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Integration and differentiation of neural information dissociate between conscious percepts

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ABSTRACT

At any given moment, we experience a perceptual scene as a single whole and yet we may distinguish a variety of objects within it. This characteristic of perception instantiates two general properties of phenomenological experience: integration and differentiation. While integration is the property of experiencing a collection of objects as a unitary percept, differentiation is the property of experiencing these objects as different percepts. Little is known about how these two phenomenological properties are dynamically indexed by the brain in terms of information processing. Here we evaluated the dynamics of neural information underlying phenomenological integration and differentiation in bistable perception. Participants listened to auditory bistable stimuli, a sequence of tones experienced either as a –single– integrated percept (phenomenological integration) or as two –parallel– differentiated percepts (phenomenological differentiation). We computed neurophysiological indices of information integration and information differentiation with electroencephalographic and direct cortical recordings in human participants. We focused specifically on the gamma-band dynamics within the frontoparietal network, commonly implicated in conscious processing. In electrical recordings at the scalp and intracranially, the phenomenologically integrated percept generated an increase in neural information integration and a decrease in differentiation between frontal and parietal regions, whereas the opposite pattern was observed for the phenomenologically differentiated percept. This effect was not observed in the auditory control task. Furthermore, this dissociation was not observed when computing traditional measures of neural oscillatory integration (phase synchronization) within the same frontoparietal network and frequency range. However, this frontoparietal phase synchrony was able to distinguish between a stable perceptual window and the transitional period between the two percepts. These theoretically-motivated neural indices of information dynamics dissociated phenomenological integration and differentiation that indices of oscillatory dynamics did not. By incorporating theoretically motivated measures of information theory in the characterization of perceptual content, we contribute to the construction of a testable framework to investigate the neuroscience of conscious experience.

Keywords: contents of consciousness, bistable perception, wSMI, K complexity, integrated information theory, EEG.

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INTRODUCTION

Brains continuously coordinate information for creating coherent internal states underpinning perception, cognition and action. Thus, investigating neural information processing seems crucial for understanding complex cognitive phenomena. Under this information-theory framework, processes such as the information flow, information complexity and information transfer have been recently explored as potential dynamical mechanisms underlying cognition and consciousness. For instance, the dynamic of information transfer within cortical networks has been useful for unravelling the mechanisms of sensorimotor integration (Lungarella and Sporns, 2006; Siegel et al., 2015), visual perception (Hanslmayr et al., 2013; Ince et al., 2016), working memory (Salazar et al., 2012), and pathological states of consciousness (King et al., 2013).

During the last years, consciousness research has benefited, primarily at the theoretical level (and to a certain degree, empirically), from the application of information theory for investigating the neural dynamics of conscious processing. Importantly, current theories of consciousness propose that the information generated by the dynamics of neural activity is crucial for the emergence of conscious experience (Dehaene and Changeux, 2011; Dehaene et al., 2014; Koch et al., 2016; Tononi et al., 2016). However, empirical research derived from these theories have focused primarily on investigating conscious states and conscious access rather than on its potential role on underpinning conscious experience itself (Dehaene et al., 2014). For instance, the role of information dynamics has been investigated for distinguishing between pathological (Casali et al., 2013; King et al., 2013; Sitt et al., 2014) and pharmacological (Casali et al., 2013; Sarasso et al., 2015; Schartner et al., 2015, 2017) conscious states, and for discriminating between conscious and unconscious processing during conscious access tasks (Gaillard et al., 2009). However, the potential role of information dynamics for indexing conscious experience has not yet been tested. Here we describe a testable framework for studying the general properties of conscious experience using theoretically motivated informational measures of brain activity.

According to current theories of consciousness, although conscious experience cannot be divided into discreet independent components (that is, it is phenomenologically integrated; Tononi et al., 2016), it can contain different assortment of events and objects (that is, it is phenomenologically differentiated; Tononi et al., 2016). We propose that these two general properties of conscious experience can be neurophysiologically investigated during auditory bistability. During auditory bistability, an invariant sequence of tones is experienced as forming either a phenomenologically integrated percept (one stream) or a phenomenologically differentiated percept (two streams) (Snyder et al., 2012) (Figure 1).

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Neurophysiologically, conscious experience is thought to require the joint presence of information integration and information differentiation (Oizumi et al., 2014; Tononi et al., 2016). In particular, the emergence of conscious percepts are believed to involve the integration of information coming from multiple, specialized brain areas to form a phenomenologically unified whole (Dehaene and Changeux, 2011; Dehaene et al., 2014; Tononi et al., 2016). Therefore, a reasonable assumption is that a phenomenologically integrated percept (one stream, as the one used in this experiment) should be associated with correspondingly higher neural information integration (NII). Recently, NII has been empirically measured in a direct manner by computing the amount of information shared between long-distance EEG signals, and it has been used to discriminate between vegetative and minimally conscious patients (King et al., 2013; Sitt et al., 2014). This NII measure can detect non-oscillatory coupling between signals as compared to classical measures of neural oscillatory integration (NOI) such as phase synchronization. In the case of auditory bistability, we expect higher neural information integration for the perceptually integrated percept (one-stream) compared to the perceptually differentiated percept (two-streams), as the former would require information about tones of two different frequencies to form a single, integrated percept.

Complementary to NII, empirical indices of neural information differentiation (NID) have been used to separate levels of consciousness by estimating the degree of compressibility of EEG signals (Casali et al., 2013; Sitt et al., 2014; Schartner et al., 2015, 2017). For instance, a decrease in NID has been observed in patients in vegetative states compared to minimally conscious states (Sitt et al., 2014), showing that differentiation of neural information is associated with a cognitively more advanced - clinically defined- state of consciousness. On the other hand, the only study providing preliminary indication that neurophysiological differentiation might be related to perceptual processes is a fMRI study (Boly et al., 2015), showing that NID was highest when participants watched a coherent movie, intermediate when scenes were scrambled, and minimal for 'TV noise'. However, it is unclear whether neurophysiological differentiation was specifically related to conscious awareness since factors such as low-level visual processing, expectations and top-down attention might be influencing the differences observed between conditions. During auditory bistability, we can specifically evaluate phenomenological differentiation directly since what is changing is not the stimulus itself but how it is subjectively experienced. If the neural information associated with a conscious percept is highly differentiated, NID is expected to be high since information is not easily compressible. In contrast, neural differentiation is expected to be low if EEG signals are processing information in a stereotypical way because information is highly redundant and can be easily compressed. Following this rationale, we expect that the phenomenologically differentiated percept (two stream) should be associated with higher neural information differentiation.

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Neurophysiological studies of auditory bistable perception, including those on streaming, have often been optimised for detection of activity in auditory-related cortices. Convergent results from several EEG, MEG, and fMRI studies indicate greater stimulus-locked activity on the superior temporal plane for the perception of two-streams percept than for that of one-stream (Gutschalk et al., 2005; Hill et al., 2011; Szalardy et al., 2013). Relatively fewer studies have shown percept-related activation beyond the auditory cortices. These have demonstrated that a wider set of brain areas (including subcortical sites; Kondo and Kashino, 2009) and the intraparietal sulcus (Cusack, 2005; Teki et al., 2011) are involved in, or reflect, auditory bistability. Recent computational models of auditory bistable perception (Mill et al., 2013; Schroger et al., 2014) have emphasized predictive and inferential processing for auditory streaming, suggesting the involvement of high-order cortical (e.g. frontoparietal network) areas in the emergence of auditory percepts, albeit this has not yet been experimentally verified. Importantly, content-specific experimental studies have revealed that a broad frontoparietal network is activated during visual (Hipp et al., 2012) and auditory (Basirat et al., 2008) tasks that contrast alternating conscious percepts. These results suggest that the awareness of conscious percepts might require the widespread broadcasting of neural information within the frontoparietal network (Dehaene and Changeux, 2011; Dehaene et al., 2014).

Alongside, there is ample and rapidly growing evidence that endogenous or 'ongoing' brain activity in the gamma band (30-70 Hz) is neither meaningless nor random but instead carries functional information which largely determines the way incoming stimuli are interpreted (Engel et al., 2001, 2013; Varela et al., 2001; Freeman, 2015). For instance, studies in the visual systems have shown that neural oscillatory integration (NOI) in the gamma-band is involved in the alternation between visual conscious percepts (Doesburg et al., 2005; Hipp et al., 2012). Thus, drawing upon these results and a wealth of previous research that has identified gamma band activity as relevant for conscious perception (e.g. Engel et al., 2013; Levy et al., 2015; Melloni et al., 2007), we analyse information and oscillatory dynamics of ongoing activity in the gamma band. However, we specifically evaluate the theoretical prediction (Koch et al., 2016) that information dynamics (NII and NID) but not oscillatory dynamics (NOI) of ongoing activity underpins phenomenological integration and differentiation.

By measuring high-density scalp EEG and Local Field Potentials (LFP) from direct cortical recordings in humans, we tested the hypothesis that during the formation of conscious percepts, phenomenology goes along with neurophysiology. Specifically, we predict that the phenomenologically integrated percept goes along with high frontoparietal neural information integration in the gamma band and conversely, that the phenomenological differentiated percept goes along with high neural information differentiation within frontal and parietal regions.

