

Electrophysiological signatures of conscious perception: The influence of cognitive, cortical and pathological states on multisensory integration

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Mai 2017

Publikationsbasierte Habilitationsschrift

Eingereicht beim Fachbereich
Erziehungswissenschaft und Psychologie
der
Freien Universität Berlin

Danksagung

Wissenschaft ist ein gemeinschaftliches Unternehmen und viele haben Anteil am Gelingen dieser Arbeit. Mein Dank dafür gilt:

Daniel Senkowski: Ein Großteil der Arbeit an dieser Habilitation entstand in der Arbeitsgruppe Multisensorische Integration an der Charité – Universitätsmedizin Berlin. Ohne Prof. Dr. Daniel Senkowski würde diese Arbeit nicht existieren – vielen Dank für Deine Unterstützung und Dein Vertrauen. Mein Dank gilt ebenso meinen Kolleginnen und Kollegen der Arbeitsgruppe: Johanna Balz, Mathis Kaiser, Martin Krebber, Georgios Michail, James Moran, Yadira Roa Romero und Ulrich Pomper. Darüber hinaus danke ich allen Studentinnen und Studenten, Hilfwissenschaftlerinnen und Hilfwissenschaftlern, Praktikantinnen und Praktikanten, die mich in meiner bisherigen Arbeit in Berlin unterstützt haben.

Marc Schönwiesner: Meine erste Stelle nach der Promotion führte mich an das International Laboratory for Brain, Music and Sound Research an der Université de Montréal. Marc Schönwiesner nahm mich in seiner Arbeitsgruppe auf und gab mir die Möglichkeit frei zu forschen. Ebenso gilt mein Dank Iria SanMiguel und Jana Timm für ihre Unterstützung.

Mein tiefer Dank gilt ebenso allen meinen Mitautoren, ohne die keine der hier zusammengefassten Arbeiten existieren würde. Darüber hinaus danke ich der Deutschen Forschungsgemeinschaft für die finanzielle Unterstützung meiner Arbeit (KE1828/2-1 und KE1828/4-1).

Schlussendlich danke ich meinen Eltern und meinen Brüdern für ihre Zuversicht und Unterstützung. Ganz besonders danke ich Katja Scherle: Vielen Dank, dass du immer, immer noch und immer wieder für mich da bist.

Julian Keil

Mai, 2017

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- Study 5:** Roa Romero, Y., Senkowski, D., Keil, J., 2015. Early and late beta-band power reflect audiovisual perception in the McGurk illusion. *J Neurophysiol* 113, 2342–2350. doi:10.1152/jn.00783.2014 56
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- Study 7:** Keil, J., Senkowski, D. (in press). Individual Alpha Frequency Relates to the Sound-Induced Flash Illusion. *Multisensory Research*. 58
- Study 8:** Pomper, U., Keil, J., Foxe, J.J., Senkowski, D., 2015. Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices. *Hum Brain Mapp* 36, 3246–3259. doi:10.1002/hbm.22845..... 59
- Study 9:** Keil, J., Pomper, U., Feuerbach, N., Senkowski, D., 2017. Temporal orienting precedes intersensory attention and has opposing effects on early evoked brain activity. *NeuroImage*. doi:10.1016/j.neuroimage.2017.01.039 60

Ausgewählte Publikationen und Arbeitsanteil

Study 1: Keil, J., Pomper, U., Senkowski, D., 2016. Distinct patterns of local oscillatory activity and functional connectivity underlie intersensory attention and temporal prediction. *Cortex* 74, 277–288. <https://doi.org/10.1016/j.cortex.2015.10.023>

Intersensory attention (IA) describes our ability to attend to stimuli of one sensory modality, while disregarding other modalities. Temporal prediction (TP) describes the process of directing attention to specific moments in time. Both attention mechanisms facilitate sensory stimulus processing, yet it is not understood whether they rely on common or distinct network patterns. In this electroencephalography (EEG) study, we presented auditory cues followed by visuo-tactile stimuli. The cues indicated whether participants should detect visual or tactile targets in the visuo-tactile stimuli. TP was manipulated by presenting stimuli block-wise at fixed or variable inter-stimulus intervals. We analysed power and functional connectivity of source-projected oscillations. We computed graph theoretical measures to identify networks underlying IA and TP. Participants responded faster when stimuli were presented with fixed compared to variable inter-stimulus intervals, demonstrating a facilitating effect of TP. Distinct patterns of local delta-, alpha-, and beta-band power modulations and differential functional connectivity in the alpha- and beta-bands reflected the influence of IA and TP. An interaction between IA and TP was found in theta-band connectivity in a network comprising frontal, somatosensory and parietal areas. Our study provides insights into how IA and TP dynamically shape oscillatory power and functional connectivity to facilitate stimulus processing.

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Study 2: Keil, J., Roa Romero, Y., Balz, J., Henjes, M., Senkowski, D., 2016. Positive and Negative Symptoms in Schizophrenia Relate to Distinct Oscillatory Signatures of Sensory Gating. *Frontiers in Human Neuroscience* 10, 639. <https://doi.org/10.3389/fnhum.2016.00104>

Oscillatory activity in neural populations and temporal synchronization within these populations are important mechanisms contributing to perception and cognition. In schizophrenia, perception and cognition are impaired. Aberrant gating of irrelevant

sensory information, which has been related to altered oscillatory neural activity, presumably contributes to these impairments. However, the link between schizophrenia symptoms and sensory gating deficits, as reflected in oscillatory activity, is not clear. In this electroencephalography study, we used a paired-stimulus paradigm to investigate frequency-resolved oscillatory activity in 22 schizophrenia patients and 22 healthy controls. We found sensory gating deficits in patients compared to controls, as reflected in reduced gamma-band power and alpha-band phase synchrony difference between the first and the second auditory stimulus. We correlated these markers of neural activity with a five-factor model of the Positive and Negative Syndrome Scale. Gamma-band power sensory gating was positively correlated with positive symptoms. Moreover, alpha-band phase synchrony sensory gating was negatively correlated with negative symptoms. A cluster analysis revealed three schizophrenia phenotypes, characterized by (i) aberrant gamma-band power and high positive symptoms, (ii) aberrant alpha-band phase synchrony, low positive, and low negative symptom scores or (iii) by intact sensory gating and high negative symptoms. Our study demonstrates that aberrant neural synchronization, as reflected in gamma-band power and alpha-band phase synchrony, relates to the schizophrenia psychopathology. Different schizophrenia phenotypes express distinct levels of positive and negative symptoms as well as varying degrees of aberrant oscillatory neural activity. Identifying the individual phenotype might improve therapeutic interventions in schizophrenia.

