incentives and social contexts ($F_{(4,168)} = 5.4$, $p = 0.004$), consistent with force production being proportional to the product of incentive-related and context-related variations in personal utility. No other significant interaction was observed. Third, subjects produced more force when the opponent performed better, regardless of social context ($F_{(1,42)} = 42.1$, $p < 0.001$).

To disentangle the specific effects of social contexts from their effect through modulation of personal utility, we conducted a multiple linear regression across trials (Fig. 2B, left). At the group level, regression coefficients (β values) were significant for personal utility ($r = 0.42$, $t_{(43)} = 9.7$, $p < 0.001$), collaboration ($r = 0.06$, $t_{(43)} = 2.7$, $p = 0.009$), position ($r = 0.05$, $t_{(43)} = 7.9$, $p < 0.001$), and fatigue (indexed by trial number, $r = -0.23$, $t_{(43)} = -10.2$, $p < 0.001$) but not for competition ($t_{(43)} = -1.2$, $p = 0.25$). Therefore, the effect of social context appeared primarily driven by changes in personal utility. However, collaboration induced a small, but significant, deviation from utilitarianism that we termed collaboration bias and defined as the coefficient of the collaboration regressor.

To verify the social nature of the collaboration bias, we conducted two control studies. The task was modified such that participants thought they were interacting alternately with a human or a computer (Fig. 1B). One study contained only collaborative trials (Task 2) and the other only competi-

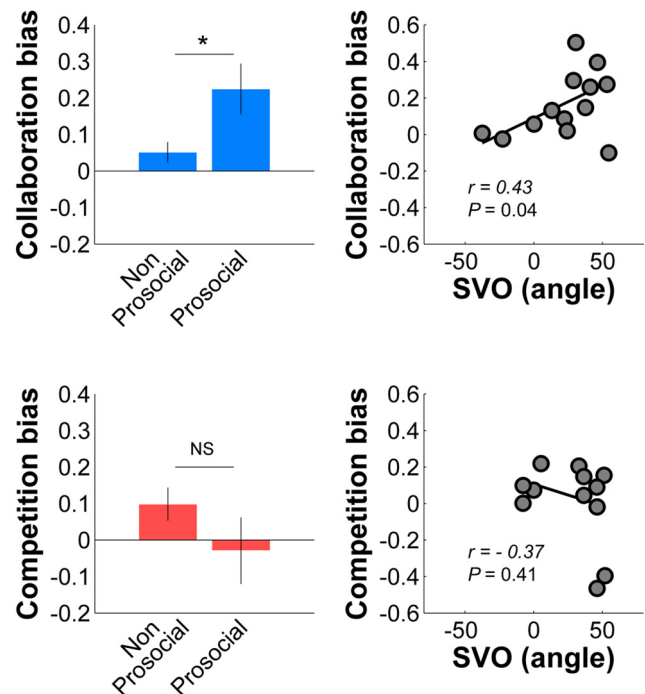


Figure 3. Relationship between SVO and collaboration (top) or competition (bottom) bias. Diagrams on the left show collaboration and competition biases for subjects classified as pro-social or non-pro-social. Error bars are intersubject SEMs. * $p < 0.05$; NS, nonsignificant. Scatter plots on the right show how collaboration or competition biases vary with SVO measure of pro-sociality. Each dot is a subject. r and p are Pearson's coefficient and the robust fit p value of the linear regression.

tive trials (Task 3). The main effects of monetary incentive and social position were replicated in both studies (Fig. 2A, top and bottom). Collaboration with a human yielded a significant increase in force production relative to collaboration with a computer ($t_{(12)} = 3.2$, $p = 0.007$; Fig. 2B, middle). On the contrary, competition with a human did not induce any significant effect ($t_{(11)} = 0.2$, $p = 0.83$; Fig. 2B, right). Furthermore, participants in Tasks 2 and 3 were categorized as pro-social or non-pro-social by an independent measure of social orientation (Liebrand and McClintock, 1988). Although the two groups shared similar pro-sociality scores ($t_{(23)} = -0.54$, $p = 0.59$) and similar proportions of pro-social subjects ($\chi^2 = 0.07$, $p = 0.79$), it was only in Task 2 that we found a significant correlation with behavioral results: the collaboration bias was significantly greater in subjects categorized as pro-social (Fig. 3). Thus, behavioral results suggest that competition may not affect effort production beyond the change in effort personal utility, whereas the collaboration context may reveal a purely pro-social tendency that is independent of personal utility maximization.