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RESULTS

Twenty-nine healthy participants and one patient implanted with intracranial electrodes listened to a repeating pattern of three tones followed by a temporal gap, that are experienced either as a one-stream percept (phenomenological integration) or as a two-streams percept (phenomenological differentiation) (Figure 1, upper panel). Participants were asked to press a button when perceiving that one-stream percept had fully changed into two-streams percept and a second button when perceiving that two-streams percept had fully changed into one-stream percept (Figure 1, middle panel). As an experimental control, we used a condition in which the stimuli were physically manipulated (varying the length of the silence between tones) in order to generate two externally-driven alternating percepts (exogenous condition), and participants had to perform the same task as in the endogenous condition. On the one hand, the exogenous condition was designed to control for stimuli-related differences, allowing us to characterize the neural dynamics specifically triggered by the external changes in the stimuli (the two alternating patterns) and to contrast them with the dynamics of internal neural activity elicited by the endogenous condition (bistability). On the other hand, the exogenous condition allowed us to control for top-down attention in the absence of bistability by creating externally driven switches between percepts as oppose to the internally driven ones induced endogenously.

Information integration in frontoparietal ongoing activity.

We first investigated the dynamics of neural information integration in the gamma range (NII_γ). After comparing activity occurring during a 500-ms window before a perceptual change with that occurring after the change (see Experimental Procedures), repeated-measures ANOVA (RANOVA) revealed a significant triple interaction between condition (endogenous, exogenous), window (before change, after change), and percept (one stream, two streams) for NII_γ (τ = 6 ms) ($F_{1,28}$ = 5.73, P = 0.024, Cohen's d = 0.90, Bayes factor (Bf) in favour of the alternative = 2.73). Bonferroni's *post hoc* test revealed higher NII_γ in one-stream compared to two-streams percept in the before-change (BC) window ($F_{1,28}$ = 7.92, P = 0.009, Cohen's d = 1.06, Bf in favour of the alternative = 6.42) (Figure 2a,c). Interestingly, ~1 s later in the after change (AC) window, NII_γ showed again higher values for one-stream than two-streams percept ($F_{1,28}$ = 5.51, P = 0.026, Cohen's d = 0.87, Bf in favour of the alternative = 2.49) (Figure 2a,c). These findings suggest that the phenomenologically integrated percept consistently involved a higher level of gamma neurophysiological integration than the phenomenologically differentiated one.

Interestingly, while NII_γ discriminated between conscious percepts during the endogenous condition (Figure 2a), did not show any difference between percepts in the exogenous condition (BC: $F_{1,28}$ = 0.34,

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P = 0.561; AC: $F_{1,28}$ = 0.90, P = 0.349, Bf in favour of the null = 3.26) (Figure 2b), suggesting that frontoparietal NII_{γ} may be specifically indexing endogenously generated percepts. Furthermore, no differences were observed in the mean level of NII_{γ} between endogenous and exogenous conditions ($F_{1,28}$ = 1.39, P = 0.248, Bf in favour of the null = 2.12) or between windows ($F_{1,28}$ = 0.11, P = 0.918, Bf in favour of the null = 3.59), indicating that the overall amount of information sharing within the frontoparietal network was similar between conditions. This index of information integration was hence sensitive to endogenously driven perceptual changes and may specifically underlie the formation of conscious auditory percepts.

In addition to NII_{γ}, we investigated whether neural information integration in the alpha band (NII_{α}) dissociates between auditory percepts, as alpha activity has been previously related to perceptual bistability (Flevaris et al., 2013; Handel and Jensen, 2014). However, the ability of frontoparietal NII to track and distinguish between different endogenous percepts seems to be specifically related to the gamma range since no differences were found between percepts in frontoparietal NII_{α} ($F_{1,28}$ = 1.01, P = 0.321, Bf in favour of the null = 2.48) (Supplementary Figure 1). Finally, to establish the specific role of frontoparietal areas, we computed inter-hemispheric NII_{γ} between temporal electrodes. We found no significant triple interaction in temporotemporal NII_{γ} ($F_{1,28}$ = 1.51, P = 0.228, Bf in favour of the null = 2.02) (Supplementary Figure 2), implying relative specific involvement of frontoparietal networks in the emergence of endogenous auditory percepts.

Information differentiation of frontal and parietal ongoing activity

We next investigated the dynamics of neural information differentiation (NID) within frontal and parietal electrodes during bistable perception (Figure 3). The RANOVA revealed a significant triple interaction between condition (endogenous, exogenous), window (before change, after change), and percept (one stream, two streams) for NID ($F_{1,28}$ = 7.05, P = 0.013, Cohen's d = 1.00, Bf in favour of the alternative = 4.57). Bonferroni's *post hoc* test revealed higher NID in two- compared to one-stream percept in the BC window ($F_{1,28}$ = 7.49, P = 0.011, Cohen's d = 1.03, Bf in favour of the alternative = 5.41) (Figure 3a) and a similar pattern in the AC window, showing higher NID values for two-streams than one-stream percept ($F_{1,28}$ = 6.64, P = 0.016, Bf in favour of the alternative = 3.88, Cohen's d = 0.97) (Figure 3a). These results show that the phenomenologically differentiated percept exhibits higher neurophysiological differentiation than the phenomenologically integrated one.

Like in the case of NII_{γ}, information differentiation did not change between percepts in the exogenous condition (B.C: $F_{1,28}$ = 0.84, P = 0.366, Bf in favour of the null = 2.66; A.C: $F_{1,28}$ = 1.94, P = 0.174, Bf in favour of the null = 1.68) (Figure 3b). Furthermore, no differences were observed in the mean level of NII between endogenous and exogenous conditions ($F_{1,28}$ = 1.39, P = 0.248, Bf in favour of the null =

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2.12) or between windows ($F_{1,28}$ = 0.15, P = 0.228, Bf in favour of the null = 3.53), indicating that the overall information differentiation within the frontoparietal network was similar across conditions. Finally, no triple interaction was observed in NII between temporal electrodes (right and left hemispheres) ($F_{1,28}$ = 3.59, P = 0.069; Bf in favour of the null = 0.86) (Supplementary Figure 3). In agreement with the wSMI results, this index of information complexity dissociated endogenous percepts. However, NID showed an opposite pattern compared to NII in the directions of the effects between one and two streams, suggesting that NID is capturing a different but complementary aspect of neural information dynamics associated with conscious percepts.

Information integration and differentiation in direct cortical recordings (LFP)

In order to validate these findings (in a similar manner as we performed elsewhere (Canales-Johnson et al., 2015), we repeated the experiment in a patient implanted with intracranial electrodes for epilepsy surgery. We benefited from the high spatial resolution of intracranial recordings, which allowed us to directly test the hypothesis that it is specifically the information sharing between frontal and parietal areas that differentiates between the two auditory percepts. We computed NII_{γ} on direct cortical recordings (local field potentials; LFP) between the superior parietal lobe (SPL) and middle frontal gyrus (MFG) obtained from the intracranial patient performing the same task as above (Figure 4a-c). As in the healthy participants, the RANOVA showed a triple interaction between (endogenous, exogenous), window (before change, after change), and percept (one stream, two-streams) for NII_{γ} ($F_{1,56}$ = 36.02, P < 0.001, Cohen's d = 1.73, Bf in favour of the alternative > 100). Simple effects within the BC window showed higher NII_{γ} for one- compared to two-streams percept in the endogenous ($F_{1,56}$ = 18.96, P < 0.001, Cohen's d = 1.24, Bf in favour of the alternative > 100) (Figure 4b) but not the exogenous condition ($F_{1,56}$ = 0.84, P = 0.362, Bf supporting the null = 3.43) (Figure 4c). In the case of the AC window, one-stream percept again showed higher NII_{γ} than two-streams percept in the endogenous ($F_{1,56}$ = 6.20, P = 0.016, Bf supporting the alternative = 3.10) (Cohen's d = 0.70, Figure 4b) but not in the exogenous condition ($F_{1,56}$ = 0.33, P = 0.857, Bf in favour of the null = 4.31) (Figure 4c). Furthermore, no differences were found between these percepts in the same LFP recordings within the alpha band (NII_{α}) ($F_{1,56}$ = 0.58, P = 0.569, Bf in favour of the null = 3.84) (Supplementary Figure 4).

Next, we investigated NID dynamics on LFP signals in the intracranial patient within SPL and MFG (Figure 4d,e). Again, RANOVA showed a triple interaction between (endogenous, exogenous), window (before change, after change), and percept (one stream, two streams) ($F_{1,56}$ = 8.32, P = 0.008, Cohen's d = 1.13, Bf in favour of the alternative = 7.67). In agreement with the scalp EEG results, simple effects analysis within the BC window showed higher NID for the phenomenologically differentiated percept compared to phenomenologically integrated percept in the endogenous ($F_{1,56}$ = 19.08, P < 0.001,

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Cohen's d = 1.71, Bf in favour of the alternative > 100) (Figure 4d) but not in the exogenous condition ($F_{1,56}$ = 2.10, P = 0.159, Bf in favour of the null = 1.97) (Figure 4e). In the case of the AC window, two-streams percept again showed higher NID than one-stream percept in the endogenous ($F_{1,56}$ = 10.57, P = 0.003, Cohen's d = 1.27, Bf in favour of the alternative = 20.15) (Figure 4d) but not in the control (exogenous) condition ($F_{1,56}$ = 0.49, P = 0.488, Bf in favour of the null = 4.02) (Figure 4e). These findings demonstrate strong convergent evidence between scalp EEG and direct cortical recordings, further supporting the hypothesis that phenomenology goes along with neurophysiology of conscious percepts, specifically indexed by the frontoparietal ongoing activity.

