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Should I stay or should I go? The cerebral bases of street-crossing decision

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Abstract

An observer willing to cross a street must first estimate if the approaching cars offer enough time to safely complete the task. The brain areas supporting this perception, known as Time-To-Contact (TTC) perception, have been mainly studied through non-invasive correlational approaches. We carried out an experiment in which patients were tested during an awake brain surgery electrostimulation mapping to examine the causal implication of various brain areas in the street-crossing decision process. Forty patients were tested in a gap acceptance task before their surgery to establish a baseline performance. The task was individually adapted upon this baseline level and carried out during their surgery. We acquired and normalized to MNI space the coordinates of the functional areas that influenced task performance. A total of 103 stimulation sites were tested, allowing to establish a large map of the areas involved in the street-crossing decision. Multiple sites were found to impact the gap acceptance decision. A direct implication was however found mostly for sites within the right parietal lobe, while indirect implication was found for sites within the language, motor, or attentional networks. The right parietal lobe can be considered as causally influencing the gap acceptance decision. Other positive sites were all accompanied with dysfunction in other cognitive functions, and therefore should probably not be considered as the site of TTC estimation.

KEYWORDS

awake brain surgery, brain mapping, direct electrostimulation, street-crossing decision, time-to-contact estimation

1 | INTRODUCTION

Humans frequently interact with moving objects in their environment. Among these interactions, one crucial action is our ability to

safely cross a street. In such a situation, an observer has to accept or reject a gap between oncoming vehicles for crossing. In other words, the observer first has to estimate how long an oncoming vehicle will take to reach his path, to decide whether or not he has

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enough time to safely cross the street. Such an estimation is also known in the literature as time-to-contact (TTC) perception. It has been demonstrated that TTC perception can be accurately achieved under specific constraints like uniform velocity by relying principally on the inverse relative expansion rate of the object's image on the retina ("tau") or its derivative ("tau-margin") (Lee, 1976). In addition, previous research suggests that several factors influence street-crossing decisions in pedestrian or driver situations, including the observer's age, the approaching vehicle's speed or distance (Lobjois & Cavallo, 2007), the relative size of the object (the size-arrival effect, DeLucia and Warren (1994)), and the density of vehicles (Baurès et al., 2014).

To our knowledge, the cerebral bases supporting the street-crossing decision have never been investigated in a street-crossing task per se. However, street-crossing tasks are very similar to other tasks used to investigate TTC perception. In coincident timing (CT) or prediction motion (PM) protocols, an observer has to press a button to indicate the arrival time of a moving object at a specific place, while the target remains visible (CT protocol) or after the target is occluded (PM, see Battaglini and Ghiani (2021), and Teichmann et al. (2021) for recent reviews). All tasks, street-crossing, CT and PM, have been shown to rely on the same visual information, with tau, velocity and distance being the main cues used by the observers (e.g., Yan et al. (2011), Lobjois and Cavallo (2007), Benguigui et al. (2008)). We can therefore hypothesize from CT and PM protocols the areas which could be involved in street-crossing scenarios. Using CT or PM protocols, it has been shown that TTC perception involves activations in area V1 (Coull et al., 2008) and in the MT/V5+ complex (Bosco et al., 2008; Delle Monache et al., 2017; Dessing et al., 2013; Schenk et al., 2005). Depending on the task demands (e.g., manually intercepting the object) and context (e.g., implied gravity acceleration), activations have also been documented in the superior parieto-occipital cortex (Dessing et al., 2013), temporoparietal junction, and in the insula (Delle Monache et al., 2017; Indovina et al., 2005). Interestingly, it has been shown that when the object approaches the observer directly, primary sensorimotor areas, the inferior parietal lobule, the ventral premotor cortex, and the supplementary motor area (SMA) are engaged (Coull et al., 2008; Field & Wann, 2005) as well as the anterior insula (Billington et al., 2011).

Recently, we performed a PM task while participants were undergoing an awake brain surgery (Baurès et al., 2021). In the task, the participants saw a ball moving toward them in a corridor. The ball disappeared at a variable TTC, and the participants had to press a key to indicate the estimated arrival time. That task was done during a control condition to estimate the baseline performance of each participant. Then, a subset of the task was done during the awake brain surgery, while the neurosurgeon stimulated, hence transiently de-activated, various areas. Our results showed a partial agreement with previous studies using fMRI (Billington et al., 2011; Coull et al., 2008; Field & Wann, 2005). On the one hand, we found a direct implication of the right intraparietal sulcus (IPS) for short occlusion times. Stimulations in the right frontal cortex were accompanied by a deficit in TTC estimation (as compared with a control condition),

