Social and Non-social Brain Areas in Risk Behaviour: The Role of Social Context

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Abstract—The human brain contains social areas that become active when interacting with another human. These are located in the ventral prefrontal and mediodorsal cortices, adjacent to areas involved in reward processing and cognitive control. Human behaviour is strongly influenced by the social context. This is particularly evident when observing greater risk propensity in the presence of a peer, particularly during adolescence and emerging adulthood. We explored the widely held view that enhanced risk propensity is the consequence of weak cognitive control. We used brain activity, estimated from EEG recordings in a sample of 114 emerging adult dyads whilst performing a risk perception task, to predict risk behaviour in a subsequent driving simulation task. Being with a peer reduced the ability to discriminate riskiness in images of traffic scenes, biased responses towards the perception of no-risk, and increased the rate of accidents in the driving simulation. Risk perception involved three sets of clusters showing activity only when being with a peer, only when being alone, and in both social contexts. Functional connectivity between the clusters accounted for the later driving simulation performance depending on the peer's presence. In the light of our findings, greater risk-taking, when a peer is present, seems to be triggered by the activation of a different, less efficient brain network for risk-processing. © 2021 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Key words: driving simulation, emerging adults, functional connectivity, peer-effect, risk perception.

INTRODUCTION

Adolescence and emerging adulthood are characterized by the maturation of cognitive, emotional and social abilities, along with a heightened propensity towards risk-taking behaviour, encouraged by the presence of peers (Crone and Dahl, 2012; Albert et al., 2013; Silva et al., 2016; Knoll et al., 2017). In fact, risk-behaviour is the main causal factor of fatalities in youths, with road traffic accidents being the leading cause of death (World Health Organization, 2018), particularly when speeding with peers (Allen and Brown, 2008).

This enhanced tendency to take risks (Steinberg, 2008) has been interpreted as stemming from differences in the development of the brain network underlying the processing of affect, incentives and reward, and that of the network supporting cognitive control and behaviour regulation (Casey, 2015). Thus, a heightened sensitivity to reward and sensation seeking, along with a weak impulse control system that is not yet strong enough to regulate behaviour under highly emotional situations,

could account for impulsive and risky behaviour (Shulman et al., 2016; Romer et al., 2017; Steinberg et al., 2018; Yoneda et al., 2019). Given that the behaviour of youths is highly influenced by the opinions of their peers (Gorrese and Ruggieri, 2013; Reiter et al., 2019), the presence of peers is suggested to affect activity in areas involved in the processing of rewards, such as the ventral striatum or the orbitofrontal cortex (Chein et al., 2011; Leung et al., 2014; Telzer et al., 2015; Sherman et al., 2018, 2019), which might foster risk-taking behaviours (Gardner and Steinberg, 2005; Figner et al., 2009). Support for this idea is provided by studies showing greater activity in the reward network (ventral striatum and orbitofrontal cortex (OFC)) in adolescents whilst performing an urgent decision-making task observed by peers (Chein et al., 2011).

However, findings related to differences in the cognitive control network in adults and youths as a function of the social context are not yet clear. This network, which supports the regulation of actions and thoughts in accordance with current goals, includes a large number of areas, including the frontoparietal, the cingulo-opercular networks, and some subcortical structures (Fan et al., 2014). Few studies have found effects of the social context (peer influence) on the

activation or connectivity of these areas, whilst others have failed to find any differences (Chein et al., 2011; Breiner et al., 2018; Smith et al., 2018; Sherman et al., 2019). Using the go/no-go task, which is suggested to recruit response inhibition, (Smith et al., 2018) observed no behavioural effect of peer presence and minimal activation in the right posterior middle frontal gyrus, a region not commonly thought to support cognitive control. Moreover, (Chein et al., 2011) found no differential activity in cognitive control areas using the Stoplight task. However, using a social go/no-go task, (Breiner et al., 2018) observed differences in brain activation as a function of peer presence/absence, but only in 13–17 year old participants and using a non-corrected whole brain statistical approach. In stark contrast, (Sherman et al., 2019) observed greater connectivity of the anterior insular cortex in the peer than in the alone condition with the stoplight task, but not with the go/no-go task. Moreover, behavioural peer effects were observed in neither the stoplight or in the go/no-go tasks.

These results suggest that the cognitive control network is minimally affected by the presence of peers, which is unexpected on the basis of the maturational theoretical approach, and difficult to accommodate within this framework. However, it is possible that factors such as age, behavioural task or ecological validity of the peer manipulation could underlie these mixed results.