Oscillatory integration of frontoparietal ongoing activity

Finally, we evaluated the theoretical prediction that information dynamics but not oscillatory dynamics of brain activity underpins the emergence of conscious percepts (Koch et al., 2016). Thus, we investigated whether neural oscillatory integration (NOI) of ongoing activity might also capture the dynamics of auditory bistability. Specifically, we investigated whether frontoparietal gamma phase synchronization (Weighted Phase-Lag Index ($wPLI_\gamma$)) could differentiate between endogenous percepts. Unlike NII_γ, RANOVA revealed no triple interaction between condition (endogenous, exogenous), window (before change, after change), and percept (one stream, two streams) for NOI_γ ($F_{(1,28)}$ = 0.12, P = 0.726, Bf in favour of the null = 3.58) (Figure 5a,b). However, a (weak) significant interaction between condition (endogenous, exogenous) and window (before change, after change) was found ($F_{(1,28)}$ = 4.22, P = 0.049, Cohen's d = 0.77, Bf in favour of the alternative = 1.50) (Figure 5c,d). Bonferroni's *post hoc* test showed that NOI_γ significantly decreased in the AC window compared to the BC window in the endogenous ($F_{(1,28)}$ = 6.51, P = 0.016, Cohen's d = 0.93, Bf in favour of the alternative = 3.73) (Fig 5c) but not in the exogenous condition ($F_{(1,28)}$ = 1.47, P = 0.236, Bf in favour of the null = 2.04) (Figure 5d). Furthermore, the same null result for NOI_γ between percepts was observed in the intracranial patient (RANOVA (condition x window x percept): $F_{(1,56)}$ = 0.12; P = 0.726, Bf in favour of the null = 4.73) (Fig 6). As with the scalp EEG, the intracranial patient showed an interaction between condition and window ($F_{(1,56)}$ = 13.51, P = 0.001, Cohen's d = 0.99, Bf in favour of the alternative = 68.09) in NOI_γ, showing a decrease in phase synchrony in the AC window compared to the BC window only in the endogenous condition (Bonferroni's *post hoc* test in endogenous condition: $F_{(1,56)}$ = 12.90, P = 0.001, Cohen's d = 0.96, Bf in favour of the alternative = 53.48; and exogenous condition: $F_{(1,56)}$ = 2.16, P = 0.147, Bf in favour of the null = 1.92) (Fig 6.d,e) between SPL and MFG electrodes. These findings suggest that oscillatory integration does not index the identity of auditory percepts but follows the duration of percept stability: phase synchrony maxima occur in the BC window (before the end of a stable percept) and phase synchrony minima in the AC window (just at the onset of percept stability).

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DISCUSSION

Here we demonstrate that only information dynamics in frontoparietal ongoing neural activity differentiates alternative conscious percepts during auditory bistability. By means of studying neural dynamics (EEG and direct cortical recordings), we show that empirically tractable measures of neurophysiological information integration and neurophysiological information differentiation go along with auditory percepts experienced either as phenomenologically integrated (one stream) or differentiated (two stream), respectively. Furthermore, phase synchronization of oscillatory gamma activity in the frontoparietal network does not differentiate between auditory percepts, nor it does the information between temporal networks.

Neural correlates of consciousness, information integration and differentiation.

Our results expand the understanding of the neural correlates of consciousness (NCC) (Koch et al., 2016) in several ways. First, our experimental findings directly support information-based theories of consciousness (Dehaene and Changeux, 2011; Dehaene et al., 2014; Tononi et al., 2016); in their current instantiation, the Integrated Information Theory (IIT) (Tononi et al., 2016) and the Global Neuronal Workspace Theory (GNWT) (Dehaene and Changeux, 2011) of consciousness emphasize both the role of information exchange in generating conscious percepts. Although both theories conceptualize information differently, their proposed empirical indices are based on classical Shannon-entropy information framework. Using these measures of information dynamics, our results show convergent evidence supporting both GNWT and IIT predictions by demonstrating a role of neural information in the emergence of contents of consciousness. The interpretation of these results is albeit different between the IIT and GNWT.

However, our results suggest a differential role of information integration vs. information differentiation in the emergence of conscious percepts. According to IIT, the neural activity associated with conscious percepts should reflect the joint presence of neurophysiological integration and neurophysiological differentiation. Under this theoretical framework, integration is expected – in principle – to be paralleled by differentiation of neural activity. Contrary to this prediction, our results show dissociation between neurophysiological integration and neurophysiological differentiation of frontoparietal ongoing activity. Interestingly, while the phenomenologically integrated percept (one stream) showed a relative increase in NII and relative decrease in NID, the perceptually differentiated percept (two streams) exhibited the opposite pattern, that is, a decrease in NII and increase in NID. Together, these dissociated patterns suggest that each measure is instead directly associated with the phenomenology of conscious percepts: whereas information integration of neural activity is capturing

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phenomenological integration (one-stream percept), information differentiation may be capturing phenomenological differentiation (two-streams percept).

Second, we demonstrate a potential mechanistic role of information integration and differentiation in the formation of conscious percepts. Why do these measures capture the neural dynamics of conscious percepts? Coordination in the brain has been classically studied by computing phase synchronization between neural oscillations (Uhlhaas et al., 2009; Engel et al., 2013). Synchronization is a highly-ordered form of neural coordination that primarily captures the linear (or proportional) phase relationship between signals at specific frequencies (phase-locking). Thus, a mechanism of coordination-by-synchrony captures only certain regimes of neural coordination that are periodic. However, brain dynamics exhibits both a tendency to integrate information (synchronization) and a tendency for the components to differentiate information (independent function) (Dehaene and Changeux, 2011; Tognoli and Kelso, 2014; Tononi et al., 2016). During auditory bistability, conscious percepts typically alternate continuously without becoming locked into any one percept for long periods. We propose that underlying this dynamical process are ensembles of neurons that are repeatedly assembled and disassembled, and that this non-trivial dynamic might be instantiated by a mechanism of coding-by-information that captures complex, nonlinear patterns of neural activity and not merely simple proportional associations between neural signals.

Interestingly, NII dynamics suggest that integrating two tones into a single perceptual stream requires higher information-sharing than integrating two tones into two separate streams. What exactly is it about integrating A and B tones (one-stream percept) that requires higher information sharing than perceptually grouping an A tone with subsequent A tones (and B tones with subsequent B tones, i.e. two-streams percept)? Some theories of streaming (Fishman et al., 2001) propose that for tones sufficiently close in frequency, integration is the default (initial) percept because overlapping neural populations respond to the two tones, until adaptation gives rise to a separation in these populations (and a corresponding emergence of two auditory streams). Arguably, once those two streams have emerged, more information sharing would be required across those neural populations to re-integrate them into a one-stream percept. Conversely, NID dynamics suggest that neural information of the two-streams percept is more differentiated than neural information associated with one-stream percept. What is it about segregating A and B tones into two parallel streams (two-streams percept) that requires higher neurophysiological differentiation than integrating them (one-stream percept)? Following the abovementioned rationale, a higher variety of information patterns are expected across neural populations responding to each individual tone as compared to an overlapping neural population responding to the two tones (A and B).

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Conscious auditory percepts and ongoing neural activity.

The frontoparietal patterns of neural information are a manifestation of the interaction between the external stimulation and the endogenous, ongoing brain activity, as opposed to activation purely imposed by the auditory stimuli. Thus, NII and NID patterns do not merely reflect stimulus-driven neural activity but rather the intrinsic coordination of endogenous frontoparietal neural activity. Indeed, in the endogenous condition of our study, internally generated changes in neural activity triggered changes in conscious percepts in the complete absence of any change in the auditory stimuli. In line with our results, recent studies in the visual system have shown that long-distance integration of ongoing oscillations reflects internally coordinated activity associated with conscious perception (Hipp et al., 2012; Engel et al., 2013; Helfrich et al., 2016). Here, by directly measuring the amount of information integration and information differentiation contained in the ongoing neural activity, we demonstrate a functional role of information dynamics in the emergence of auditory conscious percepts and in general in perceptual integrative processes

Although the pioneering electrophysiological studies supporting the active role of ongoing activity in perception and cognition date from the 70's (Freeman, 1976, 2000), over the last decade ongoing brain activity has been mainly studied in the context of "resting state networks" (Fox and Raichle, 2007). In these recent studies, fluctuations in ongoing activity between spatially segregated networks (brain regions) are correlated when a participant is not performing an explicitly defined task. In the present study, by taking advantage of the high temporal resolution of EEG and direct cortical recordings, we show that patterns of neural information are transiently coordinated during the active discrimination of internally generated auditory percepts. Furthermore, our results also allowed us to differentiate the contribution of information in frequency-space, showing that gamma but not alpha NII differentiates auditory percepts during bistable perception.

Auditory bistable perception and frontoparietal activity.

