



Review

Look now and hear what's coming: On the functional role of cross-modal phase reset



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ABSTRACT

In our multisensory environment our sensory systems are continuously receiving information that is often interrelated and must be integrated. Recent work in animals and humans has demonstrated that input to one sensory modality can reset the phase of ambient cortical oscillatory activity in another. The periodic fluctuations in neuronal excitability reflected in these oscillations can thereby be aligned to forthcoming anticipated sensory input. In the auditory domain, the example par excellence is speech, because of its inherently rhythmic structure. In contrast, fluctuations of oscillatory phase in the visual system are argued to reflect periodic sampling of the environment. Thus rhythmic structure is imposed on, rather than extracted from, the visual sensory input. Given this distinction, we suggest that cross-modal phase reset subserves separate functions in the auditory and visual systems. We propose a modality-dependent role for cross-modal input in temporal prediction whereby an auditory event signals the visual system to look now, but a visual event signals the auditory system that it needs to hear what is coming.

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1. Introduction

As we explore our environment, a sound might render one element of the visual scene more salient. Similarly a movement we see may help us identify a sound that we hear. Our sensory systems are constantly receiving information from the environment around us, and much of this information is interrelated and must somehow be integrated. In this article we review the current body of evidence from human studies that input to one sensory modality systematically reorganises the ambient cortical activity in another. Evidence in favour of this view comes for instance from studies of cortical plasticity after sensory deprivation. Following auditory sensory loss, activation of the auditory cortex by visual stimulation can be observed (e.g. Sandmann et al., 2012), which demonstrates how closely the sensory systems interact. In the normal, undeprived brain, the data on cross-modal phase reorganisation per se seem robust, but the evidence of directly-consequent perceptual or

behavioural benefit is rather sparse. We argue that notable differences between the available auditory and visual data relate to the contrasting roles of temporal prediction in the auditory and visual systems, and propose a function for cross-modal input that differs in a subtle but important manner across modalities.

Even in the absence of overt stimulation our sensory neural systems remain active, and distinct patterns of neuronal oscillatory activity are evident in cortical regions (e.g. Lakatos et al., 2005). Cortical oscillations are thought to reflect periodic fluctuations in neuronal activity between states of high and low excitability (Schroeder et al., 2008), and many recent studies have linked the phase of these oscillations to periodic fluctuations in sensory performance (Busch et al., 2009; Busch and VanRullen, 2010; Drewes and VanRullen, 2011; Henry and Obleser, 2012; Mathewson et al., 2010, 2009; Neuling et al., 2012; Ng et al., 2012; Stefanics et al., 2010; VanRullen et al., 2011). A growing number of studies have also now shown that oscillatory phase in one sensory modality can be perturbed or reorganised by events in another (Diederich et al., 2012; Fiebelkorn et al., 2011, 2013; Kayser et al., 2008; Lakatos et al., 2007, 2009; Naue et al., 2011; Romei et al., 2012; Thorne et al., 2011), and this effect seems to span several sensory modalities (see Fig. 1). However the potential benefits of such a cross-modal

Abbreviations: A1, primary auditory cortex; CMPR, cross-modal phase reset; SOA, stimulus onset asynchrony; V1, primary visual cortex

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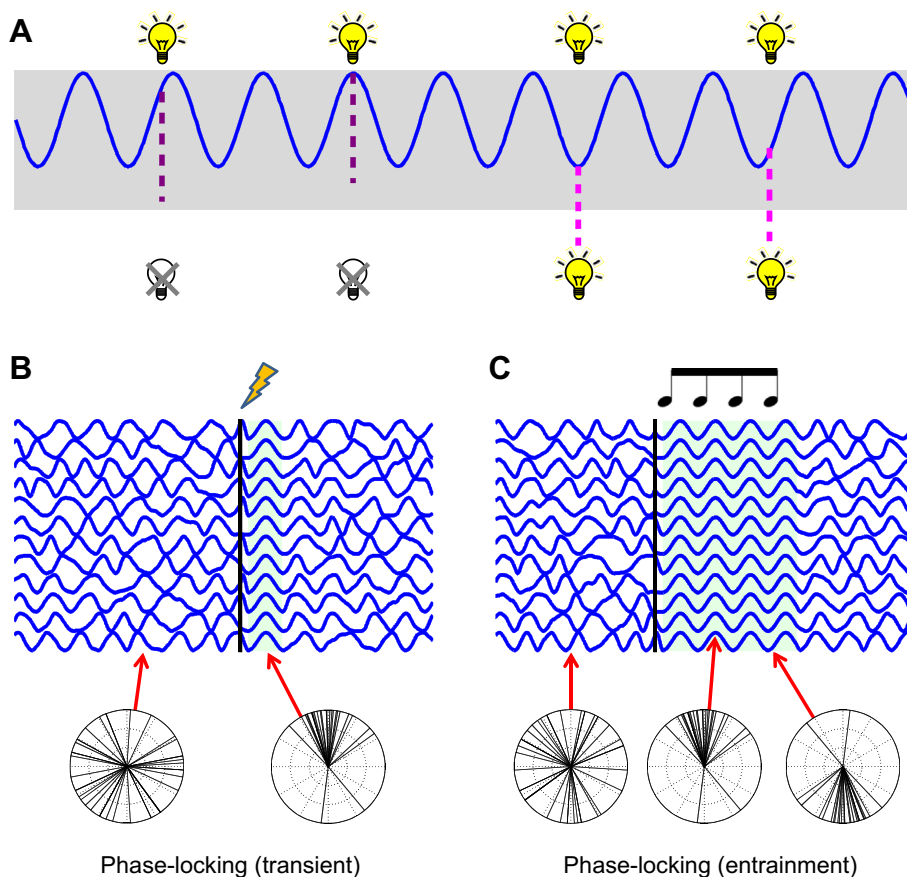


