

Gamma and beta neural activity evoked during a sensory gating paradigm: Effects of auditory, somatosensory and cross-modal stimulation

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Abstract

Objective: Stimulus-driven salience is determined involuntarily, and by the physical properties of a stimulus. It has recently been theorized that neural coding of this variable involves oscillatory activity within cortical neuron populations at beta frequencies. This was tested here through experimental manipulation of inter-stimulus interval (ISI).

Methods: Non-invasive neurophysiological measures of event-related gamma (30–50 Hz) and beta (12–20 Hz) activity were estimated from scalp-recorded evoked potentials. Stimuli were presented in a standard “paired-stimulus” sensory gating paradigm, where the S1 (conditioning) stimulus was conceptualized as long-ISI, or “high salience”, and the S2 (test) stimulus as short-ISI, or “low salience”. Three separate studies were conducted: auditory stimuli only ($N = 20$ participants), somatosensory stimuli only ($N = 20$), and a cross-modal study for which auditory and somatosensory stimuli were mixed ($N = 40$).

Results: Early (20–150 ms) stimulus-evoked beta activity was more sensitive to ISI than temporally-overlapping gamma-band activity, and this effect was seen in both auditory and somatosensory studies. In the cross-modal study, beta activity was significantly modulated by the similarity (or dissimilarity) of stimuli separated by a short ISI (0.5 s); a significant cross-modal gating effect was nevertheless detected.

Conclusions: With regard to the early sensory-evoked response recorded from the scalp, the interval between identical stimuli especially modulates beta oscillatory activity.

Significance: This is consistent with developing theories regarding the different roles of temporally-overlapping oscillatory activity within cortical neuron populations at gamma and beta frequencies, particularly the claim that the latter is related to stimulus-driven salience. © 2006 International Federation of Clinical Neurophysiology. Published by Elsevier Ireland Ltd. All rights reserved.

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1. Introduction

Stimulus-driven salience, a property that reflects an unexpected sensory element's relative importance to an individual, is automatically (i.e., involuntarily) determined by the physical features of that stimulus (James, 1890; Naatanen, 1992; Treisman and Gelade, 1980). The specific stimulus properties that confer salience in a stimulus-driven manner have been documented in the autonomic orienting literature (Sokolov, 1963) and include stimulus intensity

(Edwards, 1974; James and Hughes, 1969), stimulus novelty (Berlyne et al., 1963; Siddle et al., 1983), and the degree of contrast between a stimulus and its sensory background (Ben-Shakhar et al., 2000; Lyytinen et al., 1992). Another property that confers stimulus-driven salience, and the focus of the present report, is inter-stimulus interval (ISI) which is related to a stimulus' rarity (Gatchel and Lang, 1974; Graham, 1973). In general, “stimulus-driven” salience is to be distinguished from “task-driven” salience, the latter being voluntarily assigned by an individual's top-down allocation of selective attention (Kastner and Ungerleider, 2000; Schneider and Shiffrin, 1977; Theeuwes, 1994; van Zoest and Donk, 2004).

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It has recently been proposed that bottom-up processing of stimulus-driven salience by cortical neuron populations corresponds to oscillatory neural activity within specific separable frequency bands. Using *in vitro* preparations and computer simulations, Traub et al. (1999) have shown that neuron populations respond to stimulation with action potential bursts that recur at a gamma rhythm (30–100 Hz). When the stimulation was relatively intense, the action potential bursts subsequently transitioned to a beta rhythm (10–25 Hz). This transition did not occur after stimulation at lower stimulus intensities, although the gamma rhythm was still observed. Scalp-recorded electroencephalographic measures of neuron population activity in the intact human brain have been shown to exhibit a similar pattern of response to stimulus-driven salience: Haenschel et al. (2000) demonstrated that an evoked gamma-band response was followed by a robust beta-band response, but only when the auditory stimulus suddenly changed from the ongoing acoustic background. This apparent gamma-to-beta transition occurred within 150 ms of stimulus onset in response to these high salience stimuli. Thus, although Traub et al. (1999) and Haenschel et al. (2000) employed substantively different neurophysiological measures of neuron population activity, and although they operationalized “salience” differently, they both highlighted the sensitivity of evoked beta-band activity to stimulus-driven salience.

