Temporal pattern of odor administration alters hemispheric processing in humans

Tyler S. Lorig, Megan Rigdon and Alexander Poor

Department of Psychology, Washington and Lee University, Lexington, Virginia, USA

Correspondence and requests for reprints to Dr Tyler S. Lorig, Ph.D, Department of Psychology, Washington and Lee University, Lexington, VA 24450, USA
Tel: +1 540 458 8839; fax: +1 540 458 8047; e-mail: tlorig@wlu.edu

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Evidence from a variety of sensory modalities has suggested that the left hemisphere may be 'tuned' to process more rapidly changing stimuli than the right and some have suggested that this difference forms the foundation of the functional dichotomy often drawn between the two hemispheres. Odors may be thought to engage these same temporally dependent processes as portions of an odor mixture may come to be transduced into a phasic series of neural events. Using brain electrical activity, we show that the temporal sequence of the odor alters the pattern of brain electrical activity. Estimates of the source localization for this activity indicate that rapidly changing odors, like sounds, visual and tactile stimuli, show increased activity in the left hemisphere. NeuroReport 17:231–234 © 2006 Lippincott Williams & Wilkins

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Introduction

More than 40 years ago, Efron [1] proposed that the hemispheric specialization for language was due to the temporal nature of the sensory coding of language. He argued that it was the rapid stimulus change in word sounds that led to their differential hemispheric processing rather than some intrinsic specialization for language. Recent research by Belin et al. [2] and others [3–5] has supported this hypothesis. Curiously, it may be that odors, like language, also involve the processing of a temporal series of neural events that lead to differential hemispheric specialization.

Almost all odors found in the environment are mixtures of chemicals. Even though each chemical component of the mixture is transduced individually, they are not transduced simultaneously. In fact, the activity of some olfactory receptors is quite rapid while that of others is much slower [6]. This leads an odor mixture to be transduced as a phasic sequence of neural events that is similar to the sequence of activity elicited by successive speech sounds making up a word [7].

Over the past several years, findings from our laboratory (see [8] for a summary) have shown that some odors tend to alter the way language tasks are performed. These findings led to the hypothesis that perception of some odors, typically complex mixtures, involves the use of the same neural resources needed for performing language tasks [7]. In one recent study, an odor mixture altered symbolic information processing whereas each component of the mixture had no effect on brain potentials related to the task [9]. As it is likely that an odor mixture must unfold temporally because of transduction properties of its various chemical constituents, the rapidity of this unfolding—like the rapidity of speech sounds—might lead to increased activity in the left hemisphere and, in particular, the left temporal lobe [2] where it could compete for resources with symbolic processing.

A direct test of the hypothesis that rapidly changing components of odor mixtures differentially engage the left hemisphere is difficult. If one were to use different sets of odor mixtures and find changes in left hemisphere activity for one or two of these mixtures, it would only address the fact that some odor mixtures are processed differently than others. Even if a mixture known to produce rapidly phased bulbar activity were found to produce an increase in left hemispheric activity, one could not attribute that finding to the rapidity of the activity because of components of the odor mixture. Some other feature of the mixture such as its pleasantness or complexity might be responsible for the effect. To be compelling, a thorough test of this hypothesis must use the same odor chemicals presented for the same durations at the same concentration. Only the timing of these stimuli should change.

Materials and methods

The 10 study participants (six male, four female) were undergraduate students at Washington and Lee University and were between 18 and 22 years of age. All were right handed and were surveyed for any health problems or drug use known to be associated with altered electroencephalogram (EEG) responses. Participants reporting extreme sensitivity or insensitivity to odors were not tested. All participants detected the odors used in the study and gave their informed consent prior to their participation.
Odor administration

Three odors were used in the study (citral 10% b/v, vanillin 13% b/w, and phenylethyl alcohol 20% b/v all diluted in mineral oil). Odors were delivered by means of a constant flow olfactometer [10,11]. Each trial consisted of the presentation of a sequential odor mixture in a 600-ms-long bolus imbedded in the constant flow and administered at the onset of a nasal inhalation. Each bolus contained a series of four individual odor components with each lasting 150 ms. For example, an odor bolus would have contained a sequence such as ‘citral citral vanillin vanillin’ or ‘citral vanillin citral vanillin.’ In the former case (slow transition), there is one transition between different odors and in the latter (fast transition), there are three transitions, thus leading to more transitions within the 600-ms stimulation period (see stimulus bars in Fig. 1). This procedure led to a stimulus sequence that delivered the same amount of each odorant for the same total duration in both the slow and fast conditions. Thus, these conditions differed only in the number of stimulus changes between the two conditions. In this way, the odors in the fast change condition become an analog for rapid phonemic transitions such as ‘abab’ which are known to produce developmental activity in the left hemisphere [2]. Odor stimuli were administered in randomized order and participants typically were exposed to approximately 16 stimuli of each category with an interstimulus interval of at least 30 s. The participants’ task was to rate the intensity and pleasantness immediately following each odor administration on a 10-point Likert scale.