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When touching and viewing a moving surface our visual and somatosensory systems receive congruent spatiotemporal input. Behavioral studies have shown that motion congruence facilitates interplay between visual and tactile stimuli, but the neural mechanisms underlying this interplay are not well understood. Neural oscillations play a role in motion processing and multisensory integration. They may also be crucial for

visuotactile motion processing. In this electroencephalography study, we applied linear beamforming to examine the impact of visuotactile motion congruence on beta and gamma band activity (GBA) in visual and somatosensory cortices. Visual and tactile inputs comprised of gratings that moved either in the same or different directions. Participants performed a target detection task that was unrelated to motion congruence. While there were no effects in the beta band (13–21 Hz), the power of GBA (50–80 Hz) in visual and somatosensory cortices was larger for congruent compared with incongruent motion stimuli. This suggests enhanced bottom-up multisensory processing when visual and tactile gratings moved in the same direction. Supporting its behavioral relevance, GBA was correlated with shorter reaction times in the target detection task. We conclude that motion congruence plays an important role for the integrative processing of visuotactile stimuli in sensory cortices, as reflected by oscillatory responses in the gamma band.

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In everyday life we are confronted with inputs of multisensory stimuli that need to be integrated across our senses. Individuals vary considerably in how they integrate multisensory information, yet the neurochemical foundations underlying this variability are not well understood. Neural oscillations, especially in the gamma band (> 30 Hz) play an important role in multisensory processing. Furthermore, gamma-aminobutyric acid (GABA) neurotransmission contributes to the generation of gamma band oscillations (GBO), which can be sustained by activation of metabotropic glutamate receptors. Hence, differences in the GABA and glutamate systems might contribute to individual differences in multisensory processing. In this combined magnetic resonance spectroscopy and electroencephalography study, we examined the relationships between GABA and glutamate concentrations in the superior temporal sulcus (STS), source localized GBO, and illusion rate in the sound-induced flash illusion (SIFI). In 39

human volunteers we found robust relationships between GABA concentration, GBO power, and the SIFI perception rate (r -values = 0.44 to 0.53). The correlation between GBO power and SIFI perception rate was about twofold higher when the modulating influence of the GABA level was included in the analysis as compared to when it was excluded. No significant effects were obtained for glutamate concentration. Our study suggests that the GABA level shapes individual differences in audiovisual perception through its modulating influence on GBO. GABA neurotransmission could be a promising target for treatment interventions of multisensory processing deficits in clinical populations, such as schizophrenia or autism.

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The McGurk illusion is a prominent example of audiovisual speech perception and the influence that visual stimuli can have on auditory perception. In this illusion, a visual speech stimulus influences the perception of an incongruent auditory stimulus, resulting in a fused novel percept. In this high-density electroencephalography (EEG) study, we were interested in the neural signatures of the subjective percept of the McGurk illusion as a phenomenon of speech-specific multisensory integration. Therefore, we examined the role of cortical oscillations and event-related responses in the perception of congruent and incongruent audiovisual speech. We compared the cortical activity elicited by objectively congruent syllables with incongruent audiovisual stimuli. Importantly, the latter elicited a subjectively congruent percept: the McGurk illusion. We found that early event-related responses (N1) to audiovisual stimuli were reduced during the perception of the McGurk illusion compared with congruent stimuli. Most interestingly, our study showed a stronger poststimulus suppression of beta-band power (13–30 Hz) at short (0–500 ms) and long (500–800 ms) latencies during the perception of the McGurk illusion compared with congruent stimuli. Our study demonstrates that auditory perception is influenced by visual context and that the

subsequent formation of a McGurk illusion requires stronger audiovisual integration even at early processing stages. Our results provide evidence that beta-band suppression at early stages reflects stronger stimulus processing in the McGurk illusion. Moreover, stronger late beta-band suppression in McGurk illusion indicates the resolution of incongruent physical audiovisual input and the formation of a coherent, illusory multisensory percept.

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Transcranial magnetic stimulation (TMS) influences cortical processes. Recent findings indicate, however, that, in turn, the efficacy of TMS depends on the state of ongoing cortical oscillations. Whereas power and phase of electromyographic (EMG) activity recorded from the hand muscles as well as neural synchrony between cortex and hand muscles are known to influence the effect of TMS, to date, no study has shown an influence of the phase of cortical oscillations during wakefulness. We applied single-pulse TMS over the motor cortex and recorded motor-evoked potentials along with the electroencephalogram (EEG) and EMG. We correlated phase and power of ongoing EEG and EMG signals with the motor-evoked potential (MEP) amplitude. We also investigated the functional connectivity between cortical and hand muscle activity (corticomuscular coherence) with the MEP amplitude. EEG and EMG power and phase in a frequency band around 18 Hz correlated with the MEP amplitude. High beta-band (~34 Hz) corticomuscular coherence exhibited a positive linear relationship with the MEP amplitude, indicating that strong synchrony between cortex and hand muscles at the moment when TMS is applied entails large MEPs. Improving upon previous studies, we demonstrate a clear dependence of TMS-induced motor effects on the state of ongoing EEG phase and power fluctuations. We conclude that not only the sampling of incoming information but also the susceptibility of cortical communication flow depends cyclically on neural phase.

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Study 7: Keil, J., Senkowski, D., 2017. Individual Alpha Frequency Relates to the Sound-Induced Flash Illusion. *Multisensory Research* 30(6), 565–578. <https://doi.org/10.1163/22134808-00002572>

Ongoing neural oscillations reflect fluctuations of cortical excitability. A growing body of research has underlined the role of neural oscillations for stimulus processing. Neural oscillations in the alpha band have gained special interest in electrophysiological research on perception. Recent studies proposed the idea that neural oscillations provide temporal windows in which sensory stimuli can be perceptually integrated. This also includes multisensory integration. In the current high-density EEG-study we examined the relationship between the individual alpha frequency (IAF) and cross-modal audiovisual integration in the sound-induced flash illusion (SIFI). In 26 human volunteers we found a negative correlation between the IAF and the SIFI illusion rate. Individuals with a lower IAF showed higher audiovisual illusions. Source analysis suggested an involvement of the visual cortex, especially the calcarine sulcus, for this relationship. Our findings corroborate the notion that the IAF influences the cross-modal integration of auditory on visual stimuli in the SIFI. We integrate our findings with recent observations on the relationship between audiovisual integration and neural oscillations and suggest a multifaceted influence of neural oscillations on multisensory processing.

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Knowledge about the sensory modality in which a forthcoming event might occur permits anticipatory intersensory attention. Information as to when exactly an event

occurs enables temporal orienting. Intersensory and temporal attention mechanisms are often deployed simultaneously, but as yet it is unknown whether these processes operate interactively or in parallel. In this human electroencephalography study, we manipulated intersensory attention and temporal orienting in the same paradigm. A continuous stream of bisensory visuo-tactile inputs was presented, and a preceding auditory cue indicated to which modality participants should attend (visual or tactile). Temporal orienting was manipulated blockwise by presenting stimuli either at regular or irregular intervals. Using linear beamforming, we examined neural oscillations at virtual channels in sensory and motor cortices. Both attentional processes simultaneously modulated the power of anticipatory delta- and beta-band oscillations, as well as delta-band phase coherence. Modulations in sensory cortices reflected intersensory attention, indicative of modality-specific gating mechanisms. Modulations in motor and partly in somatosensory cortex reflected temporal orienting, indicative of a supramodal preparatory mechanism. We found no evidence for interactions between intersensory attention and temporal orienting, suggesting that these two mechanisms act in parallel and largely independent of each other in sensory and motor cortices.

