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Neural bases of social facilitation and inhibition: how peer presence affects elementary eye movements

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Abstract:

Social Facilitation/Inhibition (SFI) refers to how others' presence influences task performance positively or negatively. Our previous study revealed that peer presence modulated saccadic eye movements, a fundamental sensorimotor activity. Pro- and anti-saccades were either facilitated or inhibited depending on trial block complexity (Tricoche et al., 2020). In the present fMRI study, we adapted our paradigm to investigate the neural basis of SFI on saccades. Considering inter- and intra-individual variabilities, we evaluated the shared and distinct neural patterns between social facilitation and inhibition. We predicted an involvement of the saccade-related and attention networks, alongside the Theory-of-Mind (ToM) network, with opposite activity changes between facilitation and inhibition. Results confirmed peer presence modulation in fronto-parietal areas related to saccades and attention, in opposite directions for facilitation and inhibition. Additionally, the ventral attention network was modulated during inhibition. Default mode regions, including ToM areas, were also modulated. Finally, pupil size, often linked to arousal, increased with

peers and correlated with dorsal attention regions and anterior insula activities. These results suggest that SFI engages task-specific and domain-general networks, modulated differently based on observed social effect. Attention network seemed to play a central role at both basic (linked to arousal or vigilance) and cognitive control levels.

Keywords: social influence, fMRI, prosaccades, antisaccades, attention, DMN

Total number of words: 8045

Introduction

When another person is present while we perform a task, our performance happens to be modulated, either positively or negatively. Called Social Facilitation/Inhibition (SFI), this effect of mere presence has been identified by social psychology a long time ago (see review in Guerin, 2010). In particular mere presence has generally been established to help us when the task is simple or well-mastered (i.e. social facilitation), whereas it impedes our performance in complex or newly acquired tasks (i.e. social inhibition) (Zajonc, 1965). However, no study has so far highlighted the neural mechanism and processes leading to a social facilitation *versus* inhibition.

Theories from social psychology suggested an attentional mechanism of SFI accounting for its opposite effects according to task difficulty. One such theory assumes that other presence is distracting and diverts attention away from the task at hand. This creates an attentional conflict, a situation where attention must be split between the task and the nearby person, reducing the attention focus devoted to the task. This leads in turn to a paradoxically better performance in simple tasks (few salient stimuli, few peripheral distractors) because the reduced attention is less likely attracted by distractors away from

the salient targets. Conversely, for complex tasks (many crucial stimuli, many distractors) the performance is impaired because attentional demands are so high that any attentional diversion is detrimental (Baron, 1986; Belletier et al., 2019; Huguet et al., 1999). However, this attentional hypothesis has not been supported by neuroimaging studies so far. Indeed, as detailed in the next paragraph, they did not clearly establish the implication in the SFI mechanism of attention processes and associated brain networks; moreover, none of them distinguished between social facilitation and social inhibition.

The cortical network of attention is well defined (Buschman & Kastner, 2015; Corbetta & Shulman, 2002; Katsuki & Constantinidis, 2014). This fronto-parietal network consists of dorsal areas (superior parietal lobule-SPL, intra-parietal sulcus-IPS, frontal eye field-FEF) and ventral areas (temporo-parietal junction-TPJ, inferior frontal gyrus-IFG, part of the median frontal gyrus-MFG). This attention network has been included in the brain models of social behavior only recently (Chang et al., 2013; Patel et al., 2019). Mere presence modulates this network in monkeys (Monfardini et al., 2015), as well as in human (Dumontheil et al., 2016; Liu et al., 2017; Yoshie et al., 2016). When analyzed at the light of behavioral results, the increased activity in the attention areas disclosed by Dumontheil and collaborators was associated with social inhibition, whereas the deactivation of the attention network found by Yoshie and collaborators was associated with social facilitation. But, as these studies did not vary the tasks difficulty levels, they could not address the mechanisms underlying the bi-directionality of social effect. Moreover, the above studies showed that modulations were not restricted to the attention network, but extended to areas of the Theory of Mind (ToM) or motivation domain-general networks. In a previous study we found that these three

networks were modulated by peer presence on two cognitive tasks relative to education (Tricoche et al., 2023).

Some behavioral studies have investigated the specific effects on attention tasks of social facilitation *versus* social inhibition, but found conflicting results. Particularly, Yu and Wu, as well as Liu and Yu showed an effect of social presence on reaction time (RT) in a visual search task, which depended on the task difficulty parametrically controlled by the number of visual distractors present in the scene (Liu & Yu, 2017; Yu & Wu, 2015). Claypoole and Szalma showed only a social facilitation in a Go/NoGo vigilance task (Victoria L Claypoole & Szalma, 2018a, 2018b; Victoria Lynne Claypoole et al., 2019). Using saccade tasks, McFall, Jamieson and Harkins also showed only a social facilitation on RT, regardless of whether subjects performed blocks of reflexive prosaccades (saccades toward the target) or voluntary antisaccades (saccades away from the target, towards its mirror location) (McFall et al., 2009). On the contrary, Oliva and collaborators who also tested prosaccades and antisaccades in separate blocks found only a social inhibition on antisaccades' RT, with no effect on prosaccades RT (Oliva et al., 2017). These studies are indicative of the high inter- but also intra-individual variabilities of SFI (Sanna, 1992; Uziel, 2007, 2010), an effect rarely explored as the majority of studies investigated SFI at group level.

Recently we re-investigated whether these three attention tasks (visual search, vigilance and saccade tasks) can exhibit clearly dissociated social facilitation versus social inhibition effects according to their difficulty level (Tricoche et al., 2020), but still looking at group but not individual level. Our participants performed either the tasks alone, or in the mere presence of a familiar peer. Our main prediction was a social facilitation for easy trials and a social inhibition for complex trials. The results indicated that only the saccade task revealed a

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social effect which varied with task difficulty, whereas no significant SFI effect was found in the two other tasks. More precisely, participants performed pro- or anti-saccades either in two distinct pro- and anti-blocks (easy trials) or mixed together at random in the same block (complex trials). Results showed a social inhibition effect on both RT and peak velocity in complex trials, where pro- and anti-saccades were initiated later and were slower in peer presence than alone; whereas in easy trials both pro- and anti-saccades were initiated earlier and were faster in peer presence than alone. Therefore, the social effect did not depend on the saccade type itself (pro- or anti-) but on the global task difficulty related to the presentation schedule (randomly mixed or blocked). This study leads to the following intriguing questions: are such peer presence effects on saccades associated with a modulation of the attention network, given its strong involvement in saccade generation? In the affirmative, are other domain-general networks like ToM and motivation also involved? Does the modulation of these different networks differ according to the direction of the social behavioral effect observed at the group or individual level?

The present imaging study used the same saccade task as in Tricoche et al 2020. Adult participants were scanned while performing easy trial blocks (pro- and anti-saccades separated) and complex trial blocks (pro- and anti-saccades mixed together) during two different sessions: one with a familiar peer present in a neighboring room and observing the participant as he/she performed the task (Observation condition), and the other alone, without any observation (Alone condition). Our main hypothesis was that the domain-general fronto-parietal attention network, also involved in saccades (task-specific network), will be modulated by the observation condition compared to the alone condition. In addition, the ToM and motivation domain-general networks will also be modulated by peer

presence (Dumontheil et al., 2016; Liu et al., 2017; Tricoche et al., 2023; Yoshie et al., 2016). Finally, all three networks will be differently modulated according to social facilitation or social inhibition. We made two alternative predictions depending on how the distraction related to the peer presence is processed: 1) this distractor effect is counterbalanced by an increased attention dedicated to the task, thanks to a greater involvement of the endogenous attention network, yielding social facilitation; 2) the distraction effect wins, associated with an increase of activity in the exogenous attention network, and impairs task performance (social inhibition). To discriminate between these two predictions, physiological responses at the levels of whole-brain and saccadic ROIs were analyzed separately for socially facilitated *versus* socially inhibited blocks, taking advantage of inter-individual variabilities. We analyzed two parameters reflecting the attentional performance (saccadic RT and eye peak velocity) and one additional parameter (pupil diameter) reflecting notably the state of arousal and vigilance (Joshi & Gold, 2020) and previously found modulated by social contexts (Ebitz et al., 2014; Liu & Yu, 2017).

