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Research Report

The effects of attentional load on auditory ERPs recorded from human cortex

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ABSTRACT

Responses to acoustic input were recorded from human temporal cortex using subdural electrodes in order to investigate in greater anatomical detail how attentional load modulates exogenous auditory responses. Four patient-volunteers performed a dichotic listening task in which they listened for rare frequency deviants in a series of tones presented to both ears at interstimulus intervals (ISIs) of 400, 800, and 2000 ms. Across all ISIs, stimuli presented contralateral to electrode location produced the strongest deflections in the averaged ERP at approximately 90 and 170 ms post-stimulus on average (labeled N90stg and P170stg). Maximal recording sites for these peaks most often occurred over the Sylvian fissure or the upper bank of the posterior superior temporal gyrus. Neither ISI nor selective attention exhibited substantial effects on peak latencies. However, as presentation rates increased (decreasing ISI), overall averaged event-related potential (ERP) amplitudes declined significantly, while attending to the contralateral stimulus significantly increased both the N90stg and P170stg peaks for most patients. This effect of attention increased with decreasing ISI for both components most clearly in the difference between the grand-average ERPs for attending to vs. ignoring the contralateral stimulus, and even more dramatically in the percentage ratio of that difference over the mean peak amplitude. This amplifying effect of attention with increasing load, along with its anatomical location, suggests that attention can enhance exogenous sources in auditory cortex.

1. Introduction

It is well known that attention directed toward particular aspects of sensory input (i.e., selective attention) can modulate the baseline physiological response to that input. Human electrophysiological research has resulted in two competing models of the effects of auditory selective attention. In one view, Hillyard and colleagues have proposed an early enhancement of the exogenous auditory evoked response potential (ERP) waveform deflection occurring approximately 70–120 ms post-stimulus, commonly labeled N1 (i.e., the “N1 effect”, Hillyard et al., 1973; Näätänen and Picton, 1987; Woods, 1990). Its primary auditory source is believed to reside along the supratemporal plane (STP) (Liégeois-Chauvel et al., 1994; Picton et al., 1999; Yvert et al., 2001; Godey et al., 2001), which, along with its

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early latency, tonotopicity, and sensitivity to the state of the listener, has lead many to view the N1 as an obligatory (i.e., exogenous) sensory response (see Näätänen, 1992, for a review). Its attentional modulation would therefore indicate that selective attention can intervene early and directly in sensory processing.

Conversely, Näätänen and colleagues have proposed that the attentional modulation of late auditory ERP deflections arises primarily from an endogenous generator independent of that producing the N1 (Näätänen, 1992). In this view, selective attention adds a distinct negative component to the ERP labeled the "processing negativity" (PN), which is considered a physiological index of an endogenous perceptual comparison process. The broad temporal effect of the PN can not only add negativity to attended ERPs at N1 latencies, thus creating the N1 effect, but also to later positive deflections such as the P2, which would thus shift negatively in attend relative to ignore conditions (Näätänen, 1992; Teder et al., 1993).

A fast stimulus presentation rate was initially viewed essential for creating the N1 effect because it was thought to increase information load to the point where attention must intervene early in sensory processing to achieve target set selection (Hillyard et al., 1973; Schwent et al., 1976; Hansen and Hillyard, 1984). For example, Woldorff and colleagues reported an early attentional modulation of the positive mid-latency deflection occurring around 20–50 ms post-stimulus (known alternately as P20–50 or P1), but only under conditions of high load created with very short ISIs (e.g., 200 ms) (Hackley et al., 1990; Woldorff and Hillyard, 1991; Woldorff et al., 1993). The generators of these enhanced ERP components have also been localized to the STP, further supporting the view that exogenous auditory responses can be directly modulated by attention (Woldorff et al., 1993; Woods et al., 1994; Giard et al., 2000). Reports of a more positive P2/P190, along with the more positive P20–50 and more negative N1, also suggest that attention generally enhances responses in sensory cortex beyond the contributions of putative endogenous components (Woldorff and Hillyard, 1991). This association of greater attentional load or cognitive effort with greater activation in sensory cortex has found growing support in both EEG (Alcaini et al., 1995; Sussman et al., 2003) and neuroimaging studies (O'Leary et al., 1997; Alho et al., 1999; Jäncke et al., 1999; Zatorre et al., 1999; Petkov et al., 2004; Shomstein and Yantis, 2004).

