PSYCHOPHYSIOLOGY SPR | WILEY

Brain signatures of catastrophic events: Emotion, salience, and cognitive control

Laura Mas-Cuesta[1] | **Sabina Baltruschat[1]** | **Antonio Cándido[1]** | **Andrés Catena[2]**

[1]Mind, Brain and Behavior Research Center, University of Granada, Campus de Cartuja s/n, Granada, Spain

[2]School of Psychology, University of Granada, Campus de Cartuja s/n, Granada, Spain

Correspondence
Laura Mas-Cuesta, Mind, Brain and Behavior Research Center, University of Granada, Campus de Cartuja s/n, Granada 18011, Spain.
Email: lauramas@ugr.es

Abstract

Anticipatory brain activity makes it possible to predict the occurrence of expected situations. However, events such as traffic accidents are statistically unpredictable and can generate catastrophic consequences. This study investigates the brain activity and effective connectivity associated with anticipating and processing such unexpected, unavoidable accidents. We asked 161 participants to ride a motorcycle simulator while recording their electroencephalographic activity. Of these, 90 participants experienced at least one accident while driving. We conducted both within-subjects and between-subjects comparisons. During the pre-accident period, the right inferior parietal lobe (IPL), left anterior cingulate cortex (ACC), and right insula showed higher activity in the accident condition. In the post-accident period, the bilateral orbitofrontal cortex, right IPL, bilateral ACC, and middle and superior frontal gyrus also showed increased activity in the accident condition. We observed greater effective connectivity within the nodes of the limbic network (LN) and between the nodes of the attentional networks in the pre-accident period. In the post-accident period, we also observed greater effective connectivity between networks, from the ventral attention network (VAN) to the somatomotor network and from nodes in the visual network, VAN, and default mode network to nodes in the frontoparietal network, LN, and attentional networks. This suggests that activating salience-related processes and emotional processing allows the anticipation of accidents. Once an accident has occurred, integration and valuation of the new information takes place, and control processes are initiated to adapt behavior to the new demands of the environment.

KEYWORDS
accident, brain network, EEG, effective connectivity, simulator, unpredictable

1 | INTRODUCTION

The human brain is primarily designed to predict the future and thus optimize behavior. This anticipatory brain activity is triggered by environmental cues or regularities that signal an upcoming event (Breska & Ivry, 2018; Coull, 2009). However, there are certain situations that are statistically unpredictable due to their very low frequency or lack of regularity and can have severe consequences if not avoided. One striking example of such

situations is traffic accidents, which result in significant physical and psychological harm and account for more than 1.3 million deaths per year worldwide (World Health Organization, 2021). However, the study of the neural mechanisms underlying the anticipation and processing of unexpected events in dynamic ecological contexts, such as accidents, has received little attention in the scientific literature, despite its potential practical application in the field of human–machine integration to improve driver state monitoring and optimize driver assistance (Duma et al., 2017). Therefore, there remains a gap in our understanding of what occurs in the brain when we are confronted with situations that we could not foresee.

Electroencephalography studies indicate that contingent negative variation (CNV) and stimulus preceding (SPN), two types of event-related potentials (ERPs), serve as reliable indicators of the anticipation of expected events, even in situations of uncertainty (Catena et al., 2012; Guo et al., 2019; Mento, 2017). Furthermore, source analysis suggests that these ERPs are distributed across brain regions such as the supplementary motor area (SMA), insula, anterior cingulate cortex (ACC), and medial and lateral frontal cortices (Kotani et al., 2015; Mento et al., 2015). Some studies have raised the question of whether anticipatory brain activity can still be observed when events are statistically unpredictable. For example, Radin et al. (2011) observed significant differences in cortical activity between meditators and non-meditators before the random presentation of a light flash or tone, equating this with SPN. In fact, the concept of predictive anticipatory activity (Mossbridge et al., 2014) allows us to distinguish between stimuli with different characteristics that are randomly presented (Duggan & Tressoldi, 2018). However, it is important to note that most of these studies were conducted with stimuli presented in non-real-life settings with irrelevant consequences. Our study focuses on accidents, events that have catastrophic consequences when they occur in real life. Additionally, these accidents are highly uncommon and unexpected, but this does not necessarily preclude the possibility that they can be anticipated.

Driving is a complex task that relies on visual perception and multi-domain executive functioning (Calhoun et al., 2002; Ware et al., 2020). Studies on effective connectivity, which examine how one brain node influences another (Friston, 2011), have revealed the involvement of various processes in driving, such as visual attention, episodic memory retrieval, goal direction, motor planning, and inhibitory control pathways (Almahasneh et al., 2018; Choi et al., 2020; Liu et al., 2017). Normal driving activates brain regions including the lateral occipital, superior and inferior parietal, and inferior temporal cortices, as well as the frontal gyrus, motor areas, and cerebellum (Kan

et al., 2013; Ware et al., 2020; Yan et al., 2019). However, when driving presents distractions or becomes more challenging, areas associated with cognitive control networks, relevant stimulus processing, and error monitoring, such as the superior frontal cortex, ACC, and insula, are also activated (Oba et al., 2022; Yuen et al., 2021). In the context of crashes, some studies have noted changes in the power of different EEG frequency bands in the moments before and after a simulated crash (Li et al., 2022; Zhang & Yan, 2023). Additionally, Sun et al. (2013) observed a rapid shift in ERPs occurring 500 ms after a collision in a simulated driving task compared to normal driving. Furthermore, Duma et al. (2017) observed increased negativity in frontocentral electrodes in both the "accident" (where an unpredictable simulated accident occurred) and "baseline" (where there was the certainty that an accident would not occur, inducing a strong expectancy about the end of the trial) conditions, in the interval between 1000 and 0 ms pre-accident. In other words, the authors found anticipation markers in the accident condition, which arose before the occurrence of a statistically unpredictable and unavoidable stimulus. However, these studies have primarily focused on sensor-level analysis, leaving a gap in our understanding of which brain networks are involved in these effects, the point at which specific brain areas are recruited, and their connectivity during the peri-accident period.

This study aimed to explore the markers of anticipatory brain activity when individuals are confronted with unavoidable, catastrophic events (accidents in simulated driving contexts). Additionally, we aimed to investigate how the brain processes the occurrence of accidents and how connectivity between different brain networks evolves during the peri-accident periods. Based on previous evidence, we hypothesized that brain regions associated with expectation and uncertainty would be activated in the pre-accident period, leading to increased connectivity within the limbic and attentional networks responsible for emotional processing and salience. Conversely, all brain networks (Yeo et al., 2011) will be involved during the post-accident period, initiating the control and regulatory processes inherent to driving (Ware et al., 2020).

2 | METHOD

2.1 | Participants

A total of 161 (54 women) healthy participants with no history of head injury or neurological disorders took part in this study, which was carried out as part of a larger study on the neural basis of risk behavior in driving. All participants had a valid driver's license. The mean age of

the participants was 32.6 years, ranging from 18 to 68 years (SD = 13.76), with a medium–high educational level. After being debriefed on the aims of the study and their rights, all participants signed an informed consent form. All participants were paid for their participation in the study and were treated according to the Helsinki Declaration (World Medical Association, 2013). The study was approved by the Ethics Committee on Human Research of the University of Granada (n° 204/CEIH/2016). The sample size was calculated using G*Power 3.1.9.7 (Faul et al., 2009), with a moderate effect size ($f = 0.25$), an alpha error of 0.05, and a power of 0.90 ($n = 130$). A further 24% of participants were added to the sample to account for potential dropouts.

2.2 | Procedure

The participants visited the research center and took part in the HRT motorcycle simulator, described elsewhere (Di Stasi et al., 2009; Megías et al., 2017). In brief, this simulator is a realistic but static setup equipped with a seat, handlebar, pedals, accelerator, brakes, turn indicators, and horn. The simulation session consisted of two main parts: a practice and a driving task. Following the practice session, participants drove through a night circuit featuring eight risky scenarios (e.g., doors opening suddenly and pedestrians crossing) while their electrical brain activity was being recorded. Accident occurrence (crash resulting in the fall of the motorcycle) depended on the driver's behavior during the circuit. The road scenario was projected on a screen measuring 110×180 cm, positioned 185 cm in front of the driver. The screen had a refresh rate of 30 Hz and a resolution of 1024×768 pixels. The duration of the driving task, which depended on factors such as speed and the occurrence of accidents, averaged approximately 5 minutes. Our analysis focused exclusively on the data obtained during the risky scenarios and accident events recorded by the HRT motorcycle simulator. On average, participants experienced 1.16 accidents (SD = 0.91, range = 1–4). Specifically, 56 participants had only one accident, 18 had two accidents, 11 had three, 5 had four, and the remaining 64 participants experienced no accidents. On average, participants had 6.42 no accident periods (min/max = 4/8).

2.3 | EEG recordings

Electrical activity of the brain (EEG) was recorded during the motorcycle riding task using a 64-channel active system (Brain Products, Inc.) mounted on an elastic cap and arranged according to the extended 10–20 system. The data were sampled at a rate of 1000 Hz, amplified with a 0.016–1000 Hz band-pass filter, and referenced online to FCz. Electrode impedances were maintained below 25 kΩ, as recommended by the manufacturer.