Our results also suggest a fruitful new approach to conceptualizing and investigating auditory bistable perception. We demonstrate that the dynamics of auditory conscious percepts can be associated with the long-distance coordination of neural activity. Previous neural signatures of auditory bistability have mainly been identified in sensory cortices; in our report we demonstrate a role of long-distance sharing of neural information across associative, frontoparietal areas. One possibility is that this network activity reflects attention being drawn to (or directed to) subsets of the sounds; such processes are known to influence the perceptual organization of ABA… sequences (Carlyon et al., 2001; Snyder et al., 2006; Billig and Carlyon, 2015). Alternatively, it may instantiate the ongoing (and automatic) prediction of upcoming sounds based on patterns extracted from earlier stimulation, as

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has been proposed in theories that consider auditory perceptual objects as generative models (Winkler and Schröger, 2015).

These findings provide convergent evidence about the role of frontoparietal networks in the dynamics of formation and maintenance of the contents of consciousness. Research in visual bistability has focused on characterizing content-related activity predominantly in local brain areas or networks (Sterzer et al., 2009). Of those few studies that have expanded their scope to associative cortices and wider networks, one has recently proposed mechanistic accounts on visual percepts using multivariate pattern analysis (MVPA) of fMRI data (Wang et al., 2013). The results showed differential patterns of BOLD activity in high-order frontoparietal regions between visual percepts during bistable perception. The present study complements these results by showing a role for the frontoparietal network in indexing percepts in the auditory modality. Furthermore, the temporal resolution of our EEG and LFP data enabled us to characterize the fine-grained temporal dynamics of neural information integration associated with specific auditory percepts within the frontoparietal network. These results represent convergent evidence towards a possible general mechanism of information integration underlying the emergence of the contents of consciousness under invariant stimulation.

In conclusion, we have presented experimental evidence that conscious percepts may require both information integration and differentiation of ongoing neural activity in order to emerge. We have also highlighted the stark differences between fleeting endogenous percepts, where neurophysiological integration and differentiation parallel the corresponding integrated and differentiated percepts, and those that are externally triggered, for which no differences between these measures were observed. Importantly, the conceptual mapping between phenomenology and the neurophysiology that we have highlighted here should be considered as a fruitful approach for measuring the different dimensions of phenomenology in an experimentally testable manner, in light of some of the main current theoretical framework of conscious perception (IIT and GNWT).

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Materials and Methods

Healthy participants and patient

Twenty-nine right-handed healthy participants (14 males; mean ± SD age = 21.30 ± 2.2 years) and one left-handed epileptic patient (female; 29 years) gave written informed consent to take part in the experiment. The study was approved by the institutional ethics committee of the Faculty of Psychology of Universidad Diego Portales (Chile) and the Institutional Ethics Committee of the Hospital Italiano de Buenos Aires, Argentina, in accordance with the Declaration of Helsinki. The patient suffered from drug-resistant epilepsy from the age of 8 years and was offered surgical intervention to alleviate her intractable condition. Drug treatment at the time of implantation included 600 mg/d oxcarbazepine, 200 mg/d topiramate, and 750 mg/d levetiracetam. Computed tomography (CT) and magnetic resonance imaging (MRI) scans were acquired after insertion of depth electrodes. The patient took part in the current study one day before the surgery. She was attentive and cooperative during testing, and her cognitive performance before and one week after the implantation was indistinguishable from healthy volunteers. The patient was specifically recruited for this study because she was implanted with electrodes covering frontal and parietal regions.

Stimuli

In the endogenous condition, a high-frequency pure tone A alternated with a low-frequency pure tone B, in a repeating ABA- pattern. The frequency of A was 587 Hz and that of B was 440 Hz (5 semitones difference). The duration of each tone was 120 ms. The silence ('-') that completed the ABA… pattern was also 120 ms long, thus making the A tones isosynchronous (Pressnitzer and Hupé, 2006). In the exogenous (control) condition, the ABA- pattern alternated with an AB-- pattern. This second pattern had the same parameters (frequencies and duration) and same silence duration as the ones used for the endogenous condition (ABA- pattern). Duration of both patterns (ABA- and AB--) were randomly set between 4-8 seconds, which suppressed the effect of endogenous bistability, and ABA- was most often perceived as a one stream, whereas AB-- as two streams.

For both experimental conditions, the auditory stimuli consisted of 4 min long sequences. Each sequence was presented 12 times per condition with a 30 second pause between sequences. Stimuli were presented binaurally using Etymotics ER-3A earphones, and the sound level was individually adjusted to a comfortable level. The order of experimental conditions was counterbalanced between participants.

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Experimental conditions

There were two experimental conditions. In the endogenous condition (bistability), we used a bistable auditory stimulus(Carlyon et al., 2001),(Gutschalk et al., 2005),(Pressnitzer and Hupé, 2006). Participants listened to a pattern of three tones (ABA) separated by a silence ('-') (see Stimuli section below) that are experienced either as a one-stream percept or as a two-streams percept (Figure 1a). Participants were instructed to press a button with one hand when perceiving that one-stream percept had fully changed into two streams and a second button with the other hand when perceiving that two-streams percept had fully changed into one stream (Figure 1, middle panel). In the exogenous condition (control), participants listened to two alternating patterns of three (ABA) and two (AB) tones separated by a period of silence ('-') (see Stimuli section below). As in the endogenous conditions, participants were instructed to press a button with one hand when perceiving that ABA- had fully changed into AB- and another button with the other hand when pattern AB- had fully changed into ABA-. The exogenous condition allowed us to characterize the dynamics of neural activity specifically related to external changes in the stimuli (the two alternating patterns) and to contrast them with the dynamics of internal neural activity elicited by the endogenous condition (bistability). The endogenous and exogenous conditions used physically similar stimuli, as described in the next section, with the latter sometimes having one fewer A tone. Because the analysis windows were not time-locked to the stimuli, differences in the evoked responses to specific tones are unlikely to account for the observed pattern of results.

Electroencephalography (EEG) recordings, pre-processing and analysis

EEG signals were recorded with 128-channel HydroCel Sensors using a GES300 Electrical Geodesic amplifier at a sampling rate of 500 Hz using the NetStation software. During recording and analyses, the electrodes' average was used as the reference electrode. Two bipolar derivations were designed to monitor vertical and horizontal ocular movements. Following Chennu *et al* (Chennu et al., 2014), data from 92 channels over the scalp surface were retained for further analysis. Channels on the neck, cheeks and forehead, which reflected more movement-related noise than signal, were excluded. Eye movement contamination and other artefacts were removed from data before further processing using an independent component analysis(Delorme and Makeig, 2004). All conditions yielded at least 91% of artefact-free trials. Trials that contained voltage fluctuations exceeding ± 200 µV, transients exceeding ± 100 µV, or electro-oculogram activity exceeding ± 70 µV were rejected. The EEGLAB MATLAB toolbox was used for data pre-processing and pruning(Delorme and Makeig, 2004). MATLAB open source software FieldTrip (Oostenveld et al., 2011) and customized scripts were used for

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calculating weighted symbolic mutual information (wSMI), K complexity and weighted phase lag index (wPLI).

Local field potential (LFP) recordings and pre-processing

Direct cortical recordings were obtained from semi-rigid, multi-lead electrodes that were implanted in the patient. The electrodes had a diameter of 0.8 mm and consisted of 5, 10 or 15 contact leads that were 2-mm wide and 1.5-mm apart (DIXI Medical Instruments). The electrode strips were implanted in different regions of the frontal, temporal, central and parietal cortices and subcortical structures. For the purposes of the current study, local field potentials (LFP) were analysed from the left middle frontal gyrus and left superior parietal lobe. MNI coordinates of the depth electrodes were obtained from MRI and CT images using SPM (Friston, 2006) and MRIcron (Rorden and Brett, 2000) software. The recordings were sampled at 1024 Hz and down-sampled to 500 Hz for further analysis. The exact MNI coordinates and cortical regions of the selected electrodes are reported in Supplementary table 1. Open-source BrainNet Viewer software was used for visualization of selected electrodes (Xia et al., 2013).

Analysis of ongoing neural activity

A classical experimental approach for studying endogenous, or “ongoing” activity in the EEG related to internal fluctuations during cognitive tasks is by analysing the EEG window before the onset of motor responses when participants report internal changes. This approach has been used for studying neural signatures of conscious awareness, such as in bistable perception(Parkkonen et al., 2008), binocular rivalry (Doesburg et al., 2005)·(Frässle et al., 2014) and intrusions of consciousness (Noreika et al., 2015). Here, ongoing EEG and LFP activity (not time-locked to stimuli) preceding the onset of each response (button press) was analysed in terms of connectivity (wSMI and wPLI) and complexity (K complexity).

Window size selection was based on the following procedure. In the exogenous condition, we calculated the mean reaction times in the group of healthy participants (M = 1342 ms; SD = 101 ms). Then, in the endogenous condition, we calculated the minimum temporal gap between responses such that epochs would not overlap (2500 ms). Since mean reaction times in the exogenous condition corresponded to roughly half of the minimal window size of the endogenous condition, we selected a 2500 ms window for both conditions (from -2500 to 0 ms relative to button press) (Figure 1, lower panel). Importantly, this window included the onset of the exogenous auditory patterns ('ABA-' and 'AB--'), making the exogenous and endogenous conditions comparable from a stimulus perspective.

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The same procedure was repeated for the intracranial data (reaction times in the exogenous condition: M = 1380 ms, SD = 79 ms; window size in the endogenous conditions: 2500 ms).

