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PARIETO-FRONTAL GAMMA BAND ACTIVITY DURING THE PERCEPTUAL EMERGENCE OF SPEECH FORMS

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ABSTRACT

The multistable perception of speech refers to the perceptual changes experienced while listening to a speech form cycled in rapid and continuous repetition, the so-called Verbal Transformation Effect. Because distinct interpretations of the same repeated stimulus alternate spontaneously, this effect provides an invaluable tool to examine how speech percepts are formed in the listener's mind. In order to track the temporal dynamics of brain activity specifically linked to perceptual changes, intracerebral EEG activity was recorded from two implanted epileptic patients while performing a verbal transformation task. To this aim, they were asked to carefully listen to a speech sequence played repeatedly and to press a button whenever they perceived a change in the repeated utterance. For both patients, 300-800 ms prior to the reported perceptual transitions, high frequency activity in the gamma band range (> 40 Hz) was observed within the left inferior frontal and supramarginal gyri. An additional auditory decision task was used to rule out the possibility that the increased gamma band activity was due to the patients' motor responses. These results suggest that articulatory-based representations play a key part in the endogenously driven emergence of auditory speech percepts. The findings are interpreted in relation to theories assuming a link between perception and action in the human speech processing system.

Keywords: Multistable perception, Verbal Transformation Effect, Perceptual awareness, Intracerebral EEG, Gamma band activity, Speech perception, Speech production.

INTRODUCTION

Multistable perception phenomena refer to the perceptual alternation between two or more mutually exclusive conscious interpretations of an unchanging sensory stimulation. Because different interpretations of the same stimulus alternate spontaneously, multistable perception provides a rare opportunity to examine the neural processes underlying endogenously driven conscious perception. In the visual domain, multistable perception has been described for a wide range of stimuli, such as ambiguous figures, binocular rivalry (e.g., Leopold and Logothetis, 1999, for a review). While adaptation or inhibition mechanisms at the sensory level have been suggested as the loci of multistable visual perception, perceptual alternation might also depend on an interplay between bottom-up, sensory and internal, top-down, neural processes (see Leopold and Logothetis, 1999; Kast, 2001; Blake and Logothetis, 2002, for a review). From this view, coordinated neuronal activations among widely distributed visual, parietal and frontal brain regions might be critical for perceptual awareness (Dehaene and Nacache, 2001; Crick and Koch, 2003).

Although multistable perception has been studied mainly in the visual modality, alternating perceptual interpretations of an unchanging auditory speech stimulus has also been reported, the so-called Verbal Transformation Effect (Warren and Gregory, 1958; Warren 1961). This effect refers to the perceptual changes experienced while listening to a speech stimulus cycled in rapid and continuous repetition. Initially, a percept matching the original form is heard, but at some point another percept suddenly arises. For example, the rapid repetition of the word “life” produces a perceptual transform into “fly”, “fly” back into “life” and so on. This transformation process persists throughout the repetition procedure, leading to perceptual

switches from one speech form to another (or back to the original form). Previous studies have reported that perceptual changes relative to the auditory input mainly range from auditory streaming/perceptual grouping (Pitt and Shoaf, 2001, 2002), to phonological (Warren, 1961; Warren and Meyers, 1987) and lexical transformations (Warren, 1961; Shoaf and Pitt, 2002). While verbal transformations have initially been studied as a pure auditory perceptual effect, they appear to occur also when subjects repeatedly utter the speech stimulus in both an overt and a covert mode (Reisberg et al., 1989; Smith et al., 1995; Sato et al., 2006). With this production procedure, the number of verbal transformations has been shown to gradually decrease from a condition of complete externalization to one of complete internalization, when subarticulation is blocked by a concurrent articulatory task, through a condition of partial externalization (i.e., whispering, mouthing; Reisberg et al., 1989). Sato and colleagues (2006) further showed that verbal transformations are specifically influenced by articulatory synergies. They analysed the stability of sequences i.e. the number of times a given sequence was not transformed and the attractivity, i.e. the number of times a sequence was selected as a transformation. They observed that both perceptual stability and attractivity of a sequence depend on articulatory constraints. In addition, the fact that verbal transformations may depend on articulatory constraints appears also consistent with the finding that a concurrent silent articulation decreases the number of reported perceptual changes while listening to a repeating word (MacKay et al., 1993).

The fact that, besides auditory, phonological and lexical influences, articulatory constraints may act on the emergence and stabilization of verbal transformations suggests that they partly rely on motor neural processes. This hypothesis is in keeping with two recent functional magnetic resonance imaging (fMRI) studies examining neural activities during a

verbal transformation task (Sato et al., 2004; Kondo and Kashino, 2007). Using a block-design paradigm, Sato and colleagues (2004) contrasted a verbal transformation condition involving the mental repetition of speech sequences with an active search for verbal transformation, with a baseline condition involving the simple mental repetition of the same items. When compared to the baseline, the verbal transformation condition showed a predominantly left-lateralized network of brain activations within the inferior frontal gyrus, extending into the anterior part of the insular cortex, the supramarginal gyrus and the superior temporal gyrus. The authors suggest that this temporo-parieto-frontal neural network likely reflects the online analysis of the rehearsed speech sequence and the temporary storage of the recently built representation. Additional activations were also observed within the right anterior cingulate cortex and the cerebellum bilaterally and were assumed to reflect attentional control and/or comparison of speech forms during the active search for verbal transformations. In an event-related fMRI study, Kondo and Kashino (2007) attempted to identify brain regions activated at the time of perceptual transitions during a purely auditory verbal transformation condition and during a tone detection condition. Both conditions involved bilateral activations within the primary auditory area, the posterior part of the superior temporal gyrus, the supramarginal gyrus and within the left insular cortex. However, the anterior cingulate cortex, the prefrontal cortex and the left inferior frontal gyrus were found to be activated only in the verbal transformation condition.

Despite methodological differences, similar frontal, parietal and temporal areas were found to be activated in these two fMRI studies, including the anterior cingulate cortex, the inferior frontal gyrus extending into the insular cortex, the supramarginal gyrus and the superior temporal gyrus. Besides the activation of the anterior cingulate cortex, which is likely to reflect

some competition mechanisms between different possible representations (e.g., Carter et al., 1998), these brain areas strongly resemble those observed during previous brain imaging studies of speech perception in which a left-lateralized network, including the posterior superior temporal gyrus, the inferior parietal lobule and the inferior frontal gyrus, has been consistently identified (see Hickok and Poppel, 2007, for a review). It has been proposed that this temporo-parieto-frontal ‘dorsal stream’ provides a mechanism for the development and maintenance of parity between sound-based representations in the superior temporal gyrus and articulatory-based representations in the inferior frontal gyrus, via sensorimotor recoding in the inferior parietal lobule (Hickok and Poeppel, 2000, 2004, 2007; Scott and Johnsrude, 2003). Taken together, these results suggest that perceptuo-motor interactions play a key part in the conscious emergence and stabilization of speech percepts.