Neuroimaging

To identify the neural pathways that mediate the influence of personal utility, social context, and position on effort production, we tested parametric modulations of brain activity modeled as a single boxcar over the trial period. After FWE correction for multiple comparisons over the whole brain ($p < 0.05$ at the cluster level), we found that personal utility was mainly reflected in the basal ganglia (Fig. 4; Table 1). The principal activation foci were neighboring the ventral pallidum (VP), a region that has been conceived as a final common pathway for the limbic system

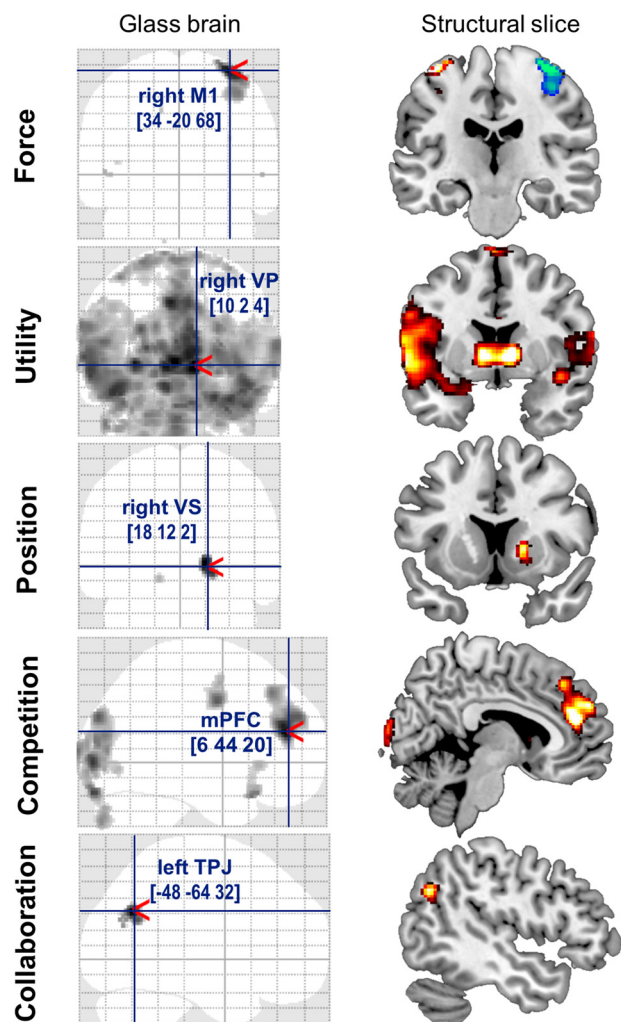


Figure 4. Statistical parametric maps of brain activity. The top row illustrates the contrasts of left-hand – right-hand (blue) or right-hand – left-hand (red) force production. The four rows below illustrate significant correlations with parametric regressors (personal utility, social position, competition, and collaboration). Coronal and sagittal slices were taken at the global maxima of interest indicated by red pointers on glass brains and were superimposed on structural scans. $[x, y, z]$ coordinates of the maxima refer to the MNI space. All activations survived a statistical threshold of $p < 0.05$, after clusterwise whole-brain correction for multiple comparisons, except for social position, to which a more liberal threshold was applied ($p < 0.001$, uncorrected). M1, Primary motor cortex.

(Smith et al., 2009) and implicated in translating expected reward into behavior energization (Pessiglione et al., 2007). Secondary activation foci were observed over motor and visual regions, as well as anterior insula, and might possibly reflect that higher effort was associated with greater motor output, attentional focus, and physical pain. Note that the activations reported here were obtained with a parametric modulation by global personal utility, i.e., the product of incentive- and context-related utility, which was found to drive effort production. We have also tested parametric modulations of brain activity by incentive- and context-related utility separately. The two regressions yielded similar activations, with no significant difference between the two maps. Moreover, the main clusters obtained in the conjunction of these two maps overlapped with the VP clusters activated with global personal utility.