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Study 9: Keil, J., Pomper, U., Feuerbach, N., Senkowski, D., 2017. Temporal orienting precedes intersensory attention and has opposing effects on early evoked brain activity. *NeuroImage* 148, 230–239. <https://doi.org/10.1016/j.neuroimage.2017.01.039>

Intersensory attention (IA) describes the process of directing attention to a specific modality. Temporal orienting (TO) characterizes directing attention to a specific moment in time. Previously, studies indicated that these two processes could have opposite effects on early evoked brain activity. The exact time-course and processing stages of both processes are still unknown. In this human electroencephalography study, we investigated the effects of IA and TO on visuo-tactile stimulus processing within one paradigm. IA was manipulated by presenting auditory cues to indicate whether participants should detect visual or tactile targets in visuo-tactile stimuli. TO was manipulated by presenting stimuli block-wise at fixed or variable inter-stimulus intervals. We observed that TO affects evoked activity to visuo-tactile stimuli prior to IA. Moreover, we found that TO reduces the amplitude of early evoked brain activity,

whereas IA enhances it. Using beamformer source-localization, we observed that IA increases neural responses in sensory areas of the attended modality, whereas TO reduces brain activity in widespread cortical areas. Based on these findings we derive an updated working model for the effects of temporal and intersensory attention on early evoked brain activity.

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Zusammenfassung

Jederzeit erreichen uns Informationen über unsere verschiedenen Sinnesorgane und Wahrnehmungssysteme. Um in dieser Menge an Informationen den Überblick zu behalten, müssen zusammengehörige Informationen zu einer kohärenten Wahrnehmung zusammengefügt werden. In den letzten Jahren hat die Hypothese, dass synchrone neuronale Oszillationen eine wichtige Rolle bei der Verarbeitung von unisensorischen und multisensorischen Reizen spielen, viel Unterstützung erfahren. Neueste Befunde befördern weiterhin die Idee, dass lokale Oszillationen und funktionale Konnektivität aufsteigende und absteigende Prozesse bei multisensorischer Integration und Wahrnehmung widerspiegeln. In dieser Arbeit werde ich einen Überblick über die neuesten Befunde zur Rolle neuronaler Oszillationen bei bewusster, multisensorischer Wahrnehmung geben. Anschließend werde ich ein integratives Netzwerkmodell multisensorischer Wahrnehmung präsentieren, welches die kortikalen Korrelate bewusster, multisensorischer Wahrnehmung, den Einfluss von Schwankungen oszillatorischer neuronaler Aktivität auf darauffolgende Wahrnehmung, sowie den Einfluss kognitiver Prozesse auf neuronale Oszillationen und Wahrnehmung beschreibt. Ich schlage vor, dass neuronale Oszillationen in umschriebenen, gleichzeitig aktiven Frequenzbändern die verschiedenen Verarbeitungsschritte widerspiegeln, welche multisensorischer Wahrnehmung zugrunde liegen.

Summary

At any given moment, information reaches us via our different sensory systems. In order to navigate this multitude of information, associated information needs to be integrated to a coherent percept. In recent years, the hypothesis that synchronous neural oscillations play a prominent role in unisensory and multisensory processing has received substantial support. Current findings further convey the idea that local oscillations and functional connectivity reflect bottom-up as well as top-down processes during multisensory integration and perception. In the current work, I review recent findings on the role of neural oscillations for conscious multisensory perception. Subsequently, I present an integrative network model for multisensory integration that describes the cortical correlates of conscious multisensory perception, the influence of fluctuations of oscillatory neural activity on subsequent perception, and the influence of cognitive processes on neural oscillations and perception. I propose that neural oscillations in distinct, coexisting frequencies reflect the various processing steps underlying multisensory perception.

Clocks tick, bridges and skyscrapers vibrate, neuronal networks oscillate

György Buzsáki and Andreas Draguhn

Introduction

Why does seeing a speaker's lip movements improve speech comprehension in noisy environments (Sumby and Polack, 1954)? Why does simultaneous ringing and vibrating help us to answer a phone faster (Pomper et al., 2014)? Why do individuals usually respond faster to multisensory stimuli than to unisensory stimuli (Miller et al., 1982; Cappe et al., 2009)? The study of multisensory integration at the behavioral level can provide valuable information about the conditions under which information from different senses interact. In addition, functional neuroimaging approaches are well suited to study which cortical regions are involved in the perception and processing of multisensory information (Calvert et al., 2000; 2001). Furthermore, electrophysiological approaches are practical for mapping the neural network dynamics underlying multisensory processing, integration and perception (Senkowski et al., 2008). The combined knowledge from behavioral, functional neuroimaging, and electrophysiological studies allows a comprehensive understanding of how sensory information is integrated across the different senses. In the present work, I focus on the electrophysiological correlates of conscious perception. More specifically, I elucidate the influence of cognitive, cortical and pathological states on multisensory integration.

First, in the present work I will provide an introduction to neural oscillations, with a focus on the role of neural oscillations in conscious perception. Second, I will summarize how multisensory integration and conscious perception are reflected in oscillatory cortical activity. Third, I will review the cortical states influencing multisensory perception. Fourth, I will summarize the cognitive influences on cortical activity and multisensory perception. In a fifth part, I will briefly highlight the relationship between aberrant cortical oscillations and multisensory perception in psychiatric disorders. Finally, I will present an integrative model to summarize the different aspects presented above. **Figure 1** gives an overview of the key elements investigated in the current work.

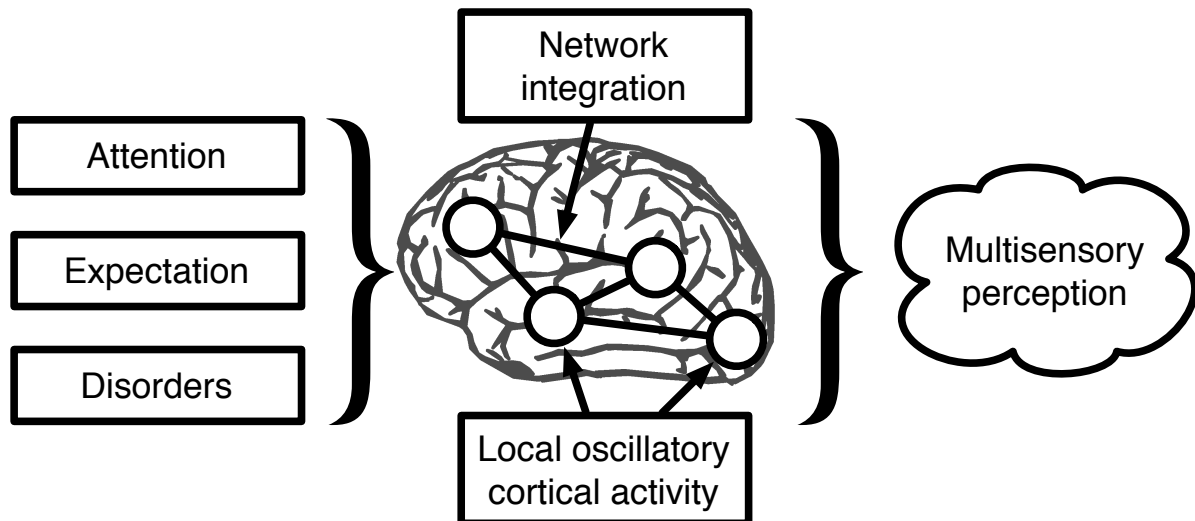


Figure 1: Key elements of the current work. Conscious multisensory perception is reflected in local neural oscillations and functional connectivity networks. In turn, local neural oscillations and functional connectivity networks influence processing and perception of upcoming multisensory stimuli. Cognitive processes such as attention and expectations influence local neural oscillations and functional connectivity networks and also multisensory perception. Psychiatric disorders are related to aberrant neural oscillations and influence multisensory perception.