Materials and Methods

Participants

We recruited 16 duos of participants *via* web posting (mean age: 21.77 years, SD: 1.83, range: 19-27 years, 22 females), who were native French speakers with normal or corrected vision, no MRI contra-indications and no neurologic or psychiatric history. All duos were age-matched (+/- 3 years) familiar partners, friends or lovers, with a mean closeness score assessed by the Inclusion of Other in the Self scale (on 7 points) of 4.96 (range: 3-7),

indicating typical close relationships (Aron et al., 1992; Gächter et al., 2015). One participant was excluded before the scanning due to a match with an exclusion criterion. Three participants were excluded from all analyses (both sessions), and two participants were excluded from analyses of the second session only, due to recording issues. Our final sample included 26 participants who completed both sessions, and 2 additional participants who completed only one session. Two power analyses were conducted to validate this sample. The first one was based on our previous behavioral study where we found the significant Condition x Task difficulty interaction we expected in the present experiment (Tricoche et al., 2020): for a similar effect size ($f=0.40$, $\eta p^2=0.14$) with a power of 80% and with $\alpha= 0.05$, the *a priori* power analysis using GPower indicated a required sample size equal to 12. For imaging data, we used our previous fMRI study where a Condition x Task interaction was found with a medium effect size ($f=0.29$, $\eta p^2=0.08$) (Tricoche et al., 2023): expecting in the present study a Condition x Task difficulty interaction (see below) with a similar effect size, the power analysis indicated a sample size of 18. Based on these power analyses, we decided to increase our sample size above 20, as we also investigated the main Condition effect by separating facilitated and inhibited sets of trials.

The study was approved by the Ethics Committee (CPP Sud-Ouest & Outre-Mer II) on Oct 3, 2019 (ID-RCB: 2019-A01027-50) and conducted according to the guidelines of the Declaration of Helsinki. All participants signed an informed consent before inclusion, and received a 70€ compensation for their participation.

Sessions timeline

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Participants performed two scanning sessions with at least three weeks in between. In one session the two familiar partners of a duo came together (Observation condition). Each member of the duo alternatively took the actor and the observer roles. While the actor performed the task inside the scanner, his/her partner observed him/her remotely from an adjacent room. The observer was facing a computer screen displaying the live video streams of three cameras placed in the scanner room and filming, respectively, the actor's face, the actor's body and the task's screen (focusing on the feedback about the actor's performance). The observer was instructed to watch these 3 video streams and particularly the performance feedback and to give his/her opinion about the actor's performance at the end of each run by choosing among "Fair", "Good" or "Excellent" rating. This evaluation scenario was used to improve the peer presence effect (Belletier et al., 2015; Cohen, 1980). In the other session, each participant came alone and performed the task without observation (Alone condition). The order of the two sessions was counterbalanced across participants.

For each session the actors performed the same saccade task during approximately 30 minutes. This task was divided in four runs of 7 minutes each. At the end of the second run, a 6-minute anatomical T1 scan was conducted (Figure 1A). At this time, in the Observation condition, the actor and the observer could see each other via video cameras in order to reinforce the actor's sense of being watched by the observer. In the Alone condition, the actor saw the same, but now empty, room. At the end of the task, there was a 9-minute resting state scan, not analyzed in the present paper. In both conditions, the experimenters remained during the whole session out of sight in the scanner's monitoring room (whose window overlooking the scanner was obtruded by a curtain) and refrained from any unnecessary verbal contact with the actor in order to minimize third-party presence.

Saccade task

The saccade tasks were programmed using the EyeLink® Experiment Builder software (<https://www.sr-research.com/experiment-builder/>). The stimuli were projected onto a screen viewed by the actor through a mirror attached to the head coil. For each trial (Figure 1B), the actor fixed a dark dot at the center of the screen for a pseudo-randomized duration of 1,000 or 1,500 ms. Then a colored dot appeared on the left or on the right at 10° of eccentricity on the horizontal axis, simultaneously with the fixation dot disappearance. If the stimulus was green, the actor should make a saccade toward it (prosaccade); if the stimulus was red, he/she should perform a saccade away from it, toward its mirror location (antisaccade). Participants were asked to be as fast and accurate as possible. Stimuli remained visible until the saccade initiation or the 1,000 ms timeout was reached (trials with a saccade latency > 1,000 ms were considered as misses). At the end of each trial, an iconic performance feedback appeared at the center of the screen during 100 ms: a thumb-up indicated a correct trial (saccade toward the expected direction), whereas a thumb-down indicated an incorrect trial (saccade toward the wrong direction) or a miss trial. Participants performed 4 runs, each composed by 16 saccade blocks and 7 interleaved fixation blocks. Each saccade block comprised 8 trials (4 trials in each direction, pseudo-randomly), yielding a total of 512 saccade trials per session. Easy blocks of trials (Figure 1C) comprised a single type of saccade (8 pro or 8 anti) whereas complex blocks of trials (Figure 1D) comprised the two saccade types in random order (4 pro and 4 anti). The 4 runs were always performed in the following order: two runs of complex trial blocks, one run of prosaccades easy trial blocks, and one run of antisaccades easy trial blocks (Figure 1A). We then obtained (and

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analyzed) 4 sets of trials: easy prosaccades, easy antisaccades, complex prosaccades and complex antisaccades. For the fixation blocks, participants should fixate a dark cross at the center of the screen during 10 seconds.

At the beginning of each session, participants completed a training phase composed by one

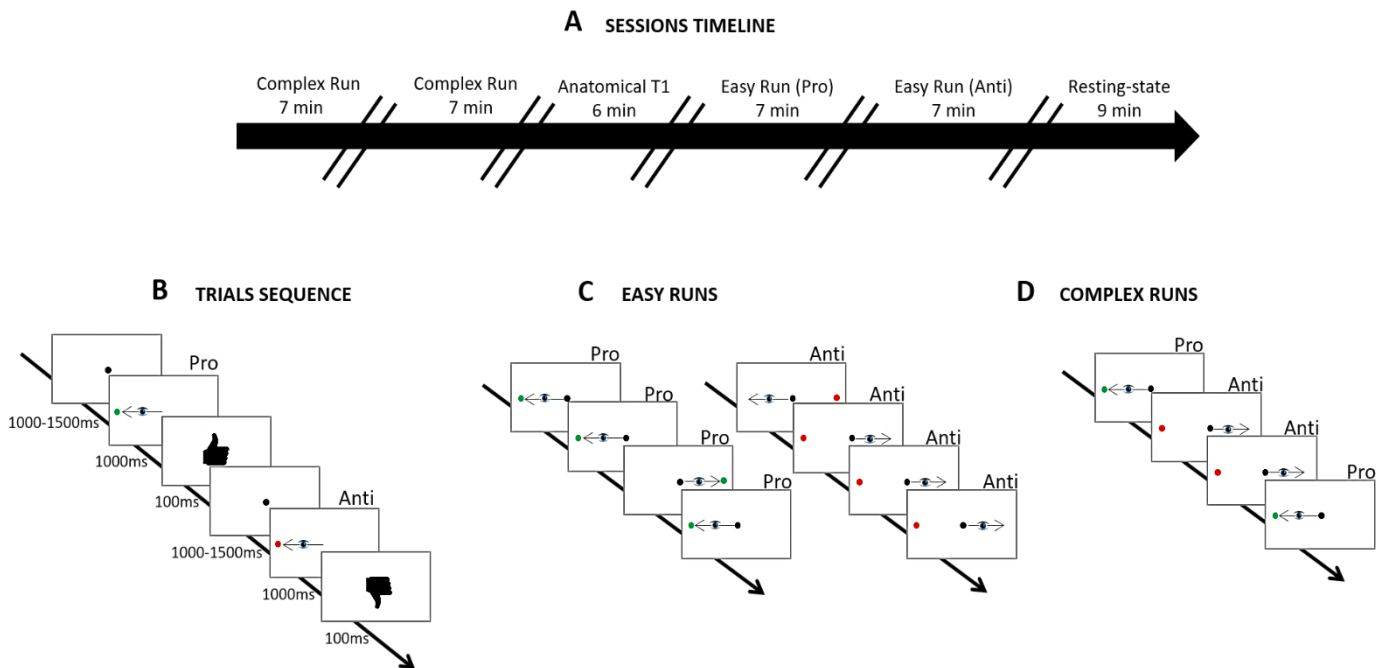


Figure 1: (A) During the MRI session, participants completed first the two Complex runs, followed by the anatomical T1, and then the two Easy runs. The session ended with a resting-state acquisition. (B) For each trial, participants fixated a dark dot at the center of the screen for a pseudo-randomized duration (1,000 to 1,500ms). Then a colored dot appeared on the left or on the right. Participants had to make a prosaccade if the stimulus was green or an antisaccade if the stimulus was red. At the end of each trial, a performance feedback appeared (thumb-up or thumb-down). (C) Easy runs: the pro- and anti-saccades were presented in separated blocks, (D) Complex runs: the pro- and anti-saccades were randomly mixed together.

block of 8 prosaccades trials and one block of 8 antisaccades trials.