Significance

When a car approaches a pedestrian, it is of crucial importance for him to determine if he can safely cross the street. What are the brain areas engaged in that decision? We tested patients suffering from brain tumors during their surgery during which we deactivated various brain areas and compared their performance to a baseline condition. Here we demonstrate that a region in the parietal area is causally engaged in the street-crossing decision, possibly by affecting the arrival time estimation of the car. Incidentally, we also report that deactivating language areas in the left hemisphere also interfered with the decision process.

but also with involuntary hand or eye movements. As such, these areas may not be directly involved in the TTC estimation per se, but may be more likely to play a role in the motor preparation or execution following the estimation. Finally, we found that stimulating language areas in the left temporal cortex also impaired TTC estimations. We hypothesized that the TTC and language networks share a common attentional component located downstream of the initial TTC processing. This partial disagreement also argues for the use of various neuroimaging methods in investigating the cerebral bases of cognitive processes, as the possibilities and limits of MRI or DES does not overlap (Vaidya et al., 2019).

It is, however, important to notice that in addition to the TTC estimation per se, numerous processes take place in the PM protocol we used. In the first place, the participants must cope with an occlusion of the object. As such, the observer needs to both extract from the visual cues the object's TTC and mentally process the occlusion time (Bosco et al., 2015; Makin, 2018). In addition, as the object looms toward the observer, it will eventually enter into his peripersonal space (PPS). The frontal and parietal areas have been demonstrated to be involved in all these processes (Assmus et al., 2003; Harrison et al., 2010). Consequently, more work is required to determine if the IPS is involved in the TTC perception per se or in an auxiliary process (as motion extrapolation, that is, mentally representing the position or TTC of the occluded object, PPS construction, visuospatial attention) supporting the TTC estimation. This is in line with (Kurashige et al., 2019), who demonstrated that different cognitive processes may require the same neural substrates (as could, for example, do motion extrapolation and TTC estimation), and inversely, hidden relationships among cognitive functions may appear from brain imaging studies (as we demonstrated by the interference between language disruption and TTC estimation).

We therefore decided to extend our study with a street-crossing task in which the incoming vehicle would remain visible for its entire trajectory in both pre- and per-surgery conditions (i.e., respectively, the day before the patient's surgery and during the patient's surgery). We aimed to compare the current results with the results

obtained in Baurès et al. (2021). While the approaching car would not disappear nor approach directly toward the observer, the current experiment should be able to disentangle the exact role of the brain areas tested, that is, to demonstrate if they were implicated in the TTC estimation process or in an auxiliary process only.

2 | METHODS

2.1 | Patients

Language and TTC functions were mapped by electrostimulation using an awake brain mapping technique in the left and right hemisphere of 40 patients (mean \pm SD age: 51.80 ± 14.22 years old, range 22 to 74 years old, 13 females) suffering from a brain tumor in various (non-occipital) brain areas (See Table S1 for details). Patients were identified for inclusion in the study by the neurosurgeon during his pre-surgery visit. Basic clinical data and neurological examinations were performed by the neurosurgeons and oncologists caring for the patients. For all patients, complete preoperative assessments by a speech therapist and a physical therapist were performed before the surgery to confirm that their language and motor functions were normal. In addition, more detailed tests were conducted preoperatively by the resident neuropsychologist in the department. All patients performed a MMSE test before the first experimental session (mean score = 28.52, SD = 1.59, minimal score = 25), indicating functional cognitive behavior. Neglect was evaluated with a French battery test called the Batterie d'Evaluation Negligence (Rousseaux et al., 2001; Roux et al., 2011). This consisted of a bell cancellation test, scene copying, clock drawing, two line bisection tasks, identification of overlapping figures, text reading, writing, and a representational task based on a map of France, also investigating the difference between performance in the right and left hemispaces. Four patients were unable to perform the task accurately in the pre-surgery condition and their results were therefore not analyzed.

2.2 | Exclusion criteria

Criteria for exclusion were as follows: patients under 18 years of age, patients with preoperative spatial neglect, complete hemianopsia or quadrantanopsia, dysphasic patients, and more generally, patients unable to understand the TTC tasks. Overall, 11 patients were excluded for this study.