2.4 | Data processing

Seven participants did not fully complete the task and were excluded from the analysis. Of the 154 remaining participants, only 90 experienced at least one accident during the course (accident condition). Therefore, these 90 participants were used to compare their brain activity before and after having an accident with their non-accident periods (referred to as the baseline condition). The remaining 64 participants (no accident condition) were used for between-group comparisons with the accident and the baseline conditions.

The preprocessing of the continuous EEG signals was conducted using EEGlab software (Delorme & Makeig, 2004; https://sccn.ucsd.edu/eeglab) using the following protocol: (1) The continuous EEG recording was initially down-sampled to 250 Hz; (2) the data were then re-referenced offline to the average reference; (3) any problematic channels were identified and removed based on their spectral characteristics using EEGlab's default parameters (channels with a flatline duration of more than 50 s or with more line noise relative to its signal (4SD)); (4) band-pass filtering was applied to the data (0.5–37 Hz); and (5) the data were segmented into epoch [−6000 to 1500 ms], which were time locked to the trigger corresponding to either the occurrence of an accident (for participants with accidents) or the risky scenario trigger associated with safe segments without accidents (for these participants and those who did not experience an accident). These triggers were provided by the simulator software and integrated into the EEG recording. As accidents could occur at any time during the circuit, the triggers of the risky situations were used as a reference for comparisons. In cases where an accident occurred, the triggers for both the preceding and subsequent scenarios were deleted. This was done to ensure a minimum of 20 seconds between the accident and the next trigger, or between the risky scene and the next scene trigger. The average time distance between the accident and the previous risky scene trigger was 8688 ms (min/max = 1073/68,261 ms), but as triggers were deleted for those cases, the time distance between the accident and the previous risky scene was 28,536 ms. The average temporal distance between the accident and the subsequent risky scene trigger was 36,111 ms (min/max = 1147/146,495 ms). Therefore, when the immediately subsequent triggers were removed, the average distance was 41,407 ms. When no accident happened, the only triggers were the risky scenes.

Subsequently, independent component analysis (ICA) was computed using the second-order blind identification (SOBI) algorithm (Tang et al., 2005), and ocular and electromyographic artifacts were removed using the IClabel plugin implemented in EEGlab (https://github.com/sccn/ICLabel). Removed channels were interpolated using the spherical spline method. The online FCz reference was restored, and the averaged epochs data were then analyzed using standardized low-resolution brain electromagnetic tomography software (sLORETA; Pascual-Marqui, 2002; http://www.uzh.ch/keyinst/loreta.htm). This software was employed to calculate the current source density (CSD) of brain sources underlying the recorded EEG signals. As we do not have the exact location of the channel, the exact Loreta (eLORETA) approach was used, with sLORETA computing the CSD using 6239 voxels and using the Montreal Neurological Institute (MNI) standard template as the solution space.

Next, following Baltruschat et al. (2020), we used the Brainnetome Atlas (BNA; Fan et al., 2016; http://atlas.brainnetome.org) to compute the effective connectivity between and within the seven brain networks identified by Yeo et al. (2011). For this purpose, we used the multivariate Granger causality software developed by Seth (2010; https://users.sussex.ac.uk/~lionelb/MVGC/html/mvgchelp.html) (model order average=4; maximum number of lags=1000). The atlas provides 210 cortical nodes, distributed for each network as follows: 34 for visual network (VN), 33 for somatomotor network (SMN), 30 for dorsal attention network (DAN), 22 for ventral attention network (VAN), 26 for limbic network (LN), 26 for frontoparietal network (FPN), and 36 for default mode network (DMN) (see Fan et al., 2016, for more detail). Coordinates were translated to the sLORETA template, centered at the Brainnetome atlas node coordinates. The time series for each network and each one of its nodes were spatially averaged using the first eigenvariate of the singular value decomposition of the cluster of voxels. So, the time series for each network, and the time series for each node of each network, were then submitted to Seth's Granger causality software.

2.5 | Statistical analysis

Two separate analyses were conducted, one focusing on the estimated brain activities and the other on the estimated effective connectivity. We used the permutation-based statistical software included in the sLoreta distribution to obtain the corrected p values for each network/node and each time frame (Blair & Karniski, 1993; Groppe et al., 2011). In both cases, we employed a non-parametric permutation t test using t-max statistics. This involved generating 5000 random samples to account for multiple comparisons, while an adjusted significance level was set at 0.05. Two main

comparisons were conducted. First, a within-subjects analysis involved comparing the accident condition against the baseline (accident–baseline). Second, a between-subjects analysis was conducted to compare the accident condition against the no accident condition (accident–no accident). Separate comparisons were also carried out for the pre- and post-accident periods. For the connectivity analysis, in each case, comparisons were made between the networks and between the nodes within the networks. Additionally, as a control test, the no accidents condition was compared with the baseline condition (Figure 1).

3 | RESULTS

3.1 | Brain activity

During the pre-accident period, significant differences were observed for the within-subjects comparison accident–baseline (Figure 2). At 896 ms before the accident, there was a difference favoring the accident condition in the right area 40 in the inferior parietal lobe (IPL). At 144 ms before the accident, the difference was located in the left area 32 (ACC), and 60 ms before the accident, the difference was found in the right insula.

For the between-groups comparison accident–no accident, we observed significant differences favoring the accident condition at area 40 (880 ms), at right area 5 (232 ms), and at left area 32 and right area 40 (approximately 112 ms before the accident).

At post-accident (Figure 3, upper panel), we observed a substantial number of significant differences between the accident and baseline conditions, which can be summarized into three distinct time intervals: early (104–192 ms), middle (788–880 ms), and late (1260–1404 ms). These differences were associated with specific brain regions. The difference during the early period was identified in bilateral area 11, in the medial orbitofrontal gyrus, and in the right area 40. During the middle period, the difference was located in bilateral (but mostly left hemisphere) area 24 in the cingulate gyrus, in the right area 6 of the middle frontal gyrus, and in bilateral areas 9 and 11 in the medial frontal gyrus. During the late period, the difference was located in bilateral areas 10/11 in the medial frontal gyrus, and bilateral area 32 (predominantly the right hemisphere). Similar differences emerged when comparing the accident with the no accidents condition (Figure 3, lower panel). The difference during the early period was observed at around 104 ms post-trigger and located in bilateral area 11, whereas differences during the middle period appeared at 772 ms and were located in the right area 11 and bilateral area 32. Differences during the late period emerged at 1264 ms and were located in the right area 32, bilateral
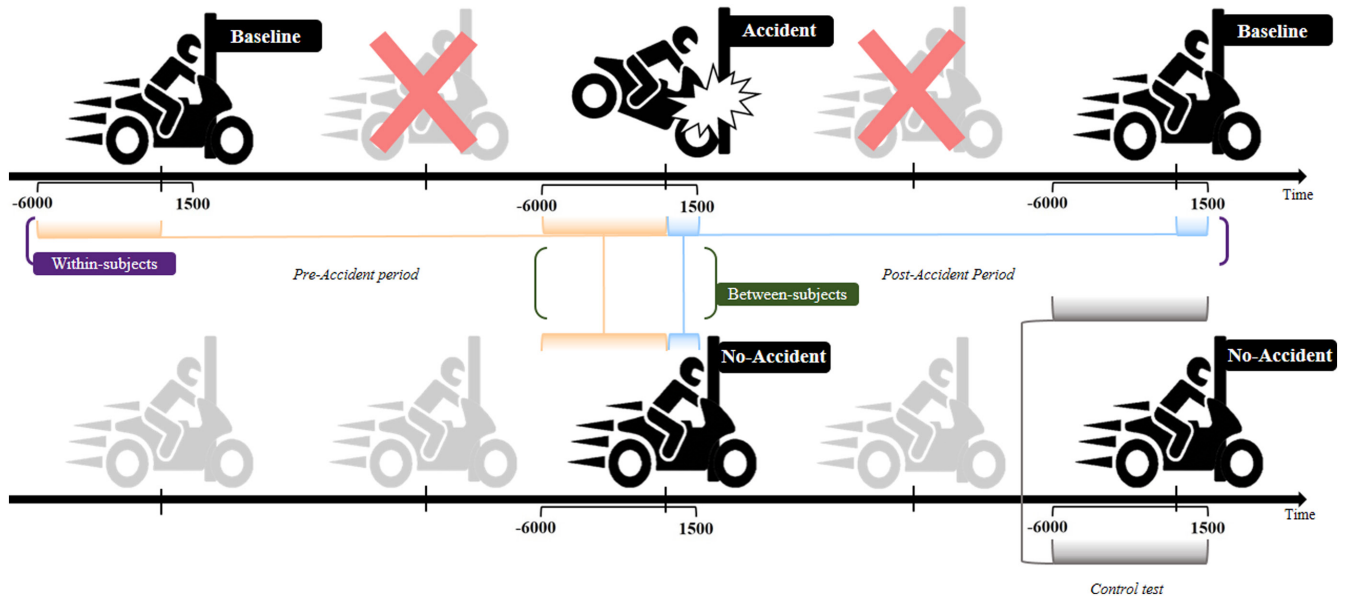
FIGURE 1 Timeline and segmentation of the driving task in the accident (upper part) and no accident (lower part) conditions along with comparisons made in the pre-accident (left) and post-accident (right) periods, and control test.
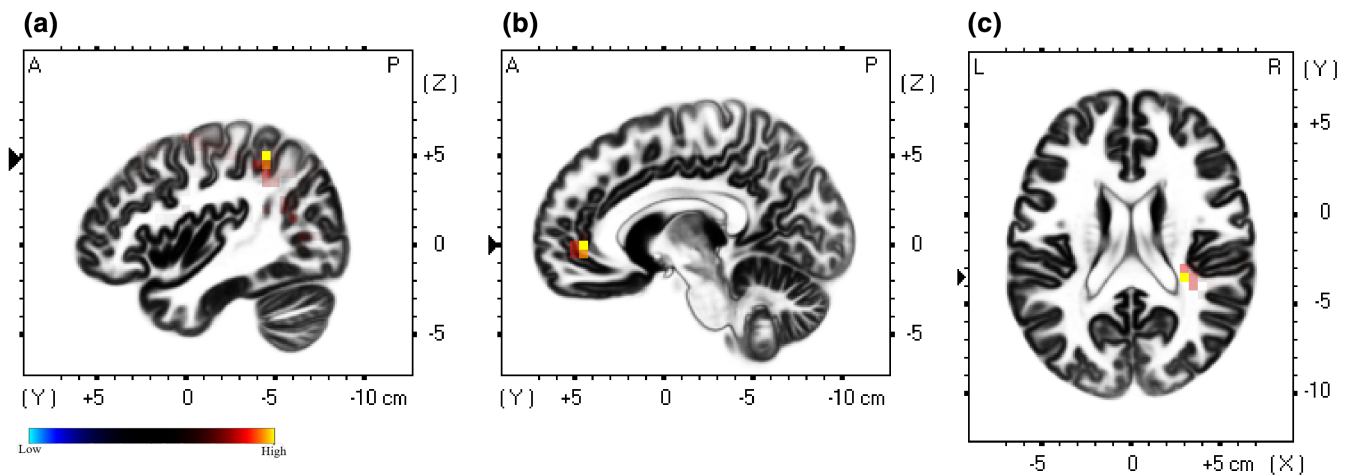

