RESEARCH ARTICLE

Does the insula contribute to emotion-related distortion of time? A neuropsychological approach

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Abstract

The literature points to a large distributed brain network involved in the estimation of time. Among these regions, the role of the insular cortex is still poorly understood. At the confluence of emotional, interoceptive, and environmental signals, this brain structure has been proposed to underlie awareness of the passage of time and emotion related time dilation. Yet, this assumption has not been tested so far. This study aimed at exploring how a lesion of the insula affects subjective duration, either in an emotional context or in a non-emotional context. Twenty-one patients with a stroke affecting the insula, either left or right, were studied for their perception of sub and supra second durations. A verbal estimation task and a temporal bisection task were used with either pure tones or neutral and emotional sounds lasting between 300 and 1500 ms and presented monaurally. Results revealed that patients with a right insular lesion, showed less temporal sensitivity than both control participants and patients with a left insular lesion. Unexpectedly, emotional effects were similar in patients and control participants. Altogether, these results suggest a specific role of the right insula in the discrimination of durations, but not in emotion related temporal distortion. In addition, an ear $\times$ emotion interaction in control participants suggests that temporal processing of positive and negative sounds may be lateralized in the brain.

KEYWORDS

emotion, insula, time estimation

1 | INTRODUCTION

Time perception is crucial to our way of experiencing the world and the generation of appropriate behaviors. It underlies most of—if not all—our daily activities, cognitive processes, and social abilities. Despite the major importance of the subjective passage of time in experience and cognition, its neural underpinnings remain unclear. Functional magnetic resonance imaging (fMRI) studies have reported that estimating sub-second to second durations involves a large distributed network, mostly right-lateralized, including the supplementary motor area (SMA), the basal ganglia, the cerebellum, the dorsolateral prefrontal cortex (PFC), the anterior cingulate cortex (ACC), the right parietal cortex, and the insular cortex (Harrington, Haaland, & Knight, 1998; Merchant, Harrington, & Meck, 2013; Pouthas et al., 2005). Prefrontal and parietal areas have been associated to memory and attention processes involved in time perception (Ferrandez et al.,

2003), the cerebellum to event timing and temporal prediction (Ivry & Schlerf, 2008) and the basal ganglia and SMA are thought to underlie core timing processes (Ferrandez et al., 2003; Grondin, 2010; Merchant et al., 2013). The role of insula in time processing is less understood and has so far been neglected in time perception models (see, however, Wittmann, 2013). The present study aims at elucidating the role of the insula in time estimation mechanisms, by exploring how a lesion of insula affects time perception.

1.1 | Insula and time perception

Previous studies report a specific role of the insula in the experience of duration. Using a temporal discrimination task, Lewis and Miall (2003) observed an activation of the anterior insula both in sub-second and supra-second duration estimation. Trying to isolate the brain structures specifically involved in time perception, Nenadic et al. (2003) compared

brain activations during a duration discrimination task versus a frequency discrimination task, and reported specific activation of the insular cortex as well as of the ventrolateral PFC and the putamen. Similarly, Livesey, Wall, and Smith (2007) compared brain activations of color versus duration discrimination of the same stimuli. They observed a specific activation of the insula in the timing condition, suggesting a genuine role of this structure in time processing.

1.2 | Time perception and interoception

In a model attempting to take into account the subjective nature of time perception, Craig (2009a) proposed that the insular cortex mediates the relation between immediate self-perception and the notion of time. This brain structure has been shown to be specifically involved in the integration of emotional and interoceptive states of the body, which is thought to underlie immediate self-awareness (Craig, 2002, 2009b; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004). According to this model, the subjective passage of time would result from a cinematic view of the immediate self that would rely upon activity in the insula. Following this idea, some authors proposed that the right insula constitutes the neural underpinning for subjective distortion of time, by accumulating information about physiological changes in the body (Schirmer, 2011; Wittmann, Simmons, Aron, & Paulus, 2010). Consistent with this, there are several reports in the literature of a link between interoceptive awareness and subjective duration (Di Lerna et al., 2018; Meissner & Wittmann, 2011; Wittmann et al., 2014). For example, both mindfulness and cardiac awareness have been positively related to accuracy in time estimation (Meissner & Wittmann, 2011; Wittmann et al., 2014). In addition, shorter subjective durations were observed in individuals less sensitive to bodily information (Di Lerna et al., 2018).