The most common types of peer manipulation employed are virtual peers (simulated people not related to the participant in any way, (Breiner et al., 2018; Sherman et al., 2019)), the sole presence of a peer (usually observing from an adjacent room, (Chein et al., 2011; Smith et al., 2015)), or the mere knowledge about the presence of peers (Kwon et al., 2014; Vorobyev et al., 2015). It has been shown that the mere presence of peers (friends) does not appear to influence risky decision making (Somerville et al., 2019), whilst the belief that a social interaction is taking place with another human as opposed to a computer driven system activates different brain areas, particularly the prefrontal cortex (Pfeiffer et al., 2014). However, no research has considered the ecological validity of social context manipulation, with the exception of (Cascio et al., 2015), who used a confederate in their driving simulator session. They found that control cognitive network activation (basal ganglia and right inferior frontal gyrus) predicts safer driving in the presence of cautious passengers. It is worth noting that (Cascio et al., 2015) used a car simulator to assess the peer effect, which suggests that ecological validity of the social context could be a factor to consider when attempting to explain the discrepant results on the cognitive control network and risk behaviour. It is also surprising that no studies have yet considered the gender of the peer, although some research has suggested that it could be a determining factor in observing different types of risk-taking behaviours (Simons-Morton et al., 2005; Eisenberg et al., 2014). Furthermore, using videos of real peer interactions, (Ambrosia et al., 2018) have observed that activity in the ventromedial prefrontal cortex moderates the association between the reciprocal positive affect of peers and risky behaviour.

Our study aimed to explore the role of three key variables in risk behaviour: actual *social context*, so that each participant was asked to perform the task whilst in close proximity to a good friend (Ambrosia et al., 2018), who was seated behind the participant whilst also performing the task; the *type of dyad*, with three types: man-man, woman-woman and woman-man/man-woman; and *authentic potentially risky settings*: photographs of high-/low-risk traffic scenes to assess risk perception, and simulator riding (Cascio et al., 2015) to quantify risky behaviour in medium-fidelity scenes. Within a brain-as-predictor scheme, we used brain sources estimated from high-density EEG recordings of the risk perception task as predictors of the driver's behaviour on the motorcycle simulator, from which we consider the number of accidents and average speed as indicators of risky driving. To enhance the ecological validity of our social context manipulation, the drivers performed the risk perception task whilst seated in the motorcycle simulator.

EXPERIMENTAL PROCEDURES

Participants

A total of 114 dyads took part in this study. The dyads were friends of a similar age, and of either the same or different gender. All participants had a driver's license and were aged 18–28 years ($M = 21.43$, $SD = 2.13$). The mean age difference between the dyads was 1.71 years ($SD = 1.12$). The sample size was calculated as 100 dyads with G-power (for a power of 0.8, $\alpha = 0.05$, and a small effect size Cohen's $d = 0.25$). We added 14 dyads to ensure a sufficient sample size in case of possible dropouts. Since the experiment was conducted in dyads, 114 of the participants were contacted and asked to bring a close friend of the same or the opposite gender (3 dyads were not included in the analyses due to EEG recording errors), resulting in two different dyad types, 78 same-sex (39 woman-woman) and 33 different-sex pairs (woman-man/man-woman). Each participant was paid for their participation in the study and informed about their rights according to the Helsinki declaration (World Medical Association, 2008).

Procedure

The participants first gave written informed consent and filled in a questionnaire to collect information on demographic variables. They performed the risk perception task with the dyad seated in the motorcycle simulator, one in the rider's seat and the other in the passenger's location (Peer condition, the "driver" and the "passenger"), or separated in different rooms (Alone condition), while brain activity was recorded with Electroencephalogram (EEG).

Risk perception task

We used the *SR Research Experiment Builder* (SR Research Ltd., Missessauga, Ontario, Canada) to present a set of 140 real traffic pictures taken from the driver's perspective. The pictures were selected from a database of traffic risk (Megías et al., 2015; Baltruschat et al., 2020), with 70 of the pictures depicting a high-risk scene (for instance, crossing pedestrians, animals on the road, or cars which are about to cross in front), and the other 70 depicting a low level of risk. All stimuli were displayed with a refresh rate of 60 Hz at a distance of 185–200 cm on a screen (180 × 110 cm) projected on the wall in front of the participants. In the Peer condition, participants were not allowed to interact, but they were in close contact, as they were both sitting on the seat of the motorcycle simulator, with the peer seated on the motorcycle just behind the driver. In the Alone condition, the driver performed the task in the same room, whilst the passenger completed the task in another room of the laboratory with stimuli displayed with a refresh rate of 100 Hz at distance of 100 cm on 40 × 30 cm screen.

Each trial of the task began with a 750 ms fixation point in the centre of a white screen followed by an image of a traffic scene for 2000 ms. The task required the participant to indicate whether or not the depicted traffic scene was risky, responding only when the scene was perceived as risky, and not responding at all if he/she perceived the scene as non-risky. After 2000 ms, a black screen was displayed for 750 ms (for examples and task description see Supplementary Fig. S1). The driver always responded with the motorcycle controls whilst the passenger responded by clicking mouse buttons. Immediately after the risk perception task, the driver drove two circuits of the simulator, one with the peer sitting behind him/her in the Peer condition and alone in the Alone condition.

The proportions of hits (yes responses to a high-risk scene) and false alarms (yes responses to a low-risk scene) were computed for each subject, as well as signal detection theory discrimination (d') and response bias indices.