An overview of neural oscillations

Oscillatory neural activity recorded through electroencephalography (EEG) or magnetoencephalography (MEG) can be understood as the synchronous waxing and waning of summed postsynaptic activity of large neural populations in circumscribed brain regions (Purpura, 1959; Lopes da Silva, 1991; Wang, 2010; Cohen 2017). The properties of the resulting waveform can be dissected into different frequency bands with distinct amplitudes and phases (Walter et al., 1966; Mitra and Pesaran, 1999; Herrmann and Mecklinger, 1999). Two types of neural oscillations, which reflect different aspects of neural activity, can be distinguished: evoked and induced oscillations (Tallon-Baudry and Bertrand, 1999). The former are closely related to the onset of an external event and are strictly phase- and time-locked to the stimulus onset. Phase-locking of oscillatory responses can be quantified as inter-trial coherence (ITC; Cheron et al., 2007) and the summation over trials of identical phase can result in event-related potentials (ERP, Luck, 2005). Induced oscillations can be elicited by stimulation but are also present independent of external stimulation. Induced oscillations do not have to be strictly phase- and time-locked to the onset of stimuli (Tallon-Baudry and Bertrand, 1999). In addition, functional connectivity, the interaction between neural oscillations in different cortical regions, can be reflected in phase coherence. Neural

oscillations of two brain regions are considered to be phase coherent when there is a constant relationship between the phases of the two oscillations over time (Tass et al., 1998; Fries 2005; Senkowski et al., 2008). In general, the analysis of neural oscillations in the cortex, but also in the peripheral nervous system, can provide valuable information on local processes and network interactions underlying perception.

Neural networks in mammals exhibit oscillatory activity ranging between approximately 0.05 Hz and 350 Hz (Penttonen and Buzsáki, 2003). In humans, oscillatory activity patterns were among the first signals recorded using EEG (Berger, 1929; Bremer, 1958). Within one neural network, neighboring frequency bands can compete with each other and can be associated with different cortical states (Ray and Cole, 1985; Engel et al., 2001; Buzsáki and Draguhn, 2004). Moreover, multiple rhythms coexist at the same time, which results in complex waveforms consisting of different high- and low-frequency oscillations (Steriade, 2001; **Figure 2**). Berger described the EEG as being dominated by ongoing 8-12 Hz oscillations, which were later termed alpha band activity (Berger, 1929). Interestingly, Berger observed that alpha band activity changed with the participant's behavior: Its amplitude increased when participants closed their eyes and decreased when they opened the eyes (Berger, 1929). Ray and Cole (1985) proposed that oscillatory activity in different frequency bands reflects different cognitive processes. In two experiments, the authors established that alpha band activity relates to attentional processes and is increased if attention is not required. Additionally, ongoing alpha band oscillations influence subsequent perception (Lange et al., 2014). Recently, the alpha band has been ascribed an important role in attention and the routing of information processing (Jensen and Mazaheri, 2010; Klimesch, 2012). Below the alpha band, Walter (1936) described the delta band, which comprises oscillatory activity below 4 Hz. In the frequency range of 4-7 Hz, i.e. between the delta- and alpha band, Walter (1963) identified the theta band. Both, delta- and theta band activity have been related to memory processing (Klimesch, 1999; Sauseng et al., 2005). More recently, theta band activity has been linked to cognitive control mechanisms such as attention and predictions (Cavanagh and Frank, 2014). Above the alpha band, Berger (1929) identified the beta band (13-30 Hz). Besides motor functions, beta band activity relates to cognitive and emotional processing and might possibly reflect cortical feedback processing (Ray and Cole, 1985; Pfurtscheller 1992; Engel and Fries, 2010; Michalareas et al., 2016; Keil et al., 2016a, **Study 1**). Cortical activity in frequencies

above the beta band (i.e. > 30 Hz) has been termed gamma band activity (Adrian, 1942; Bressler, 1990). Some researchers speculate that oscillatory activity in the gamma band forms a mechanism for feature representation of a given stimulus (Lopes da Silva, 1991). Findings from the auditory and visual domain support this notion. For example, Chatrian et al. (1960) described a rhythmic response to visual stimulation at a frequency of around 50 Hz using intracranial recordings from the calcarine region of the visual cortex. Moreover, in response to auditory stimuli, Pantev et al. (1991) described a transient oscillatory response at around 40 Hz. Interestingly, changes in this transient oscillation could be used to characterize psychiatric disorders (Keil et al., 2016b, **Study 2**). On the other end of the frequency spectrum, slow wave activity below 1 Hz has been described (Birbaumer et al., 1990; Penttonen and Buzsáki, 2003). Oscillatory slow wave activity plays a prominent role in sleep and memory (Diekelmann and Born, 2010), but might also reflect changes in cortical excitability related to task performance (Birbaumer et al., 1990; Rockstroh et al., 1992). In summary, oscillatory activity in different frequency bands relates to perceptual and cognitive processes, and reflects functional states of neural networks (Lopes da Silva, 1991).