Despite the rather coherent portrait of brain activations observed during verbal transformation tasks, little is known about the temporal dynamics of brain activity linked to verbal transformations, that is activations occurring prior to the consciously reported perceptual transitions. Brain imaging as well as non-invasive electro-encephalographic (EEG) techniques do not provide the combined spatial and temporal resolution necessary to track activity in localized cortical regions in a period of time restricted to basically a few hundred of milliseconds. However, intracerebral EEG (iEEG) recordings, by means of electrodes stereotactically implanted inside the brain of some epileptic patients as part of their presurgical evaluation, enable to track cortical activity with high selectivity both in time and in space. The high spatial resolution in this study (approximately of 5 mm) excludes the problem of source localisation that exists in scalp EEG recordings (Lachaux et al., 2002; Lachaux, Rudrauf and Kahane, 2003,

Lachaux et al., 2007). In the present study, iEEG activity was recorded over a wide frequency range (1-160 Hz) from two implanted epileptic patients, while performing a verbal transformation task. Although the implanted sites of the two patients were selected entirely for clinical purposes with no reference to the present study, their implantation sampled a large number of temporal, parietal and frontal regions previously found to be activated during a verbal transformation task (Sato et al., 2004; Kondo and Kashino, 2007). iEEG recordings detect local neural activity related to cognitive processes as transient spectral energy variations in several characteristic frequency bands, including the theta (4-7 Hz), alpha (8-12 Hz), beta (15-30 Hz) and especially gamma (above 30 Hz and up to 200 Hz) bands.

Recent iEEG studies have put a strong emphasis on gamma band activations in particular, in association with a wide range of cognitive processes, including memory (Fell et al., 2001; Howard et al., 2003; Mainy et al., 2007), visual attention and perception (Brovelli et al., 2005; Lachaux et al., 2000, 2005; Tallon-Baudry et al., 2005; Tanji et al., 2005), audition (Bidet-Caulet et al., 2003; Crone et al., 2001; Edwards et al., 2005), somatosensory and motor processes (Crone et al., 1998; Crone, Sinai and Korzeniewska, 2006; Lachaux et al., 2005; Aoki et al., 1999; Pfurtscheller et al., 2003; Szurhaj et al., 2005), and language (Crone et al., 2001) . Importantly, in all those studies, gamma band activity was observed only in very specific brain regions, dependant on the tasks, and in good agreement with the functional networks revealed by fMRI (Lachaux et al., 2007).

The exact function of gamma band activity is still a matter of debate; initial studies have mostly related this phenomenon with visual integration, for instance for the perception of gestalt-like visual stimuli (Keil et al, 1999; Tallon-Baudry and Bertrand, 1999, for review), but this

interpretation seems to be too restrictive : for instance, several studies have found modulation of gamma band activity during speech perception (Palva et al., 2002, Kaiser et al., 2005, Ford et al., 2005). In fact, recent reviews have suggested that gamma band activity may in fact subserve a general mechanism facilitating and channelling local and global communication among neurons (Fries, 2005; Varela et al., 2001; Fries, Nikolić and Singer, 2007), which would explain why gamma band activity would play a role in processes as different as visual integration and speech perception.

That is, gamma band responses occur precisely in cortical regions associated with major cognitive functions, presumably reflecting local neural communication (Fries et al., 2007); as such, they constitute a candidate of choice to detect and describe the precise timing of short episodes of neural activity associated with verbal transformations. Based on this interpretation, our basic assumption in this study was that neural activity specifically associated with the emergence of a new percept in the verbal transformation task should be observed in the brain regions observed in fMRI studies (Sato et al., 2004; Kondo and Kashino, 2007), the left inferior frontal gyrus and the left supramarginal gyrus, prior to the conscious identification of a change in perception by subjects, and that activity should translate into energy increase in the gamma band in local iEEG recordings of those regions. We found that, for both patients, these two areas showed enhanced gamma band activity 300-800 ms prior to the reported perceptual transitions.

MATERIALS AND METHODS

Participants

Two right-handed patients, suffering from drug-resistant partial epilepsy and candidates for surgery, participated in the study (Pt1: female, 32 year old; Pt2: female, 27 year old; handedness was assessed by means of the Edinburgh Inventory, Oldfield, 1971). Both patients were native speakers of French and reported no hearing or speech disorders. Informed consent was obtained from each participant before the experiment.

Electrodes implantation

Magnetic resonance imaging (MRI) of the brain showed a left hippocampal sclerosis in patient Pt1 and Pt2. Because the location of the epileptic focus could not be identified using non-invasive methods, the two patients underwent iEEG recordings by means of stereotactically implanted multilead depth electrodes (for explanation of this methodology, see Kahane et al., 2004). 12 and 14 semi-rigid electrodes were implanted in patients Pt1 and Pt2, respectively, in various cortical areas depending on the suspected origin of seizures. Each electrode had a diameter of 0.8 mm and comprised 10 or 15 leads of 2 mm length, 1.5 mm apart (Dixi, Besançon, France), depending on the target region. The electrode contacts were identified on each individual stereotactic scheme, and then anatomically localized using the proportional atlas of Talairach and Tournoux (Talairach and Tournoux, 1988). In addition, the computer-assisted matching of post-implantation CT-scan with a pre-implantation 3-D MRI provided a direct visualization of the electrode contacts with respect to the brain anatomy of each patient (IVS Solution, Germany).

Although the implanted sites were chosen entirely for clinical purposes with no reference

to the present experimental protocol, the two patients were selected to enter this study because their implantation sampled several cerebral regions previously found to be activated during a verbal transformation task (Sato et al., 2004; Kondo and Kashino, 2007). During the experiment, 126 sites were recorded from each of the two patients in the left hemisphere (see Figure 1 and Table 1). Both patients performed the experiment four days after the implantation of the electrodes.