Motorcycle riding simulation

The Honda Riding Trainer motorcycle simulator (HRT) consisted of a seat, handlebar, pedals, accelerator, brakes, turn indicators and a claxon (see Di Stasi et al., 2009, for a full description of the HRT simulator). The simulation was projected with the same dimensions as the stimuli of the risk perception task. Participants rode through an urban road scenario that included 8 risk situations (e.g., sudden opening of the doors of parked cars or pedestrians suddenly crossing the road). Both the number of accidents and average speed were calculated for each participant and peer condition.

Brain sources estimated from EEG recordings

Electrical brain activity was recorded with a 62 active channel system (Brain Products, Inc.) with active tin electrodes mounted on an elastic cap arranged according to the extended 10–20 system. EEG recordings were referenced online to FCz, sampled at 1000 Hz and amplified using a 0.016–1000 Hz band-pass filter. During the recording, impedances were below 25 kΩ, which is the value recommended by the manufacturer of the system.

EEGLAB toolbox for MATLAB (Delorme and Makeig, 2004, http://sccn.ucsd.edu/eeglab) was used for the off-line pre-processing. EEG recordings were down-sampled to 250 Hz, re-referenced offline to average reference, and FCz activity was recovered. Channels with flat-line duration of more than 50 seconds or with excessive line noise relative to its signal (4 *SD*) were identified using the EEGLAB plugin cleanrawdata (freely available at https://sccn.ucsd.edu/wiki/EEGLAB_Extensions). Bad channels were interpolated with the spherical spline method included in EEGLAB software. Bad channels average was 3.5 (*SD* = 3.0). Recordings were then segmented from −200 to 1600 ms time-locked to the stimulus onset, and baseline corrected. Independent Component Analysis (ICA) was applied using the Second Order Blind Identification algorithm (SOBI, Tang et al., 2005, and ocular and muscle artifacts were removed using the EEGLAB plugin ADJUST (Mognon et al., 2011) http://www.unicog.org/pm/pmwiki.php/MEG/RemovingArtifactsWithADJUST), after visual inspection of ICA classification. An average of 30.6 ICAs (*SD* = 20.5) were discarded. EEG segments were averaged for each channel, risk condition, and participant.

Average ERPs for each participant and condition were used to estimate the brain sources of scalp potentials using the standardized low resolution brain electromagnetic tomography software (sLORETA; Pascual-Marqui, 2002, which estimates the current source density in the sLORETA solution space based on the Montreal Neurological Institute (MNI) atlas.

Statistical analyses

Our statistical analyses were conducted in three phases according to a brain-as-predictor scheme. First, behavioural data from the risk perception task were used to determine the effect of the Dyad Type (between groups: man-man (MM), woman-woman (WW), mixed: women-man (WM)/ man-woman (MW)), Social Context (repeated measures: Peer, Alone), and Picture Risk Level (repeated measures: high-risk, low-risk). Therefore, three repeated measures ANOVA were conducted in each group (passengers and drivers). Taking proportions of risk responses consisting of hits and false alarms (yes responses in high- and low-risk scenes, respectively as dependent variables), we employed a 2 × 2 × 3 experimental design with Social Context (Peer and Alone) and Picture Risk Level (low- and high-risk) as within-subject factors, and Dyad Type (MM, WW, WM/MW) as the between-group factor. Using the discrimination index d' and response bias as dependent variables, we employed a 2 × 2 experimental design with Social Context (Peer and Alone) as the within-subject factor, and Dyad Type (MM, WW, WM/MW) as a between-group factor. Age and gender did not covary with either the dependent or

independent variables, and were therefore not subject to further analysis. Analyses of these data were conducted with IBM SPSS statistical software (Version 21.0., IBM Corp., Armonk, NY, 2012).

Second, estimations of brain activity were analysed for the highest interaction observed in the behavioural analysis, comparing high- vs low-risk pictures in both the Peer and Alone condition. This analysis was conducted in sLORETA, and clusters were labelled using the Brainnetome atlas (Fan et al., 2016, http://at-las.brainnetome.org).

Our third goal was to predict behavioural performance of the motorcycle simulation (total number of traffic accidents and average speed) from functional connectivity, using a backward stepwise multivariate multiple regression analysis. The functional connectivity between the significant clusters observed in the Risk Perception Task was computed on the average of voxels within the cluster with the L1-regularized partial correlation FSLnets (fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLNet s). Tested lambda regularization values ranged from 0 to 100 in steps of size 10. The selected lambda value (=30) was the one with the minimum sum of squared prediction errors. All the analyses for the brain activation and connectivity data were conducted on averages normalized by participant. Corrections for the multiple comparison problem were carried out using a permutation-based two-tailed paired max t-test.