1.3 | Time perception, interoception, and emotion

This interrelation between interoceptive awareness and subjective duration may explain temporal distortions observed in salient situations, such as when experiencing emotions (Craig, 2009a; Schirmer, 2011). Thus, relevant internal or external stimuli would make interoceptive states more salient and change inner passage of time. Studies investigating how emotion influences time perception mostly report an overestimation of emotional stimuli durations by comparison to neutral stimuli durations, especially concerning highly arousing stimuli (Droit-Volet & Meck, 2007; Mella, Conty, & Pouthas, 2011; Noulhiane, Mella, Samson, Ragot, & Pouthas, 2007; Tipples, 2008). Pollatos, Laubrock, and Wittmann (2014) investigated the relationships between interoception, emotion, and time perception. The authors reported that attention to interoceptive states increased the emotion-related temporal distortion. Interestingly, errors in temporal processing of threatening stimuli have been associated with activation of the right insula, together with the putamen and the right amygdala (Dirnberger et al., 2012). More recently, Pfeuty, Dilharreguy, Gerlier, and Allard (2015) showed that the estimation of both emotional and neutral pictures duration involved activation of the right insular cortex, together with other regions classically involved in time perception, but they reported a specific activation of the right inferior frontal

cortex related to the subjective lengthening of negative pictures duration. Investigating temporal processing of emotional and neutral faces, Tipples, Brattan, and Johnston (2015) showed that activity in the junction of the right inferior frontal gyrus and anterior insula, together with the right SMA, was modulated by emotion, but only in the most difficult decision making condition. fMRI studies of emotion duration estimation are then not univocal concerning the role of insula in temporal distortion.

1.4 | Neuropsychological studies

Neuropsychological studies show a mixed pattern of results. Griffiths et al. (1997) reported a deficit in analyzing temporal sequences of sounds in a patient with a bilateral lesion of the insula. More recently, using a time reproduction task with negative and neutral pictures, Monfort et al. (2014) showed that a focal lesion of the right anterior insula was associated to aberrant reproduction times, suggesting that this structure would be involved in temporal precision independently of the nature of the stimulus. Lastly, a voxel based symptom-lesion mapping study showed that lesions in the white matter posterior to the insula as well as in the insula were related to larger errors in time estimation (Trojano, Caccavale, De Bellis, & Crisci, 2017). However, this study did not address interval timing abilities, but the capacity to correctly recall the timing of self-relevant events. Overall, if results from these studies suggest that the insula plays a substantial role in the relationship between subjective duration, emotion, and interoception, they do not allow clearly precisifying its specific role in emotion-related temporal distortions.

1.5 | The present study

In the present study, we investigated duration processing in brain-damaged patients with a focused lesion of the insula as well as in healthy controls, using temporal paradigms with either pure tones or neutral and emotional sounds. Previous studies report a duration processing network that is preferentially right-lateralized (Benau, DeLoretta, & Moelter, 2018; Ivry & Schlerf, 2008; Lewis & Miall, 2006; Livesey et al., 2007; Mella et al., 2011; Pfeuty et al., 2015; Pouthas et al., 2005). The right lateralization has been especially consistent concerning the insula (Dirnberger et al., 2012; Lewis & Miall, 2006; Pfeuty et al., 2015; Tipples et al., 2015; Wiener, Turkeltaub, & Coslett, 2010). Patients with both left and right lesions of the insula were then recruited and parsed into two groups, with the expectation that right lesion patients would show greater alterations of time processing. Using two groups of lesions also allowed controlling for the general impact of a stroke on time processing. Two different time perception tasks were used to address distinct components of temporal processing: A temporal bisection task enabled exploring temporal sensitivity (or precision) as well as emotion-related temporal distortions, while a verbal estimation paradigm allowed investigating both emotion-related temporal distortions and duration effects, that is, whether specific to a certain range of durations (from 300 to 1500 ms). Finally, a monaural listening paradigm was used to maximize the potential effects of a lateralized lesion. As auditory processing is mostly contralateral (Jäncke, Wüstenberg, Schulze, & Heinze, 2002),

effects of a lesion of the right insula should be enhanced when the sound is presented in the left ear, while effects of a lesion of the left insula should be greater when the sound is presented in the right ear. Predictions concerning effects of the side of presentation of the sounds may also be formulated for control participants: Based on the right lateralized processing of duration in the brain, one may expect that subjective duration would be more precise when the sound is presented in the left ear, potentiating the right hemisphere processing. This hypothesis may be proposed for pure tones and neutral stimuli, but additional effects of lateralization of emotion processing might be observed (Wager, Phan, Liberzon, & Taylor, 2003) and remains exploratory.

2 | METHOD

2.1 | Participants

2.1.1 | Patients

Twenty-one patients with an acute ischemic stroke affecting mainly the right (11 patients) or the left (10 patients) insula, defined following MR acquisition, participated in this study. All patients were recruited during the acute stage (mean time post-onset: 11 days, range: 3–22) in the University Hospitals of Geneva and gave their informed consent for the experiment, approved by the Ethical committee of the University Hospitals of Geneva. Inclusion criteria were: 18–85 years, an acute ischemic stroke involving predominantly the insula on the MRI. Exclusion criteria were: a history of neurodegenerative or psychiatric disorders, hemineglect, or hypacusia. A description of the patients is given in Table 1.

