



Steady state responses to temporally congruent and incongruent auditory and vibrotactile amplitude modulated stimulation



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ARTICLE INFO

Article history:

Received 11 February 2013

Received in revised form 26 May 2013

Accepted 4 June 2013

Available online 11 June 2013

Keywords:

Cross-modal correspondence

Amplitude modulation

Steady-state response

Temporal information

Multisensory integration

Perceptual sensitivity

ABSTRACT

Recent research suggests that multisensory integration may occur at an early phase in sensory processing and within cortical regions traditionally thought to be exclusively unisensory. Evidence from perceptual and electrophysiological studies indicate that the cross modal temporal correspondence of multisensory stimuli plays a fundamental role in the cortical integration of information across separate sensory modalities. Further, oscillatory neural activity in sensory cortices may provide the principle mechanism whereby sensory information from separate modalities is integrated.

In the present study we aimed to extend this prior research by using the steady-state EEG response (SSR) to examine whether variations in the cross-modality temporal correspondence of amplitude modulated auditory and vibrotactile stimulation are apparent in SSR activity to multisensory stimulation. To achieve this we varied the cross-modal congruence of modulation rate for passively and simultaneously presented amplitude modulated auditory and vibrotactile stimuli. In order to maximise the SSR response in both modalities 21 and 40 Hz modulation rates were selected. Consistent with prior SSR studies, the present results showed clear evidence of phase-locking for EEG frequencies corresponding to the modulation rate of auditory and vibrotactile stimulation. As also found previously, the optimal modulation rate for SSR activity differed according to the modality, being greater at 40 Hz for auditory responses and greater at 21 Hz for vibrotactile responses. Despite consistent and reliable changes in SSR activity with manipulations of modulation rate within modality, the present study failed to provide strong evidence of multisensory interactions in SSR activity for temporally congruent, relative to incongruent, cross modal conditions. The results are discussed in terms of the role of attention as a possible factor in reconciling inconsistencies in SSR studies of multisensory integration.

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1. Introduction

Multisensory integration refers to a process whereby sensory information from different modalities is integrated to form a combined multisensory representation not otherwise available from separate senses. The ability to integrate sensory information across modalities provides a considerable adaptive advantage by enhancing stimulus detection and discrimination and speeding behavioural responses (Calvert, 2001). The dramatic perceptual impact of the multisensory 'whole' being greater than the sum of the 'parts' is apparent from the classic demonstrations of the influence that seemingly trivial cross-modal manipulations of sensory information has on perception (Shipley, 1964; McGurk and MacDonald, 1976; Shams et al., 2000).

An important limitation for perceptual investigations of multisensory integration is establishing whether multisensory enhancement reflects the integration of information at a sensory level or whether

these changes result from higher order perceptual or cognitive processes, such as perceptual grouping or attention that may operate entirely on separate unisensory input. For multisensory integration to occur, sensory information from separate modalities must be integrated at some level within the central nervous system (Foxy et al., 2002). Developing a comprehensive understanding of how the brain achieves sensory integration information across modalities represents a major challenge for research examining the neural basis of multisensory perception. In the present study we seek to extend this research by examining whether the EEG steady state response shows the stimulus–response characteristics consistent with emerging views of the neurophysiological activity underlying multisensory integration.

1.1. Neurophysiological basis of multisensory integration

Traditionally, the integration of information across sensory modalities was thought to occur subsequent to initial unisensory processing and within polysensory or association cortex (Felleman and Van Essen, 1991). The seminal discovery (Meredith and Stein, 1983) that

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neurons in superior colliculus were uniquely sensitive to multisensory stimulation challenged this view by revealing that multisensory integration was a far more low-level aspect of sensory processing than had been traditionally assumed. This research provided evidence of a variety of multisensory neural responses which may either be additive, superadditive or subadditive, relative to the sum of the corresponding unisensory responses (Stein and Meredith, 1993) and established some important principles of multisensory integration based on the cross-modal stimulus relationships. Multisensory responses were generally found to be greatest where unisensory stimuli shared common spatial or temporal characteristics (i.e. the spatial and temporal rules) (Meredith et al., 1987; Meredith and Stein, 1996).

While the majority of early neurophysiological research examined neural responses within superior colliculus, it was later established that multisensory neurons also existed in cortex and that multisensory responses in superior colliculus largely reflected the top down influence of converging inputs from unisensory cortical neurons (Wallace et al., 1993). This central role of the cortex in multisensory processing was confirmed in studies using multi-electrode techniques to directly measure local field potentials in humans and other primates, thus providing unequivocal support for the emerging view that multisensory integration occurs in primary cortical regions previously thought to be exclusively unisensory and at a much earlier stage in the sensory processing (for reviews see; Schroeder and Foxe, 2005; Ghazanfar and Schroeder, 2006). Neuroanatomical studies have also provided substantial support for the role of cortex in multisensory processing with evidence of extensive cross modal innervation of the sensory cortices including direct somatosensory and visual subcortical innervations of auditory cortex (for reviews see; Kayser et al., 2009; Musacchia and Schroeder, 2009). Further, sensory projections from secondary visual cortex to caudal auditory cortex in monkeys (Falchier et al., 2010) and direct bidirectional projections between primary auditory cortex and primary auditory cortex in the gerbil have been identified (Budinger et al., 2006). Similarly, multisensory neuroimaging studies (e.g. PET, fMRI, MEG and EEG) in humans have provided evidence that wide cortical networks are involved in multisensory integration, including superior temporal sulcus, inferior parietal sulcus, posterior insula and frontal cortex, which may vary according to the sensory modalities and multisensory experimental designs involved (for review see; Calvert, 2001).