Insert Figure 1 and Table 1 about here

Experimental conditions

Two experimental conditions were considered. In the verbal transformation condition (ENDO condition), patients were asked to listen carefully to a speech sequence (i.e., either /pata/ or /tapa/ syllables being played repeatedly), and to press a button with their left hand whenever they perceived a change in the repeated utterance, even if the utterance changed into one they had heard previously. A verbal transformation experiment using the same material showed that the main organization of the reported transformations for both speech sequences was that of a pairwise coupling between /pata/ and /tapa/ syllables, although other phonological or lexical transformations were also reported (Sato et al., 2007b). In a second condition (EXO condition), patients were asked to listen carefully to randomly alternating repetitions of two syllables (i.e., /...papapa...tatata...papapa.../), and to detect any transition between them by pressing a button with their left hand. The EXO condition was designed to disentangle neural activity specifically linked to endogenously driven perceptual changes in the ENDO condition from those related to motor activities due to the patients' responses. Most specifically, the expectation was that the same motor activity due to button pressing should occur in both conditions and that an increase

in neural activity due to the perceptual changes in the EXO condition cannot be expected apart from the temporal interval between the syllable transition and the button-pressing event. This reaction time being estimated in the EXO condition, a modulation of spectral energy appearing in the ENDO condition at latencies prior to those observed in the EXO condition would likely be related to neural activity specifically associated with the emergence of a new verbal percept. For both patients, the EXO condition was performed before the ENDO condition.

Stimuli

Multiple utterances of /pa/ and /ta/ syllables were recorded in a soundproof room by a trained phonetician, native French speaker (J.-L.S.). The speaker pronounced each syllable naturally at a conversational rate, maintaining an even intonation and vocal intensity while producing the sequences. The items were digitized (16 bit resolution) and sampled at 44.1-kHz sampling rate directly to disk on a PC computer. One clearly articulated token was selected for each sequence, /pa/ and /ta/ syllables being matched as closely as possible for acoustic durations (as checked by a spectrogram analysis using the Praat software, Institute of Phonetic Sciences, University of Amsterdam, the Netherlands).

The speech sequences used in the ENDO condition (i.e., /...patapatapata.../) and in the EXO condition (i.e., /...papapa...tatata...papapa.../) were constructed by concatenating the /pa/ and /ta/ syllables, with a 100 ms silent period inserted between the offset of the vowel and the onset of the following consonantal burst. With this procedure, the duration of each consonant-vowel syllable was 250 ms. For each condition, two distinct speech sequences were built, differing in the ordering of the repeated syllables (i.e., /patapata.../ and /tapatapa.../ for the ENDO condition, /papa...tata.../ and /tata...papa.../ for the EXO condition), in order to minimize

any possible priming effect. For the EXO condition, the number of repetitive /pa/ or /ta/ syllables was randomly varied from 4s to 8s (corresponding to 23 switches between the two syllables). The random distribution was used to reduce the predictability of the switches, and maintain subject's attention. Each of the four speech sequences lasted 150 s. (corresponding to the concatenation of 600 syllables). These samples are available here: <http://www.icp.inpg.fr/~basirat/stimuli.html>.

Recordings

Intracerebral recordings were conducted using an audio-video-EEG monitoring system (Micromed, Treviso, Italy), which allowed the simultaneous recording of 128 depth-EEG channels sampled at 512 Hz [0.1–200 Hz bandwidth] during the experimental procedure. One of the contact sites in the white matter was chosen as reference. This reference had the same impedance as the other contact sites, and was located in a region with no or little electrical field source. In addition, it was not contaminated by eye-movements artefacts or electromyographic activity from subtle muscle contractions. Furthermore, all signals were re-referenced to their nearest neighbour 3.5 millimetres away on the same electrode before analysis (bipolar montage). Recording sites showing clear epileptiform activities were excluded from the analysis, and among the remaining sites, monopolar and bipolar data, both raw and high-pass filtered (above 15 Hz), were systematically inspected. Any trial showing epileptic spikes in any of those traces was discarded. Note that the high-pass filtering process was done solely for artefact detection, all analysis presented in this study were performed on raw, unfiltered, signals.

Time-frequency data analysis

EEG signals were evaluated with the software package for electrophysiological analysis (ELAN-Pack) developed in the INSERM U821 laboratory (Lyon, France). For each single trial, bipolar derivations computed between adjacent electrode contacts were analyzed in the time-frequency (TF) domain by convolution with complex Gaussian Morlet's wavelets (Tallon-Baudry et al., 1997), thus providing a TF power map: $P(t, f) = |w(t, f) * s(t)|^2$ where $w(t, f)$ was for each time t and frequency f a complex Morlet's wavelet: $w(t, f) = A \exp(-t^2 / 2 \sigma_t^2) \times \exp(2i\pi f t)$ with $A = (\sigma_t \sqrt{\pi})^{-1/2}$ and $\sigma_t = 1 / (2 \pi \sigma_f)$, and σ_f a function of the frequency f : $\sigma_f = f/7$.

Task-related spectral energy modulations of iEEG signals were detected using Mann-Whitney non-parametric tests. The objective was to test, for several frequency bands up to 160 Hz, whether the spectral energy before the patients' button press was higher than the energy measured at the same frequencies in neutral episodes during which patients reported no endogenous or exogenous perceptual switches. More precisely, we defined [200 ms x 8 Hz] TF windows covering a TF region from -1000 ms to 0 ms before button press in the time domain, and from 1 to 160 Hz in the frequency domain. For each such TF window, the total wavelet time-frequency energy was measured in that window for each button press to provide N energy values (N being the number of responses from the patient). Those N energy values were compared statistically with N energy values measured in N [200 ms x 8 Hz] TF windows in the same frequency band and at 'neutral' latencies, with no perceptual switch and chosen at least one second before and one second after a button press. One Mann-Whitney test was performed for each [200 ms x 8 Hz] TF window. Tests were performed independently for the ENDO and EXO

conditions. To correct for multiple testing, we applied a Bonferroni correction taking into account the number of non-overlapping [200 ms x 8 Hz] TF tiles covering the total [1000 ms x 160 Hz] TF domain which was tested (which yielded a corrected p equal or inferior to $5e-4$ ($0.05/(20 \times 5)$)).

RESULTS

Behavioural responses

The instances where the subjects pressed the button signalling a perceptual switch was the only available behavioural information. In the EXO condition, the mean reaction time corresponding to the delay between a stimulus switch (from /pa/ to /ta/ or from /ta/ to /pa/) and a button press was of 334 ms (\pm 87) for patient Pt1 and of 601 ms (\pm 371) for patient Pt2. The mean percentage of errors, corresponding to the absence of button press within 2 s after a stimulus switch, was 2 % and 4% for patients Pt1 and Pt2, respectively. In the ENDO condition, the total number of transformations was of 70 for patient Pt1 and of 58 for patient Pt2. The number of transformations as a function of time is shown on figure 2A. In order to test whether the subjects' response pattern was different in the beginning and at the end of the experiment, we analysed the number of transformations in the first and last half of each trial. The t-test did not show any significant difference ($t(3) = -1.75$, $p = 0.179$). Analyses of inter-switch durations, that is the time of stability from one transformation to the next, showed a mean stability duration of 3.74 s (\pm 3.54) for patient Pt1 and of 4.86 s (\pm 2.48) for patient Pt2 (the histograms of inter-switch durations are displayed on Figure 2B).