For statistical analyses (see below), two time windows of 500 ms were selected based on the exogenous condition. A window after the change between auditory percepts (after-change window (AC)) was defined based on the mean reaction times at the group level (from -1342 to -842 ms). A second time window was defined at the epoch onset (before-change window (BC); from -2500 to -2000 ms). The rationale behind both time windows latencies was to select the periods when both externally driven percepts remained stable. The same window lengths and latencies were used for the endogenous condition (Figure 1).

Phase synchronization

We quantified phase coherence between pairs of electrodes as a measure of dynamical linear coupling among signals oscillating in the same frequency band. Phase synchronization analysis proceeds into two steps: (i) estimation of the instantaneous phases and (ii) quantification of the phase locking.

Estimation of the instantaneous phases

To obtain the instantaneous phases φ of the neural signals, we used the Hilbert transform approach (Foster et al., 2016). The analytic signal $\xi(t)$ of the univariate measure $x(t)$ is a complex function of continuous time t defined as:

$$(1) \qquad \xi(t) = x(t) + ix_h(t) = a_\xi(t)e^{i\varphi_\xi(t)}$$

where the function $x_h(t)$ is the Hilbert transform of $x(t)$:

$$(2) \qquad x_h(t) = \frac{1}{\pi} P.V. \int_{-\infty}^{+\infty} \frac{x(t)}{t-\tau} d\tau$$

P.V. indicates that the integral is taken in the sense of Cauchy principal value. Sequences of digitized values give a trajectory of the tip of a vector rotating counterclockwise in the complex plane with elapsed time.

The vector norm at each digitizing step t is the state variable for instantaneous amplitude $a_\xi(t)$. This amplitude corresponds to the length of the vector specified by the real and imaginary part of the complex vector computed by Pythagoras' law and is equivalent to the magnitude of the observed oscillation at a given time and frequency point.

$$(3) \qquad a_\xi(t) = \sqrt{x(t)^2 + ix_h(t)^2}$$

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and the arctangent of the angle of the vector with respect to the real axis is the state variable for instantaneous phase $\varphi_x(t)$.

$$(4) \qquad \varphi_x(t) = arctg\,\frac{ix_h(t)}{x(t)}$$

The instantaneous phase $\varphi_x(t)$ of $x(t)$ is taken equal to $\varphi_\xi(t)$. Identically, the phase $\varphi_y(t)$ is estimated from $y(t)$. This phase is thus the angle of the vector specified by the real and imaginary components. For a given time and frequency point, it corresponds to a position inside the oscillation cycle (peak, valley, rising, or falling slope).

The instantaneous phase, although defined uniquely for any kind of signal to which the Hilbert transform can be applied, is difficult to interpret physiologically for broadband signals. For this reason, a standard procedure is to consider only narrow-band phase synchronization by estimating an instantaneous phase for successive frequency bands, which are defined by band-pass filtering the time series(Le Van Quyen et al., 2001). Thus, for each trial and electrode, the instantaneous phase of the signal was extracted at each frequency of the interval 1- 60 Hz (in 1-Hz steps) by computing the Hilbert transform using a zero phase shift non-causal finite impulse filter.

Neural oscillatory integration: weighted phase lag index (wPLI)

Phase synchronization is often calculated from the phase or the imaginary component of the complex cross-spectrum between the signals measured at a pair of channels. For example, the well-known Phase Locking Value (PLV) (Lachaux et al., 1999) is obtained by averaging the exponential magnitude of the imaginary component of the cross-spectrum. However, such phase coherence indices derived from EEG data are affected by the problem of volume conduction, and as such they can have a single dipolar source, rather than a pair of distinct interacting sources, producing spurious coherence between spatially disparate EEG channels. The Phase Lag Index (PLI), first proposed by Stam *et al* (Stam et al., 2007) attempts to minimize the impact of volume conduction and common sources inherent in EEG data, by averaging the signs of phase differences, thereby ignoring average phase differences of 0 or 180 degrees. This is based on the rationale that such phase differences are likely to be generated by volume conduction of single dipolar sources. However, despite being insensitive to volume conduction, PLI has a strong discontinuity in the measure, which causes it to be maximally sensitive to noise.

The Weighted Phase Lag Index (wPLI) (Vinck et al., 2011) addresses this problem by weighting the signs of the imaginary components by their absolute magnitudes. Further, as the calculation of wPLI

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also normalises the weighted sum of signs of the imaginary components by the average of their absolute magnitudes, it represents a dimensionless measure of connectivity that is not directly influenced by differences in spectral or cross-spectral power. For these reasons, we employed the wPLI measure to estimate connectivity in our data. The wPLI index ranges from 0 to 1, with value 1 indicating perfect synchronization (phase difference is perfectly constant throughout the trials) and value 0 representing total absence of synchrony (phase differences are random). For each trial and pair of electrodes, wPLI was estimated using a 500 ms sliding window with 2 ms time step, i.e. with a 96% overlap between two adjacent windows.

Neural information integration: weighted symbolic mutual information (wSMI)

In order to quantify the coupling of information flow between electrodes we computed the weighted symbolic mutual information (wSMI) (King et al., 2013; Sitt et al., 2014). It assesses the extent to which the two signals present joint non-random fluctuations, suggesting that they share information. wSMI has three main advantages: (i) it allows for a rapid and robust estimation of the signals' entropies; (ii) it provides an efficient way to detect non-linear coupling; and (iii) it discards the spurious correlations between signals arising from common sources, favouring non-trivial pairs of symbols. For each trial, wSMI is calculated between each pair of electrodes after the transformation of the EEG and LFPs signals into sequence of discrete symbols discrete symbols defined by the ordering of k time samples separated by a temporal separation τ (King et al., 2013). The symbolic transformation depends on a fixed symbol size (k = 3, that is, 3 samples represent a symbol) and a variable τ between samples (temporal distance between samples) which determines the frequency range in which wSMI is estimated(Sitt et al., 2014). In our case, we chose τ = 32 and 6 ms to isolate wSMI in alpha ($wSMI_{\alpha}$) and gamma ($wSMI_{\gamma}$) bands respectively. The frequency specificity *f* of wSMI is related to k and τ as:

$$f = 1000 / (\tau * k)$$

As per the above formula, with a kernel size k of 3, τ values of 32 and 6 ms hence produced a sensitivity to frequencies near 55 Hz (gamma) and 10 Hz (alpha) range, respectively.

wSMI was estimated for each pair of transformed EEG and LFPs signals by calculating the joint probability of each pair of symbols. The joint probability matrix was multiplied by binary weights to reduce spurious correlations between signals. The weights were set to zero for pairs of identical symbols, which could be elicited by a unique common source, and for opposite symbols, which could reflect the two sides of a single electric dipole. wSMI is calculated using the following formula:

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$$wSMI(X,Y) = \frac{1}{\log(k!)} \sum_{x \in X} \sum_{y \in Y} w(x,y)\, p(x,y) \log\left(\frac{p(x,y)}{p(x)p(y)}\right)$$

where *x* and *y* are all symbols present in signals *X* and *Y* respectively, w*(x,y)* is the weight matrix and *p(x,y)* is the joint probability of co-occurrence of symbol *x* in signal *X* and symbol *y* in signal *Y*. Finally, *p(x)* and *p(y)* are the probabilities of those symbols in each signal and *K*! is the number of symbols - used to normalize the mutual information (MI) by the signal's maximal entropy. Temporal evolution of wSMI was calculated using a 500 ms sliding window with 2 ms time step, i.e. with a 96% overlap between two adjacent windows.

Neural information differentiation: Kolmogorov-Chaitin complexity (K complexity)

Kolmogorov-Chaitin complexity quantifies the algorithmic complexity (Kolmogorov, 1965; Chaitin, 1974) of an EEG signal by measuring its degree of redundancy (Sitt et al., 2014; Schartner et al., 2015, 2017). Algorithmic complexity of a given EEG sequence can be described as the length of shortest computer program that can generate it. A short program corresponds to a less complex sequence. K complexity was estimated by quantifying the compression size of the EEG using the Lempel-Ziv zip algorithm (Lempel and Ziev, 1976).

Algorithmic information theory has been introduced by Andreï Kolmogorov and Gregory Chaitin as an area of interaction between computer science and information theory. The concept of algorithmic complexity or Kolmogorov-Chaitin complexity (K complexity) is defined as the shortest description of a string (or in our case a time series *X*). That is to say, K complexity is the size of the smallest algorithm (or computer program) that can produce that particular time series. However, it can be demonstrated by *reductio ad absurdum* that there is no possible algorithm that can measure K complexity (Chaitin, 1995). To sidestep this issue, we can estimate an upper-bound value of K complexity(*X*). This can be concretely accomplished by applying a lossless compression of the time series and quantifying the compression size. Capitalizing on the vast signal compression literature, we heuristically used a classical open-source compressor gzip (Salomon, 2004) to estimate K complexity(*X*). It is important to standardize the method of representation of the signal before compression in order to avoid non-relevant differences in complexity. Specifically, to compute K complexity(*X*):

1. The time series were transformed into sequences of symbols. Each symbol represents, with identical complexity, the amplitude of the corresponding channel for each time point. The number of symbols was set to 32 and each one corresponds to dividing the amplitude range

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of that given channel into 32 equivalent bins. Similar results have been obtained with binning ranging from 8 to 128 bins (Sitt et al., 2014).