FIGURE 2 Differences between the accident and baseline conditions at 896 ms (a; area 40), 144 ms (b; area 32), and 60 ms (c; insula) before the accident. Colors indicate a corrected p value of .05 (red) and .01 (yellow).

area 11/10 in the medial frontal gyrus, and bilateral area 24 in the anterior cingulate. Interestingly, no significant differences were observed in this period when we compared the baseline and no accident conditions.

3.2 | Effective connectivity

3.2.1 | Pre-accident period

In the pre-accident period, no significant differences were found between networks for the within- or between-subjects comparisons. However, we found significant differences within networks when comparing the accident and baseline conditions (Table 1; Figure 4).

3.2.2 | Post-accident

The accident versus baseline comparison revealed two significant differences in the efficiency of between-network connections. The first difference was directed from the ventral attention network (VAN) to the somatomotor network (SMN) ($p = .05$). Although marginally significant, the second was directed from the default mode network (DMN) to the ventral attention network ($p = .07$). Additionally, within the same comparison, we observed a substantial number of significant connections at the within-network level (Table 2; Figure 4). Comparison between the accident and no accident conditions yielded fewer significant differences (Table 3).
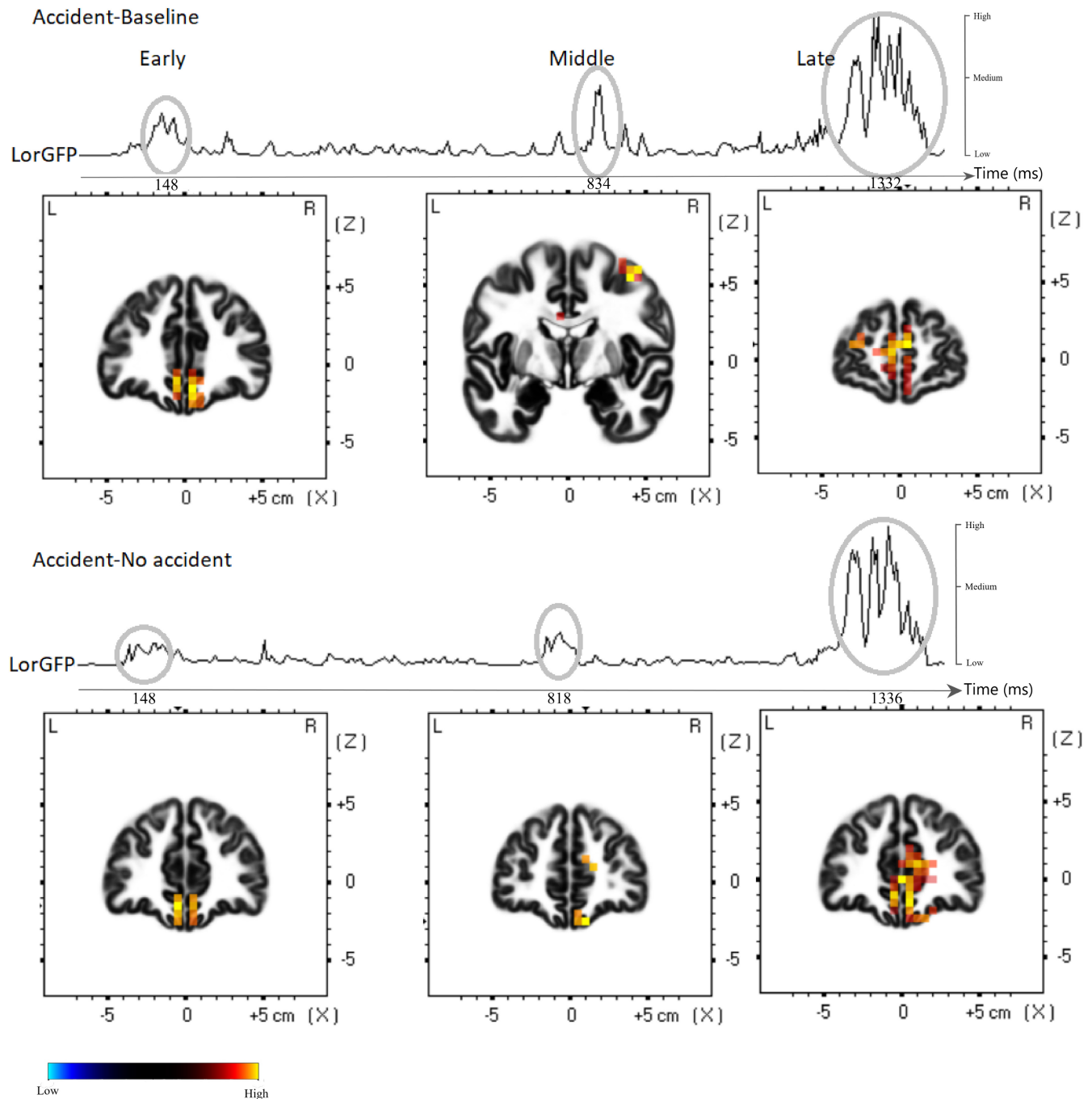
FIGURE 3 Profiles of statistical significance and significant brain areas in the post-trigger differences between the accident and baseline conditions (upper panel), and between the accident and no accident conditions (lower panel). The Loreta global field power (LorGFP) curve is marked at the three most significant points, and differential activations favoring the accident conditions are displayed in the brain maps. Colors indicate a corrected *p* value of .05 (red) and .01 (yellow).

4 | DISCUSSION

This study aimed to determine the brain activity and effective connectivity associated with the anticipation and processing of catastrophic events that are both unexpected and impossible to avoid. For this purpose, we measured brain activation patterns before and after a traffic accident in a simulated driving context. In the pre-accident period, we observed increased activity in the right IPL, the left ACC, and the right insula in the accident condition. In the post-accident period, we detected heightened activity in the bilateral orbitofrontal cortex/ventromedial prefrontal cortex (OFC/vmPFC), right IPL, bilateral ACC, and middle and superior frontal gyrus in the accident condition. Regarding effective connectivity, our analysis revealed a causal activation flow within the

TABLE 1 Within-network differences in the pre-accident period for the within-subjects comparison (accident–baseline).