Insert Figure 2

iEEG responses

Analysis of iEEG responses were designed to detect possible neural activities specifically associated with perceptual transitions in both the ENDO and EXO conditions.

ENDO condition: In patient Pt1, four sites were found with a stronger spectral energy

before the button press than in the reference period (see Figure 1A, 3 & Table 1A). These activations were observed in the gamma band (above 40 Hz) and were maximal between 800 ms and 100 ms before the button press ([-600 : -300] for q'6; [-500 : -100] for x'8; [-800 : -500] for r'8; [-600 : -400] for s'9). For patient Pt2, four sites had stronger spectral energy before the button press than in the reference period (see Figure 1A, 3 & Table 1A). As for patient Pt1, these activations were observed in the gamma band, between 600 ms and 200 ms before the button press ([-500ms : -300ms] for q'5; [-500ms : -300ms] for g'15; [-600ms : -300 ms] for s'7; [-500ms : -200 ms] for e'5). Therefore, gamma band activations common to both patients were found in the left inferior frontal and supramarginal gyri 300-800 ms prior to the reported perceptual transitions. Notice that these activities occur at a negative latency relative to the button press, which is within the reaction time in the EXO condition for patient Pt2, but generally quite larger for patient Pt1. This rules out, for this patient at least, the possibility that the increase in activity is only due to the preparation of the button pressing action *per se*.

Insert Figure 3 about here

EXO condition: Some of the previous sites mentioned above also demonstrated significant gamma band increases in the EXO condition, but these were found much later always after -200 ms before the button press (Pt1: s'9, r'8, x'8; Pt2: s'7). In addition, the EXO condition was characterized by gamma band increases after -200 ms in the superior temporal gyrus (Pt1: t'7, u'4, u'10; Pt2: u'9 - see Figure 1B, 3, and Table 1B).

DISCUSSION

The present study was designed to examine the temporal dynamics of brain activity linked to perceptual changes during a verbal transformation task. To this aim, iEEG activities were recorded from two implanted epileptic patients, while they listened to an auditory speech sequence played repeatedly and reported any perceptual change. For both patients, an increase in gamma band activity was observed 300-800 ms prior to the reported perceptual transitions within the left inferior frontal and supramarginal gyri, while no modulation occurred in temporal areas. In an additional auditory decision task, an increase of gamma band activities was also observed but in a shorter latency relative to the patients' motor responses and mainly in the left superior temporal and supramarginal gyri.

Before discussing these results, it is important to highlight some limitations of the present study. One limitation, inherent to patient studies, is the possible long term effects of epilepsy on cognitive abilities (e.g., Jokeit and Ebner, 2002; Hermann et al., 2006). Although cognitive deficits cannot be excluded, it is worthwhile noting that the two patients performed the tasks correctly and that neural activity found for both patients (who do not have the same epilepsy) were in brain areas previously reported for the verbal transformation effect using fMRI (Sato et al., 2004; Kondo and Kashino, 2007). In addition, the epileptogenic zone of the two patients - as precisely defined by intracerebral recordings - was restricted to antero-mesial temporal lobe structures. A second limitation comes from the fact that intracranial electrodes did not allow sampling of all the cerebral regions previously found to be activated during the verbal transformation effect (Sato et al., 2004; Kondo and Kashino, 2007). Notably, given the patients' implantation and the fact that verbal transformations mainly involve left-lateralized activations

(Sato et al., 2004), neural activity was recorded only in the left hemisphere. Finally, a third limitation comes from the fact that no information on the precise nature of the transformations was available. However, a previous verbal transformation experiment using the same material showed that the main organization of the reported transformations for both speech sequences was that of a pairwise coupling between /pata/ and /tapa/ syllables, although various other transformations were reported (Sato et al., 2007b). From these results, the reported transformations in the present study are likely to be strongly linked to a syllabic parsing process, rather than to auditory streaming or lexical competition mechanisms, as also sometimes observed in verbal transformations (see Sato et al., 2006, 2007a, 2007b).

Nethertheless, the present study provides the first direct recordings of neural activity preceding, or simultaneous with, a verbal transformation. A coherent portrait of neural activity was observed for both patients, in the inferior frontal and the supramarginal gyri in the ENDO condition, as well as in the superior temporal and supramarginal gyri in the EXO condition. Given the restricted number of subjects, we will focus on these brain areas found to be activated for both patients. Note also that the modulation of spectral energy observed before the patients' responses is relative to some neutral periods, selected in the same condition but in which no perceptual transitions were reported. Therefore, the absence of modulation in a particular brain region does not necessarily mean that this region is not activated during the task but, possibly, it is not differentially activated than in neutral periods.

Altogether, the observed increase of gamma band activity in the EXO condition appeared around 200 ms prior to the motor responses in the temporal and, to a lesser extent, parietal regions. Activations observed within the left temporal areas likely reflect the auditory

identification of the new syllable. The left temporal lobe has long been implicated in the perception of speech sounds (e.g., Zatorre et al., 1992; Binder et al., 2000; Scott et al., 2000; Binder et al., 2004). While processing of the spectrotemporal features of both speech and non-speech sounds has been attributed to the primary auditory cortex and dorsolateral portions of the superior temporal gyrus (Binder et al., 2000), phonetic processing of speech signals involves mainly the left anterior superior temporal gyrus and the adjacent superior temporal sulcus extending both anteriorly and posteriorly (Binder et al., 2000; Scott et al., 2000). Furthermore, a direct relationship between identification accuracy and neural activations has been also observed in the anterolateral aspect of Heschl's gyrus and adjacent lateral superior temporal gyrus during a syllable discrimination task (Binder et al., 2004). Finally, the present neural modulation in temporal areas also appears in line with previous electrophysiological and neuromagnetic studies of speech perception, showing a mismatch negativity response in the auditory cortex elicited by infrequent deviant sounds presented among frequent standard sounds (see Näätänen, 2001, for a review). Indeed, each transition from /pa/ to /ta/ and /ta/ to /pa/ could be considered as an oddball, just as in the mismatch negativity paradigm. The specific signification of increased gamma band activities observed in the supramarginal gyrus is less clear. The supramarginal gyrus has been associated with temporary storage of phonological material (Paulesu, Frith and Frackowiak, 1993; Cohen et al., 1997; Jonides et al., 1998; Honey, Bullmore and Sharma, 2000), phonological judgements (Romero, Walsh and Papagno, 2006), motor preparation (Deiber et al., 1996), and motor attention (Rushworth, Krams and Passingham, 2001). The present study cannot disambiguate the specific contribution of the supramarginal gyrus to these processes.

