Traveling waves appear and disappear in unison with produced speech

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Abstract

In Rapela (2016) we reported traveling waves (TWs) on electrocorticographic (ECoG) recordings from an epileptic subject over speech processing brain regions, while the subject rhythmically produced consonant-vowel syllables (CVSs). In Rapela (2017) we showed that TWs are precisely synchronized, in dynamical systems terms, to these productions. Here we show that TWs do not occur continuously, but tend to appear before the initiation of CVSs and tend to disappear before their termination. During moments of silence, between productions of CVSs, TWs tend to reverse direction. To our knowledge, this is the first study showing TWs related to the production of speech and, more generally, the first report of behavioral correlates of mesoscale TWs in behaving humans.

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1 Introduction

Findings of spatio-temporally organized neural activity (i.e., traveling waves, TWs) are not new. However, their functional role is still unclear.

In non-human animals TWs have been related to the perception of visual stimuli by monkeys (e.g., Benucci et al., 2007) and by turtles (e.g., Precht et al., 1997), and to movement preparation by monkeys (e.g., Rubino et al., 2006). In humans, macroscopic TWs have been associated to reaction speeds (e.g., Patten et al., 2012) and to memory consolidation during sleep (e.g., Muller et al., 2016), among others. However, to our knowledge, no study has reported TWs during the production of speech or has found behavioral correlates of mesoscopic TWs in behaving humans.

In Rapela (2016) we reported the existence of TWs in a speech processing brain region. In Rapela (2017) we showed that, at times of CVS transitions, TWs are precisely synchronized, in dynamical systems terms, to the production of CVSs. Here we show that TWs tend to appear before initiations of productions of CVSs, tend to disappear before the their terminations, and sometimes reverse direction during moments of silence.

2 Results

We describe findings from the analysis of TWs in recording session EC2_B105 of subject EC2. We report results from the analysis of TWs moving over the ventral sensorimotor cortex between electrodes 135 and 142 (Figure 1) at the median frequency of CVS production of this subject, 0.62 Hz.

We say that there is a wave event (WE) at a sample time when recorded neural activity at this time is spatiotemporally organized as a TW (Section 4.1). We say that there is a contiguous wave event (CWE) from time $t_0$ to time $t_1$ when WEs are detected at all sample times between $t_0$ and $t_1$ (Section 4.3).

As we quantify below, TWs moving in the ventro-dorsal direction (from electrode 135 to 142) were not continuous, but tended to appear only during the production of CVSs. The start and end times of CWEs was aligned to initiations and terminations of CVSs with a sub-second precision. Also, we observed few TWs moving in the dorso-ventral direction (from electrode 142 to 135), which appeared most often during periods of silence between productions of CVSs.
The abscissa of a blue dot in Figure 2 marks the time at which a WE was detected, and the ordinate gives the speed of the corresponding TW. Blue/red lines in Figure 2 mark start/end times of CWEs. Solid and dashed gray lines in Figure 2 indicate initiations and terminations, respectively, of the CVSs at the top of the plot. For instance, the blue and red lines at 326.3 and 327.1 seconds mark the start and end times of a CWE and the solid and dotted black lines at 326.4 and 327.2 seconds mark the initiation and terminations of the CVS zaa. We see that for ventro-dorsal TWs (i.e., CWEs with negative speed) tend to start a little before initiations of CWEs (i.e., blue vertical lines corresponding to blue dots with negative speed appear a little to the left of solid vertical gray lines) and end a little before terminations of CWEs (i.e., red vertical lines corresponding to blue dots with negative speed appear a little to the left of dashed vertical gray lines).

We observed 1293 ventro-dorsal WEts (i.e., moving from electrode 135 to 142). The proportion of significant such events occurring between 0.3 seconds before the start time of the production of a CVS and the end time of this production was 86%, and this proportion was significantly different from chance (p<1e-4, permutation test, Section 4.5). We observed 116 dorso-ventral WEts and these events occurred most often during periods of silence. The proportion of significant dorso-ventral WEts in periods of silence was 90%, and this proportion was significantly different from chance (p=0.006, permutation test, Section 4.5). That is, ventro-dorsal TWs tended to occur during CVSs productions and these TWs tended to reverse direction during silence.