Node net 1	Net 1		Node net 2	Net 2	*p*
RH medial area 38	LN	>	LH area 13	LN	.05
RH rostral area 20	LN	>	LH area 13	LN	.02
RH rostral area 35/36	LN	>	LH area 13	LN	.04
RH TI (T agr insular cortex)	LN	>	LH area 13	LN	.00
RH TI (T agr insular cortex)	LN	>	LH area 4	VAN	.05
LH area 1/2/3 (lower limb region)	VAN	<	LH ventrolateral area 37	DAN	.05

Abbreviations: <, causal link from Node 2 to Node 1; >, causal link from Node 1 to Node 2; DAN, dorsal attention network; FPN, fronto-parietal network; LN, limbic network; RH/LH, right/left hemisphere; VAN, ventral attention network.
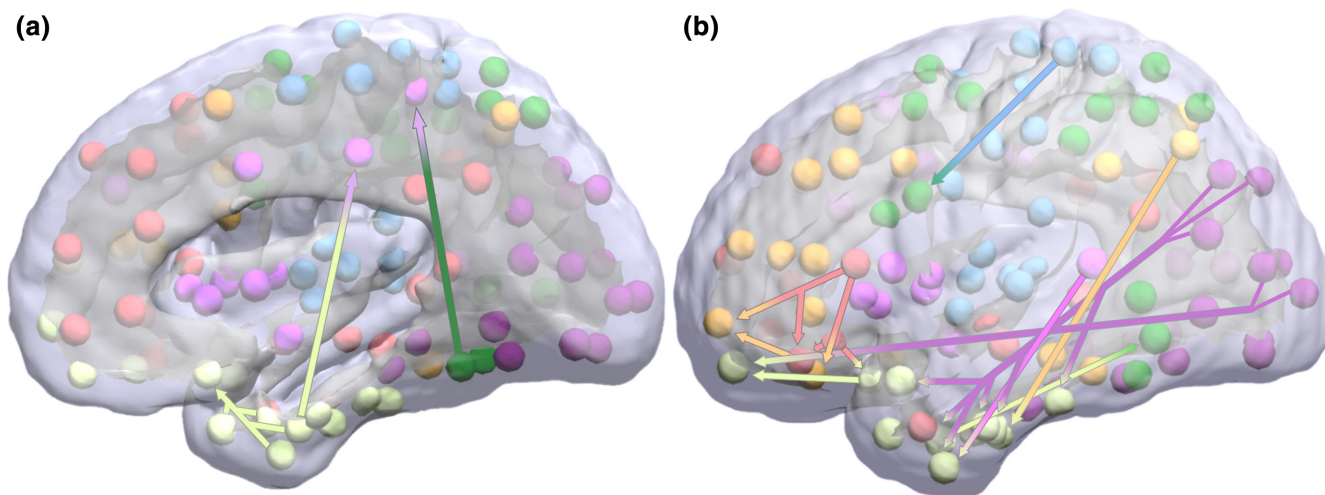

FIGURE 4 Within-network effective connectivity in the pre-accident (a) and post-accident periods (b) for the within-subjects comparison. Node color represents the network they are forming part of: purple (visual) blue (somatomotor), green (dorsal attention), violet (ventral attention), cream (limbic) orange (frontoparietal), and red (default mode). Arrow direction represents the causal activation flow from one node to another. Adapted from Baltruschat et al. (2020).

various nodes of the LN and between the nodes of the attentional networks during the pre-accident period. In the post-accident period, we also observed greater effective connectivity between networks, from the VAN to the SMN and from nodes in the VN, VAN, and DMN to nodes in the FPN, LN, and attentional networks.

4.1 | Brain activity

4.1.1 | Pre-accident period

Our findings revealed notable activation in the right IPL, left ACC, and right insula when comparing accident and baseline conditions. We observed similar activation patterns when comparing the accident and no accident groups. These findings align with previous research indicating the involvement of these brain regions

during driving and the anticipation of unexpected and potentially dangerous situations. Specifically, IPL activation has been linked to anticipating outcomes following decision-making processes as well as reinforcing or aversive stimuli (Gaudio & Quattrocchi, 2012; Liu et al., 2011; Seidel et al., 2015). In this regard, the IPL is associated with monitoring attentional shifts in space, and with visuospatial perception and memory functions (Chen et al., 2012; Chung et al., 2014). The ACC has been associated with uncertainty processing, conflict detection, and error monitoring from the time an action is performed to the results of this action (Ernst & Paulus, 2005; Grupe & Nitschke, 2013). In addition, Calhoun et al. (2002) also identified the activation of an attentional modulation network during driving, which includes the ACC and the IPL. On the other hand, the insular cortex responds to painful stimuli and the anticipation of harm (Centanni et al., 2021; Drabant et al., 2011; Seidel et al., 2015).

TABLE 2 Significant within-network connections during the post-accident period in the within-subjects comparison (accidents–baseline).

Node net 1	Net 1		Node net 2	Net 2	*p*
LH area 4ul, (upper limb region)	SMN	>	RH dorsal area 44	DAN	.02
LH caudal cuneus gyrus	VN	>	RH opercular area 44	VAN	.05
RH lateral area 10	FPN	<	RH lateral area 11	FPN	.02
LH caudal cuneus gyrus	VN	>	RH lateral area 11	FPN	.01
LH occipital polar cortex	VN	>	RH lateral area 11	FPN	.03
RH area 13	LN	>	LH medial area 11	LN	.02
LH lateral superior occipital gyrus	VN	>	RH medial area 38	LN	.03
LH caudal area 39	VN	>	RH intermediate ventral area 20	LN	.04
LH rostrodorsal area 39	FPN	>	RH rostral area 20	LN	.02
LH dorsomedial parietooccipital sulcus	VN	>	RH rostral area 20	LN	.04
LH lateral superior occipital gyrus	VN	>	RH rostral area 20	LN	.01
LH caudal area 39	VN	>	RH intermediate lateral area 20	LN	.02
LH lateral superior occipital gyrus	VN	>	RH caudoventral of area 20	LN	.01
RH dorsolateral area 37	DAN	<	RH area TI (T agr insular cortex)	LN	.03
RH caudoposterior sup temporal sulcus	VAN	>	RH TI (T agr insular cortex)	LN	.01
LH dorsomedial parietooccipital S	VN	>	RH area TI (T agr insular cortex)	LN	.03
RH lateral area 10	FPN	<	RH rostroventral area 24	–	.03
RH orbital area 12/47	DMN	<	RH rostroventral area 24	–	.02
RH lateral area 11	FPN	<	RH rostroventral area 24	–	.01
RH orbital area 12/47	DMN	<	RH subgenual area 32	DMN	.05
RH area 13	LN	<	RH subgenual area 32	DMN	.03

Abbreviations: <, causal link from Node 2 to Node 1; >, causal link from Node 1 to Node2; DAN, dorsal attention network; DMN, default mode network; FPN, fronto-parietal network; LN, limbic network; RH/LH, right/left hemisphere; SMN, somatomotor network; VAN, ventral attention network; VN, visual network.

Specifically, it represents conscious feelings and body states related to interoceptive awareness (Craig, 2009; Uddin et al., 2017). Together with the ACC, this structure forms the "salience network" (SN; Seeley et al., 2007) that is activated in response to behaviorally relevant and novel stimuli rather than expected events (Corbetta et al., 2008). Furthermore, in a functional magnetic resonance study where a group of taxi drivers played a driving video game, Spiers and Maguire (2007) found increased activation in the medial occipital, posterior middle temporal, posterior parietal and lateral prefrontal cortices, ACC, precuneus, and insula when responding to road hazards. Effective connectivity studies have also demonstrated that information enters the salience network via the insula, which acts as an "out-flow hub" regulating the interaction between large-scale networks (Ham et al., 2013; Sridharan et al., 2008). In other words, the insula serves as a final step in hierarchical information processing, integrating relevant sensory, interoceptive, emotional, and cognitive information (Kurth et al., 2010).

In summary, the evidence indicates that the IPL, ACC, and insula are activated during driving and these structures are also linked to attentional shifts based on stored

information. These processes enable the interpretation of the environment, detection of errors, and monitoring of potential conflicts. Moreover, these brain regions are essential for integrating emotional and interoceptive information, allowing individuals to identify certain features of the environment that are relevant for anticipating unexpected or potentially threatening situations. In line with previous research (Duma et al., 2017), our findings support the existence of anticipatory brain activity in response to catastrophic events. Specifically, we observed that the IPL, ACC, and insula become active in the milliseconds (ms) preceding a simulated driving accident. Therefore, it seems that the activation of internal processes, including emotional, cognitive, and interoceptive awareness, forms the basis for anticipating unpredictable situations that cannot be avoided.

4.1.2 | Post-accident period

The accident–baseline comparison revealed activation in several key brain regions, including the bilateral OFC/vmPFC, right IPL and bilateral ACC, and middle and

TABLE 3 Significant within-network connections during the post-accident period in the between-subjects comparison (accidents–no accidents).