In the ENDO condition, an increase of gamma band activity was observed for both

patients around 300-800 ms prior to the motor responses within the left inferior frontal and supramarginal gyri. Note that these activities occur at a negative latency relative to the motor responses, which for both patients is quite earlier than that observed in the corresponding areas in the EXO condition. This result therefore clearly rules out the possibility that the increase in activity could be due to the preparation of the button pressing action *per se*. The activities observed in the present study in frontal and parietal areas are consistent with our previous study on verbal transformations, which did not involve button pressing at all. This further suggests that button pressing does not modify the multistability phenomenon itself. It confirms the role of this fronto-parietal network in the verbal transformation process. Moreover, the precise temporal localisation allowed by iEEG enables the confirmation of the specific role of this network in perceptual switches and decision making. Furthermore, the fact that most transformations in this kind of sequences are towards /pata/ and /tapa/ sequences rather than related to auditory streaming processes (Sato et al., 2007b) strongly suggests that this network plays a role in speech perception.

Actually, in past studies, the inferior frontal gyrus has been repeatedly found to be activated during phonological processing, in phoneme monitoring, syllable counting and rhyming tasks (e.g., Démonet et al., 1992, 1994; Paulesu et al., 1993; see Poldrack et al., 1999; Démonet, Thierry and Cardébat, 2005; Vigneau et al., 2006, for a review), as well as during auditory speech perception (e.g., Wilson et al., 2004; Watkins and Paus, 2004; Pulvermuller et al., 2006; Wilson and Iacoboni, 2006). This region thus appears well adapted to syllable parsing process in the present verbal transformation task (Sato et al., 2004), and to speech segmentation in general (Burton and Small, 2006). As previously noted, the supramarginal gyrus has been

associated with both temporary storage of phonological material (Paulesu, Frith and Frackowiak, 1993; Cohen et al., 1997; Jonides et al., 1998; Honey, Bullmore and Sharma, 2000) and phonological judgements (Romero, Walsh and Papagno, 2006). Given that the verbal transformation task appears to require at least minimal verbal storage (Smith, Reisberg and Wilson, 1995; Sato et al., 2004), this region is thus likely to be involved in the temporary storage of the present percept until the emergence of a new one. Altogether, the present fronto-parietal coupling, involved in both syllable parsing processes and temporary storage of the latterly built representation, could therefore provide a well-adapted platform for phonological comparison and decision-making processes before the conscious emergence of a new speech form.

In summary, the observed increase of gamma band activity within the left inferior frontal and supramarginal gyri, 300-800 ms prior to the reported perceptual transitions, suggests that articulatory-based representations may play a key part in the endogenously driven emergence of auditory speech percepts. This result appears consistent with recent neurobiological models of speech perception and language understanding that claim for a tight connection between speech perception and production systems (Hickok and Poeppel, 2000, 2004, 2007; Scott and Johnsrude, 2003; Callan et al., 2004; Wilson and Iacoboni, 2006; Skipper et al., 2007).

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TABLES

Table 1: Anatomical locations for each recorded site exhibiting enhanced energy in the gamma band (A) in the verbal transformation condition (ENDO condition) and (B) in the auditory decision task (EXO condition). Anatomical regions were drawn from the individual MRI of the patients, not from standard atlases.

A)

Patient ID	Site ID	Anatomical localization	Talairach x, y, z
Pt1	s'9	Inferior parietal lobule (BA40)	-59, -22, 18
Pt1	r'8	Inferior frontal gyrus (BA44/BA6)	-55, 6, 12
Pt1	q'6	Inferior frontal gyrus (BA44)	-44, 16, 11
Pt1	x'8	Brevis anterior gyrus of the insula	-31, 16, 5
Pt2	s'7	Inferior parietal lobule (BA40)	-61, -24, 21
Pt2	g'15	Inferior frontal gyrus (BA45/46)	-48, 38, 13
Pt2	q'5	Inferior frontal gyrus (BA45)	-39, 19, 4
Pt2	e'5	Fusiform gyrus (BA36)	-37, -18, -26

B)

Patient ID	Site ID	Anatomical localization	Talairach x, y, z
Pt1	s'9	Inferior parietal lobule (BA40)	-59, -22, 18
Pt1	r'8	Inferior frontal gyrus (BA44/BA6)	-55, 6, 12
Pt1	x'8	Brevis anterior gyrus of the insula	-31, 16, 5
Pt1	t'7	Anterior part of the superior temporal gyrus (BA41)	-59, -3, -6
Pt1	u'4	Superior temporal gyrus (BA41) and Heschl Gyrus	-36, -25, 10
Pt1	u'10	Posterior part of the superior temporal gyrus (BA42)	-59, -25, 10
Pt2	u'9	Posterior part of the superior temporal gyrus (BA42)	-31, 16, 5
Pt2	s'7	Inferior parietal lobule (BA40)	-61, -24, 21