Out of 92 ventro-dorsal CWEs, 92 of them (100%) overlapped with the production of a CVS. For 90% of these overlapping CWEs their start time occurred between -0.40 and 0.18 seconds from the start time of the overlapping CVS (dotted blue lines in Figure 3), and their end time occurred between -0.38 and 0.16 from the end time of the overlapping CVS (dotted blue lines in Figure 4). That is, start and end times of ventro-dorsal CWEs were aligned to start and end times of productions of CVSs with a sub-second precision.

We tested the hypothesis that this alignment did not occurred by chance by comparing statistics on start and end times in experimental datasets and in surrogate datasets reflecting the null hypothesis of no alignment between CVSs and overlapped ventro-dorsal CWEs (Section 4.4). The mean of differences between start (end) times of ventro-dorsal CWEs minus start (end) times of overlapping CVSs productions was -0.06 sec (-0.11 sec), which was significantly smaller than chance, p=0.0185 (p<1e-4) (permutation test, Section 4.5). That is, on average CWEs started and ended significantly before overlapping CVSs. The variance of differences between start (end) times of ventro-dorsal CWEs minus start (end) times of CVSs productions was 0.03 sec$^2$ (0.03 sec$^2$), which was significantly smaller than chance, p<1e-4 (p<1e-4) (permutation test, Section 4.5). Thus, the alignment between start and end times of overlapping CWEs and CVSs was significantly more precise than expected by chance.

3 Discussion

This is the third article in a series characterizing TWs related to the production of CVSs. In Rapela (2016) we showed for the first time that during the production of CVSs field potentials over speech processing brain regions are spatio-temporally organized as TWs. In Rapela (2017) we showed that these TW are precisely synchronized, in dynamical systems terms, to the initiation of the production of CVSs. Here we demonstrated that these TWs tend to appear before the start of the production of CVSs and they tend to disappear before the end of these productions, with a sub-second precision. To our knowledge, this is the first report of TWs related to the production of speech, and the first demonstration of a behavioral correlate of mesoscale TWs in behaving humans.

In future research we will investigate the relation between features of these TWs (e.g., velocity, propagation direction, duration) and phonetic features of produced CVSs. We will also study possible neural mechanisms generating these reversing direction TWs and their synchronization to produced CVSs.
Figure 2: During the production of CVSs traveling waves tend to propagate in the ventro-dorsal direction (i.e., have negative speed). They tend to appear before the initiation of CVSs and disappear before their termination. In moments of silence, TWs tend to reverse direction and propagate in the dorso-ventral direction (i.e., have positive speed). Gray vertical lines indicate behavior; solid and dashed lines mark initiations and terminations of productions of CVSs, respectively. Colored dots and vertical lines indicate physiology; blue dots mark WEs, blue and red vertical lines indicate starts and ends, respectively, of CWEs. In most cases CWEs start and end before the initiation and termination of CVSs (i.e., blue vertical lines appear a little before solid gray vertical lines and red vertical lines appear a little before gray dashed lines). Click on the figure to access its online version plotting the full ten-minutes recording session.
Figure 3: Histograms of latencies between the start of ventro-dorsal CWEs and the initiation of CVSs. The blue and red histograms correspond to experimental and surrogate datasets (Section 4.4). Dotted blue vertical lines indicate 5% and 95% percentiles of the experimental dataset histogram. 90% of CWEs started between 0.4 sec before and 0.18 sec after the initiation of a CVS. The mean latency in the experimental dataset was -0.06 sec, which was significantly smaller than chance (p=0.0185, permutation test, Section 4.5), suggesting that on average CWEs started before the initiation of productions of CVSs. The variance of latencies in the experimental dataset was 0.03 sec$^2$, which was significantly smaller than chance (p<1e-4, permutation test, Section 4.5), suggesting that on average CWEs started closer to the initiation of productions of CVSs than expected by chance.
Figure 4: Histograms of latencies between the end of ventro-dorsal CWEs and the termination of CVSs. Save format at in Figure 3. 90% of CWEs started between 0.34 sec before and 0.19 sec after the termination of a CVS. The mean latency in the experimental dataset was -0.11 sec, which was significantly smaller than chance (p<1e-4, permutation test, Section 4.5), suggesting that on average CWEs ended before the termination of productions of CVSs. The variance of latencies in the experimental dataset was 0.03 sec², which was significantly smaller chance (p<1e-4, permutation test, Section 4.5), suggesting that on average CWEs ended closer to the termination of productions of CVSs than expected by chance.
Figure 5: Detection of a Wave Event at time 78.99 sec between electrodes 135 and 142, using electrode 142 at reference electrode. The abscissa plots distances of electrodes 142 to 135 to the reference electrode. The ordinate plots phase difference between electrodes 142 to 135 and the reference electrode. There is a significant linear relation between phase differences and distances (skipped Pearson correlation coefficient $r=0.89$; $p=0.002$, permutation test) indicating a WE at time 78.99 sec.