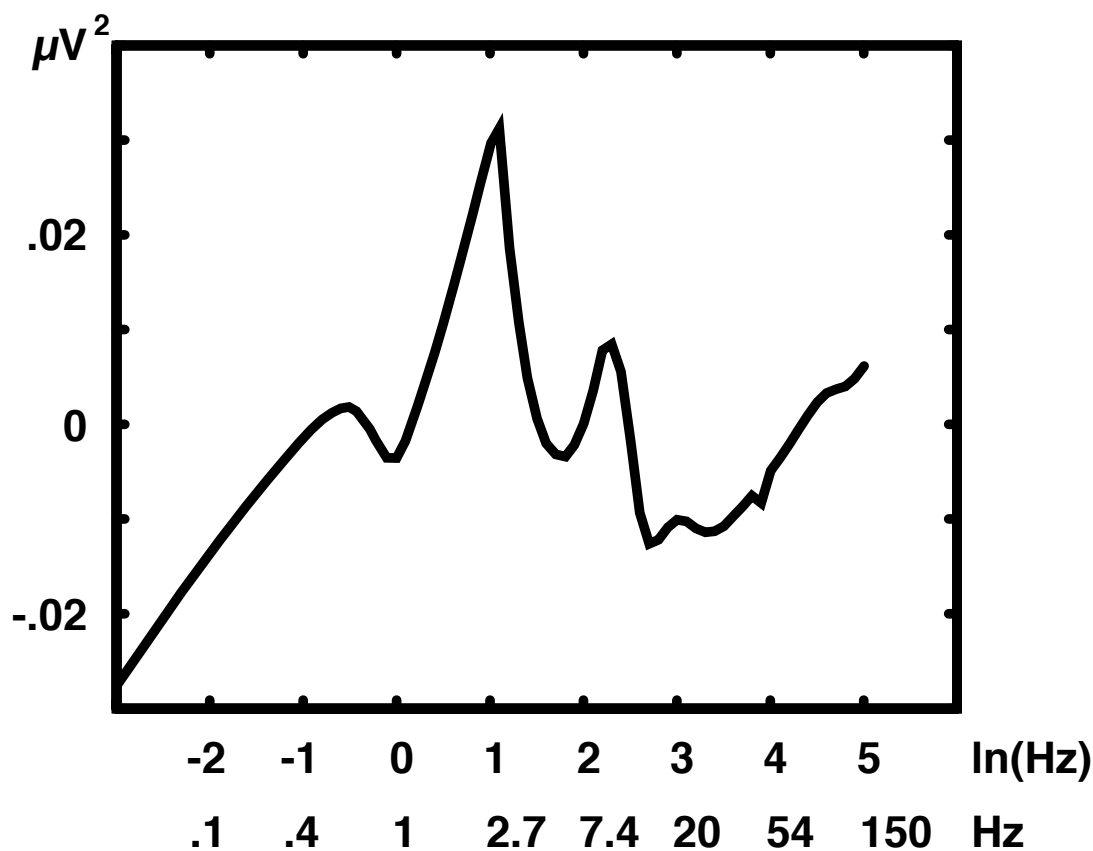


Figure 2: Example log-transformed power spectrum of human EEG (sample of 8 subjects, 5 minutes eyes-open resting-state EEG, average of 126 active electrodes). Prominent peaks in the spectrum at approximately log-transformed integers underline the delta (~3 Hz), alpha (~10 Hz), beta (~20 Hz), and gamma (above 30 Hz) bands. The theta band (~6 Hz) has been identified between the delta and alpha bands. Oscillatory activity below 1 Hz is referred to as slow wave activity (unpublished data).

Oscillatory network activity underlying conscious perception

Information processing, as well as transfer and storage in the cortex presumably rely on flexible cell assemblies, which are defined as transiently synchronized neural networks (Engel et al., 2001; Buzsáki and Draguhn, 2004; Senkowski et al., 2008). A mechanism that has been proposed for the transfer of information between cortical areas is neural phase coherence, as reflected in synchronized oscillatory activity (Fries 2005; 2015). The transient synchronization of cell assemblies by oscillatory activity depends on the coupling strength between neurons, as well as on the frequency distribution: As long as the frequencies of coupled cell assemblies are similar, the synchronization within the neural network can be sustained with weak synaptic links (Wang, 2010).

In order to provide a cognitive theory of consciousness, Baars (1993) established key elements needed for conscious experience. He postulated the necessity of distributing information across a global workspace and a balance between novelty and redundancy: Redundant stimuli will fade from consciousness and novel stimuli lacking context cannot be processed properly. Implicit in this theory is the notion that information has to be passed on between cortical areas and that information already present in a global workspace influences processing of upcoming stimuli. This implicit notion has been formalized in the predictive coding hypothesis (Rao and Ballard, 1999; Engel et al., 2001; Friston, 2005; Huang and Rao, 2011), which states that information in the global workspace can be represented in ongoing oscillatory activity. Based on the idea that the human brain constantly tries to update knowledge about the world in order to predict upcoming events, stimulus evoked activity is thought of as a marker of “surprise”: The less expected a stimulus is, the larger the evoked activity will be. Predictions are transferred from frontal cortical areas to primary sensory areas by synchronized neural oscillations in lower frequency ranges, as recently observed in intracranial recordings in monkeys (Van Kerkoerle et al., 2014; Bastos et al., 2015). Taken together, knowledge about the world is presumably represented in cortical networks spanning primary sensory and higher-order cortical networks. Prior

information influences stimulus processing and new information modifies existing knowledge. Consciousness integrates separate and independent brain functions (Baars, 2002).

Extending the notion of a global workspace, Dehaene et al. (2006) proposed a model for the transfer of information between primary sensory areas and a global cortical network representing consciousness. A key element of this model is attention: unattended stimuli are processed in sensory cortices, but the information is not transferred to a global cortical network and thus does not become conscious (Baars, 2002). As an extension of this model, Weisz and colleagues (Weisz et al., 2014; Ruhnau et al., 2014) recently formulated the idea of “windows to consciousness”. According to this idea, oscillatory activity represents dynamic phases in which stimuli can elicit cortical responses and these responses are transmitted within larger cortical networks.

In line with the idea of global cortical networks representing consciousness, Crick and Koch (2003) have argued that novel objects need to be integrated by perceptual binding (see Aru et al., 2012 for a review). Thus, the activity of several cortical areas must act together for stimuli to become conscious (Baars, 2002; Noppeney et al., 2016). Similarly, Siegel et al. (2012) have argued that cognitive processing and information integration is achieved through the formation of large transient coalitions of neurons. The authors propose that frequency-specific oscillations in distributed cortical networks may provide indices, or “fingerprints”, of the networks that underlie cognitive processes. Thus, conscious perception requires a cascade of interacting network processes, which represent prior information and new sensory input. Oscillatory processes presumably represent short-term states in which networks can interact. The temporal, spatial and spectral characteristics of this interaction, however, are still largely unknown.

Neural fingerprints of multisensory integration and perception

Unisensory perception can be accomplished by stimulus processing within primary sensory areas. Traditionally, multisensory integration has been assumed to rely on the convergence of inputs from different sensory modalities in convergence cells (Meredith and Stein, 1986). Electrophysiological and neuroimaging studies identified both cortical and subcortical convergence zones such as the superior colliculus or superior temporal gyrus (Calvert et al., 2000; 2001). More recently, multisensory phenomena have been

reported to involve processing in sensory specific cortical areas and cross-modal interactions between sensory modalities (Driver and Noesselt, 2008; Faivre et al., 2017). A number of studies support this idea by providing evidence for multisensory cross-modal influence in low-level sensory cortices (Schroeder and Foxe, 2005; Ghazanfar and Schroeder, 2006). Thus, in contrast to unisensory stimulus processing, cross-modal influence appears to require activity in primary sensory areas as well as the formation of neural networks to allow the information transfer between sensory cortical areas. Moreover, the formation of coherent, integrated, conscious multisensory percepts likely involves distributed neural networks comprising primary sensory and higher-order cortical areas (Baars, 2002; Senkowski and Engel, 2012).