2. The time series were compressed using the compressLib library for Matlab, this library implements the gzip algorithm to compress Matlab variables.
3. K complexity(*X*) was calculated as the size of the compressed variable with time series divided by the size of the original variable before compression. Our premise is that, the bigger the size of the compressed string, the more complex the structure of the time series, thus potentially indexing the complexity of the electrical activity recorded at a sensor.

For each trial and channel, K complexity was estimated using a 500 ms sliding window with 2 ms time step, i.e. with a 96% overlap between two adjacent windows.

EEG electrode cluster analysis and epoch correction

Clusters of electrodes were selected for complexity analysis and connectivity analysis (wPLI and wSMI) by selecting the canonical frontal, parietal, right-temporal and left-temporal electrodes. In the case of spectral power analysis, power values within frontal and parietal electrodes were averaged per condition and participant. In the case of frontoparietal wPLI, wSMI and K complexity analyses, we calculated the mean connectivity that every electrode of the frontal cluster shared with every electrode of the parietal cluster. Connectivity values between pairs of electrodes and between parietal pairs of parietal electrodes were discarded from the analysis. Similarly, in the case of temporotemporal connectivity analyses, we calculated the mean connectivity that every electrode of the of the right-temporal cluster shared with every electrode of the left-temporal cluster, discarding connectivity values within pairs of right-temporal electrodes and pairs of left-temporal electrodes. This procedure allows us to specifically test the role of long-distance interactions (frontoparietal and temporotemporal) during bistable perception. K complexity, wSMI and wPLI values of the corresponding regions of interest were averaged per condition and participant.

In order to make both conditions comparable (endogenous vs exogenous), after transforming data into complexity (K complexity) and connectivity (wPLI and wSMI) time series and creating the corresponding electrode clusters, we subtracted the mean activity between -2500 to -700 ms from each data point per epoch and condition. Motor-related activity in the gamma band has been reported ~-200 ms before the button press during bistable perception (Basirat et al., 2008). Thus, although it is a common procedure to analyse response-evoked activity by correcting epochs using the mean of the entire window (Doesburg et al., 2005), we used a more conservative approach by baseline correcting each epoch from -2500 to -700 ms relative to the button press in order to avoid possible contamination due to motor-related artefacts.

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Statistical analysis

For K complexity, wPLI and wSMI analyses of EEG and LFPs data, repeated-measures ANOVA between conditions (endogenous, exogenous), window (before change, after change) and percept (one stream, two streams) were performed using Bonferroni corrections for *post hoc* comparisons, and Bayes Factors of the null and alternative hypothesis were reported (Masson, 2011; Jarosz and Wiley, 2014). Statistical analyses were performed using Statistical Product and Service Solutions (SPSS, version 20.0, IBM) and open-source statistical software JASP (JASP Team (2017), version 0.8.1.1).

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FIGURES

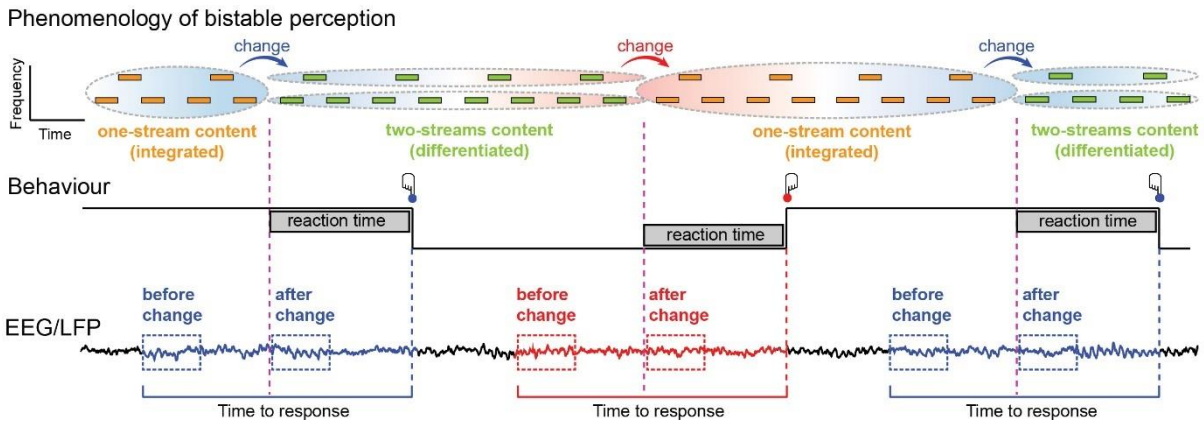

Figure 1. Experimental design and analysis of ongoing brain activity. *Top row*: Phenomenology during auditory bistable illusion. Participants listened to a series of tones of two different frequencies separated by a temporal gap (see Experimental Procedures). Tones are experienced either as one stream (phenomenologically integrated percept; orange blocks surrounded by one ellipse) or as two streams (phenomenologically differentiated percept; green blocks surrounded by two ellipses). Perceptual transitions occur either in the one-stream to two-streams direction (blue arrows and blue background) or in the two-streams to one-stream direction (red arrow and red background). *Middle row*: behavioural responses during the task. Participants pressed one button when perceiving that one-stream had fully changed into two-streams percept (blue button) and another button when perceiving that two-streams had fully changed into one-stream percept (red button). *Bottom row*: dynamical analyses and windows of interest for EEG and LFP signal analyses. Ongoing activity in during both transitions was calculated using a sliding window procedure on a fixed time window locked to the onset of the button press. Window size was calculated based on the mean reaction times (RT) in the exogenous condition (1342 ms), and the minimum duration between responses that guaranteed no overlap between RT (2500 ms) (see Experimental Procedures).

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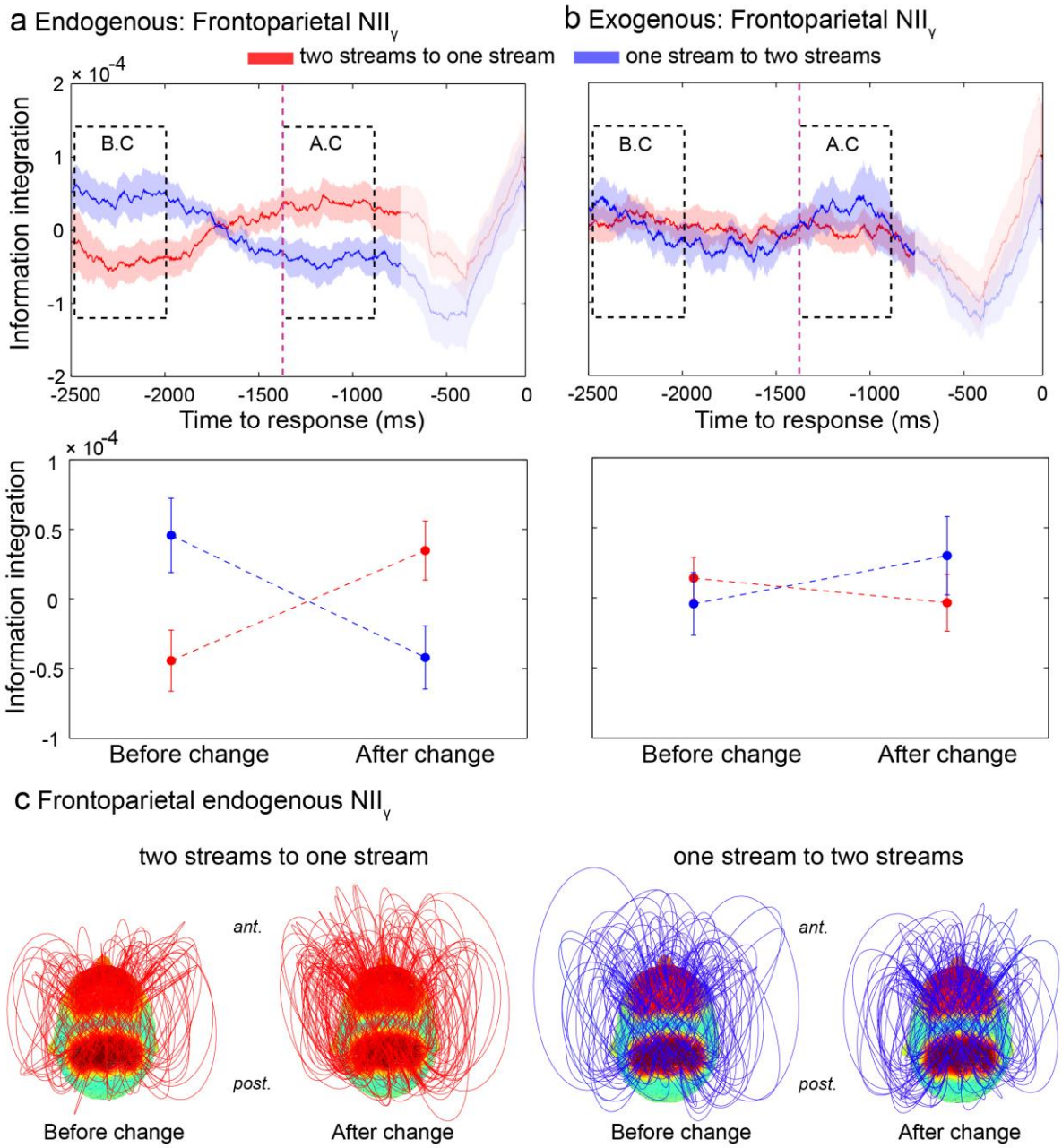

Figure 2. Frontoparietal NII dissociate alternative endogenous percepts during bistable perception. Neural dynamics of NII$_\gamma$ for transitions from two-streams to one-stream percept (red line) and from one-stream to two-streams percept (blue line) for the endogenous **(a)** and exogenous (control) conditions **(b)**. Purple dashed line marks the mean reaction time (1342 ms) of the exogenous (control) condition. Auditory percepts were directly compared in two windows of interest: the before-change (BC) and the after-change (AC) windows. **(c)** Connectivity topographies for the BC and AC windows for transitions from two-streams to one-stream percept (left panel) and from one-stream to two-streams percept (right panel) averaged over participants in the endogenous condition. Red areas on the scalp indicate regions of interest (frontal and parietal electrodes, see Experimental Procedures). The height of an arc connecting two nodes indicates the strength of the NII link between them. Values are time-

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locked to the button press (0 ms) and baseline corrected between -2500 and -700 ms relative to button press (see Experimental Procedures). Statistical analyses (bottom row) were computed on two pre-defined 500 ms windows: a BC window (-2500 to 2000 ms) and an AC window (-1342 ms to -842 ms). The onset of both windows was defined based on a control (exogenous) condition in which the stimuli physically change to generate two different percepts (see Experimental Procedures). Shaded bars (top row) and error bars (middle row) represent s.e.m.