Fig. 1. Oscillatory phase and perception. (A) Physically-identical stimuli (top) may be perceived or not (bottom) depending on the phase of underlying oscillatory activity (middle) at stimulus onset. (B) and (C) Prior to any perturbing input oscillatory phase at any point in time is random. A single stimulus can cause transient phase reorganisation (B), and regularities in the input can lead to sustained phase-locking (C) as oscillatory activity entrains to the rhythmic input.

phase reset (CMPR) mechanism have to date been described only rather generically in terms of improved performance or efficiency.

If the brain is constantly making predictions about causes of sensory input (Friston, 2005, 2012), then oscillatory activity in general may be instrumental in allowing the brain to make such predictions, not only about “what” and “where” sensory inputs are to be expected, but also about “when” they are expected to occur (Arnal and Giraud, 2012). Temporal prediction relies on extracting regularities in sensory input and using these regularities to extrapolate events into the future. Information is available both from events of the immediate past, such as from ongoing environmental rhythms, and also potentially from a repository of previously-known associations, such as the typical delays between lip and head movements and voice onsets in normal speech. This type of relationship is clearly not restricted to single sensory modalities, thus CMPR is an obvious candidate mechanism for communicating such temporal information across modalities.

The auditory environment is replete with rhythms. Indeed sounds by definition evolve over time. One such example is human speech, formed of multiple rhythms across a range of frequencies. It is proposed that auditory speech comprehension is fundamentally linked to the brain’s ability to extract the rhythms in speech in order to predict and prepare for upcoming sounds (Giraud and Poeppel, 2012). According to this model neuronal spiking in response to incoming speech causes a phase reset of activity in auditory cortex at theta (4–8 Hz) and gamma (30–80 Hz) frequencies, eventually leading to alignment of neuronal excitability with the acoustic structure of forthcoming input, and thereby

improving speech analysis. It has also been shown that movements of the head and the mouth systematically track the acoustic rhythms of speech, and the brain may utilise these movements to further improve speech intelligibility (Munhall et al., 2004). Indeed the involvement of CMPR in this process has already been proposed (Schroeder et al., 2008). Evidence therefore supports a clear role for temporal prediction in the auditory system, and moreover an opportunity for the auditory system to utilise visual information to enhance this role, particularly as visual input often precedes the auditory (e.g. Chandrasekaran et al., 2009; Vroomen and Stekelenburg, 2010).

While rhythms are clearly fundamental to auditory domains such as speech and music, there are also rhythms in the visual environment, such as biological motion. However it is far less obvious how these may be used by the visual system for prediction. Sounds evolve over time, so the future information is relevant to the auditory system, whereas this is not necessarily the case for the visual system (Bendixen et al., 2012). The role of temporal prediction in the visual system may therefore not parallel its role in the auditory system. If CMPR, in turn, plays a role in temporal prediction then the function of CMPR is also likely to depend on modality, and indeed the suggestion that there may be different CMPR systems has already been made (Diederich et al., 2012). Evidence of CMPR of visual activity may therefore not help us to understand the auditory equivalent. But if temporal prediction is fundamental to the efficient processing of auditory input, then a potential role of CMPR is to provide additional temporal information that further improves the efficiency of this process.

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