Prior to the experimental session, they were submitted to an audiogram to ensure that they had normal auditory abilities, as well as to an electroencephalogram in order to verify that patients had a good state of vigilance, which was the case for all of them. Global evaluations of their cognitive status had been conducted in the University Hospitals of Geneva upon their arrivals. All the patients showed good personal and spatial orientation, and all except for one patient showed good temporal orientation abilities. As described in Table 1, patients with a right insular lesion had a mean initial NIHSS score of 4.80 (± 2.76) and those with a left lesion a score of 5.10 (± 5.32). At the time of the tests the mean NIHSS score was of 1.27 (± 1.68) and 1.20 (± 1.87), for patients with, respectively, right and left lesions, so most patients had almost recovered from their patent symptoms.

2.1.2 | Control group

Twenty-one participants, matched for sex and age with patients, were enrolled as control participants. All of them gave their informed

consents prior to the experiment, also approved by the Ethical committee of the University Hospitals of Geneva.

2.2 | Material

According to the task, either pure tones or neutral and emotional sounds were used. Pure tones of 70 dB lasting 300, 500, 700, 900, 1100, 1300, or 1500 ms were created using Adobe Audition software and were used in the noncontextual tasks. For the contextual tasks, neutral and emotional sounds were chosen from a standardized nonverbal human sounds battery (Pollak, Holt, & Wismer Fries, 2004) and from a battery of baby's cries. From these databases, 18 sounds (6 neutral, 6 negative, and 6 positive) of 300, 500, 700, 900, and 1100 ms were created. As for the pure tones, they were adjusted to 70 dB. These new sounds were rated for their affective valence by 151 individuals (aged 19–50 years, mean age = 22.76 years) participating in a different experiment on ecological behavior (filler task). Ratings were assessed using a nonverbal scale, a smiley, ranging from 1 (negative) to 5 (positive) points. Results from these ratings confirmed that negative sounds (mean ratings = 1.61) were judged significantly more negative than neutral sounds (mean ratings = 2.75), themselves judged less positive than positive sounds (mean ratings = 4.49) ($p < .001$).

In all tasks, sounds were presented monaurally, either in the left or right ear, following a pseudo-random design.

2.3 | Procedure

Two time perception paradigms were used in this experiment. The tasks were administered on a laptop (DELL, 15 in.) using Eprime (Schneider, Eschman, & Zuccolotto, 2002). Patients were tested either in a small room dedicated to experimentation or in their hospital room. For the control group, the tasks were administered in a small room of the Psychology University building (Geneva), dedicated to experimentation.

In the verbal estimation task, the participants had to estimate the duration of each sound by moving a cursor on a visual scale ranging from 300 to 1500 ms (noncontextual part) or from 300 to 1100 ms (emotional part). The cursor was placed by default in the middle of the scale. Before starting the task, participants were presented with the two extreme durations of the range used (either 300 and 1500 ms, or 300 and 1100 ms), so that they could have a representation of these two extreme durations (binaural presentation). The noncontextual part comprised 84 trials (6 trials per condition) pseudo-randomly divided into three blocks, and the contextual task comprised 180 trials (6 trials per condition) pseudo-randomly divided into three blocks.

The temporal bisection task comprised two phases: a learning phase (binaural presentation) and an experimental phase (monaural

TABLE 1 Description of the participants

	N (male/female)	Age (years) Mean (SD)	Delay ^a (days) Mean (SD)	NIHSS scores ^b Mean (SD)
Right insular lesion	11 (5/6)	57.36 (16.27)	12.45 (3.86)	1.27 (1.68)
Left insular lesion	10 (3/7)	62.70 (12.79)	9.80 (6.71)	1.20 (1.87)
Control group	21 (8/13)	64.76 (13.78)	–	

^a Delay between the onset of the ischemic stroke and the passation of tests.

^b At the time of experimental testing.

presentation). In the learning phase, participants had to memorize two standard durations, one “short” (300 ms in both noncontextual and emotional parts) and one “long” (1500 and 1100 ms in the noncontextual and emotional parts, respectively). Both short and long standard durations were presented binaurally six times. This was followed by a pseudo-randomly presentation of 30 trials (15 for each duration), for which participants had to determine whether the sound corresponded to the “short” or to the “long” standard, using the keyboard. A feedback (“correct” or “incorrect”) followed each trial. A minimum threshold of 80% of correct responses was required before starting the experimental session.

In the experimental phase, intermediate durations (500, 700, and 900 ms for both parts, and 1100 and 1300 ms for the noncontextual part) as well as the standard durations were presented monaurally. Participants had to determine whether the presented sound was closest to the “short” standard or to the “long” standard, using the keyboard. As for the verbal estimation task, the noncontextual part comprised 84 trials (6 trials per condition) pseudo-randomly divided into three blocks and the contextual task comprised 180 trials (6 trials per condition) pseudo-randomly divided into three blocks.

The order of the tasks was randomized across participants. Overall, the experiment lasted approximately an hour and a half for the control participants and between 1 and 2 hr for the group of patients. Due to fatigue problems, some of the patients did not complete the entire protocol (a total of 20 patients, 10 left and 10 right, performed

the verbal estimation tasks; a total of 16 patients, 9 left and 7 right, performed the bisection tasks).