FIGURES

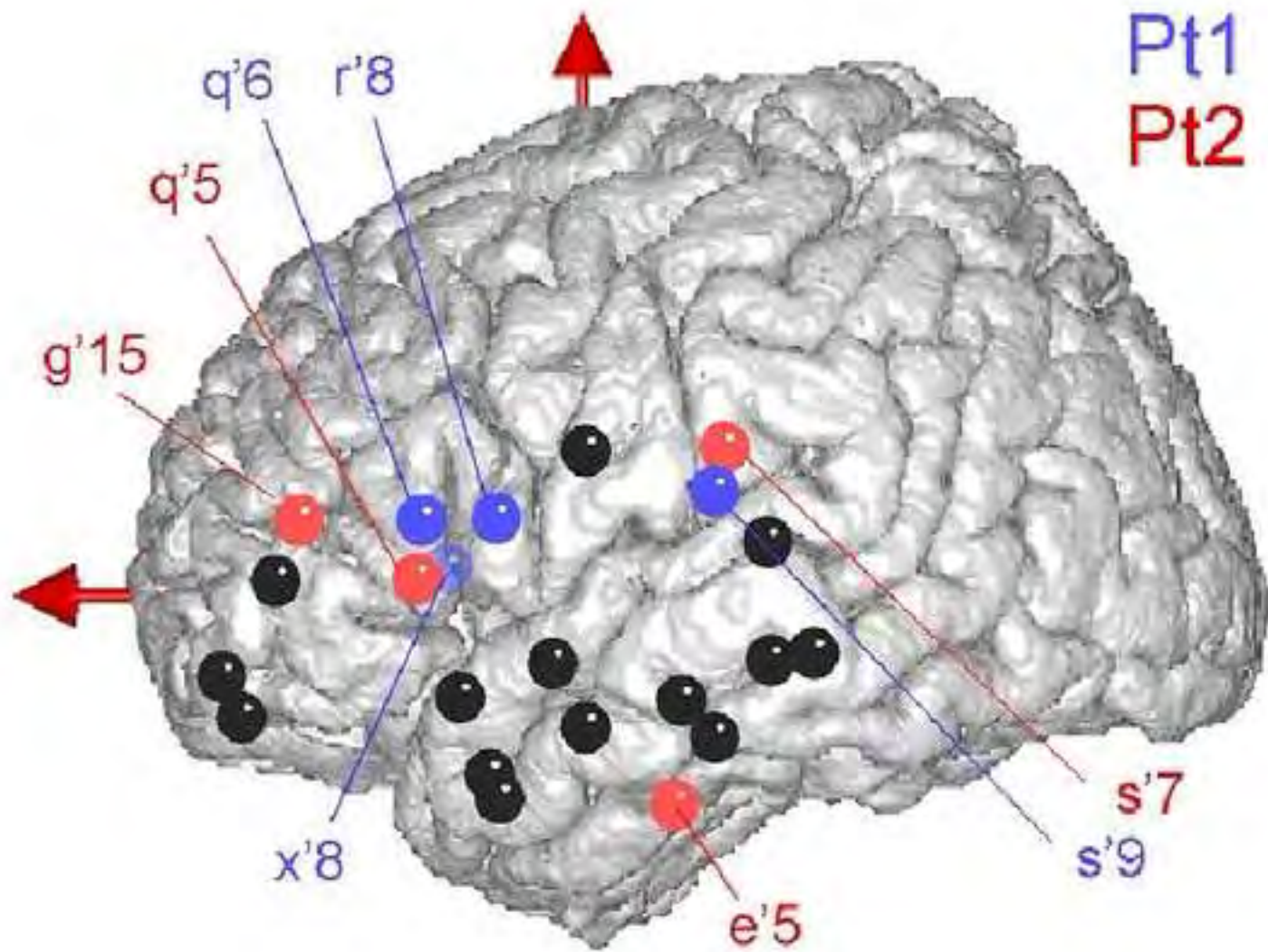
Figure 1: Entry points of the intracranial electrodes across the two patients, projected onto the lateral view of a 3D reconstruction of the Montreal Neurological Institute (MNI) single-subject MRI (after conversion from Talairach and Tournoux to MNI stereotactic space). Blue and red dots indicate the recorded sites showing enhanced gamma band energy (A) in the verbal transformation task (ENDO condition) and (B) in the auditory decision task (EXO condition) for patients Pt1 and Pt2, respectively. Black dots indicate entry points for depth electrodes with no effect. Talairach coordinates for all the implanted sites are displayed in Table 1.

Figure 2: Behavioral results in the ENDO Condition. A: Number of transformations (O and *, two trials per patient) as a function of time for patient Pt1 and Pt2 (time step = 10 sec.). B: Histograms of inter-switch durations for the two patients Pt1 and Pt2.

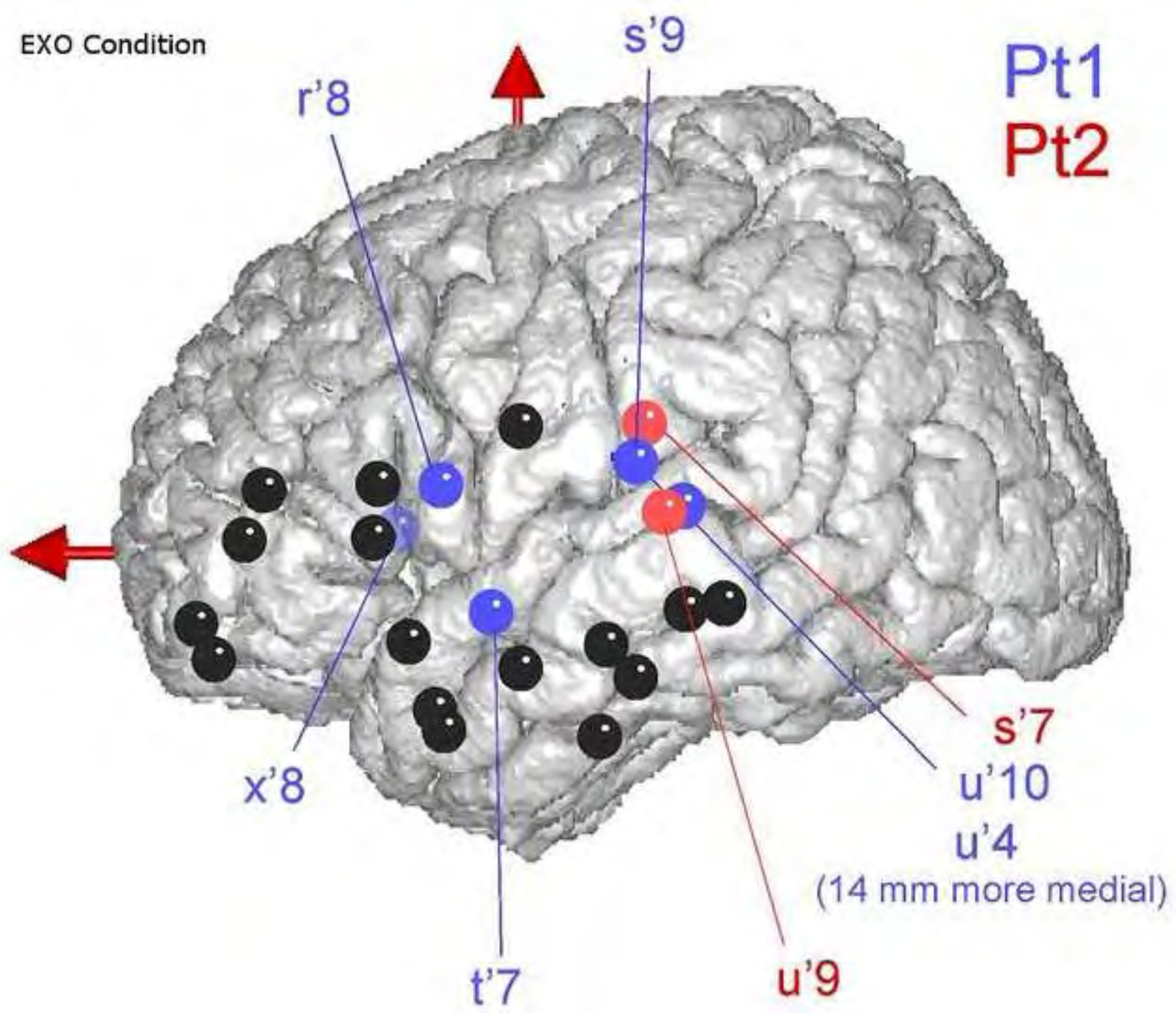
Figure 3: Time-frequency representations for the sites showing enhanced gamma band energy in the ENDO and EXO conditions for patients Pt1 and Pt2. Maps show H values of the non-parametric comparisons with the neutral periods (see text for details); H values higher than 12 correspond to significant energy increases with $p < 0.0005$. Talairach coordinates for the implanted sites are displayed in Table 1.