Behavioral analyses

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Eye movements were recorded by an eye-tracker camera (“EyeLink1000” SR-Research) placed behind the scanner and filming the eye image reflected by the mirror. Before each run, a 3-point calibration on the horizontal axis was carried out for each participant. Behavioral analyses were conducted using R (RStudio, v.1.0.136). We measured the saccade direction accuracy (percent of saccades in the correct direction, %Corr) and the speed of correct saccades initiation (reaction time, RT, between the appearance of the stimulus and the saccade initiation). We also measured saccade kinematic parameters [peak velocity (maximum eye speed during the saccade) and duration (time between saccade onset and offset)] and the pupil diameter before and after the stimulus appearance. All parameters were extracted *via* EyeLink® DataViewer and analyzed by three-way ANOVAs with the within-subject factors Condition (Observation, Alone), Saccade (Prosaccade, Antisaccade) and Task difficulty (Easy, Complex). Based on our previous study, we expected a significant Condition x Task difficulty effect on RT and peak velocity parameters (Tricoche et al., 2020).

We also analyzed for each parameter the effect of Condition (Observation *versus* Alone) at the individual level. To do so, we calculated for each set (k; easy prosaccades, easy antisaccades, complex prosaccades or complex antisaccades) and each participant (i) the performance facilitation ($\Delta > 0$) or inhibition ($\Delta < 0$) produced by the Observation relative to the Alone condition

$$[\Delta_i^k = (Mean_{Alone}^k - Mean_{Observation}^k) / Mean_{Alone}^k * 100],$$

where $Mean_{Alone}^k$ is the mean value of the parameter (RT, peak velocity or pupil diameter) for a specific k set and one i participant during the Alone condition (or during the Social condition for $Mean_{Observation}^k$). This allowed us to determine facilitated and inhibited

profiles for each participant and for each run, refining our fMRI analyses (see “fMRI data analyses” section).

MRI data acquisition

MRI scans were obtained from a MAGNETOM Prisma 3.0 T scanner (Siemens Healthcare, Erlangen, Germany) at the Lyon Primage neuroimaging platform (CERMEP, Imagerie du vivant, Lyon, France). The fMRI blood oxygenation level-dependent (BOLD) signal was measured with a multiband-accelerated echo planar imaging (EPI) sequence (acceleration factor of 2, credits for providing the sequence to CMRR, Center for Magnetic Resonance Research, Minnesota, USA). The following parameters were used: TR = 1,720 ms, TE = 30 ms, flip angle = 90°, matrix size = 92 x 88, field of view = 220 x 211 mm, voxel size = 2.4 x 2.4 mm, slice thickness = 2.4 mm, number of slices = 50.

After the two first functional runs, a high resolution T1-weighted 3D structural image was acquired for each participant (TR = 3,000 ms, TE = 3.8 ms, flip angle = 7°, matrix size = 256 x 224 mm, field of view = 224 x 256 mm, slice thickness = 1 mm, number of slices = 192).

fMRI data analyses

Preprocessing

MRI data were preprocessed using fMRIPrep 20.2.0 (Esteban et al., 2019). The two T1 images, one in each session, were merged into a single template, segmented and normalized to the MNI space. The functional images (4 task runs per session + 2 resting-state runs) were

skull-stripped, realigned, slice-time corrected, coregistered and warped to the normalized anatomical image (for a full report of the preprocessing pipeline see <https://osf.io/9p2db/>). Using SPM12, data were spatially smoothed with a Gaussian filter with a half-maximum width of approximately twice the voxel size ($4 \times 4 \times 4 \text{ mm}^3$).

Processing

Event-related statistical analyses were conducted using the general linear model (GLM). Activation was modeled as epochs with onset time locked to the presentation of the stimulus in each trial and with a duration of 1 second. Only correct trials were analysed and sorted according to 3 regressors of interest: Condition (Session 1 vs. Session 2), Saccade and Task difficulty. Fixation blocks were modeled with a duration of 10 seconds in a separate regressor for each run. Regressors of no-interest (including fixation dots before stimulus appearance and feedback periods) were added in the model, along with the six motion parameters (x, y, z, pitch, roll and yaw). All epochs were convolved with a canonical hemodynamic response function (HRF). The time series data were high-pass filtered (1/128 Hz), and serial correlations were corrected using an autoregressive AR (1) model.

Whole-brain analyses

Voxel-wise parameter estimates obtained for each participant were entered into random effect (RFX) analyses in order to identify regions exhibiting main effects and interactions in the Condition x Saccade x Task difficulty ANOVA. Group-wise statistical maps were thresholded for significance using a voxel-wise probability threshold of $p < 0.001$ (uncorrected) and a cluster-wise probability threshold of $p < 0.05$ (FWE corrected for multiple comparisons).

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As one aim of this study was to identify differential brain activity for social facilitation and inhibition taking into consideration inter- and intra-individual variabilities, we additionally constructed specific contrasts for every individuals according to their profile of social susceptibility. Based on the sign of RTs' delta scores in each participant we categorized each set as facilitated or inhibited (e.g. RT decrease *versus* RT increase when observed relative to alone, respectively). The justification and validity of this procedure is detailed in Supplementary Material 1. We then obtained group-wise statistical maps separately for facilitated and inhibited sets and we applied the Observation *versus* Alone contrast. These maps were thresholded for significance using a voxel-wise probability threshold of $p < 0.005$ (uncorrected) and a cluster-wise probability threshold of $p < 0.05$ (FWE corrected for multiple comparisons). As several participants were consistent across sets (8 were always facilitated and 2 always inhibited, see Supplementary Material 2) and thus contributed to only one map, the map of facilitated sets involved 24 participants whereas the map of inhibited sets relied on 18 participants. The same analysis strategy based on facilitated and inhibited sets was repeated for 2 other parameters, peak velocity and pupil diameter. For the peak velocity's delta score, 20 participants were included for the map of facilitated sets (e.g. where peak velocity was higher under observation than alone) and 13 participants were included for the map of inhibited sets (e.g. peak velocity was lower under observation than alone). For the pupil's delta scores, as pupil diameter is linked to vigilance level (Joshi & Gold, 2020; Murphy et al., 2014; Schneider et al., 2016) and not directly to performance (contrary to RT or peak velocity), "social facilitation" sets will correspond to those with an increased pupil size (e.g. larger pupil diameter under observation than alone) whereas "social inhibition" sets to those with a reduced pupil size (e.g. smaller pupil diameter under observation than

alone). We included 14 participants for the map of facilitated sets and 16 participants for the map of inhibited sets.

Finally, for each significant cluster, the beta value at the peak voxel was correlated separately with the 3 delta scores (of RT, peak velocity and pupil diameter) using a Pearson test or the equivalent non-parametric Spearman test.

ROI analyses

ROIs were defined as 10 mm radius spheres centered on the local maximum of each cluster (using the SPM toolbox Marsbar) obtained by the Saccade > Fixation and Fixation > Saccade contrasts (Table 1). As large clusters were found, we sometimes computed maps with a more stringent threshold (voxel-wise probability threshold of $p < 0.05$, FWE corrected for multiple comparisons) to distinguish specific ROIs inside these clusters; we could also use the mirror coordinates of a unilateral ROI to better identify the ROI center in the opposite hemisphere. Eighteen ROIs were identified for each Saccade > Fixation and Fixation > Saccade contrasts (Table 1). BOLD activity was then averaged across all voxels of each ROI, and submitted to four-way ANOVAs with the within-subject factors Condition (Observation, Alone), Saccade (Prosaccade, Antisaccade), Task difficulty (Easy, Complex) and ROI. For significant interactions in ANOVAs, pairwise comparisons with Bonferroni correction for multiple comparisons were applied. Then, as described already for the whole-brain approach, we distinguished between facilitated *versus* inhibited sets in the aim of highlighting distinct patterns of activity. To investigate the observation effect separately for facilitated and inhibited sets we applied Student tests (or the equivalent non-parametric Wilcoxon test). Statistical significance was set at $p < 0.05$.

Table 1. MNI coordinates of the significant clusters identified in the Saccade > Fixation contrast (top) and in the reverse Fixation > Saccade contrast (bottom), with a voxel-wise probability threshold of $p < 0.05$, FWE corrected for multiple comparisons. These clusters were used to define 18 ROIs for each contrast (see text). Z score = statistic obtained on the peak of each significant cluster. When the cluster contained two distinct regions, a Z score was given for the local peak of each region.