In a first EEG study on oscillatory activity and multisensory processing, Sakowitz et al. (2001) found increased gamma band power in response to audiovisual stimuli compared to auditory or visual stimuli alone. A later EEG study extended this finding by showing that the gamma band power response to audiovisual stimuli increases specifically when stimuli are attended (Senkowski et al., 2005). Interestingly, another study found increased occipital gamma band power following the presentation of incongruent audiovisual stimuli, but only when the auditory and visual stimuli were perceptually integrated (Bhattacharya et al., 2002). Whereas these studies demonstrate that multisensory perception is reflected in local gamma band power, they did not examine the underlying cortical networks. Using local field potential recordings in monkeys, Lakatos et al. (2007) showed that somatosensory stimulation modulates activity in primary auditory areas, and found evidence for a phase reset of ongoing oscillatory activity in primary auditory cortex by concurrent somatosensory input. The authors suggested that stimulus responses are enhanced when their onset falls into a high excitability phase and suppressed when the onset falls into a low-excitability phase. These observations were supported by another audiovisual study in monkeys, highlighting the role of the visually induced oscillatory phase for the modulation of auditory evoked activity (Kayser et al., 2008). Furthermore, a recent study analyzing extracellular activity in rats showed that oscillatory activity in somatosensory cortex is modulated by feed-forward projection from visual cortex (Sieben et al., 2013). Taken together, these studies have demonstrated cross-modal influences within and between primary sensory areas. Moreover, it is likely that low-frequency oscillations mediate this

cross-modal influence. However, conscious perception is difficult to judge from animal studies.

It has been proposed that conscious audiovisual perception in humans involves a network of primary visual and auditory areas, as well as multisensory regions (Schepers et al. 2013; Keil et al. 2012). The finding, that cross-modal processes influence primary sensory activity via low-frequency oscillatory activity, implies a predictive process (Schroeder et al., 2008). In many natural settings visual information precedes auditory information. For example, in audiovisual speech the lip movements precede the articulation of phonemes, and the visual information has to be transferred to the auditory cortex (Arnal et al., 2009). This network presumably reflects reentrant bottom-up and top-down interactions between primary sensory and multisensory areas (Arnal and Giraud, 2012). Cognitive processes such as attention, expectations and predictions, which are processed in frontal cortical areas, likely exert a modulatory influence on local activity in primary sensory and multisensory areas. Recent studies have suggested that this top-down influence is reflected in beta band phase synchrony (Von Stein et al., 1999; Stoll et al., 2015; Keil et al., 2016a, **Study 1**). In summary, there is robust evidence that cross-modal processes can modulate cortical activity in primary sensory areas (van Attenveld, 2014). Furthermore, as previously hypothesized (Senkowski et al. 2008), it is likely that information transfer in a network of primary sensory, multisensory, and frontal cortical areas is instantiated through synchronized oscillatory activity. Conscious multisensory perception in humans presumably requires coordinated activity within this network (Baars, 2002).

Stimulus driven multisensory integration

Bottom-up stimulation in various sensory modalities engages local cortical nodes in the gamma band (Singer, 1999; Buzsáki et al., 2004; Engel and Fries, 2010; Fries 2015). Interestingly, gamma band power is increased in response to multisensory compared to unisensory stimuli, in particular when both stimuli are attended (Senkowski et al., 2005) and integrated (Bhattacharya et al., 2002). A number of recent studies have elucidated various neural mechanisms by which multisensory stimuli are processed in a bottom-up fashion (Kayser et al., 2008).

Using intracranial recordings in humans, Quinn et al., (2013) examined the spatiotemporal profile of multisensory integration in the high gamma band power (70 –

190 Hz) and local field potentials (LFP). The study showed that multisensory integration, as indexed by modulations of high gamma band power in temporoparietal and dorsolateral prefrontal cortices, occurs relatively late, i.e. about 150 – 350 ms after stimulus presentation. Based on the findings from another human intracranial study, Mercier et al., (2015) proposed a possible mechanism for the cross-modal influence between different senses. The authors found transient synchronization of delta (3 – 4 Hz) and theta (5 – 8 Hz) band oscillations during multisensory audiovisual stimulation. Moreover, increased cross-modal phase alignment was correlated with faster behavioral responses. Similar to the results obtained from monkeys (Kayser et al., 2008) and rats (Sieben et al., 2013), the authors argue that optimally aligned phases promote communication between cortical areas and that stimuli in one modality can reset the phase of an oscillation in a cortical area of the other modality. In a human EEG study, Gleiss and Kayser (2014a) analyzed the influence of task irrelevant auditory stimuli on static visual perception. The authors found that concurrently presented spatially and temporally aligned sounds reduce visual detection thresholds. Interestingly, the multisensory enhancement correlated with a reduction in occipital alpha band (8 – 12 Hz) and beta band (13 – 30 Hz) power. In a follow-up study, the authors investigated the cross-modal influence of auditory motion stimuli on visual motion stimuli (Gleiss and Kayser, 2014b). The study revealed a reduction of occipital alpha band power during the presentation of incongruent compared to congruent audiovisual motion stimuli. More recently, Krebber et al. (2015, **Study 3**) examined the role of motion congruence for the bottom-up processing of visuotactile stimuli. In this study, EEG data for congruent and incongruent visuotactile motion stimuli were projected to visual and somatosensory cortices. Whereas motion congruence did not modulate alpha and beta band power, it enhanced gamma band power. Underscoring the behavioral relevance of this observation, the increased gamma band power during congruent stimulation was correlated with faster responses to visual and tactile target stimuli (**Figure 3**). Thus, the study suggests that motion congruence influences bottom-up processing, which is reflected in gamma band power in sensory cortices. Taken together, these studies suggest that cross-modal influence between sensory areas is reflected in synchronized low-frequency oscillations. Moreover, congruent multisensory stimulation enhances stimulus processing and is associated with increased gamma band power.