2.3.1 | MR acquisition

To localize the lesions, Diffusion-Weighted Images were acquired in a routine clinical work-up using different 1.5 T and 3 T MRI machines (Siemens, Erlangen, Germany: 1.2×1.2 mm to 2×2 mm in-plane isotropic pixel size, from 4 to 5 mm slice thickness, TE from 57 to 105 ms, TR from 4400 to 9100 ms; Philips Healthcare, Best, the Netherlands: from 0.9×0.9 mm to 1×1 mm in-plane isotropic pixel size, from 4 to 5 mm slice thickness, TE from 58 to 84 ms, TR from 3,120 to 7,684 ms). Lesions were delineated on the DWI scans and binary lesion masks were created. The obtained DWI images were registered to the Montreal Neurological Institute (MNI152) standard space, through a linear registration which we performed using FLIRT, which is part of FSL (<http://www.fmrib.ox.ac.uk/fsl/>). Figure 1 illustrates the localization of the lesions. Brain MRIs showed more or less extended lesions involving either the right ($n = 11$) or the left ($n = 10$) insula. Figure 1 shows the superimposed lesions in the left hemisphere and those in the right hemisphere. Right lesions involved the whole insula ($n = 1$), the anterior insula ($n = 1$), the posterior insula ($n = 3$), the posterodorsal insula ($n = 4$), or the posteroventral insula ($n = 2$). Left lesions involved the whole insula ($n = 1$), the anterior insula ($n = 1$), the posterior insula ($n = 3$), the posterodorsal insula ($n = 3$), or the posteroventral insula ($n = 2$). In total, the involved parts of the

FIGURE 1 Lesion probability map of the 21 patients with a stroke affecting the insula (left insula, $n = 10$, right insula, $n = 11$). The number of patients who had a lesion in a particular voxel are depicted in color (see bar on right side), where min = 1 patient; max = 10 patients with left lesion and 11 patients with right lesion (L: left hemisphere) [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Global temporal estimates in the verbal estimation task (non-contextual) according to the side of presentation of the sounds (right ear in full color and left ear in hatched color) for the control group (in black), patients with lesions affecting the right insula (in mid-gray) and patients with lesions affecting the left insula (in light-gray). Patients with lesions affecting the right insula significantly underestimated durations when the sounds were presented in the left ear. Bars represent standard errors

insula were very similar on the right side and on the left side with a clear predominance of posterior involvement of the insula on both sides (respectively, 9/11 patients and 8/10 patients).

3 | STATISTICAL ANALYSES

3.1 | Verbal estimation task

Subjective durations were transformed into T scores using the following formula: $T\text{-score} = (\text{subjective duration} - \text{real duration}) / \text{real duration}$. This transformation allowed comparisons between different ranges of duration. Repeated measure ANOVAs were conducted on these T-scores.

3.2 | Temporal bisection task

This task assesses both temporal sensitivity and distortion of temporal perception. For temporal sensitivity, the slope of the proportion of “long” responses plotted against real durations was computed for each participant using linear regressions and removing extreme values (cf. Figure 2). Distortion of temporal perception is reflected by the left or right deviation of the slope and can be assessed by computing a bisection point, that is, the stimulus value that would yield 50% “long” responses (Wearden & Ferrara, 1996). Bisection points, representing the geometric means for the short and long intervals or the point of subjective equality, were then computed for each individual and each condition using equations of the regressions (noncontextual, neutral, negative, and positive). Repeated measure ANOVAs were conducted on both individual slopes and bisection points.

For all tasks, the Huynh–Feldt correction, which makes an adjustment to the degrees of freedom was applied where sphericity assumption could not be assumed (Haverkamp & Beauducel, 2017).

When needed, post-hoc Tukey HSD tests were used to explore significant interactions.

4 | RESULTS

4.1 | Verbal estimation task

T-scores of the verbal estimation tasks are displayed in Table 2 for the noncontextual part and in Table 3 for the contextual part.

Results of the ANOVA conducted in the noncontextual task showed a significant Ear effect, $F(1, 38) = 16.50$, $p < .001$, $\eta^2 = .37$, indicating that sounds were judged to last shorter when presented in the left ear. A significant Group $\times$ Ear interaction, $F(2, 38) = 3.34$, $p = .046$, $\eta^2 = .15$, showed that duration was perceived to last shorter when presented in the left ear for right patients ($p = .029$, post-hoc HSD Tukey test), but not for left patients or control participants ($p > .10$, post-hoc HSD Tukey test) (see Figure 2). The double interaction Duration $\times$ Group $\times$ Ear interaction was also significant, $F(7, 23, 216) = 2.11$, $p = .045$, $\eta^2 = .10$, suggesting that this effect was different across duration ranges. However, post-hoc HSD Tukey tests were nonsignificant ($p > .10$). The main effect of Duration was also significant, $F(6, 228) = 22.58$, $p < .001$, $\eta^2 = .37$.