Anatomical location	MNI coordinates (mm)			Z score	Cluster size (voxels)
	x	y	z		
	<i>Saccade > Fixation</i>				
Left Superior Frontal Gyrus extending into the Anterior Cingulate Cortex	-18	40	-4	#	#
Right Superior Frontal Gyrus extending into the Anterior Cingulate Cortex	18	40	-4	6.15	55
Left Middle Frontal Gyrus	-28	40	10	#	#
Right Middle Frontal Gyrus	28	40	10	5.50	5
Left Frontal Eye Field	-27	-6	51	6.68	121
Right Frontal Eye Field	35	-6	51	5.98	88
Left Supplementary Eye Field	-9	-1	66	#	#
Right Supplementary Eye Field	9	-1	66	5.40	5
Left Parietal Eye Field (2 sub-regions)	-34	-51	56	5.69	13

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	-25	-58	58	5.30	1547
Right Parietal Eye Field (2 sub-regions)	23	-56	39	5.57	6
	16	-63	63	5.51	1518
Left Occipital Gyrus extending into the Cerebellum	-6	-75	-18	7.11	162*
Right Occipital Gyrus extending into the Cerebellum	6	-78	-16	6.97	162*
Left Putamen (2 sub-regions)	-30	1	1	7.64	437**
	-27	-8	13	7.53	437**
Right Putamen (2 sub-regions)	25	4	1	7.44	540***
	28	-8	10	7.23	540***
<i>Fixation > Saccade</i>					
Left Inferior Frontal Gyrus	-53	40	13	5.07	394
Right Inferior Frontal Gyrus	45	35	15	5.19	607
Right Middle Frontal Gyrus	30	49	32	3.85	50
Right Supramarginal Gyrus	66	-27	42	4.66	235
Left Temporo-Parietal Junction	-57	-44	25	#	#
Right Temporo-Parietal Junction	57	-44	25	4.46	58
Right Middle Occipital Gyrus	42	-80	27	5.48	188
Left Inferior Occipital Gyrus	-32	-94	-16	5.36	26
Right Inferior Occipital Gyrus	23	-99	-9	5.07	251
Pre-Supplementary Motor Area	4	23	63	5.13	167

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Middle Cingulate Cortex	2	23	34	5.55	21
Left Precuneus	-8	-37	46	5.35	17
Right Precuneus	9	-37	49	5.85	24
Posterior Cingulate Cortex extending into Precuneus	23	-58	20	5.57	885
Left Parahippocampal extending into Fusiform Gyrus	-34	-42	-26	5.85	19
Right Parahippocampal extending into Fusiform Gyrus	28	-42	-11	6.50	6936****
Left Insula	-39	-1	-9	6.09	6936****
Right Insula	40	-6	-1	6.00	1883

//***/**** Same cluster*

Mirror coordinates

Results

Behavioral analyses: group effects

As expected, a Saccade main effect was observed on both RTs and %Corr: antisaccades took longer to initiate and were less successful than prosaccades (RTs: $F(1,175)=61.55$, $p<0.001$; %Corr: $F(1,175)=96.49$, $p<0.001$). Also expected was a Task difficulty main effect revealing that easy sets led to shorter latency and better accuracy than complex ones (RTs: $F(1,175)=176.85$, $p<0.001$; %Corr: $F(1,175)=42.96$, $p<0.001$). A significant Saccade x Task difficulty interaction was disclosed for both parameters (RTs: $F(1,175)=13.70$, $p<0.001$; %Corr: $F(1,175)=11.04$, $p=0.001$), revealing that the mean latency of easy prosaccades

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(239.36ms) was the shortest relative to the other three sets (easy antisaccades: 292.09ms, complex prosaccades: 319.5ms, complex antisaccades: 337ms) and that the accuracy of complex antisaccades (mean %Corr: 72.89%) was the worst (easy antisaccades: 88.6%, complex prosaccades: 93.15%, easy prosaccades: 98.52%). Note however that all pairwise comparisons between sets were significant for both RTs and %Corr (all p 's < 0.05) with the single exception of easy antisaccades *versus* complex prosaccades for %Corr ($p=0.25$).

No Condition effect was found neither on the RTs nor on the %Corr, but a significant Condition x Saccade interaction was disclosed on RTs only ($F(1,175)=4.44$, $p=0.04$). Pairwise comparisons indicated that only antisaccades differed significantly between Observation and Alone conditions (Prosaccades: $p=1$; Antisaccades: $p=0.02$): participants initiated antisaccades earlier in the Observation condition than Alone, a facilitation effect qualified as small according to Cohen's d_z ($d_z=0.24$). Contrasting with the results obtained by Tricoche and collaborators (2020), we found no Condition x Task difficulty interaction on RTs.

Analyses conducted on the saccade peak velocity indicated a main effect of Saccade ($F(1,175)=4.05$, $p=0.05$), reflecting a higher velocity for prosaccades than antisaccades. The main effect of Task difficulty was not significant ($F(1,175)=3.26$, $p=0.07$). We additionally found no significant interaction but a significant Condition main effect ($F(1,175)=6.15$, $p=0.01$), indicating that the peak velocity was higher under observation than alone, irrespective of the saccade type and task difficulty. The associated Cohen's d_z revealed a small-sized effect ($d_z=0.33$). Analyses conducted on saccade duration revealed no modulation by the social context, as only a significant Saccade main effect was found ($F(1,175)=5.25$, $p=0.02$), antisaccades lasting longer than prosaccades. Finally, pupil diameter showed a significant main effect of Task difficulty ($F(1,175)=26.15$, $p<0.001$) as well as a Task

difficulty x Saccade interaction ($F(1,175)=4.61$, $p=0.03$), indicating a smaller pupil diameter for simple prosaccades as compared to the other three sets. No Condition main effect nor interaction was found for pupil diameter.

Behavioral analyses: individual effects

As the group results on RT, as well as peak velocity, did not allow us to replicate our previous observations of a social inhibition for simple sets and a social facilitation for complex ones (Tricoche et al., 2020), we conducted an individual analysis on those two parameters, using the delta score as a measure of each participant's susceptibility to peer presence (see Methods). The delta scores were measured for each set, yielding for each participant and each parameter four values (easy prosaccades, easy antisaccades, complex prosaccades, complex antisaccades). We also calculated the delta score for the pupil diameter, as this latter parameter is an indicator of vigilance and is modulated by social context according to a previous study (Liu & Yu, 2017). The different participants' inhibition/facilitation profiles defined based on these three parameters are given in the Supplementary Material 2. Consistent with the group effects reported above, a majority of blocks were facilitated according to the RT delta scores (61%) and to the peak velocity delta scores (65%) whereas for the pupil diameter delta scores, the two profiles were almost equally represented (47% of facilitated blocks vs 53% of inhibited blocks). The two profiles of peer influence defined for each of the three parameters -saccade RT, saccade peak velocity and pupil diameter- were used to conduct the individual-level fMRI analyses which will be presented in the following sections.

Whole-brain analyses

Using the Saccade (Pro- and Anti-saccades) > Fixation contrast across all participants and the two Conditions, we identified a network which activated in relation to eye movements. An increase of activity was shown in the typical saccadic network with extended clusters in the left or right hemisphere including FEF, SEF, PEF, SFG and subcortically, the bilateral cerebellum and a basal ganglia cluster corresponding to the bilateral putamen (Figures 2A and 2B). The reverse contrast, Fixation > Saccade, also showed significant clusters including areas frequently associated with the DMN: right MFG, right SMG, bilateral IFG, bilateral TPJ, right MOG, bilateral IOG, Prec, cingulate regions (PCC and MCC), preSMA, bilateral insula and the parahippocampal gyrus extending into the fusiform gyrus (Figure 2C). The Saccade main effect (Antisaccade > Prosaccade), as well as the Task difficulty main effect (Complex > Easy) disclosed circuitries (yellow dotted lines in Figure 2A and Figure 2B, respectively) which partly overlapped the saccadic network identified in the Saccade > Fixation contrast, involving significant clusters in the bilateral FEF, bilateral PEF, bilateral cerebellum and bilateral occipital regions including the fusiform gyrus, the parahippocampal gyrus and extending into the middle part of temporal lobe. No significant clusters were found for the reverse contrasts Prosaccade > Antisaccade and Easy > Complex.