RESULTS

Behavioural results

Risk perception task. The repeated measures ANOVA conducted on the drivers' proportion of risk responses (hits and false alarms; yes responses to high and low-risk scenes, respectively) yielded significant main effects of Social Context, $F_{1, 107} = 19.94$, $p < .001$, $\eta_p^2 = 0.157$, and Picture Risk Level, $F_{1,107} = 3448.67$, $p < .001$, $\eta_p^2 = 0.97$, as well as an interaction between these two factors, $F_{1, 107} = 21.07$, $p < .001$, $\eta_p^2 = 0.16$. No other effects of Dyad Type were significant (all $p > .24$). For the passengers, a similar pattern of results emerged: $F_{1, 107} = 39.08$, $p < .001$, $\eta_p^2 = 0.27$, $F_{1,107} = 2665.4$, $p < .001$, $\eta_p^2 = 0.96$, and $F_{1,107} = 15.16$, $p < .001$, $\eta_p^2 = 0.12$, respectively for main effects of Social Context, Picture Risk Level and the interaction between the two factors.

Further analysis of the Social Context × Picture Risk Level interaction for the drivers (Table 1) revealed that the proportion of hits was higher for the Alone (0.83, $SD = 0.16$) than for the Peer (0.79, $SD = 0.16$) condition, $p < .001$. Proportions of false alarms were, however, similar for both conditions ($p = .22$; Alone = 0.11, $SD = 0.11$; Peer = 0.10, $SD = 0.09$). Differences in the proportion of hits were also observed for passengers according to condition (0.81 vs 0.75, Alone vs Peer), but there were also differences in the proportion of false alarms ($p < .001$; Alone = 0.13, $SD = 0.12$; Peer = 0.11, $SD = 0.10$). No differences were observed between conditions in the hit reaction times (911 vs 938 ms, respectively for the Alone and the Peer conditions, $p = 0.11$) of the drivers.

Next, we used signal detection theory indexes to compute the ability to discriminate (d') high- from low-risk pictures, as well as response bias. For both drivers and passengers, we observed a higher d' for the Alone (drivers = 2.61, $SD = 0.05$; passengers = 2.41, $SD = 0.05$), than for the Peer (drivers = 2.41, $SD = 0.04$; passengers = 2.19, $SD = 0.05$) condition (drivers: $p < .001$, $\eta_p^2 = 0.22$; passengers: $p < .001$, $\eta_p^2 = 0.25$). Similarly, for both drivers and passengers, response bias was greater for the Peer (drivers = 0.27, $SD = 0.05$; passengers = 0.31, $SD = 0.05$), than for the Alone (drivers = 0.15, $SD = 0.06$; passengers = 0.13, $SD = 0.06$) condition ($p < .001$, drivers: $\eta_p^2 = 0.12$; passengers: $\eta_p^2 = 0.25$). Again, no effects of Dyad Type were observed for either drivers or passengers (all $p > .48$).

Motorcycle simulation. The number of accidents (Table 1) was higher for the Peer (0.57, $SD = 0.06$) than for the Alone (0.40, $SD = 0.06$) condition ($p < .04$, $\eta_p^2 = 0.04$). In the Peer condition, 49.5% of the drivers had at least one accident, compared with only 32.4% in the Alone condition. However, average speed (Table 1) was higher for the Alone (23.22 Km/h, $SD = 0.47$) than for the Peer (22.29 Km/h, $SD = 0.45$) condition ($p < .001$, $\eta_p^2 = 0.12$). No effects of Dyad Type were observed (all $p > 0.43$).

Differential brain activity during the risk perception task

Differences in brain activity between high- and low-risk scenes were significant for both Social Context conditions (Table 2, Fig. 1, Supplementary Table 1). No significant association was found between brain activity and motorcycle behaviour.

We observed clusters that showed this differential activity for both the Peer and the Alone condition (Table 2: Peer & Alone rows, Fig. 1: green areas), with t-peaks located at left area 13, with the cluster extending into the left medial OFC (l_mOFC (P&A)) (High < Low-Risk), right dorsal agranular insula, with

Table 1. Summary of the behavioural results observed for the drivers in the high and low risk conditions as a function of the Social Context. Accidents and average speed are also displayed for the motorcycle simulation

	High Risk		Low Risk		Reaction Time			
	Hits	No Response	False Alarms	No Response	False Alarms	Hits	Accidents	Speed
Alone	0.83	0.17	0.11	0.89	888	911	45	23.22
Peer	0.79	0.21	0.10	0.90	893	938	63	22.29

Note: The hits, no response, false alarms and no response are rates; Reaction time unit is milliseconds; Accidents is the number of accidents; speed is in Km/h.