2.3 | Protocol design in the pre-surgery condition

The visual stimulus for the street-crossing task was presented on a Dell computer equipped with a 1.6GHz i7 processor and a 13.3-in. screen (resolution 1366×768 , dimension 29.5×17 cm in horizontal by vertical), using E-Prime 3. The videos were created with Unity and consisted of an urban street (see Figure 1). A pedestrian was set



FIGURE 1 Screenshot of the video stimuli, with the car approaching the pedestrian crossing lane.

at the edge of the sidewalk, head turned left to observe any oncoming vehicle. The road was 3 m wide. A measuring tape was initially presented to the participants so they would have a better representation of the distance needed to cross the street. They were also required to walk along the tape, at their normal pace, and their time to travel the distance was registered. This was done to help the participants to better apprehend the scale of the scene, since it is well known that distances are prone to misestimation in virtual reality (e.g., Kelly (2022)). On each video, a single car moving on a road approached the participant. The car had a width of 1.77 m and height of 1.41 m, was moving with a constant velocity of 30 or 50 km/h, and was presenting an initial TTC of 2, 3, 4, 5, or 6 s. The initial position was therefore varied as a function of the initial TTC and velocity (see Table S2 for details on the car's parameters). The participants were instructed to "press the button to indicate if you feel you could safely cross the street". In the pre-surgery condition, three demo trials (randomly chosen) were performed, and finally, 150 trials (resulting from 5 different TTC and 2 velocities being presented 15 times in random order) split into three sessions. The total duration of the experiment was about 15 min. The participants had to answer using the same (ipsilesional) hand in all the conditions.

2.4 | Protocol design in the per-surgery condition

Following the pre-surgery test, we fit a psychometric function using the "quickpsy" R package (Linares & López-Moliner, 2016) to fit the gap acceptance as a function of initial TTC and velocity. For each velocity, we extracted from the model the initial TTCs leading to a 10% and 90% positive decision, for each velocity. The choice for 10% and 90% levels was made to create rather easy gap-decisions, which should be highly refused or highly accepted. From the plots, we selected the velocity which was best fit by the model, and used this velocity only in the per-surgery condition. New videos were generated so the car would now have this exact initial TTC and velocity. On average, the short gap (i.e., leading to 10% of positive decision) had a value of 2.65 s (sd = .74 s), while the long (i.e., leading to 90% of positive decision) gap had a value of 4.55 s (sd = .96 s).

During the surgery, the computer screen was positioned in front of the participant laying on his surgery bed, held by an experimenter. The screen was visible with both eyes of the patients, and any surgery-related material that could obstruct the point of view was temporarily moved away. The participant was presented one of the two videos, and was requested to do the exact same task, that is, "press the button to indicate if you feel you could safely cross the street". Each initial TTC (i.e., short TTC leading to a 10% acceptance and the long TTC leading to a 90% acceptance) was presented 4 times per stimulated area (leading therefore to 8 trials per area). For each trial, the neurosurgeon applied the stimulation on the selected area, and an experimenter started the trial 3 s after the stimulation. A break of approximately 15 s was made in-between two consecutive trials. To give their answer, the participants used a joystick held in the same hand as used during the pre-surgery test, to avoid any confound with their laterality. It has to be acknowledged that the position in the pre-surgery test (sitting on a chair) differed from the position during the per-surgery test (laying on the surgery bed). It is known that visual TTC perception may also depend on vestibular signals (Baures & Hecht, 2011; Senot et al., 2005). However, in the case of incongruent visual and vestibular information (e.g., laying on the back but seeing a stimulus from a standing perspective), it has been repeatedly shown that the visual cues overrule the vestibular information (Baures & Hecht, 2011; Indovina et al., 2005; Senot et al., 2005).

2.5 | Protocol for awake brain mapping

Our awake brain mapping protocol was based on 25 years' experience (Roux et al., 2017). The scalp was anesthetized locally with Lidocaine (1%) and initial sedation with spontaneous respiration was provided by continuous infusion of Propofol ($1\text{--}3\text{ mg kg}^{-1}\text{ h}^{-1}$). Fentanyl ($1\text{--}3\text{ }\mu\text{g kg}^{-1}\text{ h}^{-1}$) or Remifentanyl ($.01\text{--}.25\text{ }\mu\text{g kg}^{-1}\text{ h}^{-1}$) was used for analgesia. Propofol infusion was stopped during the dural opening (about 10 min before brain mapping) and the patient was fully awakened. The cortex was stimulated at 8 mA for all the patients before any surgical approach using a C2 Xplore device (Inomed) connected to a bipolar electrode (1 mm electrodes) with biphasic square wave pulses of 1 ms duration and 50 Hz trains. Intensity of stimulation was chosen based on our previous works on the topic (Roux et al., 2017). Stimulation was applied 3 s before each trial of the street-crossing task. The maximum train duration of each stimulation was 5 s. Stimulation is supposed to deactivate a very small cortical area of around 25 mm^2 (Haglund et al., 1993; Roux et al., 2017).