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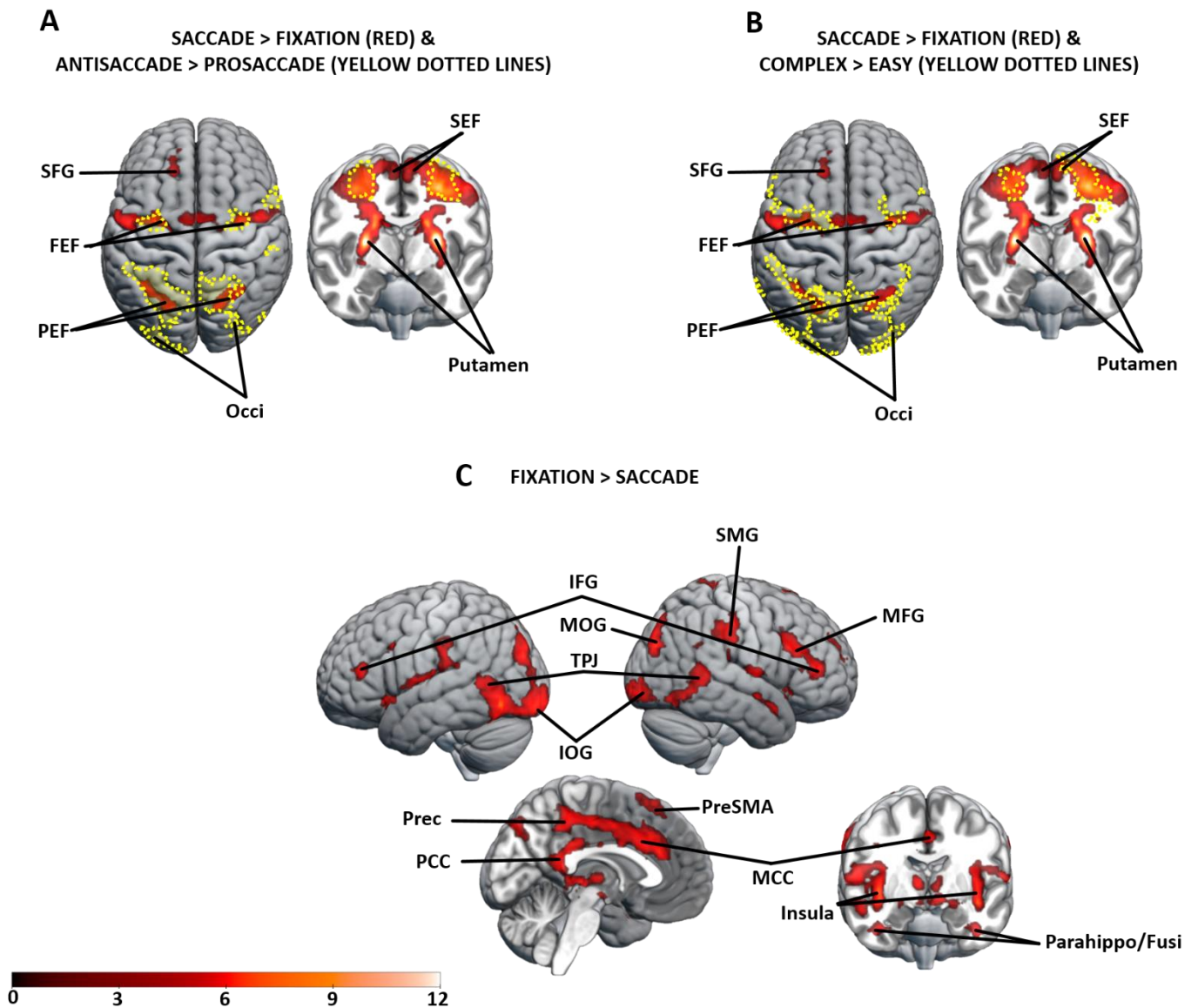


Figure 1: Brain regions activated in the Saccade > Fixation contrast (red) overlapped (yellow dotted lines) with (A) the Antisaccade > Prosaccade contrast or (B) the Complex > Easy contrast, across Conditions. (C) Brain regions activated in the reverse contrast, Fixation > Saccade, across Conditions and Task difficulties.

Moreover, whole-brain analyses revealed no main effect of Condition, nor any interaction with other factors. The absence of main effect of Condition in this group-level analysis could be due to a hypothetical difference of brain activity changes between social facilitation *versus* inhibition. To test this hypothesis, we further analyzed the effect of condition on brain activity but now according to SFI profiles defined at the individual level for the saccade RT, peak velocity and pupil diameter (delta parameters); leading to separate analyses of facilitated sets and inhibited sets. For the facilitated sets based on RTs, we found that the Observation > Alone contrast did not show significant clusters. However, for the inhibited sets based on RTs, significant clusters were found in a ventral fronto-parietal axis, with more activity during observation than alone in the bilateral SMG extending into the SPL (right: [40 -39 42], $Z=4.29$, cluster size (CS)=794; left: [-49 -39 44], $Z=3.99$, CS=852), the bilateral frontal lobe including MFG and IFG (right: [40 21 18], $Z=4.01$, CS=1022; left: [-42 42 8], $Z=3.93$, CS=706) and orbitofrontal gyrus (OFG) ([42 52 -11], $Z=3.70$, CS=100), and in a region surrounding the left posterior insula and the putamen ([-30 -20 6], $Z=3.55$, CS=93) (Figure 3A). No significant cluster was found for the Alone > Observation contrast, neither for the facilitated nor inhibited sets.

When looking at the facilitated and inhibited sets based on the peak velocity, we again did not find significant clusters for the Observation > Alone contrast for facilitated sets, but found two clusters of increased activity for inhibited sets: SEF ([2 37 44], $Z=4.58$, CS=199) and the posterior part of the left MFG surrounding FEF ([-32 25 46], $Z=4.12$, CS=145) (Figure 3B). Again, the Alone > Observation contrast did not reveal any significant region.

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Finally, analyses using profiles based on the pupil diameter showed a different pattern. Whereas no effect was found for inhibited sets, for the facilitated sets an increase of activity was revealed in dorsal fronto-parietal regions, particularly in the bilateral FEF (right: [25 4 49], $Z=3.61$, $CS=205$; left: [-27 6 66], $Z=4.01$, $CS=133$), SEF ([4 40 49], $Z=3.91$, $CS=207$), bilateral SPL (right: [35 -44 51], $Z=3.80$, $CS=359$; left: [-32 -66 46], $Z=3.81$, $CS=397$), bilateral anterior insula (right: [42 21 3], $Z=3.73$, $CS=98$; left: [-37 16 1], $Z=3.97$, $CS=97$) and ACC ([6 44 13], $Z=4.63$, $CS=85$) (Figure 3C). By correlating the beta value at the peak voxel of each cluster with the delta score of the pupil diameter for the facilitated blocks, we found a significant positive correlation between pupil diameter and neural activity, for three clusters: bilateral FEF (Pearson, right: $t=2.88$, $p=0.01$, $r=0.64$; left: $t=2.76$, $p=0.02$, $r=0.62$) and left IPS (Pearson, $t=3.07$, $p=0.01$, $r=0.66$), and a marginal effect with the right IPS (Pearson, $t=2$, $p=0.07$, $r=0.5$). The Alone > Observation contrast did not reveal any significant cluster.

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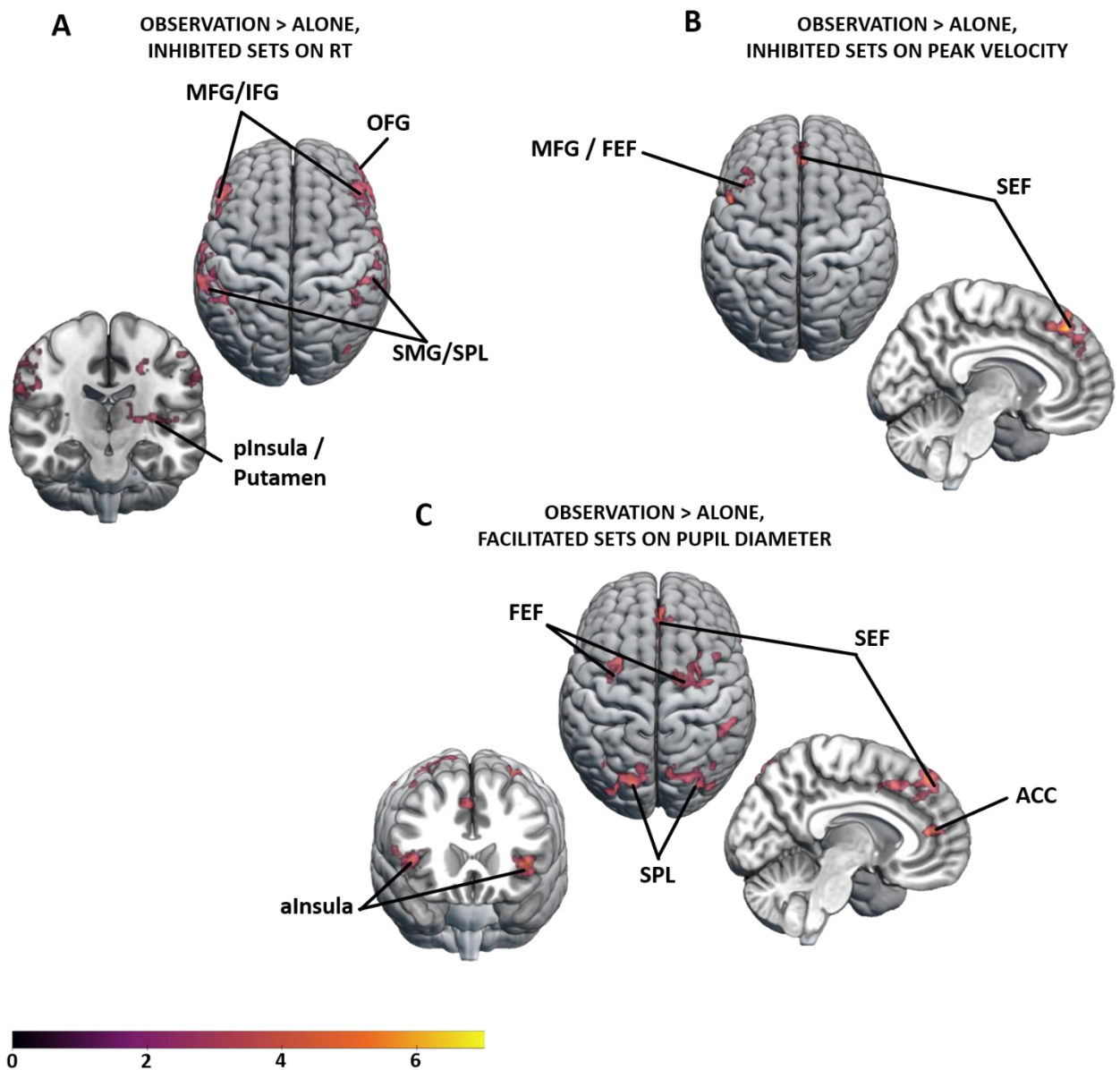