Table 2. Clusters showing differences between high- and low-risk traffic scenes as a function of the Social Context. Peer: clusters showing differential activation exclusively when the task was performed with a peer. Alone: clusters activated exclusively when the driver performed the task without a peer. Peer & Alone: clusters activated when drivers performed the risk perception task with and without the peer

| Condition | Cluster | | | | | Peak | | | | |
	Name	Location	k	H	t	X	Y	Z	Area
Peer	l_VLPFC (P)	Ventrolateral PFC	182	L	−5.53	−45	45	0	A45r
	r_mOFC (P)	Medial orbitofrontal C	6	R	−4.31	20	45	−20	A11l
	r_STG (P)	Superior temporal C	15	R	4.63	65	−30	10	A22c
Alone	bil_OFC (A)	Orbitofrontal C	161	L	−5.57	−10	25	−15	A13
	r_DMC (A)	Dorsomedial C	243	R	6.14	10	15	45	A8m
	l_DMC (A)	Dorsomedial C	14	L	5.12	−35	−30	45	A1/2/3
Peer &Alone	l_mOFC (P&A)	Medial orbitofrontal C	69	L	−5.50	−15	25	−15	A13
	r_mOFC/AI (P&A)	Medial orbitofrontal C/agranular insula	53	R	−5.68	30	25	5	dIa
	bil_CG (P&A)	Cingulate C	63	R	6.19	5	15	40	A8m

Note: H: Hemisphere; A: brain area; c, caudal; C, Cortex; G, gyrus; hf, head and face m, medial; op, opercular; r, rostral; v, ventral. X, Y, Z are in MNI space. k: number of voxels. Corrected p-values < 0.05.

/ Alone (bil ORF/ bil DMC)
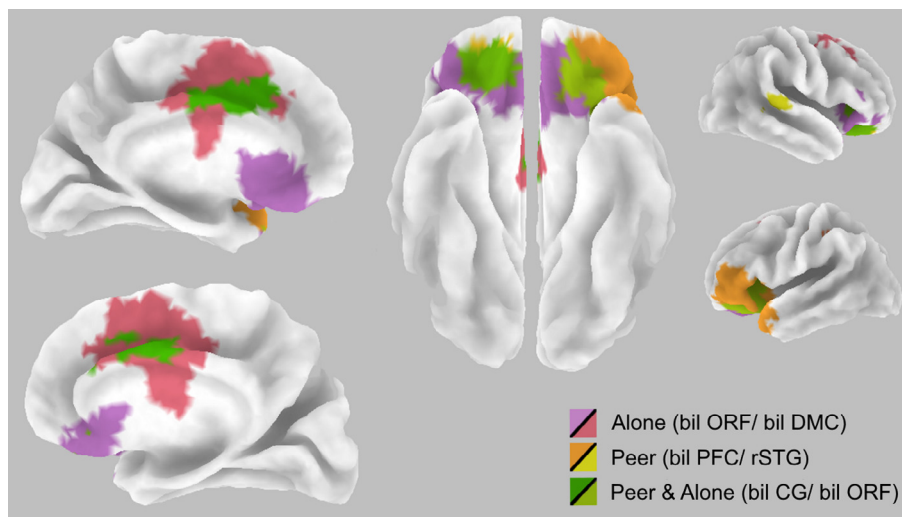/ Peer (bil PFC/ rSTG)
/ Peer & Alone (bil CG/ bil ORF)

Fig. 1. Colour-coded clusters for the High/Low-Risk contrast as a function of the Social Context manipulation, medial, ventral, and lateral views. Alone: clusters showed differential activation exclusively when the driver performed the task without a peer. Peer: clusters activated exclusively when the task was performed with a peer. Peer & Alone: clusters activated when drivers performed the risk perception task with and without the peer. Colours indicate the location of the cluster. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the cluster extending into the right medial OFC (r_mOFC/AI) (High > Low-Risk), and right medial area 8 with the cluster extending into the bilateral cingulate gyrus (bil_CG (P&A)) (High > Low-Risk).

A second type of cluster showed differences only in the Peer condition (Table 2: Peer rows, Fig. 1: orange and yellow areas), with t-peaks in the left rostral area 45 with the cluster extending into the left ventrolateral prefrontal cortex (l_VLPFC (P)) (High < Low-Risk), right lateral area 11 with the cluster extending into the right medial OFC (r_mOFC (P)) (High < Low-Risk), and right caudal area 22 with the cluster extending into the right superior temporal gyrus (r_STG (P)) (High > Low-Risk).

The third type of cluster (Table 2: Alone rows, Fig. 1: violet and pink areas) showed differences only in the Alone condition, with peaks in the left area 13 with the

cluster extending into the bilateral OFC (bil_OFC (A)) (High < Low-Risk), right medial area 8 with the cluster extending into the right cingulate gyrus and dorsomedial cortex (r_DMC (A)) (High > Low-Risk) and the left area 1/2/3 with the cluster extending into the post-central, cingulate gyrus and dorsomedial cortex (l_DMC A)) (High > Low-Risk). No effects of Dyad Type were observed (all p > .11).

Note that the comparisons involved a condition with a very different number of responses, which might indicate that differences can also be due to motor components. However, none of the significant clusters involved brain areas related to motor aspects of behaviour, which may indicate that this is a minor component of the differences observed between conditions.