Participants were first tested in one or more of three different tasks, depending on the tumor localization. The first task was a language task in which patients had to name an object presented on a paper (Roux et al., 2017). The second task was a sensorimotor task, in which the participants were either instructed to stay still, and the stimulation could trigger involuntary hand, leg, or eye movements. Alternatively, a motor interruption task could be performed, in which the participants were required to make a cyclic movement of their hand (as opening and closing their fingers, or moving the

hand up and down) at a preferential rhythm, and the stimulation was interrupting their movement (Shinoura et al., 2013). Finally, the third possible task was a line bisection task to assess their visuospatial attention performance (Roux et al., 2011). After this first set of task(s), some cortical areas already tested (whether they were positive or negative to those tasks) were tested again but now when performing the street-crossing task. Thus, these areas can be positive or negative for language, motor, neglect or TTC tasks, or positive for only one task. Because of clinical constraints, only one to eight cortical areas (numbered from A to H) were tested again to evaluate their implication in street-crossing decision. The number of sites was decided by the neurosurgeon, based on the size of the craniotomy and to comply with the medical constraints.

2.6 | Postoperative data analysis

Each patient's positive stimulation sites were positioned on the left or right 3D cortical surface reconstructions of one of the individual brains (case 12) constituting the PALS (population-average, landmark- and surface-based) atlas (Van Essen, 2005) provided in the Caret software (Van Essen et al., 2001) and normalized in the MNI space. We obtained coordinates of stimulation site locations that were per-operatively visualized and positioned on original 3D images provided by the neuronavigation software (Brain Lab). For each positive site, MNI space coordinates (X, Y, Z) were obtained and stored in an Excel database, with intraoperative photographs and detailed accounts of the evoked responses (see Table S1 for the coordinates and effect on the street-crossing task and possible interference on another task).

2.7 | Statistical analysis

By contrast with standard experiments, no analysis can be performed to compare at the group level the influence of the stimulation. Indeed, our patient presented a great heterogeneity in their profile (in particular tumor location, size, and duration) and consequently, they were not stimulated in the same areas. It therefore was not possible to perform group analysis (e.g., ANOVAs to determine the influence of the stimulation), while the stimulation differs in localization. We adopted a different strategy, in which each patient served as his own control. We therefore compared, at the patient individual level, the results of the pre-surgery condition (baseline performance) to his per-surgery condition. For this reason, if age is known to affect a pedestrian's crossing decision (Lobjois & Cavallo, 2007), it cannot explain the variation of the street-crossing decision of a single participant from the pre-surgery to the per-surgery condition. Note however that this method assumes that the pre-surgery performance of a participant is stable over the time, that is, no practice effects or perceptual learning occurs. This was controlled by performing test-retest measurements in a control population, as presented in Supplementary Results S1.

To decide whether or not a stimulation on a given area would indicate an inability to correctly perform the task, and therefore indicate the causal role of the area in the street-crossing task, we computed the probability to accept k times an initial TTC over four repetitions, given that the initial TTC led to a 10% or 90% acceptance during the pre-surgery condition. The binomial probability is given by this equation:

$$P(X = k) = \binom{n}{k} p^k (1-p)^{n-k}$$

In which

$$\binom{n}{k} = \frac{n!}{k!(n-k)!}$$

For example, for a 10% acceptance probability, the probability p to accept a gap $k=0$ time over the 4 repetitions is $p = .656$, $p = .292$ when $k=1$, $p = .049$ when $k=2$, $p = .004$ when $k=3$, and $p = .0001$ when $k=4$. As the gap is very short, its refusal should be the rule, and a too high number of acceptance suspicious. As such, we considered that accepting the short TTC two times or more was so unlikely that this would demonstrate the implication of the deactivated area in the street-crossing decision. For the long TTC, the threshold was accepting twice or less to cross the street to conclude for involvement of the area in the decision.

This method led us to define three potential outcomes: the area was identified as (1) non-engaged in the street-crossing decision if the observer mostly refused the short TTC or accepted the long TTC. In this case, the stimulation is considered as negative, that is, not influencing the street-crossing decision. Alternatively, if the observer accepted too often the short gap or refused too often the long gap, the area was considered as involved in the task and the stimulation positive. In this latter condition, the area was identified (2) as "street-crossing specific site" if neither language (as tested by a naming task), motor or visuospatial attention interferences were found in this area. We could not exclude, however, that this area defined as "specific" may lead to stimulation interferences for other functions not tested in this study. Alternatively, if the stimulation also led to language, motor, or visuospatial attention interferences, we qualified the area (3) as "street-crossing nonspecific site" indicating that the street-crossing decision was not the only function impaired by the stimulation.