Figure 2: Brain activation in the Observation > Alone contrast, by separating socially facilitated versus socially inhibited sets according to the RT, peak velocity or pupil diameter parameters. (A) Brain regions for the inhibited sets based on RT. (B) Brain regions for the inhibited sets based on peak velocity. (C) Brain regions for the facilitated sets based on pupil diameter.

ROIs analyses

In this paragraph we will focus on the main effects and interactions of the Condition factor in the Condition x Saccade x Task difficulty x ROI ANOVA (other significant effects are given in Supplementary Results 1). We first conducted this ANOVA without differentiating between facilitated and inhibited sets. Results revealed a main effect of Condition on ROIs defined by the Saccade > Fixation contrast ($F(1,3432)=4.08$, $p=0.04$) showing that, overall, beta values of the saccade network were increased in the observation condition relative to the alone condition. This main effect was not found on ROIs defined by the Fixation > Saccade contrast (reflecting DMN). However, for both contrasts a significant Condition x Saccade interaction emerged (Sacc>Fix: $F(1,3432)=8.94$, $p=0.003$; Fix>Sacc: $F(1,3432)=14.04$, $p<0.001$), as well as a significant Condition x Saccade x Task difficulty interaction (Sacc>Fix: $F(1,3432)=13.99$, $p<0.001$; Fix>Sacc: $F(1,3432)=17.1$, $p<0.001$). For the Saccade > Fixation ROIs, pairwise comparisons indicated that the condition effect occurred for complex prosaccades (Complex: pro: $p=0.002$, anti: $p>0.05$; Easy: pro: $p=1$, anti: $p=1$). For the Fixation > Saccade ROIs, again the complex prosaccades showed a significant modulation by peer presence, but this time complex antisaccades also did (Complex: pro: $p=0.02$, anti: $p=0.008$; Easy: pro: $p=1$; anti: $p=1$).

Moreover, for both contrasts, no Condition x ROI interaction was found, and none of the pairwise comparisons testing the Condition effect at the level of each ROI was significant. These results suggest that Observation modulates the entire network homogeneously but to a limited extent, such that significant effects were revealed only when all ROIs were analyzed together.

Now, as for the whole-brain analyses above, we look for hypothetical differences of brain activity modulations between social facilitation *versus* inhibition, based on the same analysis strategy separating these two social susceptibility profiles. When separating facilitated *versus* inhibited sets based on RT, we observed that in the inhibited sets, beta values of the Saccade > Fixation ROIs increased significantly in the observation condition relative to the alone condition (t-test, $t=-9.88$, $p<0.001$; 100% of the ROIs followed this pattern) whereas in the facilitated sets beta values significantly decreased (t-test, $t=2.23$, $p=0.04$; 72% of the ROIs followed this pattern; the reverse tendency being observed for the following ROIs: bilateral putamen, bilateral SFG/ACC and right PEF). An additional one-sample test against 0

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conducted on the difference between the mean beta values of the observation vs. alone conditions, confirmed that facilitated sets beta values differences were significantly lower than 0 (t-test, $\mu=0$, $t=-2.36$, $p=0.03$) and that inhibited sets beta values differences were significantly higher than 0 (t-test, $\mu=0$, $t=10.45$, $p<0.05$). Figure 4 shows the results for several ROIs (bilateral FEF, PEF, SEF and putamen) and the graph for the remaining ROIs is given in Supplementary Result 2. For the Fixation > Saccade ROIs, a reduced deactivation was found for the inhibited sets in the observation condition relative to alone (t-test, $t=-5.21$, $p<0.001$; 89% of the ROIs followed this pattern; the reverse tendency being observed for the PCC and right parahippocampal/fusiform gyrus), whereas the reverse was observed for the facilitated sets (Wilcox-test, $v=170$, $p<0.001$; 100% of the ROIs followed this pattern). One-sample t-tests confirmed that in facilitated sets, beta values differences between observation and alone conditions were significantly higher than 0 (t-test, $\mu=0$, $t=6.57$, $p<0.05$) and that in inhibited sets, beta values differences were significantly lower than 0 (t-test, $\mu=0$, $t=-5.21$, $p<0.05$). Figure 5 shows the results for several ROIs (MCC, bilateral IFG, TPJ, Prec) and the graph for the remaining ROIs is given in Supplementary Result 2. Exactly the same conclusions can be drawn when separating facilitated versus inhibited sets based on peak velocity (see Supplementary Results 3&4).

Finally, for the facilitated versus inhibited sets based on pupil diameter, a different pattern was found. For the facilitated sets, we obtained higher beta values for the Saccade > Fixation ROIs, as well as a reduced deactivation for the Fixation > Saccade ROIs in the observation condition compared to alone. The reverse was observed for the inhibited sets (see Supplementary Results 5&6).

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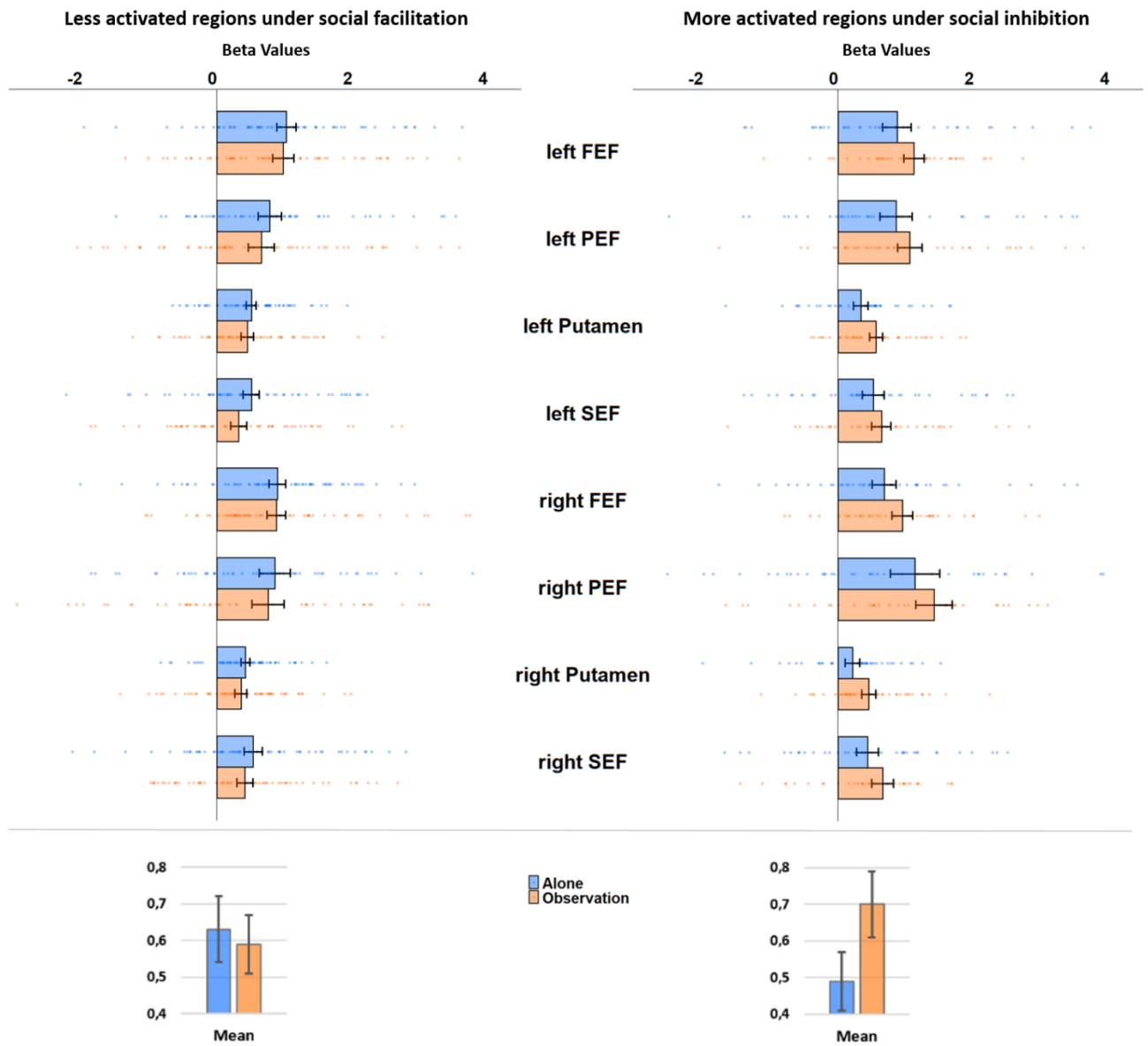


Figure 3: Condition effect (Alone in blue, Observation in orange) on several ROIs beta values. ROIs were identified from the Saccade > Fixation contrast. Left side: Facilitated sets based on RT data. Right side: Inhibited sets based on RT data. Bar plot = group mean, error bar = SEM, dots = individual data. The two lower bar plots represent the mean beta values of all ROIs in each condition.