Node net 1	Net 1		Node net 2	Net 2	p
RH area TI (T agr insular cortex)	LN	>	RH medial area 11	LN	.05
RH area TI (T agr insular cortex)	LN	>	RH area 13	LN	.01
RH dorsal agranular insula	VAN	>	RH area 13	LN	.05
LH medial superior occipital gyrus	VN	>	RH medial area 38	LN	.01
LH lateral superior occipital gyrus	VN	>	RH intermediate ventral area 20	LN	.02
LH medial superior occipital gyrus	VN	>	RH area TI (T agr insular cortex)	LN	.02
LH occipital polar cortex	VN	>	RH dorsal agranular insula	VAN	.04
RH lateral area 11	FPN	<	RH rostroventral area 24	–	.04
RH lateral area 11	FPN	<	LH subgenual area 32	DMN	.04

Abbreviations: <: causal link from Node 2 to Node 1; >: Causal link from Node 1 to Node 2; DMN: Default mode network; FPN: Frontoparietal network; LN: Limbic network; RH/LH: Right/left hemisphere; VAN: Ventral Attention network; VN: Visual network.

superior frontal gyrus. Very similar activation patterns were found in the accident–no accident comparison. Previous studies have demonstrated the role of several frontal and parietal regions in the planning phases that predict good driving performance (Oba et al., 2022; Ware et al., 2020). Furthermore, in a computerized driving task where the outcome could be a crash or successful pass, greater activation of the OFC, IPL, insula, and ACC was observed during the crash condition (Vorobyev et al., 2015). One of the main functions of the OFC/vmPFC is to integrate past and current information to effectively evaluate stimuli and guide the decision-making process (Knudsen & Wallis, 2022; Peters & Büchel, 2010). This region is involved in comparing real and expected outcomes, showing greater activation in response to highly unexpected outcomes (Ernst & Paulus, 2005). Activation of the premotor area (a6) could reflect unconscious voluntary motor planning (Drabant et al., 2011), while the ACC and premotor areas are jointly implicated in driving action in response to negative feedback (Klein et al., 2007). The ACC plays a pivotal role in task performance across all phases (Dosenbach et al., 2006) and serves as a part of the SN, contributing to error monitoring and the hierarchical initiation of control signals for activating prefrontal regions (Sridharan et al., 2008; Srinivasan et al., 2013). The superior frontal gyrus is a component of the cognitive control network responsible for inhibitory and attentional control, flexibility, and decision-making for behavioral self-regulation (Miller & Cohen, 2001; Niendam et al., 2012; Passingham & Lau, 2023). Moreover, some authors have reported changes in brain activity in the milliseconds following a simulated crash (Li et al., 2022; Sun et al., 2013). Taken together, these findings suggest that the activation of areas responsible for detecting relevant stimuli is sustained after an accident. Additionally, frontal regions responsible for the valuation of the present experience and initiating the control processes necessary for behavioral self-regulation are activated.

4.2 | Effective connectivity

4.2.1 | Pre-accident period

The accident–baseline comparison revealed a causal activation flow within LN nodes and between VAN and DAN nodes. Specifically, somatosensory regions of the VAN (left areas 4 and 1/2/3) received information from the limbic region of the right insula and the temporal area of the DAN (left area 37). On the other hand, limbic regions of the right insula, parahippocampal (right area 35/36), and superior and inferior temporal (right areas 38 and 20) gyrus showed effective connectivity to the orbital region of the LN (left area 13). The VAN is typically activated during attentional orientation and plays a role in identifying salient or novel stimuli (Corbetta & Shulman, 2002; Petersen & Posner, 2012). Previous studies have shown the collaborative interaction between DAN and VAN in redirecting attention to unexpected stimuli (Vossel et al., 2014). The insula serves as the central node of the SN, which overlaps with the VAN (Menon & D'Esposito, 2022), playing a role in event

anticipation, among other functions (see above). Area 13, part of the OFC, is responsible for the emotional valuation of stimuli by integrating information received from other brain areas (Knudsen & Wallis, 2022; Peters & Büchel, 2010; Rolls et al., 2023). This area is also responsible for the integration of past and current information and shows anticipatory activity before the presentation of stimuli (Seidel et al., 2015; Zhou et al., 2021). Other studies have demonstrated activation of the OFC when cognitive maps or sets of associations underlying a task are identified, which, in turn, facilitates behavioral learning (Schuck et al., 2016) and the prediction of rewards or punishments (Zhou et al., 2019). Therefore, the OFC appears to play a pivotal role in forming a representation of the structure of the environment to anticipate future outcomes. Additionally, anterior, inferior, and medial temporal regions are known to be involved in emotional processing, semantic representations, and episodic memory (Herlin et al., 2021; Wong & Gallate, 2012; Zhang et al., 2022). Previous research has also shown evidence of effective and structural connectivity between the insula and parahippocampal and temporal areas with the OFC (Fan et al., 2014; Lin et al., 2020; Rolls et al., 2022a). Our results on effective connectivity are consistent with those obtained on pre-accident brain activity. Moreover, they are consistent with previous evidence and suggest that relevant environmental cues are integrated with information retrieved from memory, conceptual knowledge, and interoceptive information related to potential hazards. This integration process enables the brain to form a comprehensive representation of the structure and emotional value of the situation. Therefore, it seems that the anticipation of uncertain or unexpected situations, such as accidents, is strongly associated with the activation of affective mechanisms (Seidel et al., 2015).

4.2.2 | Post-accident period

The increased effective connectivity between networks from the VAN to the SMN in the accident–baseline comparison is consistent with the findings reported by Duann et al. (2009) using an inhibitory control task. Their study revealed effective connectivity from the VAN to the SMN, where the VAN was involved in the attentional processing of novel information, and the SMN played a role in the inhibitory control of movement. These results parallel our findings and suggest that during driving, especially in the milliseconds following an accident, there is a shift in attention and activation of control and inhibitory processes that facilitate behavioral adaptation to new environmental demands.

At the within-network level, the accident–baseline comparison revealed the involvement of all brain networks. Sensory nodes within the VN, SMN, and VAN transmitted information to frontal and orbitofrontal nodes belonging to the VAN, DAN, and FPN and to temporal and insular areas of the LN. Additionally, the cingulate regions of the DMN showed effective connectivity with orbitofrontal regions belonging to the FPN, DMN, and LN, while effective connectivity was observed between nodes belonging to the same networks. The accident–no accident comparison showed similar results, although with fewer significant differences. Vorobyev et al. (2015) also found increased activation in the lateral and medial occipital areas, the junction between temporal polar, orbitofrontal, and insular cortices, and the posterior middle temporal cortex during accidents in a simulated driving task.

The occurrence of a crash (resulting in the fall of the motorcycle) leads to a complete alteration of the environmental characteristics of the driving simulator. This is reflected in the activation of occipital and parietal nodes of the VN (left occipital polar, left cuneus, left lateral occipital, left area 39, and left parietooccipital sulcus), all of which are involved in visual attention, object and motion processing, memory, and navigation (Grill-Spector et al., 2001; Malikovic et al., 2016; Rolls et al., 2022c). Previous studies have identified fixed and reciprocal connections between the VN and VAN, which facilitate spatial orientation to relevant stimuli (Vossel et al., 2012, 2014). The inferior frontal gyrus (IFG; area 44), which belongs to the VAN and the DAN (Corbetta et al., 2008), is responsible for the representation of the hierarchical sequential structure of ongoing events, using information received from precentral motor areas (Fiebach & Schubotz, 2006). These findings indicate that the connectivity from the VN and SMN to the VAN and DAN enables the formation of a representation of a sequence of events to facilitate an attentional shift from stimulus detection to goal-directed attention (Fox et al., 2006). The superior and inferior temporal regions of the LN (right areas 38 and 20) are involved in affective visual processing, semantic representations, and episodic memory (see above), and the anterior temporal cortex is part of the "meaning" network that facilitates the understanding of events for executive control (Jouen et al., 2018). Several investigations have found structural and effective connections between the occipitoparietal regions and the superior and inferior temporal cortices (Baker et al., 2018; Lin et al., 2020; Rolls et al., 2022c; Wu et al., 2016). These connections suggest the occurrence of an abstract representation of the current affective experience, which

promotes adaptive behavior. These findings are consistent with the results of Choi et al. (2020), who also identified effective connectivity from the VN to the inferior frontal, superior temporal, and inferior temporal gyrus during driving. Additionally, the insular region of the LN receives information from the superior temporal region of the VAN, which is involved in the auditory processing and perception of threatening information (Connolly et al., 2016; Rolls et al., 2022b), sending information to the temporal region of the DAN (area 37) for processing information from different sensory modalities (Hodgson et al., 2022). These patterns of effective connectivity are consistent with the idea that the insula plays a fundamental role in switching between different networks and shifting the focus from external to internal processes to facilitate the decision-making process (Lamichhane & Dhamala, 2015; Sridharan et al., 2008). In support of the above, our results suggest that, in the milliseconds following a crash, and following the notion of posterior-to-anterior patterns of information flow proposed by Mesulam (1998), the sensory association areas detect changes in the environment and relay this information to higher-order structures to initiate the information integration and cognitive control processes necessary to adapt behavior to the demands of the situation.