4 Methods

We used the methods in Patten et al. (2012) for the detection of traveling waves and for the calculation of their speed.

4.1 Wave Event

We studied TWs between electrodes 135 and 142 in the ventral sensorimotor cortex (Figure 1). We used electrode 142 as reference electrode. We say that a wave event (WE) occurred at time $t$ when there is a significant linear relation ($p<0.01$ and $|r|>0.85$) between phase differences of electrodes with respect to the reference electrode and distances of these electrodes to the reference electrode. Figure 5 illustrates the detection of a WE at recording time 78.99 sec.

In the chain of electrodes 142-135, higher numbered electrodes are more dorsal than lower ones (e.g.; electrode 142 is dorsal to electrode 141, electrode 141 is dorsal to electrode 140, . . .). A positive slope in the best fitting line in the plot Phase Difference vs Distance (red line in Figure 5) indicates a TW propagating in the dorso-ventral direction from electrode 142 to electrode 135. Similarly, a negative slope indicates a TW propagating in the ventro-dorsal direction from electrode 135 to electrode 142.

4.2 Speed

The slope of the best fitting line in the Phase Difference vs. Distance plot gives the wave number, $k$, of the TW and the speed, $v$, of the TW is $v = \frac{2\pi f}{k}$, where $f$ is the TW frequency. Blue dots
in Figure 2 indicate WEs occurring at different times and with different speeds.

4.3 Contiguous Wave Event

A Contiguous Wave Event CWE is a sequence of uninterrupted Wave Events, such that WEs were detected in all samples times from the sample time of the first WE to the sample time of the last WE. The start/end of a CWEs in Figure 2 are represented by blue/red vertical lines, respectively.

4.4 Surrogate Datasets

Datasets used in the current analysis comprise voltage recordings from the 256 electrodes in the grid plus a transcription file indicating start and end times of productions of CVSs. A surrogate dataset contained identical voltage recordings as the original dataset plus a modified transcription file, where the start and end times of productions of CVSs were randomized. Thus, in surrogate datasets there should not be synchronization between CVSs and CWEs.

The modified transcription file randomized start and end times of all CVSs in the original transcription file, but kept unchanged their durations, as explained next. The initiation time of the first CVS in the modified transcription file was that in the original transcription file plus a Gaussian random variable with mean zero and standard deviation 0.5. The termination time of the first CVS in the modified transcription file was the randomized initiation time plus the duration of the first CVS in the original transcription file. The initiation time of the second CVS in the modified transcription file was the termination time of the first CVS in the modified transcription file plus a random variable with mean and standard deviation equal to the mean and standard deviation of inter-CVS-intervals in the original transcription file. This procedure was repeated to generate randomized initiation and termination times for all CVSs in the original transcription file.

4.5 Permutation Tests

We performed one-sided permutation tests (1) to assess the reliability of proportions of WEs occurring in a given time interval (e.g., the proportion of ventro-dorsal WEs occurring between 0.3 sec before the start of the production of a CVS and the end of this production) and (2) to test the significance of the alignment between the start/end time of a CWEs and the initiation/termination time of the production of a CVSs. In both cases we first calculated a statistic on the original dataset (e.g., we computed the proportion of ventro-dorsal WEs occurring between 0.3 sec before the start of the production of a CVS and the end of this production in the original dataset). We then computed 2000 surrogate datasets (as described in Section 4.4), and we calculated the previous statistic in each of the surrogate datasets. We thus generated a collection of 2000 surrogate statistics. The p-value returned by a permutation test was the proportion of surrogate statistics smaller (for left-sided tests) or larger (for right-sided tests) than the test statistic on the original dataset.

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