This model has been questioned by other researchers, however, who have countered that fast stimulus rates do not increase the exogenous N1 peak directly but rather the onset of an attention-related negativity (i.e., PN); in such cases, the early PN onset overlaps with the N1 to create an apparent N1 effect (Parasuraman, 1980; Näätänen et al., 1981; Teder et al., 1993). The attention-related negativity has since been subdivided into earlier and later subcomponents, as measured in the negative difference wave (Nd) formed by subtracting attended from non-attended ERPs (Näätänen et al., 1981; Hansen and Hillyard, 1984; Woldorff and Hillyard, 1991; Alcaini et al., 1995; Giard et al., 2000). There is evidence that earlier Nd components may reflect true enhancements of an exogenous, modality-specific component of the N1 in auditory cortex, while later peaks arise from endogenous sources, often of more frontal origin (Näätänen et al., 1981; Hansen and Hillyard, 1984; Woldorff and Hillyard, 1991; Woods et al., 1994; Alcaini et al., 1995; Giard et al., 2000). Unfortunately, the inherent temporal and/or spatial limitations of non-invasive electromagnetic methods make it difficult to completely isolate exogenous contributions to the scalp-recorded N1 effect from potentially distinct endogenous components such as the PN (Parasuraman, 1980; Woods et al., 1991; Teder et al., 1993; Alho et al., 1994).

Patients undergoing evaluation for the surgical treatment of medically intractable epilepsy provide a rare opportunity to measure the effects of selective attention directly from human cortex. As part of their treatment, intracranial recordings (electrocorticograms, ECoG) are often made to identify the locus of seizure activity and/or map cortical areas involved in speech and language. Intracranial recordings are not susceptible to the temporal and spatial filtering of electrical sources due to the skull and scalp that are seen in EEG recordings (Srinivasan, 1999). They further limit the superimposition of distant electrical sources and therefore enhance the measurement of local generators. In the present work, electrodes were implanted for clinical purposes in patient-volunteers over the lateral temporal cortex and perisylvian areas. The increased resolution of ECoG recordings from this region should help isolate the contribution of potentially modality-specific contributors to the scalp-recorded N1 over frontal or deeper subcomponents. The goal of the current work was to investigate intracranially the effects of selective auditory attention and attentional load on human perisylvian cortex as produced in the classic dichotic auditory oddball paradigm.

2. Results

2.1. *Behavioral performance*

Table 1 presents overall mean percent correct and d-prime values in the deviant detection task averaged across both attention conditions, and from all sessions for all four patients. Previous EEG studies measuring deviant detection performance at varying ISIs reported strong trends of improved detection at faster rates (Parasuraman, 1980; Näätänen et al., 1981; Teder et al., 1993). Performance differences in the present results were not significant across ISI, however, suggesting that task difficulty increased with increasing stimulus rates for participants, countering the potential detection advantages that can occur during rapid tone presentation (Alain and Woods, 1993).

2.2. *Anatomical location and nomenclature of major negative and positive ERP peaks*

Data from four patients are reported here. Analysis will focus on changes due to attention in ERPs formed by averaging

Table 1 – Mean (±SD) p(C) and d-prime values in the deviant detection task averaged across both attention conditions, all sessions, and all patients

	400 ms ISI	800	2000
p(C)	76.4% (13.3)	77.4 (8.87)	74.5 (13.3)
d-prime	3.7 (0.7)	3.6 (0.4)	3.5 (0.6)