It is important to note that the areas of the LN that are influenced by the VN in the post-accident period (right areas 38 and 20 and temporal insular) are the same areas that influence the activation of the OFC in the pre-accident period. Before the accident, the visual scenes were identical for individuals who would later have an accident and those who would not. When the accident occurs, the limbic regions receive information from the sensory regions associated with an environment where negative consequences have occurred. This influx of new information could assist the OFC in making decisions related to the aversive consequences of the accident. In fact, in the post-accident period, the fronto-orbital areas (right areas 10, 11, 13, and 12/47) were influenced by different brain networks responsible for general task performance (Dosenbach et al., 2006), including the visual network. Previous studies have identified effective connectivity from visual regions to the OFC/VPFC when presented with aversive stimuli (Dima et al., 2016; Rolls et al., 2023). Furthermore, the effective connectivity we observed from the cingulate regions of the DMN (right areas 32 and 24) to the orbitofrontal regions belonging to the FPN, DMN, and LN support the idea that the DMN and task-positive systems are not antagonistic (Cocchi et al., 2013). The DMN is responsible for self-referential processing and internal mental state monitoring (Greicius et al., 2003), whereas the FPN is involved in planning, inhibition, and cognitive flexibility, allowing for goal modification based

on the environment and the changing demands of a task (Menon & D'Esposito, 2022; Woolgar et al., 2015). Studies of effective connectivity have revealed the cooperative interactions between the DMN and task-positive networks, with the DMN exerting an excitatory influence on the executive networks (De Pisapia et al., 2012; Pu et al., 2016; Uddin et al., 2009). In this context, the activation of orbital regions linked to cognitive control, through the influence of the cingulate cortex, can facilitate the decision-making process based on the valuation of the environment following an accident.

4.3 | Conclusions

The primary objective of this study was to explore brain activity indicators related to the processing of unexpected and unavoidable catastrophic events (accidents that occurred while driving in a simulator). In summary, our results demonstrated changes in brain activation and effective connectivity patterns during different phases of this process. During the pre-accident period, we observed activation of LN regions and attentional networks, while in the post-accident period, involvement of all brain networks was evident, ranging from sensory association regions to higher-order processing areas. These findings suggest that the activation of salience-related processes and emotional processing allows anticipating the occurrence of accidents. However, once an accident has already occurred, there is an integration and valuation of the new information, and control processes are initiated to adapt behavior to the new demands of the environment. Considering the potential development of smart systems for vehicles, this deeper understanding of the anticipation and brain processing of accidents could provide guidance to improve driver state monitoring and warning systems. This could be achieved by using EEG activity patterns and software with online analysis to optimize driver assistance. It should be noted as a limitation of the study that other behavioral indices, such as speed or handlebar control, were not taken into account. Therefore, future studies could explore the relationship between brain activity and driving performance in unpredictable risky situations.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

DATA AVAILABILITY STATEMENT

The data will be made available by the authors, upon reasonable request, to any qualified researcher.

ORCID

Laura Mas-Cuesta https://orcid.org/0000-0002-5424-6415

REFERENCES

Almahasneh, H., Kamel, N., & Khan, D. M. (2018). Variation in brain's effective connectivity due to driving using partial directed coherence. In *2018 IEEE international conference on automatic control and intelligent systems (I2CACIS)* (pp. 67–70). Institute of Electrical and Electronics Engineers (IEEE). https://doi.org/10.1109/I2CACIS.2018.8603692

Baker, C. M., Burks, J. D., Briggs, R. G., Conner, A. K., Glenn, C. A., Manohar, K., Milton, C. K., Sali, G., McCoy, T. M., Battiste, J. D., O'Donoghue, D. L., & Sughrue, M. E. (2018). A Connectomic atlas of the human cerebrum-chapter 8: The posterior cingulate cortex, medial parietal lobe, and Parieto-occipital sulcus. *Operative Neurosurgery*, *15*, S350–S371. https://doi.org/10.1093/ons/opy262

Baltruschat, S., Cándido, A., Megías, A., Maldonado, A., & Catena, A. (2020). Risk proneness modulates the impact of impulsivity on brain functional connectivity. *Human Brain Mapping*, *41*(4), 943–951. https://doi.org/10.1002/hbm.24851

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology*, *30*(5), 518–524. https://doi.org/10.1111/j.1469-8986.1993.tb02075.x

Breska, A., & Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proceedings of the National Academy of Sciences*, *115*(48), 12283–12288. https://doi.org/10.1073/pnas.1810596115

Calhoun, V. D., Pekar, J. J., McGinty, V. B., Adali, T., Watson, T. D., & Pearlson, G. D. (2002). Different activation dynamics in multiple neural systems during simulated driving. *Human Brain Mapping*, *16*(3), 158–167. https://doi.org/10.1002/hbm.10032

Catena, A., Perales, J. C., Megías, A., Cándido, A., Jara, E., & Maldonado, A. (2012). The brain network of expectancy and uncertainty processing. *PLoS One*, *7*(7), e40252. https://doi.org/10.1371/journal.pone.0040252

Centanni, S. W., Janes, A. C., Haggerty, D. L., Atwood, B., & Hopf, F. W. (2021). Better living through understanding the insula: Why subregions can make all the difference. *Neuropharmacology*, *198*, 108765. https://doi.org/10.1016/j.neuropharm.2021.108765

Chen, Q., Weidner, R., Vossel, S., Weiss, P. H., & Fink, G. R. (2012). Neural mechanisms of attentional reorienting in three-dimensional space. *Journal of Neuroscience*, *32*(39), 13352–13362. https://doi.org/10.1523/JNEUROSCI.1772-12.2012

Choi, M.-H., Kim, H.-S., & Chung, S.-C. (2020). Evaluation of effective connectivity between brain areas activated during simulated driving using dynamic causal modeling. *Frontiers in Behavioral Neuroscience*, *14*, Article 158. https://doi.org/10.3389/fnbeh.2020.00158

Chung, S.-C., Choi, M.-H., Kim, H.-S., You, N.-R., Hong, S.-P., Lee, J.-C., Park, S.-J., Baek, J.-H., Jeong, U.-H., You, J.-H., Lim, D.-W., & Kim, H.-J. (2014). Effects of distraction task on driving: A functional magnetic resonance imaging study. *Bio-medical Materials and Engineering*, *24*(6), 2971–2977. https://doi.org/10.3233/BME-141117

Cocchi, L., Zalesky, A., Fornito, A., & Mattingley, J. B. (2013). Dynamic cooperation and competition between brain systems during cognitive control. *Trends in Cognitive Sciences*, *17*(10), 493–501. https://doi.org/10.1016/j.tics.2013.08.006

Connolly, A. C., Sha, L., Swaroop Guntupalli, J., Oosterhof, N., Halchenko, Y. O., Nastase, S. A., Castello, M. V. O., Abdi, H., Jobst, B. C., Ida Gobbini, M., & Haxby, J. V. (2016). How the human brain represents perceived dangerousness or "predacity" of animals. *Journal of Neuroscience*, *36*(19), 5373–5384. https://doi.org/10.1523/JNEUROSCI.3395-15.2016

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, *58*(3), 306–324. https://doi.org/10.1016/j.neuron.2008.04.017

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755

Coull, J. T. (2009). Neural substrates of mounting temporal expectation. *PLoS Biology*, *7*(8), e1000166. https://doi.org/10.1371/journal.pbio.1000166

Craig, A. D. (2009). How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*(1), 59–70. https://doi.org/10.1038/nrn2555

De Pisapia, N., Turatto, M., Lin, P., Jovicich, J., & Caramazza, A. (2012). Unconscious priming instructions modulate activity in default and executive networks of the human brain. *Cerebral Cortex*, *22*(3), 639–649. https://doi.org/10.1093/cercor/bhr146

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Di Stasi, L. L., Álvarez-Valbuena, V., Cañas, J. J., Maldonado, A., Catena, A., Antolí, A., & Candido, A. (2009). Risk behaviour and mental workload: Multimodal assessment techniques applied to motorbike riding simulation. *Transportation Research Part F: Traffic Psychology and Behaviour*, *12*(5), 361–370. https://doi.org/10.1016/j.trf.2009.02.004

Dima, D., Roberts, R. E., & Frangou, S. (2016). Connectomic markers of disease expression, genetic risk and resilience in bipolar

disorder. *Translational Psychiatry*, *6*(1), 1. https://doi.org/10.1038/tp.2015.193

Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., Burgund, E. D., Grimes, A. L., Schlaggar, B. L., & Petersen, S. E. (2006). A core system for the implementation of task sets. *Neuron*, *50*(5), 799–812. https://doi.org/10.1016/j.neuron.2006.04.031

Drabant, E. M., Kuo, J. R., Ramel, W., Blechert, J., Edge, M. D., Cooper, J. R., Goldin, P. R., Hariri, A. R., & Gross, J. J. (2011). Experiential, autonomic, and neural responses during threat anticipation vary as a function of threat intensity and neuroticism. *NeuroImage*, *55*(1), 401–410. https://doi.org/10.1016/j.neuroimage.2010.11.040

Duann, J.-R., Ide, J. S., Luo, X., & Li, C.-S. R. (2009). Functional connectivity delineates distinct roles of the inferior frontal cortex and presupplementary motor area in stop signal inhibition. *Journal of Neuroscience*, *29*(32), 10171–10179. https://doi.org/10.1523/JNEUROSCI.1300-09.2009

Duggan, M., & Tressoldi, P. (2018). Predictive physiological anticipatory activity preceding seemingly unpredictable stimuli: An update of Mossbridge et al's meta-analysis. *F1000Research*, *7*, 407. https://doi.org/10.12688/f1000research.14330.2