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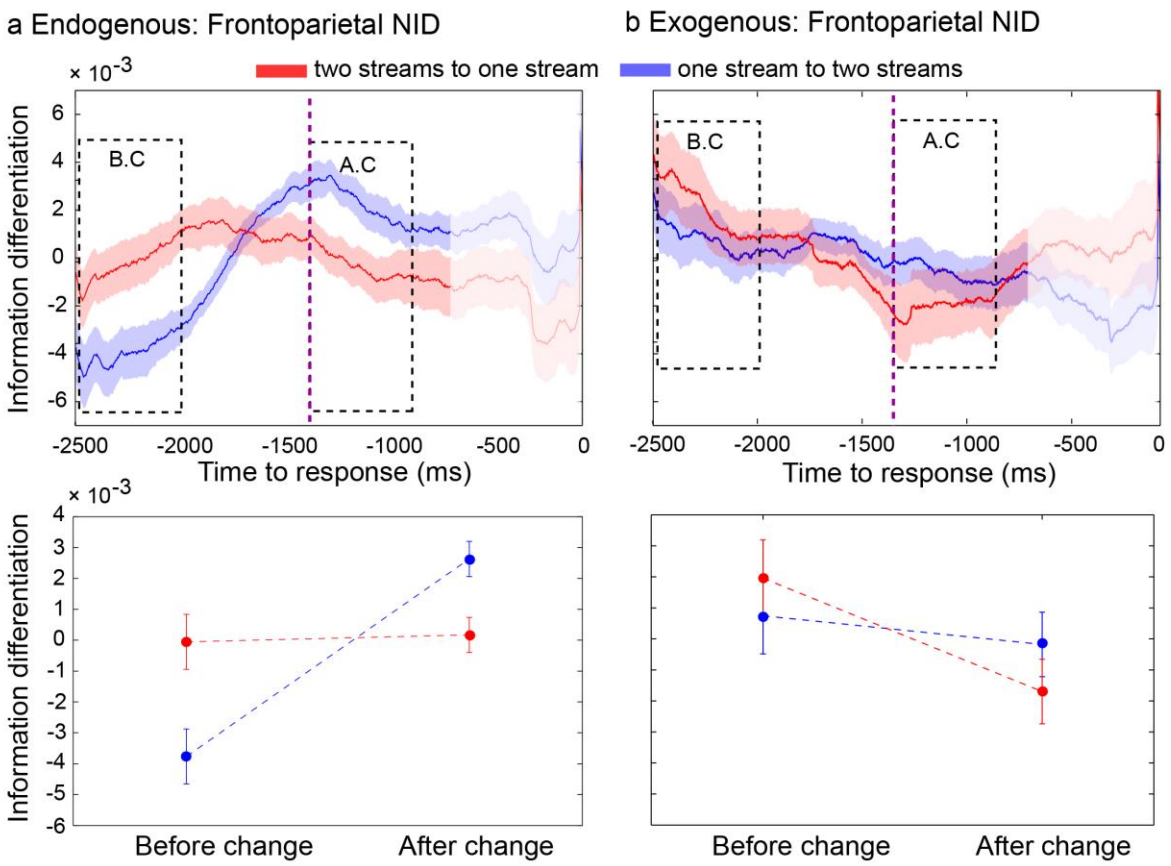

Figure 3. Frontoparietal NID dissociates alternative endogenous percepts during bistable perception. Neural dynamics of NID from two-streams to one-stream percept (red line) and from one-stream to two-streams percept (blue line) for the endogenous **(a)** and exogenous (control) conditions **(b)**. Purple dashed line marks the mean reaction time (1342 ms) of the exogenous (control) condition. Statistical analysis was performed as described in Figure 2. Shaded bars (top row) and error bars (bottom row) represent s.e.m.

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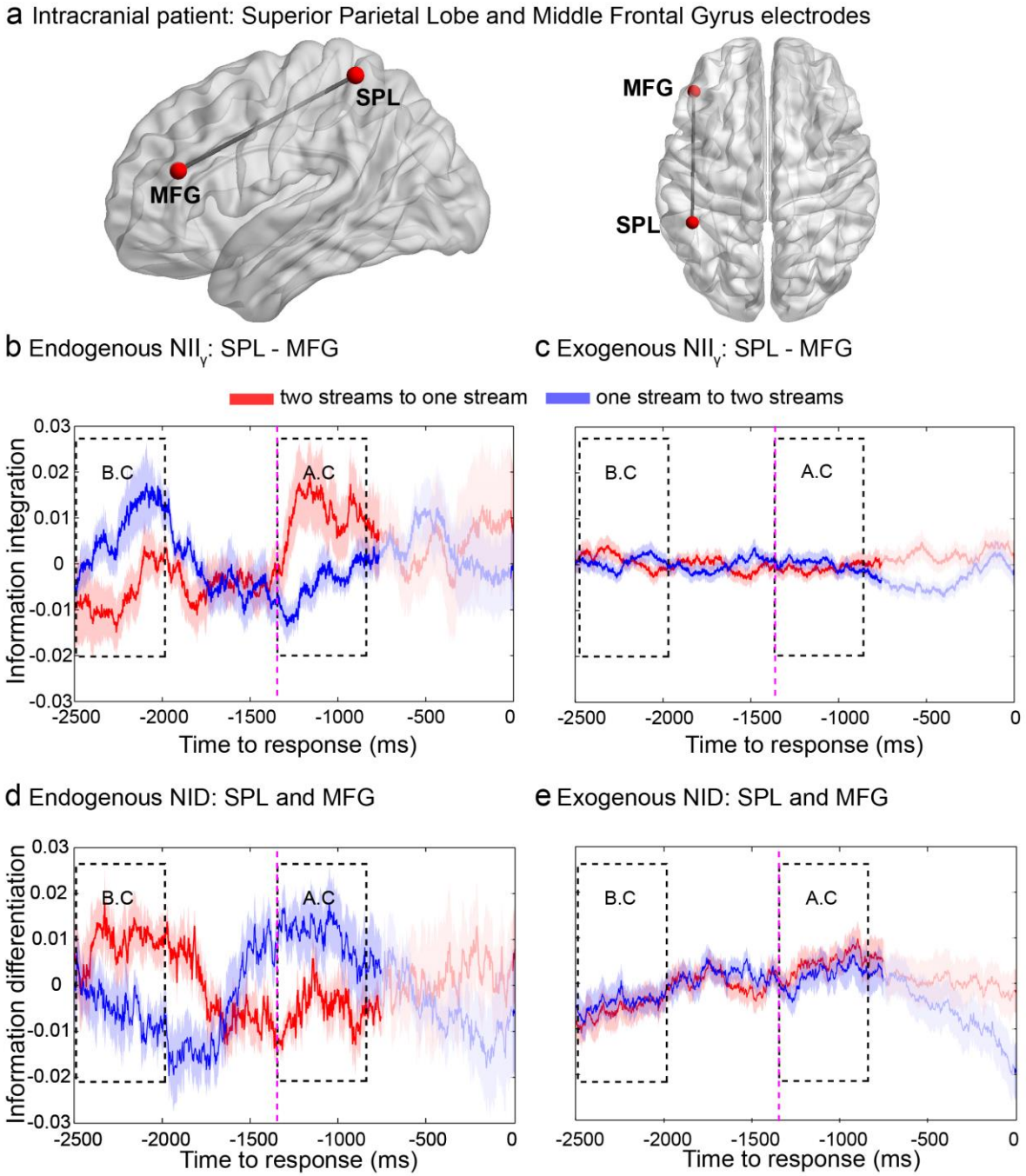

Figure 4. Frontoparietal NII and NID in local field potentials. (a) Electrodes were implanted in the left parietal lobe and left middle frontal gyrus (Supplementary table 1). Dynamics of ongoing NII_γ and NID of transitions from two-streams to one-stream percept (red line) and from one-stream to two-streams percept (blue line) in the endogenous **(b,d)** and exogenous **(c,e)** conditions, respectively. Purple dashed line marks the mean reaction time (1380 ms) of the exogenous (control) condition of the intracranial data. Statistical analyses were performed as explained in Figure 2. Shaded bars represent s.e.m.