Brain-as-predictor results

In the Peer condition, functional connectivity explained 5.6% (p < .007) of the variability in the number of accidents and 12.7% of the variability in average speed (p < .001). In the Alone condition, functional connectivity accounted for 27.3% of the variability in the number of accidents (p < .001) and 14.4% of the variability in average speed (p < .001). Fig. 2 depicts the links that make a significant contribution to these predictions. Panels A and C indicate that more links are related to the number of accidents in the Alone (A) than in the Peer condition (C). In the Alone condition, the higher the connectivity of bil_CG (P&A)) with the r_mOFC (P) and with the r_STG (P), the lower the expected number of accidents (r = −0.43 and r = −0.39, respectively). Moreover, the greater the connectivity of r_DMC(A) with r_mOFC(P) and with
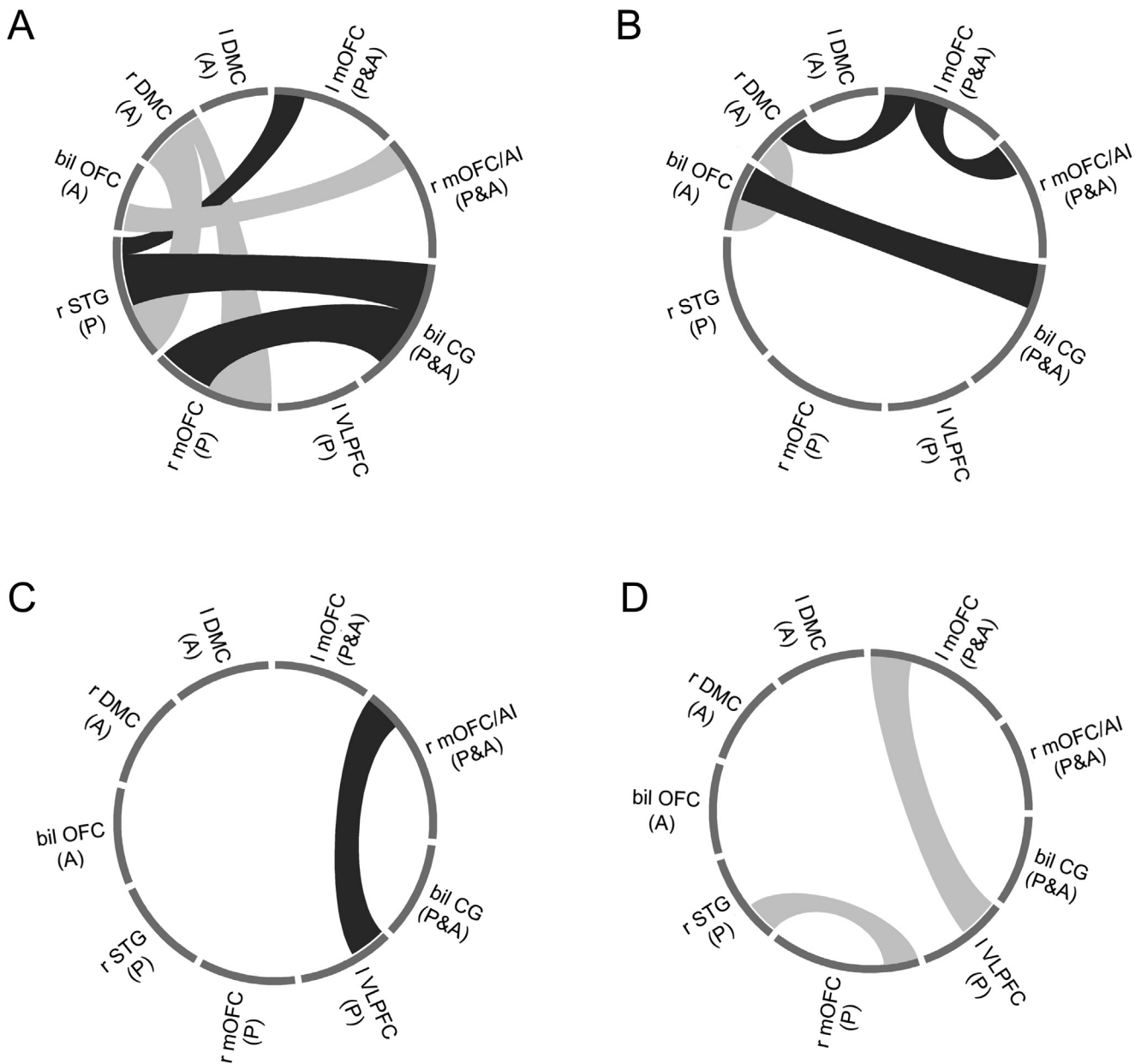
Fig. 2. Functional connectivity between significant clusters of the risk perception task, associated with performance on the motorcycle simulator. **(A)** and **(C)** display the links that account for the number of accidents when riding alone (A) and with a peer (C). **(B)** and **(D)** display the links that account for the average speed when riding alone (B) and with a peer (D). Ribbons indicate a negative (dark grey) or positive (light grey) correlation with behavioural variables. The thickness of the ribbons indicates the strength of only the significant partial correlations between brain areas that predict behavioural performance on the motorcycle simulation task.

r_STG(P), the higher the expected number of accidents ($r = 0.48$ and $r = 0.38$, respectively). The connectivity of bil_OFC (A) with r_mOFC/AI (P&A) is also positively associated with the number of accidents. In stark contrast, in the Peer condition, only the connectivity of l_VLPFC (P) with r_mOFC/AI (P&A) is (negatively) associated with the number accidents when riding with a peer.