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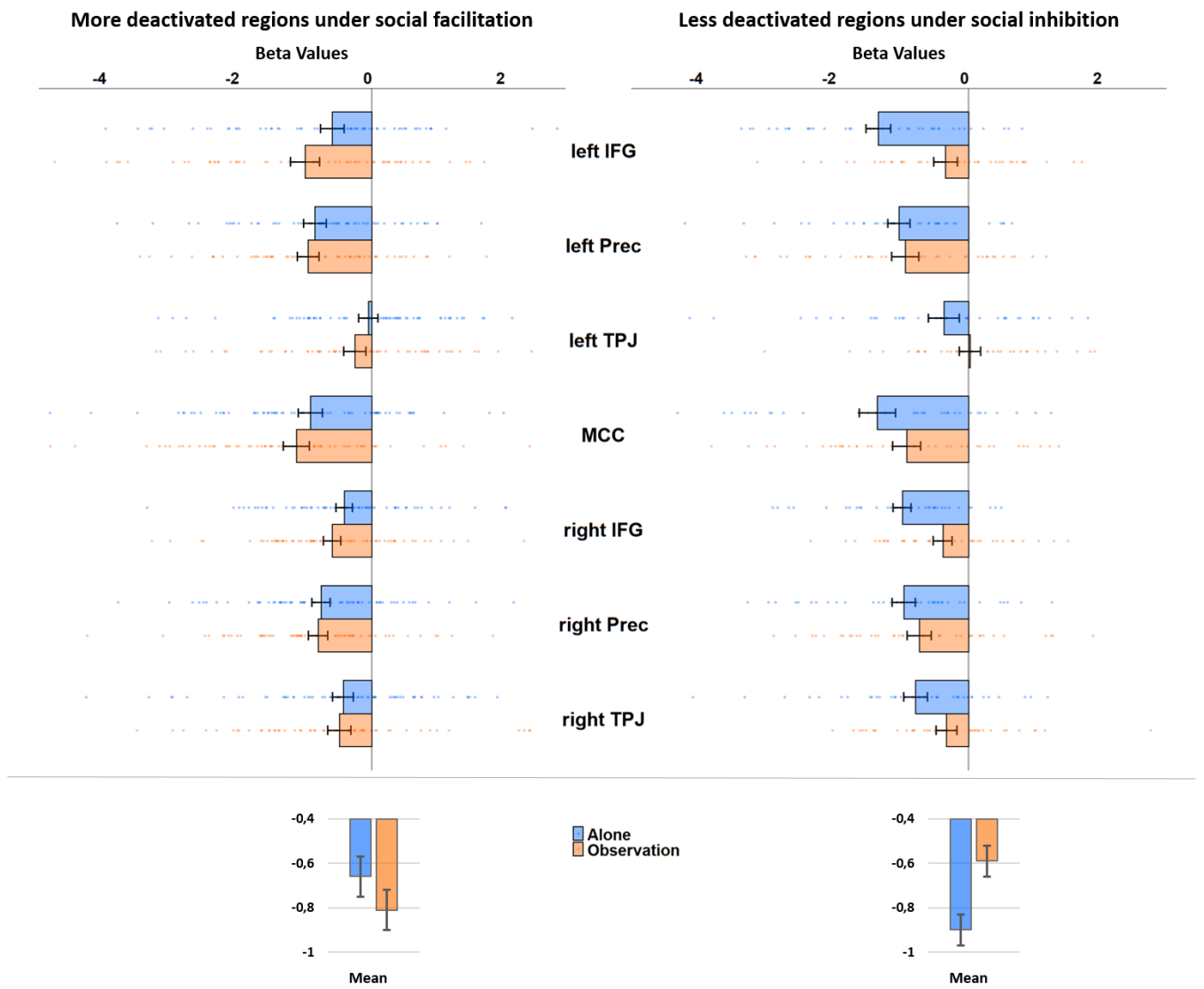


Figure 4: Condition effect (Alone in blue, Observation in orange) on several ROIs beta values. ROIs were identified from the Fixation > Saccade contrast. Left side: Facilitated sets based on RT data. Right side: Inhibited sets based on RT data. Bar plot = group mean, error bar = SEM, dots = individual data. The two lower bar plots represent the mean beta values of all ROIs in each condition.

Discussion

In the current study we scanned participants while they performed different saccade tasks either alone or being observed by a familiar peer. We wanted to highlight whether both saccade-related and domain-general networks are involved in the SFI effect. By separately analyzing social inhibition and social facilitation effects, we found a modulation of activity in the entire fronto-parietal network related to saccades, as well as a modulation of activity in the DMN, comprising areas related to the ToM network. Such task-specific and domain-general networks were both modulated differently according to the direction of the SFI effect. We also showed a modulation in ventral areas of the attention network associated to social inhibition on RTs only. The only evidence for an implication of the motivation network in a SFI revealed by a larger pupil size in the observation condition than alone, was the modulation of activity in the anterior insula. In the following paragraphs we will discuss the implication of these networks according to social facilitation *versus* inhibition.

Social Facilitation versus Inhibition at the behavioral level

We aimed at determining whether the task-specific and domain-general brain networks are modulated differently depending on whether peer presence leads to social facilitation or to social inhibition. To reach this objective, we used the same strategy as in our previous study where pro- and anti-saccades were presented either separately in different blocks of trials (simple runs) or randomly mixed together (complex runs) (Tricoche et al., 2020). Unexpectedly, our behavioral group level analyses of both saccade RT and peak velocity did not replicate our previous findings of a social facilitation for simple runs and a social inhibition for complex runs. This difference with our previous study could be explained by changes in the experimental design made to comply with fMRI conditions, potentially leading to a decreased global difficulty of the task and to higher inter- and intra-individual variabilities of performance. In fact, previous studies indicated that manipulations of task parameters could change the saccadic performance (Antoniades et al., 2013; Chiau et al., 2011; Dyckman et al., 2007; Pierce & McDowell, 2016). Nonetheless, individual-level behavioral analyses allowed us to identify facilitated *versus* inhibited sets which led to meaningful neural signatures of SFI effects.

Implication of the fronto-parietal network

The task-specific network involved in the present saccade task was the well-known oculomotor dorsal fronto-parietal network including FEF, PEF, SEF as well as basal ganglia (Coiner et al., 2019; Grosbras et al., 2005; Neggers et al., 2012). As expected, this network was more extended for antisaccades than prosaccades and for complex than simple blocks of trials (Dyckman et al., 2007). This saccadic network largely overlaps with the attention network (de Haan et al., 2008) which however also involves more ventral areas such as TPJ, SMG or IFG/MFG (Corbetta & Shulman, 2002).

At the whole-brain level, we found an increase of activity in fronto-parietal regions under observation compared to alone for the inhibited sets only, for both RT and peak velocity parameters, involving respectively ventral areas (IFG, OFG, SMG) and dorsal areas (FEF, SEF). Ventral areas of the fronto-parietal network have often been suggested to act as a “circuit breaker”, allowing to reorient attention toward new information relevant to the task (Corbetta et al., 2008; Painter et al., 2015; Poole et al., 2016) or to irrelevant information but strongly salient or with strong rewarding/emotional content, like a social information (Carretié, 2014; Frank & Sabatinelli, 2012; Klein et al., 2009; Wang et al., 2015). The activation of the ventral areas we found for inhibited RTs could reflect the processing of the present partner, which took the priority over the processing of the task-relevant stimuli and overloaded the attentional resources, leading to social inhibition (Belletier et al., 2019; Pedale et al., 2019). The increased activity in FEF and SEF found for the presence-related inhibition of peak velocity is more surprising, as a positive relationship between eye-field regions and peak velocity was previously found to reflect expected reward, whether or not including a social component (Reppert et al., 2015). Indeed, saccades performed toward a social stimulus like a face or in anticipation of a reward are faster and associated with stronger activity in the FEF (Glaser et al., 2016; Xu-Wilson et al., 2009). However, in our study the increases of FEF and SEF activity are associated with a reduced saccade velocity in the observation condition relative to alone. This suggests different neural processes in eye fields when a social distractor interfered with the saccade task as in our study, as compared to

when a direct association between the saccade goal with social and/or rewarding signals leads to better performance.