At a lower threshold ($p < 0.001$, uncorrected), higher social position specifically correlated with activity in the bilateral ventral striatum (VS), a classical reward-related region that

Table 1. Main activations during effort production

Brain region	Side	Cluster size (number of voxels)	Peak t value	Peak z score	Peak coordinates (mm)
Force (left > right hand)					
M1	R	351	5.39	4.49	34, –20, 68
Force (right > left hand)					
M1	L	232	5.29	4.43	–40, –20, 64
Personal utility					
VP	R	38411	7.23	5.50	10, 2, 4
Cuneus	L		7.18	5.47	–4, –94, 6
VP	L		6.76	5.26	–8, 4, 4
Cuneus	R		6.66	5.21	6, –88, 12
Insula	L		6.27	5.00	–44, 16, –12
Insula	R		5.91	4.80	46, 18, –8
M1	L		5.06	4.29	–24, –14, 72
M1	R		4.22	3.72	24, –20, 72
Social position					
VS	R	105	4.39	3.84	18, 12, 2
VS	L	10	3.56	3.24	–14, 10, –8
Competition					
mPFC	R	991	6.43	5.09	6, 44, 20
Middle occipital gyrus	L	868	5.55	4.59	–40, –90, 0
Cuneus	R	674	5.09	4.31	28, –86, 30
Precentral gyrus	L	276	5.09	4.31	–34, –4, 40
Inferior frontal gyrus	R	150	4.79	4.11	32, 20, –22
Cuneus	L	215	4.72	4.07	–4, –100, 8
Collaboration					
TPJ	L	191	4.48	3.90	–48, –64, 32

All voxels in the listed clusters survived a statistical threshold of $p < 0.001$, uncorrected. Except for social position, which is reported at an uncorrected threshold, all clusters included a minimum of 150 voxels, which corresponds to a threshold of $p < 0.05$ after FWE correction for multiple comparison at the cluster level. $[x, y, z]$ coordinates are given in the MNI space. M1, Primary motor cortex; R, right; L, left.

was shown to reflect positive social comparison (Fliebsbach et al., 2007; Bault et al., 2011). Therefore, these activations in the ventral basal ganglia (VP and VS) might reflect the prospect of success in terms of monetary earning or social status.

At the same period, collaboration was associated with activation in the left TPJ. The same specific activation was observed when contrasting collaborative to competitive or individual trials, separately. In contrast, competition elicited significant activation in a series of brain regions that did not include TPJ (Table 1), with a global peak in the mPFC. Thus, the collaboration versus competition manipulation dissociated the role of two regions frequently involved in social cognition (Van Overwalle, 2009; Rilling and Sanfey, 2011).

How these regions participate in the behavioral response is yet to be explained. In particular, the role of the mPFC remains elusive, because there was no specific impact of competition on force production. Regarding the TPJ, a straightforward assumption is that its activity may boost effort exertion in collaboration. Consistently, we found that, within the collaboration condition, the intertrial variability in force production not explained by personal utility was significantly predicted by TPJ activation ($t_{(31)} = 2.5$, $p = 0.019$) but not by mPFC activation ($t_{(31)} = 0.9$, $p = 0.38$). We also reasoned that, if our interpretation is correct, then interindividual variations in collaboration bias should correlate with TPJ activation. We took advantage of the high inter-participant variance, with some subjects being pure utilitarians and others great collaborators (with the collaboration bias ranging from -0.18 to 0.56), to test the correlation with the coefficient of the collaboration regressor extracted from left TPJ activation peak. We found a significant correlation, surviving robust regression methods, between the collaboration bias and left TPJ activation ($r = 0.45$, $p = 0.005$; Fig. 5A). Let us emphasize