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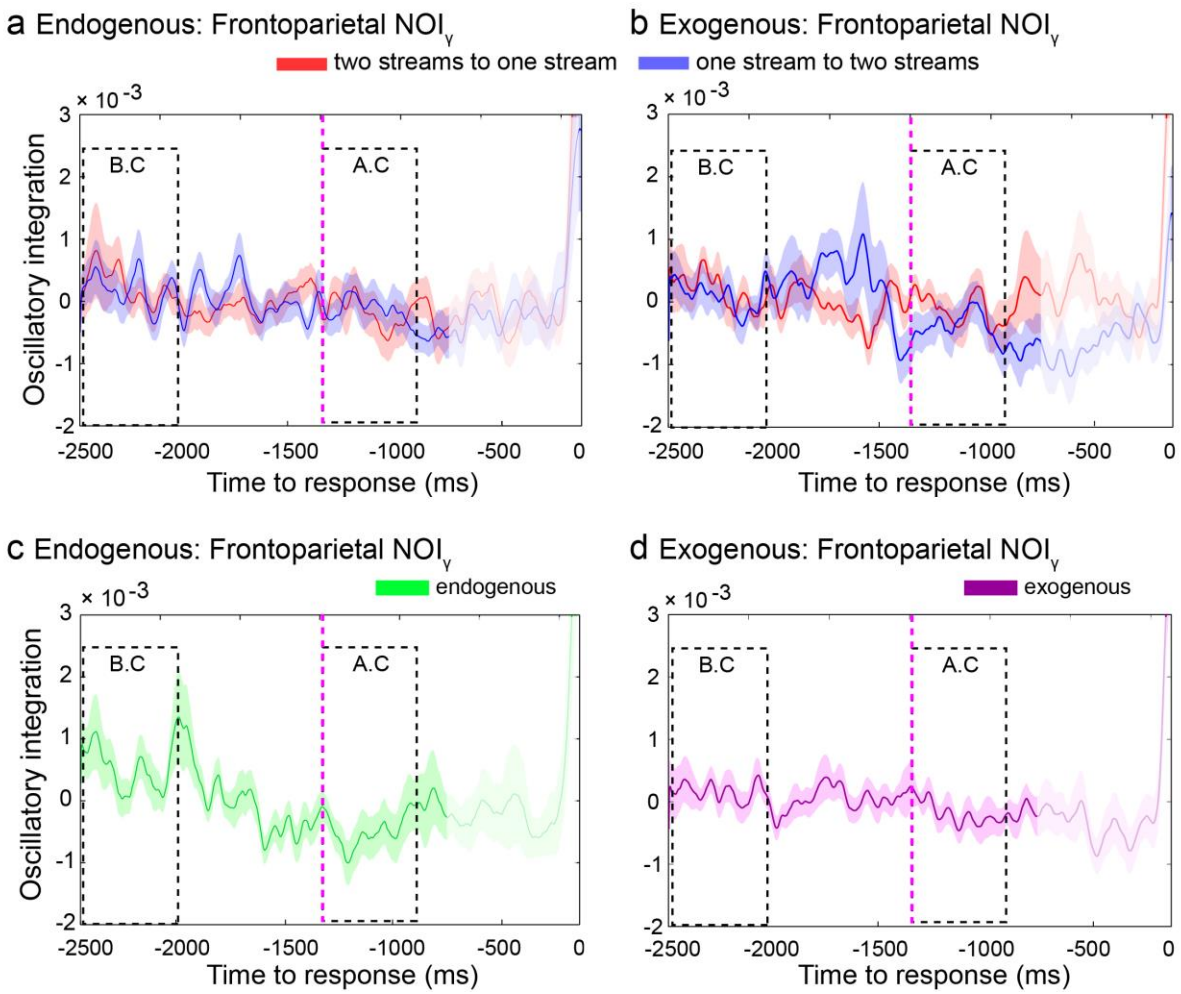

Figure 5. Frontoparietal NOI in the endogenous and exogenous conditions. Dynamics of ongoing NOI_γ from two-streams to one-stream percept (red line) and from one-stream to two-streams percept (blue line) for the endogenous **(a)** and exogenous **(b)** conditions. Ongoing NOI_γ during transitions in both directions in the endogenous **(c)** and exogenous **(d)**. Statistical analyses were performed as described in Figure 2. Shaded bars represent s.e.m.

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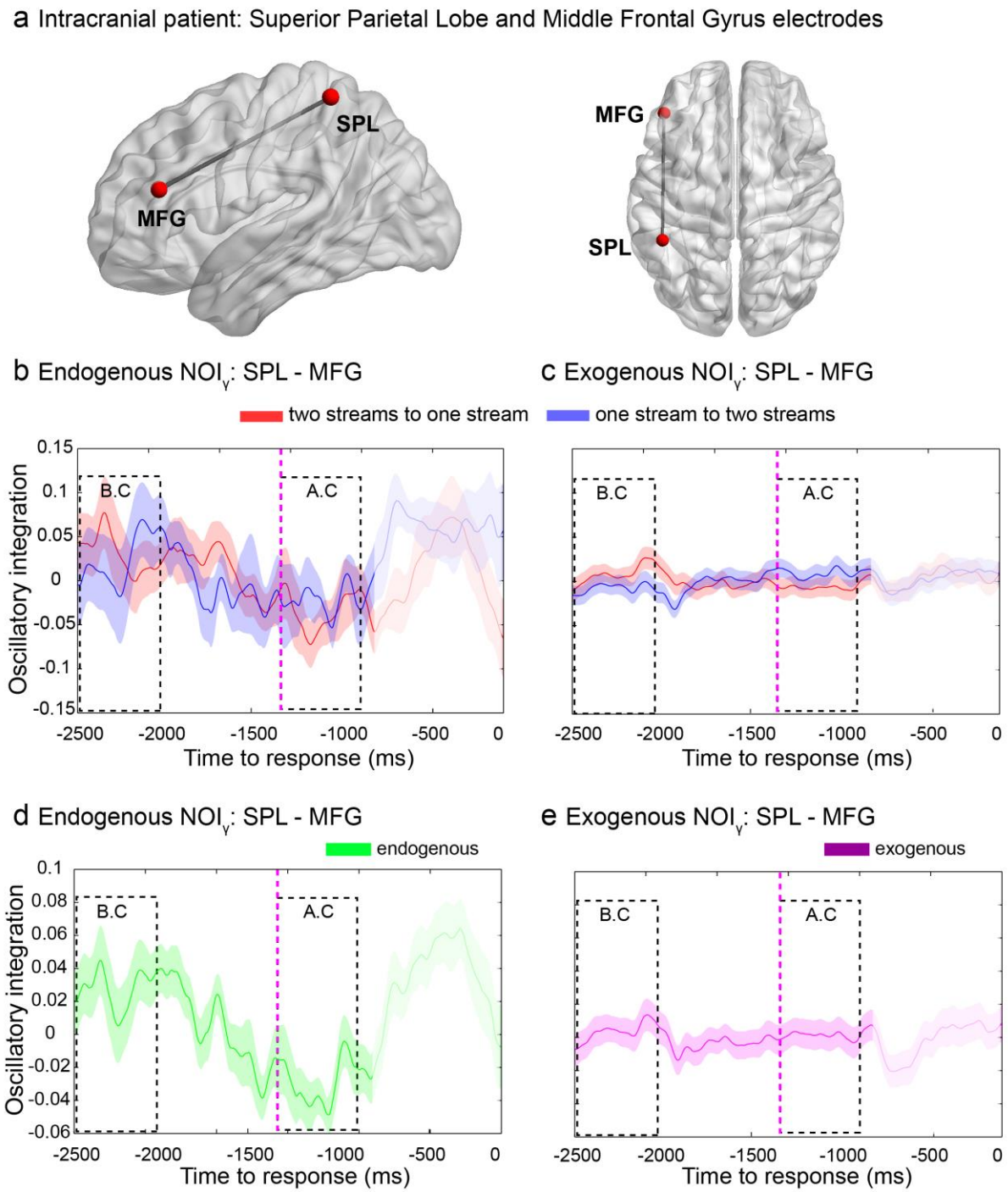

Figure 6. Frontoparietal NOI in local field potentials. (a) Intracranial electrodes implanted in the left parietal lobe and left middle frontal gyrus. Dynamics of ongoing NOI_γ for the perceptual reorganization of tones from two-streams to one-stream percept (red line) and from one-stream to two-streams percept (blue line) for the endogenous **(b)** and exogenous (control) conditions **(b)**. Ongoing NOI_γ during transitions in both directions in the endogenous **(c)** and exogenous **(d)**. Purple dashed line marks the mean reaction time (1380 ms) of the exogenous (control) condition of the intracranial data. Statistical analyses were performed as described in Figure 2. Error bars represent s.e.m.

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End notes

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Author's contributions

Conceived and designed the experiments: ACJ, TAB. Performed the experiments: ACJ, FO, AG, EM. Analysed the data: ACJ. Contributed reagents/materials/analysis tools: AB, SC. Gave access to clinical patient: MCG, WS, EV, CC. Wrote the paper: ACJ, AB, AI, VN, SC, TAB.

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Conflict of Interest

None declared.