The links that accounted for the average speed when riding with the peer are depicted in panels B and D of Fig. 2. The connectivity of the l_mOFC (P&A) clusters) with r_mOFC/AI (P&A) and r_DMC (A), and that of this last area with bil_OFC (A) are negatively associated

with speed during the Alone condition ($r = -0.25$, -0.23, and −33, respectively). However, the link between bil_OFC (A) and r_DMC (A) was positively related to average speed in this condition ($r = 0.24$). In the Peer condition, a higher speed is expected when the connectivity between l_VLPFC (P) and l_mOFC (P&A), and that of r_STG (P) with r_mOFC (P) ($r = 0.28$, 0.23, respectively) is higher.

DISCUSSION

The aim of this study was to uncover the effects of social context manipulation (Peer/Alone conditions) on the brain

activity and behaviour of late adolescents and emerging adults in relation to risk perception (discriminating high- from low-risk traffic scenes) and risk behaviour (riding a motorcycle simulator). We also took into account the dyad type (same/different sex), which was in close proximity to the participant while performing both tasks. Two main findings emerged from our study: the effect of social context, and the prediction of risk behaviour on the motorcycle simulator from functional brain connectivity measured during the risk perception task.

Our social context manipulation showed that the presence of a peer (friend) decreased the ability to discriminate high- from low-risk scenes and increased the tendency to judge the scenes as non-risky (response bias). Our data do not allow us to determine whether these effects could be observed with the mere presence of another individual. Literature showed mixed results, with some data indicating that close friendship is necessary and some other indicating that a neutral peer could be enough to produce the effect (Somerville et al., 2019). In any case, our results support that the differences observed between the Peer and Alone conditions are due to the presence of a close friend. We observed brain clusters uniquely involved in the Peer (superior temporal gyrus, orbitofrontal and ventrolateral prefrontal cortices) or the Alone (bilateral orbitofrontal, dorsomedial and postcentral cortices) condition, and areas involved in the risk perception task independently of the social context (orbitofrontal, bilateral cingulate gyrus and dorsomedial cortices). Being with a Peer—but not being Alone—engages some of the key components of the so-called social network: the posterior superior temporal, the ventrolateral prefrontal, and the orbitofrontal cortices, which are areas involved in motivational and attentional priority assigned to other individuals (Azzi et al., 2012; Watson and Platt, 2012), No evidence, however, was found for the involvement of other social network areas such as the medial or dorsolateral prefrontal areas(Wang and Olson, 2018). The superior temporal cortex has been proposed to serve as a "hub" of the social networks of the brain (Yang et al., 2015), and has also been implicated in action selection in the processing of past outcomes (Paulus et al., 2005; Peake et al., 2013), particularly in the presence of peers (Blakemore and Mills, 2014). This is possibly due to its importance for social sensitivity (van Hoorn et al., 2018) and the evaluation and adaptation of responses in social contexts (McCormick et al., 2018).

The risk perception task activated areas in the OFC that have been implicated in the processing of rewards, value-based decision-making, and the maintenance of previously successful response choices (Noonan et al., 2012; Stalnaker et al., 2015). We observed a medial-to-lateral pattern in the left hemisphere OFC, in which more medial areas (area 14 and parts of area 13) were activated in the Alone condition, while lateral areas were activated in the Peer condition (area 12, lateral area 13, lateral agranular insula, and parts of lateral area 11). Areas in the anterior and posterior orbital gyrus (medial area 13, lateral area 13, and parts of lateral area 11) were activated independently of the social context. However, in the right hemisphere, lateral areas (area 12) were involved in the Alone condition rather than in the Peer condition. These patterns of activity are in agreement with the notion that the ventral prefrontal surface is organized into different functional networks with areas belonging to the orbital or to the medial networks, and the same areas belonging to both networks (Price, 2007; Du et al., 2020), although finer distinctions have been made (Kahnt et al., 2012). We observed that the presence of peers uniquely influenced the activation of the left lateral OFC. This region has been shown to respond to a reward (or error) independently of its positive or negative value (Noonan et al., 2011) and to social contexts (Fujii et al., 2009; Domínguez D et al., 2018), whilst activation of this area is predictive of engagement in risky behaviour such as the consumption of alcohol or drugs (Wade et al., 2019).