3 | RESULTS

3.1 | Pre-surgery data

Figure 2 presents the averaged pre-surgery results of the 40 participants that correctly performed the test. In agreement with the previous literature (Baures et al., 2014; Petzoldt, 2014), the participants were more likely to accept a gap when the incoming vehicle

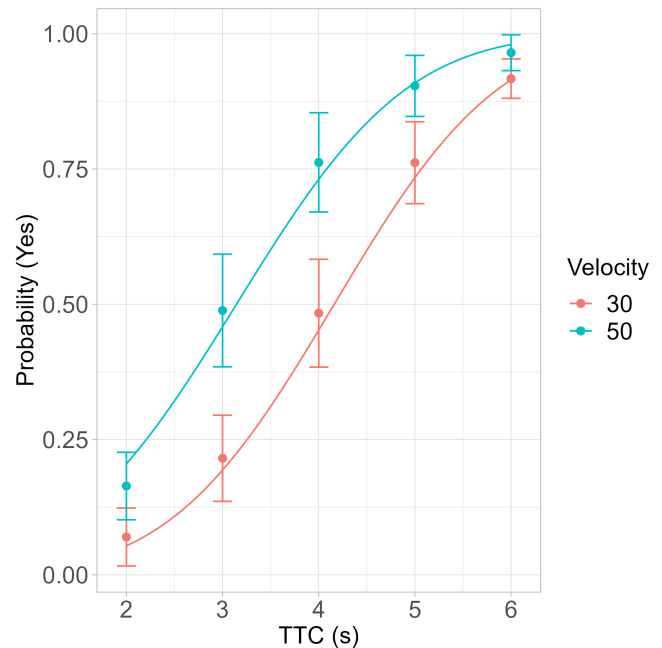


FIGURE 2 Average results of the 40 participants in the pre-surgery condition. The figure displays the probability of accepting to cross the street as a function of the car's time to contact (TTC, s) and velocity (km/h). The points represent the average probability, the error bars the 95% confidence interval of the mean and the curves of the psychometric model.

presented a greater TTC. However, the participants also exhibited a different probability to accept a given gap for the two velocities. For example, the mean accepted gaps at a probability of 50% were 4.16 and 3.12 s for the 30 and 50 km/h conditions, respectively. This agrees with many studies showing that non-temporal cues might play a role in the decision, as the car's distance or optical size (Lobjois & Cavallo, 2007; Petzoldt, 2014, 2016; Petzoldt et al., 2017). It is generally found that participants accept a shorter gap when a car moves at a higher velocity, presumably because its distance to the participant is greater and/or its optical size is smaller (compared to a slowly moving car with the same TTC). It is important to notice that this velocity effect does not disappear with the psychometric function linking the car's distance to the acceptance probability. For a given distance, the participants are more likely to cross the street for the slower (hence at a greater TTC) than for the faster (hence with a shorter TTC) car. It can be hypothesized that the task probably relies on a combination of temporal and non-temporal cues, and not purely and separately TTC specifying or distance optical cues.

The analysis of the response time (RT) of the participants indicated that participants took a shorter time (mean RT = 1.031 s) for the shortest gap value (2 s) compared to all the other conditions (mean RT = 1.228 s), without any difference among these gap values, once applied the Bonferroni correction for multiple comparisons. Participants also answered faster for positive (mean = 1.130 s) rather than negative (mean = 1.268 s) decisions. Finally, the car's velocity did not influence the RT of the decision.

3.2 | Intraoperative data

A total of 103 cortical sites were stimulated, and each was eventually classified as (1) non-engaged, (2) street-crossing specific, or (3) street-crossing nonspecific. Figure 3 displays these points (see Table S1 for the stimulation coordinates). First, in white are shown the 55 points that did not lead to a perturbation in the street-crossing decision, that is, for which the street-crossing rate does not differ from the pre-surgery session (note, however, that some of the white points may have induced errors in the other tasks). On the other hand, 48 points were considered as positive, that is, for which the street-crossing decision differs from the pre-surgery session. Among these 48 positive sites, 22 red points represent stimulation areas that led to a perturbation in the street-crossing decision only (street-crossing specific areas). The points in orange ($N=15$), green ($N=7$), or purple ($N=4$) represent stimulation sites that led to a perturbation in the street-crossing decision in addition to language issues (orange), eye movement perturbations or somatosensory sensations (green), or spatial attention issue (purple). For this reason, these last areas were defined as nonspecific street-crossing sites.