5. Figure
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ENDO Condition

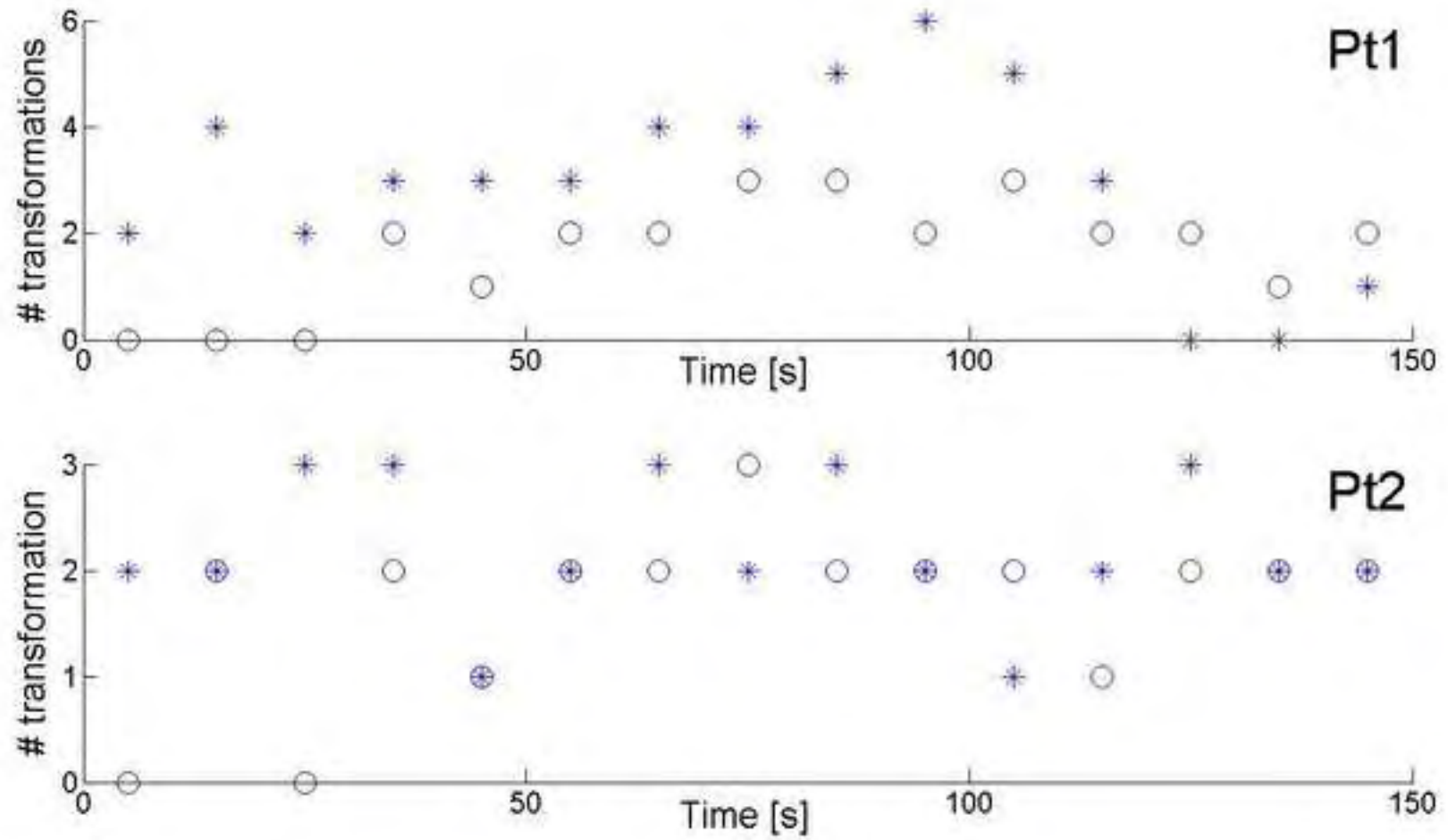


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