Total airflow through the olfactometer was 1.5 L/min with 1.0 L/min being switched into the odor vessels under computer control. Odors were administered bimonthly through a dual lumen nasal cannula that contained a 1.6 mm (inner diameter) Teflon tube. The other side of the dual lumen was used to measure air pressure changes associated with nasal breathing so that the odor stimuli might be triggered automatically during a nasal inhalation.

Electroencephalogram recording and reduction

Electrophysiological data were recorded from 80 scalp locations (extension of the 10–20 system) using a Biosemi Active2 EEG system (Amsterdam, Netherlands). Sampling rate was 256 Hz and recording bandpass was 0.01–100 Hz. Data were smoothed offline to a high frequency cut-off of 15 Hz. Monopolar recordings were made referenced to the left mastoid and re-referenced offline to a common average. Electrodes to measure vertical and horizontal eye movements were embedded in the cap that held the electrodes. As a result of the design of the active electronics inside the Biosemi electrode housing [12], impedance measurements are not possible and signal integrity is assessed by noise estimates at each electrode. Electrode noise levels were monitored during subject setup and noisy electrode placements were corrected prior to data collection. Noise levels were similar to those for low impedance (less than 5 kΩ) recordings. Offline, individual trials were smoothed, corrected for vertical and horizontal eye movements using EEGLAB4 [13], a MATLAB toolbox (The Mathworks, Natick, Massachusetts, USA). Electrodes that showed poor correlations with their nearest neighbors and excessive 60 Hz activity were presumed to have lost scalp contact during the recording session. In these cases, the values at these sites were replaced by the average of the four nearest valid neighbors. Trials exceeding ±100 μV were excluded from further analysis. Brain electrical activity from the 80 scalp sites was selected for a temporal window corresponding to the area of maximal signal positivity (800–1200 ms following odor administration; see Fig. 1) (the olfactory equivalent of the P300 [14]). The data were artifact corrected (EEGLAB4), averaged and integrated for the electrodes in each of 12 scalp regions arranged in a 3 (anterior/central/posterior) × 2 (left/right) × 2 (medial/distal) matrix.

Results

Grand means for vertex electrode in each of the two olfactory conditions are presented in Fig. 1, with timing bars (two series of small rectangles) illustrating the two different types of stimuli administered (fast/slow). The integrated peak voltages for the fast and slow odor administrations were compared across the 12-area spatial map using a four-way repeated-measures analysis of variance (odor change × anterior/central/posterior × left/right × medial/distal). As our hypothesis concerned the pattern of differences in brain activity related to the two administration types, vector filtering was not performed [15]. Results of the analysis indicated a four-way interaction such that the spatial pattern of brain electrical activity (left/right × anterior/central/posterior × medial/distal) did differ as a result of the fast and slow types of olfactory stimulation [F(2,18)=4.099, P=0.04 after Greenhouse–Geisser adjustment]. Paired t-tests of participants’ ratings for both intensity and pleasantness did not indicate differences between the fast and slow administration conditions for these attributes.

To better understand the spatial pattern of the neurophysiological differences found in the analysis of variance, the same integrated peak data were submitted to low-resolution electromagnetic tomographic analysis (LORETA [16]). This analysis converts the pattern brain electrical data into current densities and then projects them into a three-

![Fig. 1](image-url) Grand means for the two types of odor administration at electrode Cz. The large box overlapping the waveforms indicates the region of interest for the peak of positive activity. The series of small boxes illustrate the alternation between odors in the two stimulation conditions.
Dimensional model of the brain. While all attempts to estimate the source of brain potentials from scalp-recorded data can be problematic, recent research indicates that LORETA is among the more accurate and conservative approaches [17]. The results of this analysis can be seen in Fig. 2 and clearly illustrate an increase in current sources in the left temporal lobe for the fast transition condition. The slow transition condition shows a more symmetrical distribution of activity over the cortex.

Discussion
This study demonstrates that temporal unfolding of an odor stimulus has the capacity to alter human neurophysiological activity. In this study, the odors and their durations were held constant and only the number of changes per unit time differed between conditions. These temporal differences were sufficient to alter the pattern of evoked activity to the odors. Whereas inferring neural generators from scalp-recorded brain potentials can be problematic, estimates using LORETA suggest that the main difference between fast and slow administration types occurs in the hemispheric distribution of activity and, in particular, posterior aspects of the left temporal lobe. If the observed differences originate there, it would be consistent with an existing literature indicating the advantage of the left hemisphere and temporal lobe in discriminating rapidly changing stimuli in auditory, tactile and visual modalities. Furthermore, the presence of olfaction in this list of other modalities suggests that even this sense most associated with subcortical processing uses a common set of cortical resources for temporally unfolding stimuli. If rapid temporal processing is what the left hemisphere does, it is little wonder that it is strongly associated with language and all the other 'macro-category' functions attributed to this area. Perhaps it is time to reconsider what functions we are attempting to map.

References