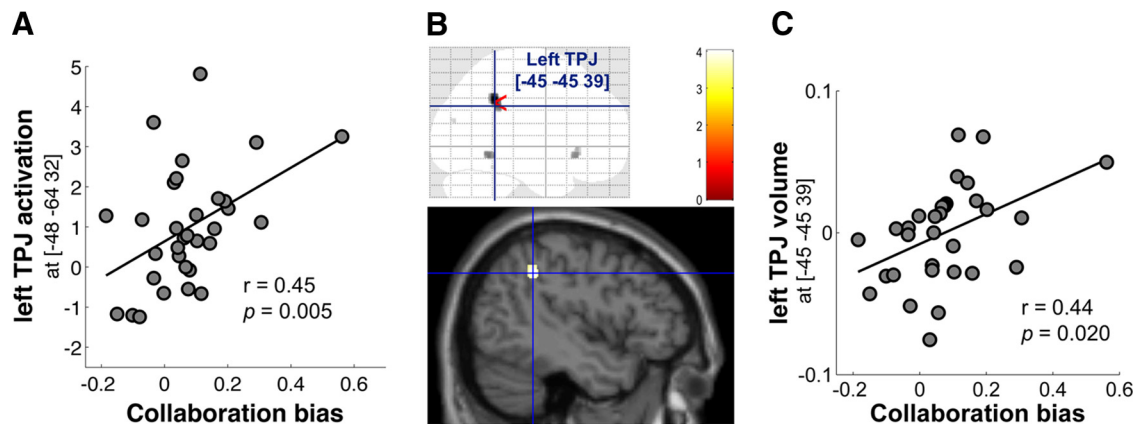


Figure 5. Individual differences in collaboration bias. **A**, Correlation between collaboration bias and left TPJ activation during collaboration. **B**, GM volume difference between collaborating and utilitarian subjects. The illustrated cluster survived a threshold of $p < 0.05$ after small-volume correction for multiple comparisons within the anatomically defined left TPJ. SPMs are displayed at an uncorrected threshold of $p < 0.001$ over the entire brain. **C**, Correlation between collaboration bias and GM volume in the left TPJ (normalized values). r and p are Pearson's correlation coefficient and robust fit p values.

that this test was independent of the intertrial regression that isolated TPJ activation during collaborative trials.

In search for another independent piece of evidence for the TPJ mediating the effect of collaboration on work motivation, we turned to brain structure. We asked whether the intersubject variability in collaboration could be predicted from variability in left TPJ volume. Using VBM analysis, we compared GM volume measures, obtained from T1-weighted anatomical images, between collaborating and utilitarian subjects. We found that collaborators had more GM than utilitarians did in a cluster that survived FWE small-volume correction within the anatomically defined left TPJ (Fig. 5*B*). Direct correlation between GM volume in this cluster and the collaboration bias was also significant (Fig. 5*C*). Thus, left TPJ anatomical volume appeared to account for part of the variance in how much individuals are motivated by collaborative situations.

Discussion

Behavioral data indicate that, across cooperative and competitive contexts, force production was mainly driven by personal utility. This replicates the well established social loafing phenomenon (Ringelmann, 1913; Karau and Williams, 1993), according to which individuals reduce their effort during collective tasks and extends the influence of personal utility to competitive contexts, in which participants produced more effort. In addition, we observed an independent motivational boost that was specifically observed when subjects believed that they were collaborating with a human partner. This was not attributable to the particular parameterization of personal utility, because it was also observed in a categorical contrast to collaboration with a computer (in Task 2). Although we conclude that collaboration induces a truly social motivation to work (by opposition to personal cost/benefit ratio), we do not claim that this motivation is purely altruistic; it might reflect a (conscious or not) desire to maintain a good reputation. In other words, we could have equally framed the collaboration-induced motivation as a purely social component in the utility function taken in a broader sense instead of reserving the term utility for financial payoff. Contrary to collaboration, competition yielded no specific motivational effect, besides those attributed to increasing personal utility. This result might mitigate the belief that competition is intrinsically motivating.