Results of the ANOVA conducted in the emotional part of the task showed a significant main effect of Emotion, $F(2, 70) = 21.03$, $p < .001$, $\eta^2 = .38$, indicating that emotional sounds' duration was perceived as longer than that of neutral sounds ($p < .001$, post-hoc HSD Tukey tests). An Emotion $\times$ Duration interaction, $F(8, 280) = 9.66$, $p < .001$, $\eta^2 = .22$, showed that this effect was observed only for short durations (300 ms, $p < .001$, post-hoc HSD Tukey tests). A significant main effect of Ear, $F(1, 35) = 5.56$, $p = .024$, $\eta^2 = .14$, revealed shorter temporal estimates when sounds were presented in the left ear, and a significant Ear $\times$ Duration interaction, $F(4, 140) = 7.00$, $p < .001$, $\eta^2 = .17$, showed that this effect

TABLE 2 Temporal estimates (T-scores) of sounds in the verbal estimation task (noncontextual sounds)

		Control participants mean (SD)	Right lesion mean (SD)	Left lesion mean (SD)
300 ms	Right ear	0.9 (1.04)	0.73 (1.21)	0.94 (0.95)
	Left ear	0.92 (1)	0.43 (0.78)	0.64 (0.76)
500 ms	Right ear	0.31 (0.44)	0.07 (0.35)	0.42 (0.63)
	Left ear	0.3 (0.42)	0.09 (0.47)	0.22 (0.49)
700 ms	Right ear	0.08 (0.26)	0.16 (0.46)	0.17 (0.38)
	Left ear	0.1 (0.25)	−0.08 (0.26)	0.16 (0.23)
900 ms	Right ear	−0.03 (0.19)	0.07 (0.36)	0.11 (0.23)
	Left ear	−0.09 (0.19)	−0.11 (0.26)	0.08 (0.2)
1100 ms	Right ear	−0.1 (0.21)	−0.09 (0.28)	0.01 (0.17)
	Left ear	−0.13 (0.14)	−0.13 (0.25)	0 (0.18)
1300 ms	Right ear	−0.18 (0.18)	−0.15 (0.24)	−0.05 (0.13)
	Left ear	−0.17 (0.18)	−0.2 (0.25)	−0.09 (0.19)
1500 ms	Right ear	−0.22 (0.18)	−0.23 (0.2)	−0.19 (0.15)
	Left ear	−0.29 (0.21)	−0.21 (0.22)	−0.18 (0.16)

TABLE 3 Temporal estimates (T-scores) of neutral, negative, and positive sounds in the verbal estimation task

			Control participants mean (SD)	Right lesion mean (SD)	Left lesion mean (SD)
Negative sounds	300 ms	Right ear	0.76 (0.58)	0.53 (0.42)	0.74 (0.42)
		Left ear	0.46 (0.26)	0.5 (0.36)	0.69 (0.32)
	500 ms	Right ear	0.16 (0.22)	0.26 (0.32)	0.28 (0.23)
		Left ear	0.16 (0.17)	0.12 (0.3)	0.25 (0.21)
	700 ms	Right ear	−0.03 (0.16)	−0.07 (0.31)	−0.06 (0.2)
		Left ear	−0.08 (0.15)	−0.1 (0.27)	−0.01 (0.16)
	900 ms	Right ear	−0.21 (0.12)	−0.21 (0.22)	−0.21 (0.15)
		Left ear	−0.22 (0.11)	−0.22 (0.25)	−0.21 (0.09)
Neutral sounds	300 ms	Right ear	−0.28 (0.12)	−0.31 (0.18)	−0.3 (0.14)
		Left ear	−0.29 (0.12)	−0.34 (0.19)	−0.31 (0.1)
	500 ms	Right ear	0.44 (0.33)	0.41 (0.29)	0.64 (0.49)
		Left ear	0.17 (0.17)	0.28 (0.27)	0.48 (0.37)
	700 ms	Right ear	0.16 (0.21)	0.05 (0.28)	0.22 (0.26)
		Left ear	0.19 (0.23)	−0.01 (0.22)	0.18 (0.18)
	900 ms	Right ear	−0.09 (0.16)	−0.15 (0.23)	−0.05 (0.18)
		Left ear	−0.05 (0.16)	−0.16 (0.23)	−0.05 (0.12)
Positive sounds	300 ms	Right ear	−0.21 (0.13)	−0.27 (0.23)	−0.21 (0.15)
		Left ear	−0.25 (0.14)	−0.33 (0.24)	−0.21 (0.12)
	500 ms	Right ear	−0.36 (0.19)	−0.39 (0.28)	−0.32 (0.16)
		Left ear	−0.3 (0.15)	−0.39 (0.2)	−0.33 (0.12)
	700 ms	Right ear	0.55 (0.28)	0.66 (0.41)	0.74 (0.55)
		Left ear	0.71 (0.42)	0.5 (0.35)	0.72 (0.36)
	900 ms	Right ear	0.23 (0.27)	0.23 (0.24)	0.18 (0.23)
		Left ear	0.09 (0.19)	0.12 (0.19)	0.16 (0.23)
	300 ms	Right ear	−0.01 (0.14)	−0.02 (0.31)	−0.01 (0.2)
		Left ear	−0.06 (0.16)	−0.07 (0.24)	0 (0.13)
	500 ms	Right ear	−0.17 (0.16)	−0.23 (0.35)	−0.18 (0.14)
		Left ear	−0.1 (0.15)	−0.19 (0.24)	−0.14 (0.16)
	700 ms	Right ear	−0.29 (0.14)	−0.29 (0.17)	−0.3 (0.13)
		Left ear	−0.33 (0.17)	−0.32 (0.2)	−0.29 (0.14)
	900 ms	Right ear			
		Left ear			