Duma, G. M., Mento, G., Manari, T., Martinelli, M., & Tressoldi, P. (2017). Driving with intuition: A preregistered study about the EEG anticipation of simulated random car accidents. *PLoS One*, *12*(1), e0170370. https://doi.org/10.1371/journal.pone.0170370

Ernst, M., & Paulus, M. P. (2005). Neurobiology of decision making: A selective review from a neurocognitive and clinical perspective. *Biological Psychiatry*, *58*(8), 597–604. https://doi.org/10.1016/j.biopsych.2005.06.004

Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., Yang, Z., Chu, C., Xie, S., Laird, A. R., Fox, P. T., Eickhoff, S. B., Yu, C., & Jiang, T. (2016). The human Brainnetome atlas: A new brain atlas based on connectional architecture. *Cerebral Cortex*, *26*(8), 3508–3526. https://doi.org/10.1093/cercor/bhw157

Fan, L., Wang, J., Zhang, Y., Han, W., Yu, C., & Jiang, T. (2014). Connectivity-based Parcellation of the human temporal pole using diffusion tensor imaging. *Cerebral Cortex*, *24*(12), 3365–3378. https://doi.org/10.1093/cercor/bht196

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: A common role for Broca's area and ventral premotor cortex across domains? *Cortex*, *42*(4), 499–502. https://doi.org/10.1016/S0010-9452(08)70386-1

Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(26), 10046–10051. https://doi.org/10.1073/pnas.0604187103

Friston, K. J. (2011). Functional and effective connectivity: A review. *Brain Connectivity*, *1*(1), 13–36. https://doi.org/10.1089/brain.2011.0008

Gaudio, S., & Quattrocchi, C. C. (2012). Neural basis of a multidimensional model of body image distortion in anorexia nervosa. *Neuroscience & Biobehavioral Reviews*, *36*(8), 1839–1847. https://doi.org/10.1016/j.neubiorev.2012.05.003

Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences*, *100*(1), 253–258. https://doi.org/10.1073/pnas.0135058100

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*(10–11), 1409–1422. https://doi.org/10.1016/s0042-6989(01)00073-6

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. *Psychophysiology*, *48*(12), 1711–1725. https://doi.org/10.1111/j.1469-8986.2011.01273.x

Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, *14*, 488–501. https://doi.org/10.1038/nrn3524

Guo, Z., Tan, X., Pan, Y., Liu, X., Zhao, G., Wang, L., & Peng, Z. (2019). Contingent negative variation during a modified cueing task in simulated driving. *PLoS One*, *14*(11), e0224966. https://doi.org/10.1371/journal.pone.0224966

Ham, T., Leff, A., de Boissezon, X., Joffe, A., & Sharp, D. J. (2013). Cognitive control and the salience network: An investigation of error processing and effective connectivity. *Journal of Neuroscience*, *33*(16), 7091–7098. https://doi.org/10.1523/JNEUROSCI.4692-12.2013

Herlin, B., Navarro, V., & Dupont, S. (2021). The temporal pole: From anatomy to function—A literature appraisal. *Journal of Chemical Neuroanatomy*, *113*, 101925. https://doi.org/10.1016/j.jchemneu.2021.101925

Hodgson, V. J., Lambon Ralph, M. A., & Jackson, R. L. (2022). The cross-domain functional organization of posterior lateral temporal cortex: Insights from ALE meta-analyses of 7 cognitive domains spanning 12,000 participants. *Cerebral Cortex*, *bhac394*, 4990–5006. https://doi.org/10.1093/cercor/bhac394

Jouen, A. L., Ellmore, T. M., Madden-Lombardi, C. J., Pallier, C., Dominey, P. F., & Ventre-Dominey, J. (2018). Beyond the word and image: II- Structural and functional connectivity of a common semantic system. *NeuroImage*, *166*, 185–197. https://doi.org/10.1016/j.neuroimage.2017.10.039

Kan, K., Schweizer, T. A., Tam, F., & Graham, S. J. (2013). Methodology for functional MRI of simulated driving. *Medical Physics*, *40*(1), 12301. https://doi.org/10.1118/1.4769107

Klein, T. A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D. Y., & Ullsperger, M. (2007). Neural correlates of error awareness. *NeuroImage*, *34*(4), 1774–1781. https://doi.org/10.1016/j.neuroimage.2006.11.014

Knudsen, E. B., & Wallis, J. D. (2022). Taking stock of value in the orbitofrontal cortex. *Nature Reviews Neuroscience*, *23*(7), 428–438. https://doi.org/10.1038/s41583-022-00589-2

Kotani, Y., Ohgami, Y., Ishiwata, T., Arai, J., Kiryu, S., & Inoue, Y. (2015). Source analysis of stimulus-preceding negativity constrained by functional magnetic resonance imaging. *Biological Psychology*, *111*, 53–64. https://doi.org/10.1016/j.biopsycho.2015.08.005

Kurth, F., Zilles, K., Fox, P. T., Laird, A. R., & Eickhoff, S. B. (2010). A link between the systems: Functional differentiation and integration within the human insula revealed by meta-analysis. *Brain Structure and Function*, *214*(5), 519–534. https://doi.org/10.1007/s00429-010-0255-z

Lamichhane, B., & Dhamala, M. (2015). The salience network and its functional architecture in a perceptual decision: An effective connectivity study. *Brain Connectivity*, *5*(6), 362–370. https://doi.org/10.1089/brain.2014.0282

Li, X., Yang, L., & Yan, X. (2022). An exploratory study of drivers' EEG response during emergent collision avoidance. *Journal of Safety Research*, *82*, 241–250. https://doi.org/10.1016/j.jsr.2022.05.015

Lin, Y.-H., Young, I. M., Conner, A. K., Glenn, C. A., Chakraborty, A. R., Nix, C. E., Bai, M. Y., Dhanaraj, V., Fonseka, R. D., Hormovas, J., Tanglay, O., Briggs, R. G., & Sughrue, M. E. (2020). Anatomy and white matter connections of the inferior temporal gyrus. *World Neurosurgery*, *143*, e656–e666. https://doi.org/10.1016/j.wneu.2020.08.058

Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews*, *35*(5), 1219–1236. https://doi.org/10.1016/j.neubiorev.2010.12.012

Liu, Z., Zhang, M., Xu, G., Huo, C., Tan, Q., Li, Z., & Yuan, Q. (2017). Effective connectivity analysis of the brain network in drivers during actual driving using near-infrared spectroscopy. *Frontiers in Behavioral Neuroscience*, *11*, Article 211. https://doi.org/10.3389/fnbeh.2017.00211

Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Kujovic, M., Palomero-Gallagher, N., Eickhoff, S. B., & Zilles, K. (2016). Cytoarchitecture of the human lateral occipital cortex: Mapping of two extrastriate areas hOc4la and hOc4lp. *Brain Structure and Function*, *221*(4), 1877–1897. https://doi.org/10.1007/s00429-015-1009-8

Megías, A., Cortes, A., Maldonado, A., & Cándido, A. (2017). Using negative emotional feedback to modify risky behavior of young moped riders. *Traffic Injury Prevention*, *18*(4), 351–356. https://doi.org/10.1080/15389588.2016.1205189

Menon, V., & D'Esposito, M. (2022). The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology*, *47*(1), 90–103. https://doi.org/10.1038/s41386-021-01152-w

Mento, G. (2017). The role of the P3 and CNV components in voluntary and automatic temporal orienting: A high spatial-resolution ERP study. *Neuropsychologia*, *107*, 31–40. https://doi.org/10.1016/j.neuropsychologia.2017.10.037

Mento, G., Tarantino, V., Vallesi, A., & Bisiacchi, P. S. (2015). Spatiotemporal neurodynamics underlying internally and externally driven temporal prediction: A high spatial resolution ERP study. *Journal of Cognitive Neuroscience*, *27*(3), 425–439. https://doi.org/10.1162/jocn_a_00715

Mesulam, M.-M. (1998). From sensation to cognition. *Brain*, *121*(6), 1013–1052. https://doi.org/10.1093/brain/121.6.1013

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*(1), 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167

Mossbridge, J. A., Tressoldi, P., Utts, J., Ives, J. A., Radin, D., & Jonas, W. B. (2014). Predicting theunpredictable: Critical analysis and practical implications of predictive anticipatory activity. *Frontiers in Human Neuroscience*, *8*, Article 146. https://doi.org/10.3389/fnhum.2014.00146

Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M., Glahn, D. C., & Carter, C. S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive, Affective, & Behavioral Neuroscience*, *12*(2), 241–268. https://doi.org/10.3758/s13415-011-0083-5

Oba, K., Hamada, K., Tanabe-Ishibashi, A., Murase, F., Hirose, M., Kawashima, R., & Sugiura, M. (2022). Neural correlates predicting lane-keeping and Hazard detection: An fMRI study featuring a pedestrian-rich simulator environment. *Frontiers in Human Neuroscience*, *16*, Article 754379. https://doi.org/10.3389/fnhum.2022.754379

Pascual-Marqui, R. D. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods and Findings in Experimental and Clinical Pharmacology*, *24 Suppl D*, 5–12.