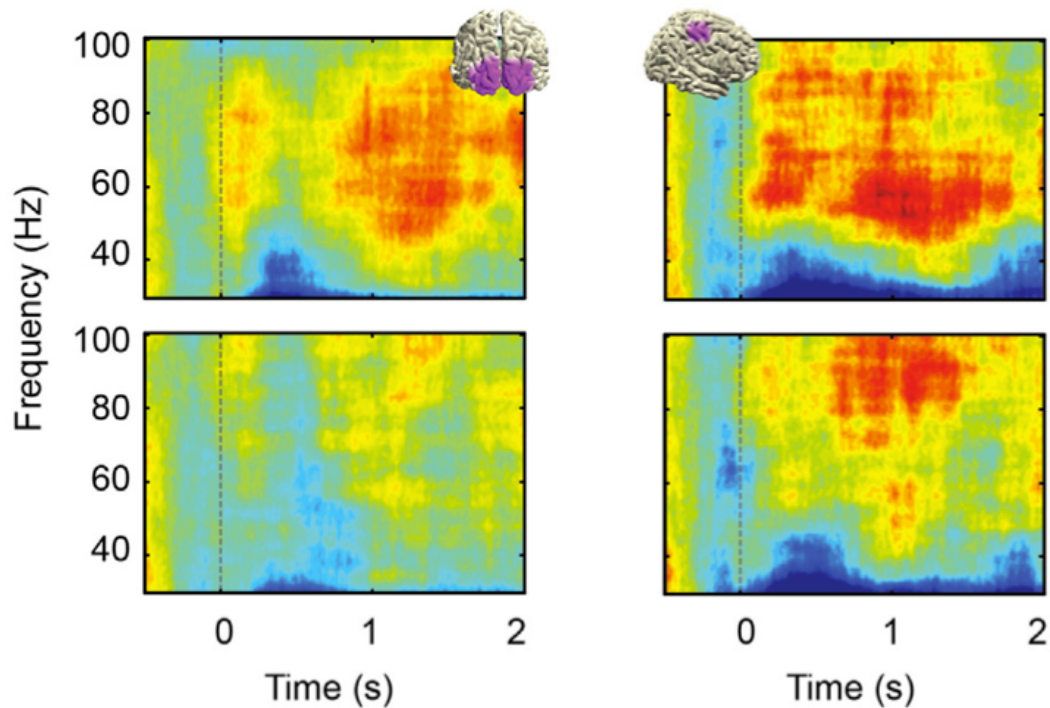


Figure 3: Increased gamma band power during congruent visuotactile motion stimulation in visual and somatosensory cortical areas. The four panels show time-frequency representations (TFR) of neural activity in the visual cortex (**left**) and sensorimotor cortex (**right**) for congruent visuotactile motion stimulation (**upper TFRs**) and incongruent motion stimulation (**lower TFRs**). Adapted from Krebber et al., 2015.

With respect to integrated audiovisual perception in addition to audiovisual stimulation, a number of studies highlight the role of gamma band power. Investigating the audiovisual sound-induced flash illusion (SIFI; Shams et al., 2000), Bhattacharya et al. (2002) found increased gamma band power over occipital electrodes during the perception of the audiovisual illusion. In this illusion, a single flash accompanied by two rapid sounds is often perceived as two flashes. Mishra et al. (2007) obtained similar results with respect to the integrated audiovisual perception. Using a visual-tactile variant of the same paradigm, Lange et al. (2011) also found increased gamma band power over occipital MEG sensors during the perception of the illusion. More recently, Balz et al. (2016a, **Study 4**) investigated the role of gamma band power in the multisensory integration area superior temporal gyrus (STG) for the SIFI. Using combined EEG and magnetic resonance spectroscopy, the authors showed a three-way relationship between the Gamma-aminobutyric acid (GABA) level in the STG, gamma-band power in the STG, and the SIFI illusion rate (**Figure 4**).

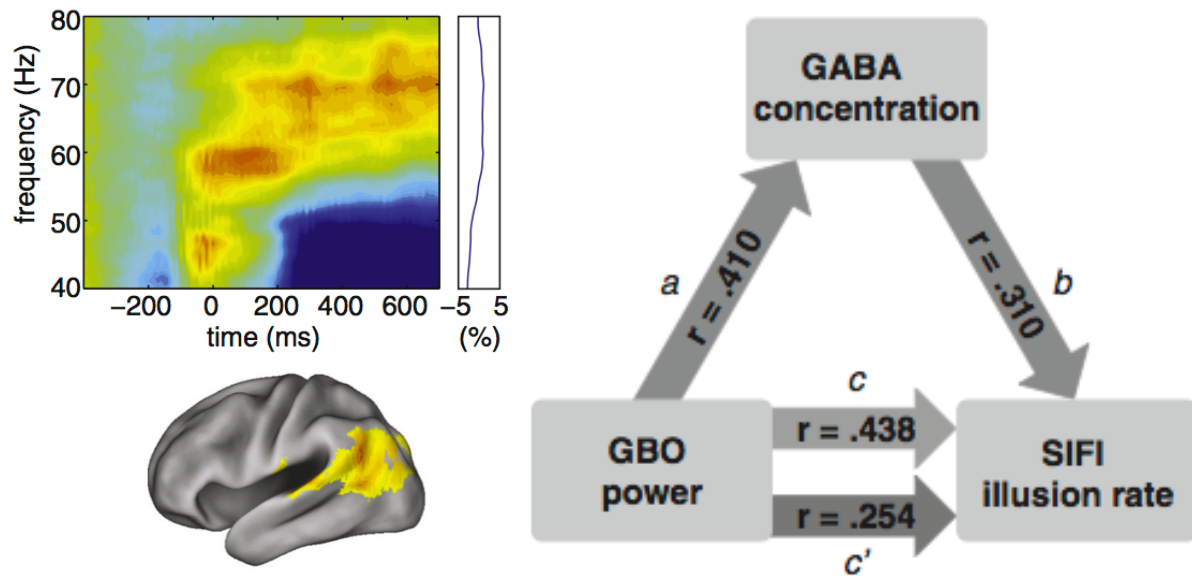


Figure 4: Audiovisual integration, as seen in the sound-induced flash illusion, is indexed by enhanced gamma band power in superior temporal gyrus. Enhanced gamma band power also correlates with increased individual illusion rate. GABA mediates this relationship. **Left:** The TFR for the region of interest in the left STG as well as the cortical source associated with the gamma band power increase relative to baseline. **Right:** The three-way relationship between gamma band power, GABA concentration and SIFI illusion rate. Adapted from Balz et al., 2016a.

In summary, the studies reviewed above suggest that bottom-up driven perception of multisensory stimuli involves two main neural mechanisms. (i) Low frequency oscillations appear to convey cross-modal influence via phase synchrony between primary sensory cortical areas and reflect local excitability (Lange et al., 2013a; 2014). (ii) High frequency oscillatory activity in primary sensory and multisensory integration areas reflects enhanced processing of integrated multisensory stimuli (Krebber et al., 2015; Balz et al., 2016a).

Multiple stages of multisensory integration

Perception of simple unisensory and multisensory stimuli can be accomplished in a bottom-up driven manner. In contrast, perception of more complex stimuli likely requires the concerted activity of multiple cortical areas and oscillatory rhythms (Peelle and Sommers, 2015). Recent studies have underlined the importance of rhythmic stimulus properties for auditory perception (Henry et al., 2012; Ng et al., 2012), especially speech perception (Giraud and Poeppel, 2012; Obleser et al., 2012). Giraud and Poeppel proposed that the phase of ongoing cortical activity aligns with slow

oscillations of the speech amplitude envelope, and that this mechanism facilitates speech processing.