The outcome of these and other investigations led to the hypotheses that event-related neural activity in the gamma band reflects obligatory processing of sensory stimulus features (Clementz and Blumenfeld, 2001; Karakas and Basar, 1998), and the subsequent beta activity “flags” a stimulus as salient (Traub et al., 1999) and thus a candidate for subsequent involuntary attention switching (Whittington et al., 1997). Further supporting evidence includes the finding that gamma oscillations are generally localized to specific sensory cortical regions (Barth and MacDonald, 1996; Pantev et al., 1991; Pantev, 1995) whereas beta activity exhibits more widespread expression across cortex and more robust synchronization between cortical regions including association areas (Roelfsema et al., 1997; von Stein et al., 1999). Nevertheless, applicability of this theory to a general neural model of stimulus-driven salience processing requires empirical demonstrations that other relevant properties, such as novelty and ISI, also appropriately modulate oscillatory neuron population activity, especially in the beta band.

Through the use of non-invasive neurophysiological measures of event-related oscillatory neural activity, the present study was designed to test predictions of the gamma-to-beta transition theory, specifically for experimental manipulation of stimulus-driven salience in the form of ISI. If gamma activity corresponds to obligatory stimulus processing and beta activity to a subsequent salience signal, then a differential pattern of modulation by ISI should be observed for neural activity within these two frequency bands. For example, if a stimulus were presented at two different ISIs, “long” and “short”, amplitude of the event-related beta response should be larger to the long-

ISI stimulus (i.e., the stimulus of higher salience) than to the short-ISI stimulus (i.e., the stimulus of lower salience). By contrast, amplitude of the gamma response, corresponding to elementary processing of the stimulus itself, should exhibit relatively little sensitivity to ISI. Further, if this model applies generally to cortical processing of stimulus-driven salience, then the predictions should hold for multiple sensory modalities (e.g., auditory and somatosensory). However, when stimuli from different modalities follow each other at short ISIs, the event-related beta response should be significantly larger than when stimuli from the same modality follow each other. This can be understood by considering that stimulus-driven salience reflects not only ISI, but also the identity of the particular stimulus. In other words, changing the identity of a stimulus (in this case from an auditory stimulus to a somatosensory stimulus, or *vice versa*) should lead to an apparent “dishabituation” pattern for the evoked beta response at short ISI (Dawson et al., 1989; Siddle and Jordan, 1993). If such a pattern were not observed, it would be difficult to rule out the possibility that reduced amplitude beta response as a function of reduced ISI simply reflects global cortical refractoriness. We did not expect this more trivial explanation for dependence of beta response on ISI to be applicable here: *within*-modality changes in stimulus identity (e.g., a change in the frequency of auditory tones), even at fixed ISI, has been shown to produce increased beta-response amplitude (Haenschel et al., 2000). A similarly robust dishabituation of event-related gamma-band activity by changing stimulus identity at short ISI was *not* expected here: even when stimuli are presented at short ISI, obligatory stimulus processing should not depend upon the physical match or mismatch to the preceding stimulus.

Neural processing of ISI has commonly been investigated with a “sensory gating” paradigm (Adler et al., 1998; Boutros and Belger, 1999; Braff and Geyer, 1990; Kisley et al., 2004). The paradigm involves the presentation of an unchanging sensory stimulus, but at varied intervals between presentations (e.g., 0.5 and 9 s). This has been described as a paired-stimulus paradigm, where stimuli separated by 0.5 s represent a “pair”, and the 9 s interval is considered the “inter-pair interval”. For the present study the stimuli were instead analyzed individually and characterized by the ISI preceding them, either short (0.5 s) or long (9 s), corresponding to “low” and “high” stimulus-driven salience, respectively. Comparing this conceptualization to previous literature, a long-ISI stimulus corresponds to the “conditioning” or S1 stimulus, and the short-ISI stimulus corresponds to the “test” or S2 stimulus. Most commonly investigated in auditory sensory gating studies are broadband event-related potential (ERP) components P1 (“P50”) and N1 (“N100”), both of which are typically larger in response to stimuli of higher salience (i.e., longer ISI) and both of which exhibit maximal deflection before about 125 ms post-stimulus. Here, by contrast, the analysis of neural activity was focused on event-related

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