Passingham, R. E., & Lau, H. (2023). Do we understand the prefrontal cortex? *Brain Structure and Function*, *228*(5), 1095–1105. https://doi.org/10.1007/s00429-022-02587-7

Peters, J., & Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, *213*(2), 135–141. https://doi.org/10.1016/j.bbr.2010.04.031

Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, *35*(1), 73–89. https://doi.org/10.1146/annurev-neuro-062111-150525

Pu, W., Luo, Q., Palaniyappan, L., Xue, Z., Yao, S., Feng, J., & Liu, Z. (2016). Failed cooperative, but not competitive, interaction between large-scale brain networks impairs working memory in schizophrenia. *Psychological Medicine*, *46*(6), 1211–1224. https://doi.org/10.1017/S0033291715002755

Radin, D. I., Vieten, C., Michel, L., & Delorme, A. (2011). Electrocortical activity prior to unpredictable stimuli in meditators and nonmeditators. *Explore*, *7*(5), 286–299. https://doi.org/10.1016/j.explore.2011.06.004

Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022a). The effective connectivity of the human hippocampal memory system. *Cerebral Cortex*, *32*(17), 3706–3725. https://doi.org/10.1093/cercor/bhab442

Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022b). The human language effective connectome. *NeuroImage*, *258*, 119352. https://doi.org/10.1016/j.neuroimage.2022.119352

Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2022c). The human posterior parietal cortex: Effective connectome, and its relation to function. *Cerebral Cortex*, *33*, 3142–3170. https://doi.org/10.1093/cercor/bhac266

Rolls, E. T., Deco, G., Huang, C.-C., & Feng, J. (2023). The human orbitofrontal cortex, vmPFC, and anterior cingulate cortex effective connectome: Emotion, memory, and action. *Cerebral Cortex*, *33*(2), 330–356. https://doi.org/10.1093/cercor/bhac070

Schuck, N. W., Cai, M. B., Wilson, R. C., & Niv, Y. (2016). Human orbitofrontal cortex represents a cognitive map of state space. *Neuron*, *91*(6), 1402–1412. https://doi.org/10.1016/j.neuron.2016.08.019

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, *27*(9), 2349–2356. https://doi.org/10.1523/JNEUROSCI.5587-06.2007

Seidel, E.-M., Pfabigan, D. M., Hahn, A., Sladky, R., Grahl, A., Paul, K., Kraus, C., Küblböck, M., Kranz, G. S., Hummer, A., Lanzenberger, R., Windischberger, C., & Lamm, C. (2015). Uncertainty during pain anticipation: The adaptive value of preparatory processes. *Human Brain Mapping*, *36*(2), 744–755. https://doi.org/10.1002/hbm.22661

Seth, A. K. (2010). Measuring autonomy and emergence via granger causality. *Artificial Life*, *16*(2), 179–196. https://doi.org/10.1162/artl.2010.16.2.16204

Spiers, H. J., & Maguire, E. A. (2007). Neural substrates of driving behaviour. *NeuroImage*, *36*(1), 245–255. https://doi.org/10.1016/j.neuroimage.2007.02.032

Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences*, *105*(34), 12569–12574. https://doi.org/10.1073/pnas.0800005105

Srinivasan, L., Asaad, W. F., Ginat, D. T., Gale, J. T., Dougherty, D. D., Williams, Z. M., Sejnowski, T. J., & Eskandar, E. N. (2013). Action initiation in the human dorsal anterior cingulate cortex. *PLoS One*, *8*(2), e55247. https://doi.org/10.1371/journal.pone.0055247

Sun, Y., Brian, A. B. A., Yu, X., & Berilla, J. (2013). The electroencephalographic response during a driving process: Normal driving, turning and collision. In *2013 39th annual northeast bioengineering conference* (pp. 147–148). Institute of Electrical and Electronics Engineers (IEEE). https://doi.org/10.1109/NEBEC.2013.143

Tang, A. C., Sutherland, M. T., & McKinney, C. J. (2005). Validation of SOBI components from high-density EEG. *NeuroImage*, *25*(2), 539–553. https://doi.org/10.1016/j.neuroimage.2004.11.027

Uddin, L. Q., Kelly, A. M., Biswal, B. B., Castellanos, F. X., & Milham, M. P. (2009). Functional connectivity of default mode network components: Correlation, anticorrelation, and causality. *Human Brain Mapping*, *30*(2), 625–637. https://doi.org/10.1002/hbm.20531

Uddin, L. Q., Nomi, J. S., Hébert-Seropian, B., Ghaziri, J., & Boucher, O. (2017). Structure and function of the human insula. *Journal of Clinical Neurophysiology*, *34*(4), 300–306. https://doi.org/10.1097/WNP.0000000000000377

Vorobyev, V., Kwon, M. S., Moe, D., Parkkola, R., & Hämäläinen, H. (2015). Risk-taking behavior in a computerized driving task: Brain activation correlates of decision-making, outcome, and peer influence in male adolescents. *PLoS One*, *10*(6), e0129516. https://doi.org/10.1371/journal.pone.0129516

Vossel, S., Geng, J. J., & Fink, G. R. (2014). Dorsal and ventral attention systems: Distinct neural circuits but collaborative roles. *The Neuroscientist*, *20*(2), 150–159. https://doi.org/10.1177/1073858413494269

Vossel, S., Weidner, R., Driver, J., Friston, K. J., & Fink, G. R. (2012). Deconstructing the architecture of dorsal and ventral attention systems with dynamic causal modeling. *Journal of Neuroscience*, *32*(31), 10637–10648. https://doi.org/10.1523/JNEUROSCI.0414-12.2012

Ware, M., Feng, J., & Nam, C. S. (2020). Neuroergonomics behind the wheel: Neural correlates of driving. In C. S. Nam (Ed.), *Neuroergonomics: Principles and practice* (pp. 353–388). Springer International Publishing. https://doi.org/10.1007/978-3-030-34784-0_18

Wong, C., & Gallate, J. (2012). The function of the anterior temporal lobe: A review of the empirical evidence. *Brain Research*, *1449*, 94–116. https://doi.org/10.1016/j.brainres.2012.02.017

Woolgar, A., Afshar, S., Williams, M. A., & Rich, A. N. (2015). Flexible coding of task rules in Frontoparietal cortex: An adaptive system for flexible cognitive control. *Journal of Cognitive Neuroscience*, *27*(10), 1895–1911. https://doi.org/10.1162/jocn_a_00827

World Health Organization. (2021). *Global plan for the decade of action for road safety 2021-2030*. WHO. https://www.who.int/publications/m/item/global-plan-for-the-decade-of-action-for-road-safety-2021-2030

World Medical Association. (2013). World medical association declaration of Helsinki: Ethical principles for medical research involving human subjects. *JAMA*, *310*(20), 2191–2194. https://doi.org/10.1001/jama.2013.281053

Wu, Y., Sun, D., Wang, Y., Wang, Y., & Wang, Y. (2016). Tracing short connections of the temporo-parieto-occipital region in the human brain using diffusion spectrum imaging and fiber dissection. *Brain Research*, *1646*, 152–159. https://doi.org/10.1016/j.brainres.2016.05.046

Yan, L., Wang, Y., Ding, C., Liu, M., Yan, F., & Guo, K. (2019). Correlation among behavior, personality, and electroencephalography revealed by a simulated driving experiment. *Frontiers in Psychology*, *10*, 1524. https://doi.org/10.3389/fpsyg.2019.01524

Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., & Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125–1165. https://doi.org/10.1152/jn.00338.2011

Yuen, N. H., Tam, F., Churchill, N. W., Schweizer, T. A., & Graham, S. J. (2021). Driving with distraction: Measuring brain activity and oculomotor behavior using fMRI and eye-tracking. *Frontiers in Human Neuroscience*, *15*, Article 659040. https://doi.org/10.3389/fnhum.2021.659040

Zhang, L., Cao, G., Liu, Z., Bai, Y., Li, D., Liu, J., & Yin, H. (2022). The gray matter volume of bilateral inferior temporal gyrus in mediating the association between psychological stress and sleep quality among Chinese college students. *Brain Imaging and Behavior*, *16*(2), 557–564. https://doi.org/10.1007/s11682-021-00524-6

Zhang, X., & Yan, X. (2023). Predicting collision cases at unsignalized intersections using EEG metrics and driving simulator platform. *Accident Analysis & Prevention*, *180*, 106910. https://doi.org/10.1016/j.aap.2022.106910

Zhou, J., Gardner, M. P., & Schoenbaum, G. (2021). Is the core function of orbitofrontal cortex to signal values or make predictions? *Current Opinion in Behavioral Sciences*, *41*, 1–9. https://doi.org/10.1016/j.cobeha.2021.02.011

Zhou, J., Gardner, M. P. H., Stalnaker, T. A., Ramus, S. J., Wikenheiser, A. M., Niv, Y., & Schoenbaum, G. (2019). Rat orbitofrontal ensemble activity contains multiplexed but dissociable representations of value and task structure in an odor sequence task. *Current Biology*, *29*(6), 897–907.e3. https://doi.org/10.1016/j.cub.2019.01.048