One limitation of our paradigm is that subjects barely knew each other and that their social interaction (collaboration or competition) switched very frequently (across trials). However, this probably attenuated collaboration effects, which might have been greater in acquainted individuals working together in the long run. Indeed, the development of interpersonal ties has been shown to enhance subsequent pro-social behavior in economic decision-making (Harrison et al., 2011; Fahrenfort et al., 2012). Furthermore, variations in social relationships or in social attributes, such as reputation and trust, also modulate regions of the social brain network (Krueger et al., 2007; Cheng et al., 2010). Thus, testing unacquainted subjects enabled assessing the intrinsic effects of social contexts without the confounding effects of preexistent social ties. Also, keeping the simulated player's behavior constant on average avoided the confounds related to subjects keeping track of dynamically evolving social attributes.

The collaboration-related motivational boost was also independent of social position, which reduced effort exertion, in the sense that subjects produced more force when running behind their partner/opponent. This is in line with the well shared notion in sports that athletes need somebody running ahead of them at the start to beat their record. In our paradigm, the social position was varied such that the teammates performed equally on average. This allowed us to match the expected payoffs of the different social contexts but limited the scope of our study to situations without inequity. It remains possible that different effects would be observed if the partner/opponent was systematically stronger or weaker.

Neuroimaging data paralleled the dissociations observed in behavioral performance. A first dissociation was found across social contexts, with collaboration recruiting the TPJ and competition the mPFC. The TPJ has been implicated in attributing mental states to others, such as intentions or beliefs (Castelli et al., 2000; Saxe and Kanwisher, 2003; Samson et al., 2004), in the management of our social image (Bhatt et al., 2010), and in social decision-making, more precisely in promoting pro-social choices (Carter et al., 2012; Morishima et al., 2012). Indeed, altruism has been shown to correlate with activity in the right TPJ (Tankersley et al., 2007; Hare et al., 2010; Morishima et al., 2012) and reciprocity with activity in

the left TPJ (van den Bos et al., 2011). The mPFC has also been involved in various social tasks, including competitive context (Decety et al., 2004). Consistent with its activation in relation to social interaction with negative valence, the mPFC has been implicated in encoding the discrepancy between self and others' preferences (Tamir and Mitchell, 2010) and in detecting deceptive intentions toward oneself (Grèzes et al., 2004; Lissek et al., 2008).

A second dissociation was observed between the collaboration context itself (represented in the TPJ) and its associated personal utility, which was reflected in the ventral basal ganglia, together with incentive-related utility. In line with our previous studies (Pessiglione et al., 2007; Schmidt et al., 2012), the ventral basal ganglia therefore appeared as the neural substrates of a motivation indexed on the personal utility of effort exertion. Activity in the ventral basal ganglia was also modulated by the social position, consistent with previous reports that social comparison influences reward-related brain activity and provides a strong drive in behavioral adaptation (Fliessbach et al., 2007; Bault et al., 2011).

In contrast, the TPJ appeared as a likely candidate for mediating the motivational boost specifically linked to collaborative situations. Indeed, both within-subject (across trials) and between-subject analyses showed that TPJ activity was linked to enhanced performance during collaboration. Furthermore, interindividual differences in the collaboration bias were also predicted by TPJ anatomical volume. Interestingly, the collaboration bias was correlated with the SVO, which is considered as a trait-like stable disposition (Van Lange, 1999). Thus, anatomical characteristics of the TPJ could constitute the neural basis for such an individual social trait. A recent study has reported that TPJ volume and activation predict another pro-social attitude: altruistic donation (Morishima et al., 2012). Significant clusters were on the right side, whereas they appeared on the left in our study. However, we would not draw strong conclusions about laterality, because we found significant clusters in the right TPJ when lowering the threshold. We also note that the anatomical and functional clusters related to the collaboration bias were adjacent but not superimposable (compare Fig. 4, bottom, with Fig. 5B). TPJ is a vast region; the functional specialization of subterritories is an issue that would require additional investigation. In any case, our findings suggest that the individual propensity to invest energy in collaborative work might have an identifiable counterpart in the brain functional architecture. They also hint that poor social collaboration, as seen in pathological conditions such as autism or psychopathy, might arise from dysfunctional TPJ.

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