We can distinguish three different patterns in the results. First, in the right hemisphere, regions around the intraparietal sulcus (IPS) and superior to inferior frontal lobe were found to be causally engaged in the street-crossing decision. When stimulated in these regions, the participants are transiently unable to perform the task as they did in the pre-surgery condition, with either unsafe decisions (short gap accepted too often) or ineffective decisions (large gap refused too often). In the same region, a couple of nonspecific sites were also found: for four of the participants, eye or hand movements were also found when stimulating the superior frontal lobe, or the stimulation within the parietal lobe triggered somesthetic sensations.

We also found that de-activating language by stimulating areas in the superior or supramarginal temporal gyri or in the frontal median gyrus of the left hemisphere interfered with the ability to make a street-crossing decision. This also happened for one left-handed participant, who therefore had his language areas in the right hemisphere.

Finally, we also found specific (red) and nonspecific (purple) sites in a region around the inferior frontal gyrus and in the inferior temporal gyrus of the right hemisphere. Stimulating these sites also sometimes induced a rightward deviation in the line bisection task, indicating an impairment in spatial awareness. Eventually, some stimulation sites were found as not involved in the TTC task (white points) were very close to positive points, even for a same patient (e.g., participants 5, 14, or 19).

Importantly, if 11 patients were stimulated in one site only, 29 patients were stimulated in more than one site, and 13 had both negative and positive sites. This led us to define the concept of positive-negative site pair, that is, two stimulation sites for a same participant, one leading to a positive response and one leading to a negative response in the street-crossing decision. There were 30 positive-negative site pairs. We computed the distance between the sites forming each positive-negative pair. On average, the distance was 14.6mm, the minimal distance was 5.7 mm, and the median distance was 9.5mm. We also found out that 16 pairs of positive-negative points were distant of <10mm, indicating that sub-centimeter cortical territories, fragmented within the lobes, are involved in the task. This is particularly true within the right parietal lobe, for which six over the nine positive-negative pairs were closer than 10mm, demonstrating that these sites engaged in the TTC estimation are parceled within the lobe instead as forming a single and larger region. It is important to note that the stimulation is supposed to deactivate a cortical area of around 25mm² (Haglund et al., 1993;

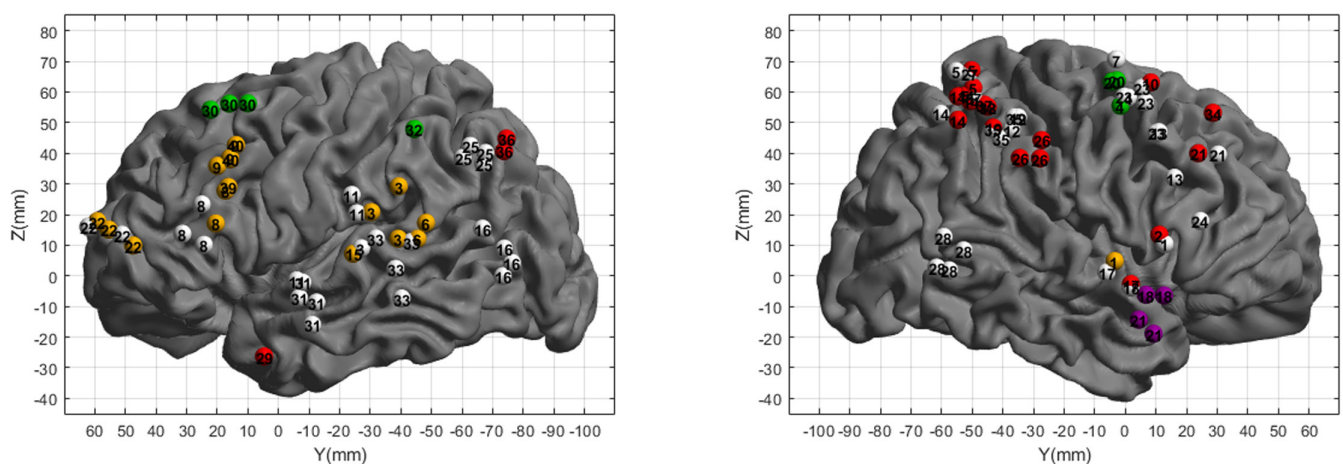


FIGURE 3 Localization of the stimulated sites on the left and right hemispheres (acquired MNI coordinates). The red points represent stimulation sites for which the participants are transiently unable to perform the task as they did in the pre-surgery condition, with either unsafe decisions (short gap accepted too often) or ineffective decisions (large gap refused too often). Points in green, orange or purple points represent nonspecific sites: eye, hand movements or somesthetic sensations (green points), language (orange points), or spatial awareness (purple points) was impaired in addition to the street-crossing decision. White points represent cortical areas not involved in the TTC task but that could lead to errors in the other tasks. Note that one left-handed patient (patient 1) had both language and street-crossing decision impairments when the right superior temporal gyrus was stimulated.