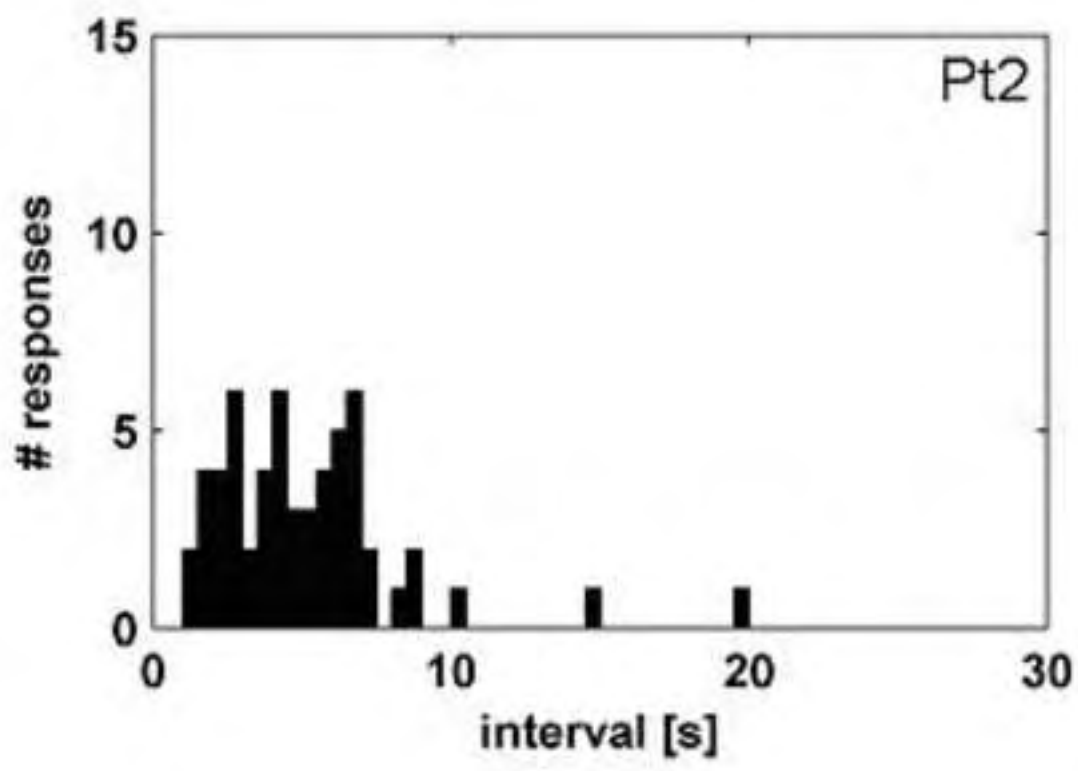
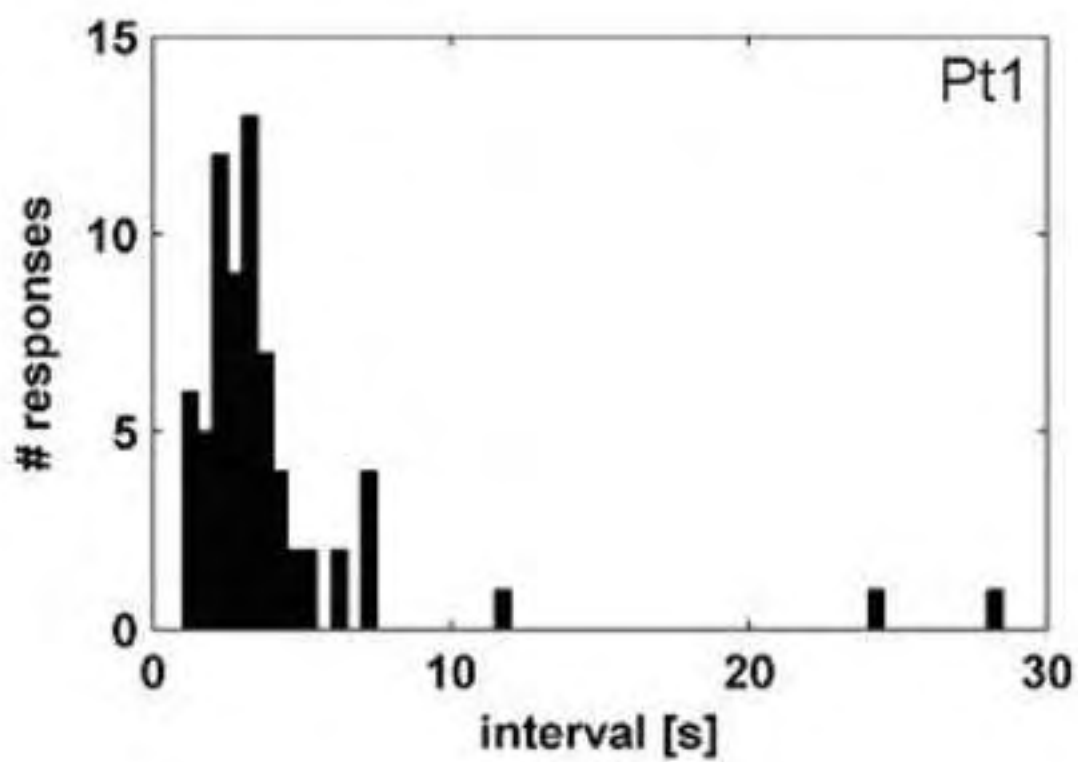


5. Figure

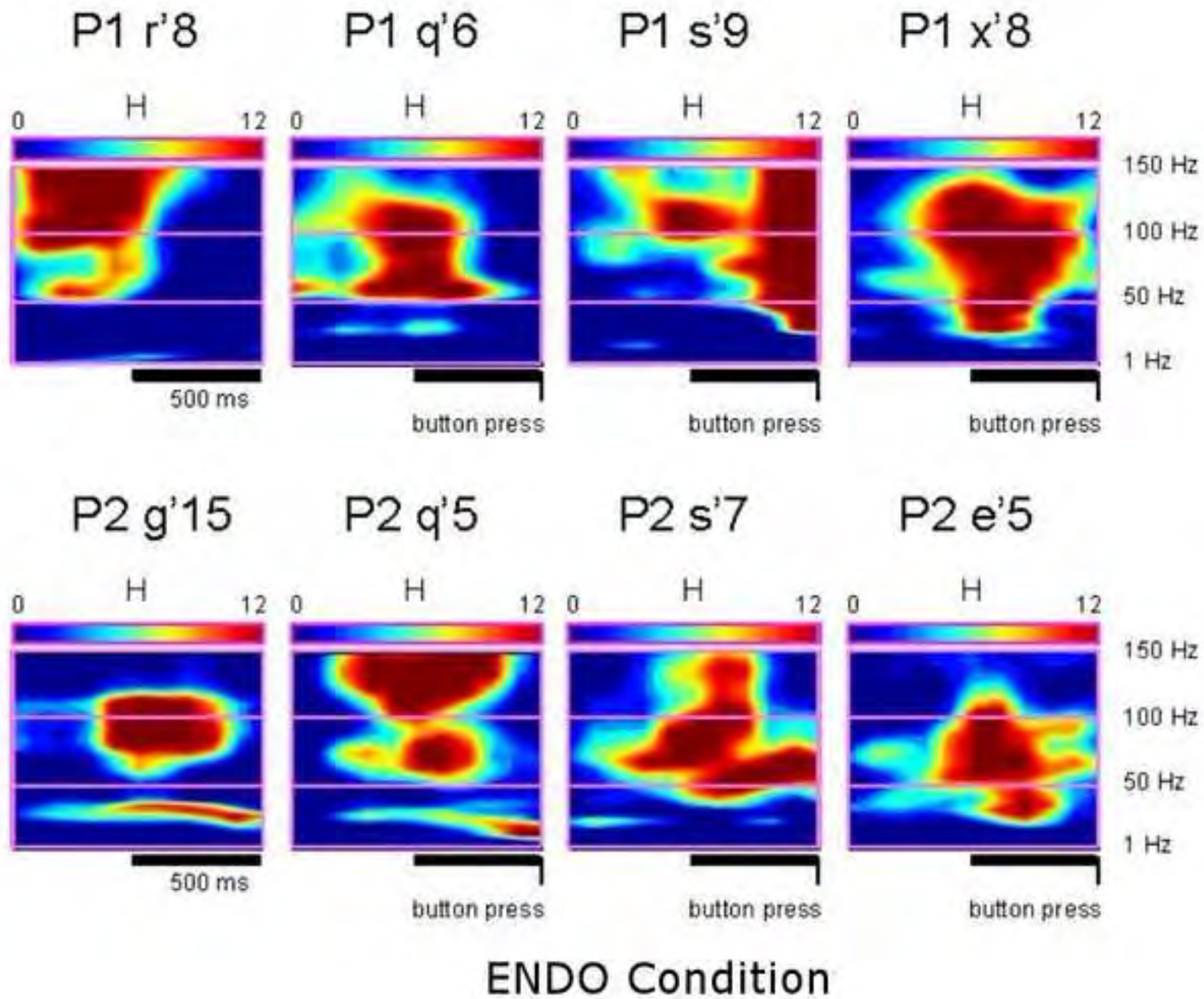
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