was significant only for short durations (300 and 500 ms, $p < .001$, and $p = .030$, respectively, post-hoc HSD Tukey tests). The double interaction Emotion $\times$ Duration $\times$ Ear was also significant, $F(8, 280) = 2.50$, $p = .014$, $\eta^2 = .07$. Post hoc HSD Tukey tests indicate that, when presented in the right ear, 300 ms emotional sounds were judged to last longer than neutral sounds ($p < .001$); while when presented in the left ear, 300 ms neutral, positive and negative sounds durations were judged to be different ($p < .001$): Negative sounds were judged to last longer than neutral ones, and positive sounds were judged to last longer than both neutral and negative sounds ($p < .001$). The Emotion $\times$ Duration $\times$ Ear $\times$ Group interaction was also significant, $F(16, 280) = 2.82$, $p < .001$, $\eta^2 = .14$. Post hoc HSD Tukey tests indicate an effect of the side of presentation for each kind of stimuli (neutral, positive, and negative) in control participants only ($p < .001$ for negative and neutral sounds; $p = .049$ for positive sounds). As illustrated in the Figure 4, negative and neutral sounds were judged to last shorter (more accurate subjective duration) when presented in the left ear, while positive sounds were judged to last shorter (more accurate subjective duration) when

presented in the right ear. The main effect of Duration was also significant, $F(4, 140) = 206.11$, $p < .001$, $\eta^2 = .85$.

4.2 | Temporal bisection task

Results concerning the non-contextual part of the task showed a significant main effect of the group on the slopes, $F(2, 27) = 6.0209$, $p = .007$, $\eta^2 = .31$, indicating that patients with a right insular lesion showed less temporal sensitivity than control participants or patients with a left insular lesion ($p < .001$, Post hoc HSD Tukey tests) (see Figure 3). No significant effects were observed on the bisection point.

Results concerning the emotional part of the task showed a significant main effect of the group on the slopes, $F(2, 26) = 3.949$, $p = .032$, $\eta^2 = .23$, indicating that patients with a lesion in the right insula showed less temporal sensitivity than control participants ($p < .05$, Post hoc HSD Tukey tests) (see Figure 4). Results also showed a tendency for Group $\times$ Emotion interaction $F(4, 52) = 2.502$, $p = .053$, $\eta^2 = .16$, suggesting that this effect was more pronounced with positive sounds (but Post hoc HSD Tukey tests showed no significant differences). Lastly, a significant main effect of Emotion on the

FIGURE 3 Proportion of “long” responses plotted against real stimulus durations for control (in black), patients with a lesion affecting the right insula (in dashed line) and patients with a lesion affecting the left insula (in gray). Patients with a right insula lesion show a lower temporal sensitivity than control subjects or than patients with a left insula lesion

intercept was observed, $F(2, 52) = 4.42$, $p = .017$, $\eta^2 = .15$, indicating that emotional sounds' duration was overestimated relatively to that of neutral ones ($p < .001$, Post hoc HDS Tukey tests).

For a better readability of the redundancy and differences of the results over the four tasks, a summary of main effects and simple interactions is provided by Table 4.

5 | DISCUSSION

The present study aimed at exploring how a stroke in the right or left insula affected time perception and emotion-related temporal distortion. Two experimental tasks with either emotional/neutral sounds or simple pure tones were used to assess both duration sensitivity (or precision) and subjective duration distortions. Our main result showed that a lesion of the right insula impaired temporal sensitivity and shortened subjective duration, by comparison with both no lesion and lesion affecting the left insula. Emotional effects were consistent with the literature, but contrary to our expectations, emotion related temporal distortions did not show any significant difference between

patients and healthy controls, suggesting that they do not rely upon engagement of the insula.