Roux et al., 2017), that is, a circle of a radius of 2.82 mm approximately. It appears therefore that two points in a positive-negative pair were never close enough to be co-stimulated at the same time, which could perturb the interpretation of the output. It is also important to have in mind that the stimulation intensity was set to have just enough strength to evoke local perturbation while avoiding after-discharge spreading (Roux et al., 2017).

4 | DISCUSSION

What are the brain regions causally engaged in a street-crossing decision when an observer needs to estimate the TTC of an approaching vehicle and decide whether or not it is safe to start his movement? We investigated this question during a brain awake surgery during which various brain areas were stimulated and compared the results with a pre-surgery condition.

The results showed that the right intraparietal sulcus was causally involved in the street-crossing decision. The current results generalize to a different and more ecological street-crossing task the findings of our previous work in which the object disappeared during its approach (Prediction Motion task). It is important to compare what the prediction motion and street-crossing tasks share in common, and what differentiate the two, to better understand the current results. The PM task, as stated in Baurès et al. (2017), first requires the sensory registration of the TTC-relevant optical variables, from which is then elaborated to get the absolute TTC estimate. Then, during the occlusion time, the observer needs to “fill the gap” (Bosco et al., 2015), that is, elaborate a mental extrapolation of the object's trajectory or TTC. Finally, the observers need to time their motor response to coincide with the estimated TTC and execute the movement when deemed appropriate. The street-crossing decision also implies the TTC sensory-registration and elaboration stages. Thus, the two tasks differ: the observer has to compare the absolute TTC estimation with his estimated crossing time (and a safety margin), to eventually press the button to indicate his ability to cross or not the street.

The similarity of the results in the two experiments, Baurès et al. (2021) and the current one, argues that the right parietal lobe would be involved in the common processes that share the two tasks. This would indicate that regions within and around the right intraparietal sulcus play a role in the TTC or distance estimation (Billington et al., 2011; Coull et al., 2008; de Azevedo Neto & Amaro Júnior, 2018; Field & Wann, 2005) and/or more generally in the visuospatial attention devoted to the vehicle (Astafiev et al., 2003; Bisley et al., 2011; Harrison et al., 2010; Jahn et al., 2012). This is in agreement with findings showing that patients with lesions or transient deactivation of these areas could suffer from visuospatial neglect (Committeri et al., 2007; Gillebert et al., 2011; Roux et al., 2011; Vallar et al., 2014) and degraded ability to avoid collisions with static or moving objects (Aravind et al., 2015). It could therefore be hypothesized that our participants, when stimulated in the right parietal lobe, would not have been able to take into consideration the

approaching car, or its TTC and/or distance parameters to the point of taking a safe street-crossing decision. All these hypotheses attribute to the parietal a purely perceptual role. It is, however, possible that the parietal would have a broader role. It has indeed been suggested that the parietal cortex accumulates sensory evidences for decision-making (e.g., Zhang et al. (2022)) and would therefore be not only engaged in the perceptual processing of the scene, but more globally in sensorimotor decisions that engage whole body responses as crossing a street.

However, it does not imply that the right parietal lobe around the intraparietal sulcus would be the unique brain area implied in the street-crossing decision. As shows Figure 3, many regions of the brain were not stimulated. For obvious ethical reasons, the participants could only be stimulated in the operative area and the size of the craniotomy was restricted to the medical interest only. Therefore, nothing can be told about these regions. It does not imply either that the right parietal lobe around the intraparietal sulcus is exclusively devoted to the TTC perception or the street-crossing decision. Again, for ethical and medical reasons, a limited number of additional tests were performed during the surgery. It is therefore plausible that this region may have been positive in another cognitive test, would we have performed this test.