A major challenge for neuroimaging studies is uncertainty regarding whether the multisensory response properties identified in single cells could be obtained in population level measures of neural activity such as fMRI and EEG. While a variety of multisensory interactions have been observed, superadditive responses to multisensory relative to unisensory stimulation is a more common criterion for assessing multisensory interaction for neuroimaging studies (Foxe et al., 2000, 2002; Brett-Green et al., 2008). However a single fMRI voxel represents the combined activity of both unisensory and multisensory neurons (Calvert, 2001). Even conservative estimates indicate that an individual fMRI voxel in human cortex could comprise approximately 2.5 million neurons, were only 37.5% (625,000) of these would be unisensory neurons and 25% (175,000) multisensory (Laurienti et al., 2005). Based on the response properties of single cells obtained in animal studies this suggests that only 28% of multisensory neurons would show superadditive responses, with the remainder showing either subadditive or additive responses. This limitation would be significantly greater for EEG and MEG as a result of the relatively lower spatial resolution and bioelectric/magnetic properties of EEG and MEG. Therefore it seems unlikely, if not impossible that superadditive multisensory responses analogous to that identified in single cell activity could be resolved using neuroimaging techniques (Laurienti et al., 2005).

Despite these limitations neuroimaging measures provide a unique opportunity to investigate the neurophysiological basis of

multisensory integration, in vivo in humans, particularly for studies examining correlations between brain activity and perceptual or attentional aspects of multisensory processing (e.g. Jacoby et al., 2012). For example, the greater temporal resolution of the EEG has been exploited by event related potential (ERP) studies to reveal that multisensory integration occurs much earlier in the sensory processing than traditionally thought. Using a variety of multisensory stimulation techniques several ERP studies have provided consistent evidence that multisensory neural responses to cross-modal stimulus combinations are evident at post stimulus latencies as brief as 50 ms for auditory–visual (Schroger and Widmann, 1998; Giard and Peronnet, 1999; Murray et al., 2001; Molholm et al., 2002) and auditory–somatosensory integration (Foxe et al., 2000; Murray et al., 2005; Butler et al., 2011).

While there has been a rapid development in knowledge regarding the neurophysiological basis of multisensory integration over the past two decades, most research has been concerned with ‘where’, and to a lesser extent ‘when’, multisensory integration takes place within the central nervous system. Much less is known about ‘how’ the brain achieves this remarkable ability. This represents a significant gap in current knowledge since the dramatic influence that multisensory stimulation may have on behavioural or neuroimaging measures does not necessarily provide evidence for the integration of information across modalities at a sensory level. As discussed, multisensory enhancement of a response may reflect perceptual or post-perceptual processes that operate entirely on unisensory input. Developing a better understanding of multisensory integration requires better knowledge of ‘how’ within the multisensory integration is achieved. Distinguishing between integration at a sensory level from the higher order behavioural or perceptual benefits that may only reflect cross-modal cue combination is required in order to better understand the neural mechanisms involved in multisensory integration (Soto-Faraco and Deco, 2009). In the next section we summarise the major theoretical approaches to understanding the neural mechanisms that may underlie multisensory integration together with evidence that the EEG steady state response may provide a unique neurophysiological measure of the integration of sensory information across modalities.

1.2. Oscillatory EEG activity and the steady state response

An alternative to the traditional ‘convergence approach’ of multisensory integration is the ‘temporal correlation hypothesis’ (von der Malsburg and Schneider, 1986; Singer and Gray, 1995), developed in the context of the ‘binding problem’ in research examining integration of stimulus features within a sensory modality. Oscillatory activity of cortical neurons reflects rapid and synchronised fluctuations of localised neural ensembles alternating between low and high excitability states (Freeman, 1975). According to this approach, multisensory integration is achieved via the synchronised oscillatory activity of ensemble cortical neurons (Engel et al., 2012). Based on a principle of ‘binding by synchrony’ (Nozaradan et al., 2012) or ‘integration through coherence’ (Senkowski et al., 2008), the temporal correlation hypothesis proposes that cross-modal coherence of synchronised neural oscillations may provide the necessary neural mechanism for flexible and context dependent binding of information across different sensory modalities.

The steady-state response (SSR) is an EEG measure of oscillatory brain activity elicited by periodic sensory stimulation. SSR activity phase-locks to the repetition rate of a range of periodic sensory stimuli and so is thought to reflect a stimulus driven ‘entrainment’ or driving of oscillatory neural activity at EEG frequencies corresponding to the stimulation rate (Picton et al., 2003). The stimulation rate at which the SSR achieves maximum amplitude varies consistently across sensory modality (Ross et al., 2012). In the auditory modality amplitude modulated sounds elicit a maximal SSR response at

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