5.1 | Less temporal sensitivity in right lesion patients

Patients with a lesion affecting the right insula showed less temporal sensitivity than control participants, when estimating the duration of pure sounds or the duration of neutral and emotional sounds. Figures 3 and 4b illustrate the major difficulties that these patients have to classify short and long durations. It may be noted on the Figure 4b that this difficulty seems to be greater for positive stimuli, although there were no significant group $\times$ emotion interaction. Performances in the bisection task suggest that, unlike left lesion patients, right lesion patients perceived intermediate durations as quite similar. This finding supports previous studies showing that the process of time is preferentially right-lateralized in the brain (Ferrandez et al., 2003; Pouthas et al., 2005). In addition, it underlines the importance of the right insula in the crucial role of temporal discrimination, that is, the difficulty to compare the encoded duration to a more general representation of a duration. This observation makes echoes to the proposition of Kosillo and Smith (2010), according to which the insula would be involved in sensory discrimination in general, that is, the ability to compare features of a stimulus, among which temporal processing would be an example, to a general representation of this feature stored in long-term memory. A functional distinction between posterior and anterior insula has been proposed by Wittmann et al. (2010), the posterior part considered to be more involved in the encoding of a duration, while the anterior part would be more involved in the reproduction of interval. As most of the patients included in our study showed lesions that affected more posterior parts of the insula (Figure 1), an encoding deficit might be responsible for the lower temporal discrimination in right lesion patients.

5.2 | Monaural listening

Monaural listening gave interesting results in the verbal estimation tasks, the durations being judged shorter when the sounds were presented in the left ear. The duration $\times$ ear interactions in both

FIGURE 4 Proportion of “long” responses plotted against stimulus durations according to the emotional content: Neutral (in gray), negative (in black) or positive (in dashed line), for control (a), right insula patients (b), and left insula patients (c). For each group, emotional sounds durations are judged to last longer than that of neutral sounds, but patients with a lesion of the right insula showed less temporal sensitivity than both control and patients with a lesion affecting the left insula. This effect was more pronounced with positive sounds

TABLE 4 Summary of the results of all experiments: Effect sizes (partial eta squared) of main effects and simple interactions

	Verbal estimation		Bisection			
	Pure	Emotional	Pure tones		Emotional	
			Slope	Intercept	Slope	Intercept
Duration	0.37**	0.85**	–	–	–	–
Ear	0.37**	0.14*	ns	ns	ns	ns
Group	ns	ns	0.31*	ns	0.23*	ns
Duration × ear	0.10*	0.17**	–	–	–	–
Group × ear	0.15*	ns	ns	ns	ns	ns
Emotion	–	0.38**	–	–	–	0.15*
Group × emotion	–	ns	–	–	0.16 ^a	ns
Duration × emotion	–	0.22**	–	–	–	–

* $p < .05$; ** $p < .001$; ^a $p < .10$; ns = nonsignificant effects or interactions. Empty cases correspond to nonrelevant conditions.

contextual and noncontextual tasks showed that this effect was significant for 300 ms (both tasks) and 500 ms (contextual tasks) sounds only. Interestingly, shortened temporal estimates for these very brief sounds also means more precise subjective duration. Consistently with our hypothesis, presenting sounds in the left ear may potentiate processing in the right hemisphere, where duration is preferentially processed (Pouthas et al., 2005; Rao, Mayer, & Harrington, 2001). This effect seems quite robust as it was observed with both pure and neutral sounds (see below for discussion about emotional sounds). However, there were no effects of monaural listening in the bisection paradigms. A possible explanation for this discrepancy may be that bisection does not allow distinguishing between short and long durations. Effects of monaural presentation in the verbal estimation tasks were specific to short durations and dependent variables in the bisection tasks are the intercepts and the slopes, which take into account the whole range of durations. Potential effects of monaural listening might then be masked by the procedure. Alternatively, ear effects might affect processes that are specific to verbal estimation paradigms, like verbal labeling. Some studies, for example, suggest that left insula is more related to language-based strategies of timing (Hinton, Harrington, Binder, Durgerian, & Rao, 2004). In verbal tasks, stimulating the left insula via right monaural listening might then increase the focus of attention on temporal cues and lengthen subjective durations. This hypothesis is speculative and future studies should specifically address this issue.

5.3 | Shortened subjective duration in right lesion patients

Patients with a lesion of the right insula showed shorter subjective durations than control participants or than patients with a left lesion, when the sounds were presented in the left ear. This lateralization effect is consistent with the expected potentiating effect of a right lesion effect by a left monaural listening. While the effect of the side of presentation of the sounds leads to more precise time estimates for very short durations in both control participants and patients, it is independent of the duration to estimate in right lesion patients, which leads them to a global underestimation of durations (see Figure 2). In addition to a discrimination deficit, a lesion of the right insula may

leads to a loss of temporal information. In the other tasks however, no such effects were observed, which makes it difficult to generalize.