It is important to note that within the right parietal lobe, some stimulation sites very close to positive points were not found to be involved in the street-crossing decision (white points). We found a piecemeal of positive sites, and not a large and uniform implication. This indicates that only sub-centimeter cortical territories, fragmented within the lobe, are involved in the task, instead of a large and well-defined region. Interestingly however, the lateralization of the process appears debated in the literature, which has either suggested a bilateral implication of the parietal area (Billington et al., 2011), a left implication (Assmus et al., 2003; Coull et al., 2008; Field & Wann, 2005) or a right implication (Baurès et al., 2021; O'Reilly et al., 2008). Our work goes with these latter articles, as it appears that we found direct implication in the right parietal area.

The current results also confirm our previous observation that disruptions to language affect the TTC judgment, or in the current case, the street-crossing decision. These nonspecific interferences were found in the left hemisphere (with the exception of one left-handed participant), within the frontal or temporal lobes. Electrostimulation of language areas can cause either a global behavior arrest or interfere more specifically with attention and short-term memory while the participants are engaged in automatic tasks (Ojemann et al., 1989). Language mapping with language comprehension tasks (Roux et al., 2015) showed the patients are not conscious of their language interferences induced by electrostimulation in the late stages of language comprehension. It is therefore plausible that the participants are simply unable to perform any cognitive task when language is transiently interrupted. Alternatively, it could be hypothesized that the elaboration of the street-crossing decision shares a common attentional component with the language network of the left hemisphere and located downstream of the initial decision

processing. Also congruent with our previous results, triggering eye movements impairs the ability to make a correct street-crossing decision. It is not surprising as eye movements have been previously found as involved in the accuracy of the TTC estimation (Bennett et al., 2010; Sudkamp et al., 2021).

In addition, we also found street-crossing nonspecific sites located within the inferior frontal gyrus and in the inferior temporal gyrus of the right hemisphere. Some of these sites were also found to impair the spatial awareness of the participants, as in previous research (Bartolomeo, 2006; Roux et al., 2011), inducing rightward deviation in a line bisection task. It is therefore hypothesized that the participants could not allocate their visuospatial attention to the left of the scene, from which the car approached. The ability to estimate the car's TTC and make a safe street-crossing decision would therefore not be impaired per se.

Finally, three sites were classified as specific, in the left (participant 29) or right (participants 2 and 17) temporal area or in the right inferior frontal gyrus. These three points are hard to interpret and not in line with the global results. A possible interpretation would be that these points are false positives. As claimed by Papagno (2017), patients may suffer from attention dropout, or stimulation could propagate along subcortical fibers producing effects in remote linked areas. More participants stimulated in these areas are required to confirm the specific nature of these areas.

Our work does not go without limits, however. As mentioned, the right parietal lobe is known to be implied in many cognitive functions particularly relevant for the task, as motion extrapolation, PPS construction, visuospatial attention. It would be necessary to carry out very specific control tasks to determine if the street-crossing decision itself is impaired, or one (or several) of its underlying sub-processes. While that work would be particularly important and relevant, the clinical constraints did not allow us to run multiple tests during the patients' surgeries.

To conclude, the current study provides new results confirming that street-crossing decision is specifically supported in a piecemeal of sub-centimeter territories within the right parietal lobe. These results suggest that this area leads participants to anticipate the object's arrival, congruently with a purpose of this network being to prepare the observer for an incoming collision and to protect themselves or move away from the object's path. Alternatively, it can be wondered if this network is specific to TTC perception or engaged in more general tasks requiring attention orientation (Gillebert et al., 2011; Rosen et al., 2015) or location information encoding (Harrison et al., 2010). More work is required to disentangle between these hypotheses.

DECLARATION OF TRANSPARENCY

The authors, reviewers, and editors affirm that in accordance with the policies set by the *Journal of Neuroscience Research*, this manuscript presents an accurate and transparent account of the study being reported and that all critical details describing the methods and results are present.

AUTHOR CONTRIBUTIONS

Robin Baurès: Supervision, Conceptualization, Methodology, Software, Data curation, Writing, and Original draft preparation. Solène Leblond: Investigation, Data curation, Writing, Reviewing, and Editing. Andrea Dewailly: Investigation. Marta Cherubini: Investigation. Lakshmi Devi Subramanian: Software. Joseph K. Kearney: Software, Writing, Reviewing, and Editing. Jean Baptiste Durand: Visualization, Writing, Reviewing, and Editing. Franck Emmanuel Roux: Supervision, Investigation, Writing, Reviewing, and Editing.

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CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/jnr.25279>.

DATA AVAILABILITY STATEMENT

The program and data that support the findings of this study are available on this link: https://osf.io/kv52t/?view_only=8b02b81622f3482da709606a1bb921a3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary Results.

Table S1.

Table S2.

Transparent Science Questionnaire for Authors

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