A specific neural signature according to the direction of the social effect.

To study the effect of peer presence on the saccade-related network, we conducted a ROI analysis based on the regions identified by this Saccade > Fixation contrast. We also used the reverse contrast (Fixation > Saccade) in order to investigate the effect of peer presence on ROIs belonging to the DMN, including mainly the TPJ, IFG, Prec/PCC, MCC, parahippocampal gyrus extending to fusiform gyrus, insula, and occipital regions. For both saccade and DMN ROIs, we found a significant social condition effect, on both RT and peak velocity parameters, when ROIs were considered together. Pairwise comparisons performed separately for each ROI did not reveal any significant effect. These results show that the whole network linked to the saccade task is modulated by the observation condition in a homogenous but limited way, no region being on its own significantly affected. Further, as the saccade-related network and attentional network are intrinsically linked, we cannot clearly establish whether this modulation by social context concerned only the task-specific saccadic network or the domain-general attention network, or both.

Modulation of the DMN and attention regions by peer presence

By looking specifically at the facilitated sets, we showed for both RT and peak velocity parameters a decrease of activity in saccade regions associated with an increased deactivation in DMN regions. For the inhibited sets, the opposite pattern was found with an increase of activity in saccade regions and a reduced deactivation in DMN regions. As generally reported in the literature, an increased activation of task-related regions, is correlated with stronger deactivation in the DMN, a symmetrical modulation which is thought to subtend our ability to successfully adapt to the difficulty of the task at hand (Corbetta et al., 2008). But in our study in contrast, both task-related and DMN networks are modulated in the same direction. This parallel modulation could be due to the activity of one network being directly boosted or inhibited by peer presence and driving the activity of the other, ultimately leading to either social facilitation or inhibition. Testing this hypothesis will require further investigations of the functional and effective connectivity between and

within the two networks, providing a better understanding of why peer presence seemed to have switched the standard anti-correlation between saccade and DMN networks into a positive correlation. A change of connectivity within the attention network during saccade tasks to social stimuli was previously found by Salvia and collaborators, namely a modulation of the functional connectivity between FEF and primary visual areas when participants made saccades toward faces compared to cars stimuli (Salvia et al., 2016). In our case, peer presence could differently modulate the functional connectivity between the attention network areas. It could divide the attention of the individual and change the attentional priority (more toward the social context or more toward the task). As this attentional priority is expressed at early-levels of treatment, i.e. visual areas (Normand et al., 2014), a change of connectivity may occur between occipital regions and other high level regions like FEF.

Modulation of the ToM and motivation networks by peer presence

In a previous study where participants performed two cognitive tasks related to education (numerosity and phonological comparisons), we found a modulation due to peer presence of TPJ, Prec/PCC and frontal regions (dmPFC) (Tricoche et al., 2023). It is well established that these three regions belong to the ToM network, being particularly involved when we think about the mental state of others (Fehlbaum et al., 2021; Frith & Frith, 2006; Preckel et al., 2018). In the present study, we cannot distinguish between the DMN network and the 'pure ToM network', but the fact that these same regions were again modulated suggests a similar mechanism of peer presence for at least three different cognitive or motor tasks.

We also predicted the motivation network to be modulated by peer presence of partners who, in our study, could have increased the motivation of the participants by evaluating them during the task. This prediction was only partly verified. Indeed, we did not find the implication of the Ventral Striatum, a region known to be particularly involved in relation to reward and motivation (Chein et al., 2011; Tricoche et al., 2023; Van Hoorn et al., 2016). We only found a modulation of the Insula activity, a region notably linked to emotional control in social contexts and sensitive to new salient stimuli (Finger et al., 2006; Wang et al., 2015). A previous study showed that anterior insula was more activated in a social context compared to a private context, but only when it was associated with a loss outcome (not with a win

one), suggesting an implication of anterior insula particularly when individuals fail in a social context (Grygolec et al., 2012).

Pupil size is sensitive to peer presence

Our last main result was that, although there was no significant change of pupil size related to peer presence at the group level, increases of pupil size in observation context were associated with higher activity in anterior insula and dorsal attentional areas, including FEF and IPS where the activity was further shown to correlate with pupil size. A social modulation of pupil size was already found in previous studies (Cos et al., 2021; Liu & Yu, 2017), but its links to attention areas in social contexts has never been investigated yet. Alnaes and collaborators indicated that pupil size signals mental effort, and is a predictor of dorsal attention network and locus coeruleus (LC) activities (Alnaes et al., 2015). Müller-Pinzler and collaborators showed that pupil size increased during public erroneous decisions and that such changes were associated with higher activation of the anterior insula (Müller-Pinzler et al., 2015). In line with these observations, our results suggest that pupil size increases in the presence condition as a result of the associated mental effort and of the apprehension to fail in our task faced to the partner.

Pupil size is often linked to LC and referred to as an indicator of vigilance or arousal (Joshi & Gold, 2020; Sara, 2009). One of the main theories of SFI developed by social psychology is that the simple presence of other increases the general level of arousal which in turn potentiates the dominant response of the given task (correct and/or fast response for a simple task, incorrect and/or slow response for a complex task) (Zajonc, 1965). Our findings, based on data sets with increased pupil size linked to peer presence, of an activation of dorsal attentional areas are consistent with this theory, even if we also found a decreased pupil size linked to peer presence in several other sets, as this last effect was not considered in this theory. A way to confirm that pupil size modulations are linked to changes of arousal level would be to measure LC activity. Unfortunately the LC is particularly difficult to track in humans (Privoulos et al., 2018) and the fMRI acquisition parameters used in our study did not allow us to detect it.

Limitations of the present study

A limitation of our study is our failure to replicate the previous behavioral findings demonstrated at the group level by Tricoche and collaborators, i.e. a social facilitation for simple trials and a social inhibition for complex trials. On the contrary, we found at the group level a social facilitation on antisaccades' RT only, but importantly we showed in addition a high intra-individual variability when we identified facilitated *versus* inhibited sets for each participant. This result enabled us to conduct more powerful analyses of fMRI data, but it also suggested that participants could be affected variably, changing between facilitation and inhibition, along the time-course of the scanning session. Therefore, considering task difficulty as the main moderator of the peer presence effect may be an over-simplification and it is crucial to better understand what are the other moderators involved (Uziel, 2007). According to our results, these moderators may fluctuate across time, and even switch between blocks of trials. One such moderator could be the confidence of the participant in succeeding the task. As during the task, feedbacks on performance were delivered after each trial, participants' confidence could have changed across time. Moreover, participants knew they were observed and evaluated by their partner whose status, depending on the participant's own confidence, could have changed from a positive motivator to a threatening evaluator, thus changing the size and even the direction of the peer presence effect.

Conclusion

The aim of our study was to investigate the effect of peer presence on brain networks during saccade tasks, taking into consideration inter- and intra-individual variabilities of behavioral effects. In accordance with previous studies (Chein et al., 2011; Demolliens et al., 2017; Monfardini et al., 2015; Müller-Pinzler et al., 2015; Somerville et al., 2013; Tricoche et al., 2023; van Hoorn et al., 2018; Van Hoorn et al., 2016; Yoshie et al., 2016), we found strong evidence for a modulation of both the task-related (saccadic) network and domain-general networks (attention, ToM and motivation). In addition, the neural signature of SFI differed according to the two directions of social effect: social facilitation disclosed by decreased RTs led to a decreased activity of the saccade-related network combined with a higher deactivation of the DMN; whereas social inhibition disclosed by increased RTs led to an increased activity of the saccade-related network with a lower deactivation of the DMN, but also recruited ventral attention areas. Finally, a modulation of pupil size, supposedly linked

to arousal state, by peer presence was associated with activation of both anterior insula and dorsal attention regions. Taken together, these results suggest that peer presence changes attention in parallel at a basic level related to arousal and at a more cognitive level directly linked to task performance. Future studies should investigate the way these networks are interconnected to better understand how peer presence can make us better or worse during a task.

Declaration of Competing Interest: The authors declare no conflict of interest.

Authorship contribution: DP, MM and LT designed the experiment. LT programmed the experiment, LT and MRH collected the data. LT analyzed the data and drafted the manuscript. LT, DP and MM wrote the article.

Data availability: Data and Supplementary materials are available on OSF following this link: <https://osf.io/9p2db/>

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