5.4 | Effect of emotion

Contrary to our expectations, emotion-related temporal distortions were not significantly different in patients and in healthy controls. The observed emotional effect was consistent with what is classically reported in the literature: Emotional sounds appeared to last longer than neutral sounds (Droit-Volet & Meck, 2007; Mella et al., 2011; Noulhiane et al., 2007; Tipples, 2008). Our result is also consistent with the single-case study of Monfort et al. (2014), showing that a focal lesion in the right anterior insula in a single patient did not lead to over-reproduction of emotional durations. However, unlike in our study, the authors report in this patient a global overestimation of durations, being with neutral or emotional stimuli. This discrepancy may lie in the fact that several important methodological points differ with our study, including a different time estimation paradigm and the use of much longer durations (up to 7 s). Monfort et al. concluded to a distorted memory representation of the encoded duration, independently of emotion. Our results, together with those of Monfort et al., did not support the hypothesis that emotion effects on time perception are mediated by the integration of bodily signals in the insula. Yet, as suggested by our results, interoceptive information processed in the right insula might serve as basis for temporal precision rather than for emotion-induced temporal distortion. An argument supporting this proposition is the finding that individuals with better accuracy at reporting their own heart-rate are more likely to accurately estimate a given temporal duration (Meissner & Wittmann, 2011). It does however not rule out the assumption that the role of the insula in timing processes may be linked to immediate self-consciousness, the feeling of “nowness” in close relation to the self, which can only emerge with the sense of time. Interestingly some epileptic seizures called ecstatic have been shown to involve mainly the insula and to include both enhanced self-awareness and time dilation (Gschwind & Picard, 2016; Picard & Craig, 2009).

Results from control participants showed an intriguing lateralization effect of emotional duration processing for very short durations (300 ms). Negative sounds were judged to last shorter when presented in the left ear, while positive sounds were judged to last

shorter when presented in the right ear. These results might be interpreted in two different ways. On the one hand, temporal estimates were more precise for negative stimuli when the right hemisphere was favored (left ear presentation), and more precise for positive stimuli when the left hemisphere was favored (right ear presentation). This observation is consistent with classical asymmetric activations underlying emotional stimuli processing, an overall right hemisphere dominance in negative emotion processing being classically described, while a left hemisphere preference is reported in the process of positive emotions (see Harmon-Jones, Gable, & Peterson, 2010 for a review). In such views, the monaural presentation congruent with emotional valence could induce a more accurate process of the sounds features, including their duration. On the other hand, one might argue that distortion of negative sounds' duration preferentially engages left hemisphere (longer temporal estimates when sounds are presented in the right ear), while distortion of positive sounds duration would rather reflect involvement of the right hemisphere. In this view, these results would go against the brain asymmetry classically reported in the literature. Some research suggests that this hemispheric lateralization is however often specific to the frontal cortex (Davidson, 2002; Davidson & Irwin, 1999) and a few brain structures do not always conform to this model, including the insula but also the amygdala (Duerden, Arsalidou, Lee, & Taylor, 2013; Wager et al., 2003; Zald, 2003). These two brain structures are presented in a recent review as potential candidates in the modulation of timing processes in an emotional context, but the underlying mechanisms are different than earlier propositions of interoceptive processes (Lake, LaBar, & Meck, 2016). The authors proposed that emotional stimuli influence the maintenance of attention toward duration estimation. More specifically, in the frame of the Striatal Beat Frequency model (Buhusi & Meck, 2005), they make the assumption that emotional stimuli would increase neural synchronization of the regions involved in both timing and attention, which would result in increased experienced duration. According to Lake and collaborators, the amygdala would be especially relevant for this function given its involvement in phasic dopaminergic activity, which plays a central role in initiating timing processes and in transient physiological arousal induced by self-relevant stimuli. Interestingly, the lateralization of emotional temporal processing was observed for very short durations in our study, which fits with a fast, short-lived process, typical of the amygdala (Öhman, 2005). Based on Lake et al.'s recent proposition and our results, we may assume that temporal distortion induced by emotional stimuli would depend more on amygdala activity than on insular activity. Involvement of the amygdala in emotional temporal distortions fits with the idea that such distortions are an adaptive phenomenon. For example, it has been argued that it could contribute to prioritization of memory (Lake et al., 2016). Alternatively, subjective time dilation has been proposed to be determined by action emergency, either by facilitating readiness potential (Droit-Volet & Meck, 2007) or by accelerating the internal rate of information processing (Tse, Intriligator, Rivest, & Cavanagh, 2004). Indeed, in extreme conditions, if time stands still, it gives the brain more time to encode environment, via enhanced sensory processing, and allows selecting the most adaptive response.

5.5 | Limitations

There are several limitations that could be highlighted in our study. First, the sample sizes were relatively small and a large number of variables were analyzed together. Therefore, interpretation of interactions between more than two variables should be interpreted with caution. Nevertheless, the Huynh-Feldt correction was applied when needed, making an adjustment to the degrees of freedom, where sphericity assumption was violated (Haverkamp & Beauducel, 2017). Furthermore, the neuropsychological testing of the patients provided information limited to the NIHSS scores.

6 | CONCLUSION

Our study is the first to investigate the effect of focal lesions of the insula on both temporal sensitivity and subjective duration, in an emotional and noncontextual context. This study brings a substantial contribution to a better understanding of the role of the insula in the processing of emotional duration and in the estimation of time more generally. Unlike what was hypothesized in the literature, this structure does not seem to be involved in the emotion-related lengthening of subjective duration, but rather in discrimination processes involved in time estimation.

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