The functions of the dorsomedial prefrontal and anterior cingulate cortices are related to executive attention, motivation and emotion, and decision-making in social contexts (Szczepanski and Knight, 2014), including belief updating based on the reliability of informants (De Martino et al., 2017). Two large subdivisions have been identified based on the influence of social context on decision-making tasks. These are non-social (cingulate sulcus, activity independent of the presence/interaction with other people), and social (a mediodorsal/ area 24 cluster, the activity of which appears to support social information) (Wittmann et al., 2018). In our risk perception task we observed two regions, one corresponding to the non-social subdivision (primarily involving parts of the cingulate cortices, including medial area 9, pregenual area 32, and caudo-dorsal area 24), which are activated independently of the presence/absence of the peer, and a social cluster located above and below the non-social subdivision, (including, among others, parts of more dorsal medial areas such as the supplementary motor area, medial area 6, medial area 8, caudal area 23 and area 24). Our social cluster, however, was activated in the absence, but not in the presence of the peer. Therefore, we did not identify a social region in its strictest sense, since we have no evidence to suggest that the presence of the peer affected activity in the cingulate cortex, although some research has also shown that different neurons are activated more strongly in response to social isolation than a social context (Demolliens et al., 2017).

Our second important result is related to how functional connectivity of the nine clusters predicts risk behaviour, as measured by the number of accidents and the average speed in the motorcycle simulation task. The number of accidents was higher, and the speed slower, when riding with the peer than when riding alone. In the Peer condition, the number of accidents was negatively associated with the strength of l_VLPFC (P) – r_mOFC/AI (P&A) connectivity. A higher number of links were needed to account for this variable when riding alone, so that the greater the strength of the connectivity of the Alone clusters (r_DMC (A) - r_mOFC (P), r_DMC (A) - r_STG (P), and bil_OFC (A) – r_mOFC/AI (P&A)), the higher the number of accidents, but the greater the connectivity of clusters active in both Peer and Alone conditions (bil_CG (P&A) - r_mOFC (P),

bil_CG (P&A) - r_STG (P), l_mOFC (P&A) - r_STG (P)), the lower the number of accidents.

The agranular insula has been linked to the valuation of rewards, the establishment of internal drives, and the regulation of affect (Wager et al., 2004), and its connectivity with other prefrontal areas have been shown to be altered by the (lack of) premeditation impulsivity trait in risk prone individuals (Baltruschat et al., 2020). Moreover, the left area 45 (l_VLPFC(P)), a part of Broca's area, is involved in conflict resolution and the inhibition of prepotent responses (Hamilton and Martin, 2005; Samrani et al., 2019). We believe that a weakening of this connection may provide l_VLPFC incomplete information on the riskiness of the simulated traffic scenario, increasing the probability of erroneous decision-making. This is supported by the fact that a much more complex network is involved in the prediction of the number of accidents in the Alone than in the Peer condition. In this network the right superior temporal and the social (dorsomedial cortex) and non-social (anterior cingulate) prefrontal cortex are the major areas involved in the accidents, with the social part being more strongly associated with an increase in the rate of accidents whilst the non-social part is involved in decrease in accident rates. The two prefrontal clusters are thought to be involved in very different components of decision-making tasks, with the anterior cingulate cortex being more predominantly involved in reward valuation whilst the dorsomedial prefrontal cortex plays a role in the integration of task information (Liu et al., 2011; Lorenz et al., 2014).

The strength of the functional connectivity of ventrolateral prefrontal (l_VLPFC (P)) and posterior superior temporal cortices (r_STG (P) with the orbitofrontal cortex (l_mOFC (PA), r_mOFC (P)) was positively associated with the average speed when riding with a peer. However, neither the superior temporal or ventrolateral prefrontal connectivity played a role in the prediction of average speed in the Alone condition, in which greater dorsomedial cortex – OFC connectivity (r_DMC (A)) – (bil_OFC (A)) was associated with higher speed, whilst greater connectivity of this OFC area with the cingulate cortex (r_DMC (P&A)) was associated with lower average speed. Thus, it appears that the control of behaviour is accomplished by two different brain networks; one is the left lateral OFC - left ventrolateral prefrontal cortex-right temporal cortex that appears to be predominantly involved in reward processing areas of the left OFC operating in the presence of peers, whilst the other is the medial orbitofrontal-mediodorsal-cingulate cortices, with rich links within the OFC that operate in the absence of peers. Notably, in this last condition all the within OFC links were negatively associated with average speed.

The social context, independently of the dyad type (same/different gender), reduced the ability to discriminate high-risk from low-risk scenes, and activated areas in the orbitofrontal, ventrolateral prefrontal, posterior superior temporal, cingulate, and dorsomedial prefrontal cortices. The pattern of OFC and medial prefrontal activation suggests a social/non-social organization. The left OFC, left ventrolateral prefrontal cortex, and right posterior superior temporal cortices are uniquely activated in the presence of peers, whilst the bilateral medial OFC and dorsomedial cortices are uniquely activated in the absence of peers. The bilateral medial OFC and portions of the cingulate gyrus are activated independently of the social context. The functional connectivity between these areas predicted performance on the motorcycle simulator in a way that was also dependent on the presence/absence of peers, that is, the cingulate/dorsomedial cortex plays a role in the absence, but not in the presence of peers. Whilst these results are compatible with the idea that the influence of peers is underpinned by the downregulation of the cognitive control network, we believe that our findings also provide evidence for the possibility that social context serves as a selector of the brain networks that are recruited to perform the task.

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APPENDIX A. SUPPLEMENTARY DATA