An important aspect of cross-modal influence in audiovisual speech perception is the predictive value of input of the visual modality for the input of the auditory modality. In an MEG study, Kaiser et al. (2005) compared cortical activity following standard, i.e. congruent, and deviant, i.e. incongruent, audiovisual speech stimuli. Importantly, the auditory stimulus was identical in standard and deviant trials. In line with the predictive coding hypothesis (Rao and Ballard, 1999; Engel et al., 2001; Friston, 2005; Huang and Rao, 2011), the authors found increased gamma band power following incongruent stimulation. The gamma band power increase likely reflects a cross-modal violation of predictions or incongruence detection. Similarly, Arnal et al. (2011) found that incongruent compared with congruent audiovisual stimulation leads to increased correlations between gamma band phase locking and evoked brain activity. The increased correlations might be due to a violation of predictions based on visual information by auditory signals. Recently, Lange et al. (2013b) compared neural oscillatory responses to incongruent vs. congruent audiovisual speech stimuli and found that incongruent stimuli evoke stronger ERPs and increased alpha band power. Interestingly, gamma band and beta band power were stronger in congruent speech stimuli. The authors suggested that the enhanced gamma and beta band power reflects evaluation of matching audiovisual information. In contrast, during incongruent audiovisual stimulation, stimulus processing beyond the initial processing of unexpected information is gated by alpha band activity. In a study comparing congruent and incongruent audiovisual speech stimuli, Ohki et al. (2016) found that the coupling between delta band phase and beta band power is indicative of audiovisual stimulus encoding. In the McGurk illusion (McGurk and MacDonald, 1976), incongruent audiovisual speech stimuli are fused to a novel percept. Using this illusion, Roa Romero et al. (2015, **Study 5**) compared congruent and incongruent audiovisual syllables that induced the same percept, and identified an early and a late stage of audiovisual integration. Both stages were marked by a stronger post-stimulus beta band power decrease following the illusion perception (**Figure 5**). This finding is in line with a recent multistage model of speech perception (Pelle and Sommers, 2015; Bizley et al., 2016). According to this model, in a first stage, visual information increases the sensitivity to auditory information. In a second stage, specific information on the speech

content is extracted. In a similar vein, Roa Romero et al. (2015) proposed that auditory and visual information are compared at an early stage and integrated at a later stage. In summary, recent findings indicate the distinct functional roles of low and high frequency oscillations in audiovisual speech perception. Whereas violations of visual predictions or incongruence between auditory and visual stimuli are reflected in gamma band power, the transfer of predictions and the integration of mismatching information into a coherent conscious percept seems to be primarily reflected in beta band power.

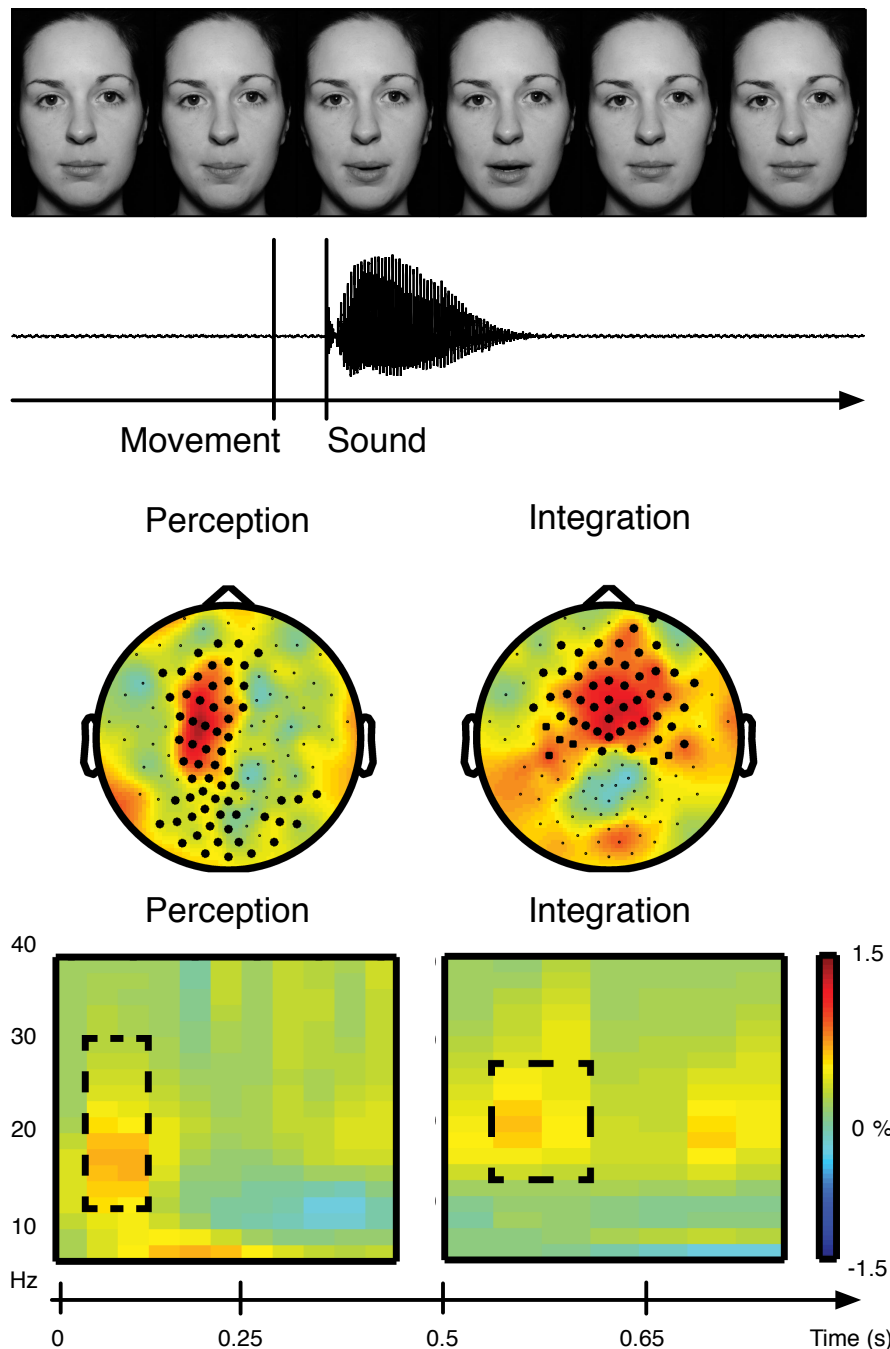


Figure 5: In naturalistic speech, visual information precedes the onset of the auditory signal. **Top:** Predictions regarding the auditory signal can be formed based on

visual information. Audiovisual speech perception and integration possibly involve separate stages. Both the early perception stage and the late integration stage are reflected in beta band oscillations. **Middle:** The topographic distribution of t-values for the comparison between congruent and McGurk illusion trials for the perception and integration stages. **Bottom:** The difference in relative change between the congruent and McGurk illusion trials for the perception and integration stages. The dashed lines mark the time-frequency windows in which increased power during the illusion was found. Adapted from Roa Romero et al., 2015.

Cortical states and stimulus processing

A common, at least implicit assumption in cognitive neuroscience is that there is an “inactive” baseline, meaning that processes in the prestimulus period bear no importance for upcoming stimulus processing. In contrast, many theories have postulated the idea that ongoing cortical activity influences stimulus processing and perception (Jensen & Mazaheri, 2010; Lange et al., 2014). Indeed, fluctuations in cortical activity were among the first phenomena observed in human electrophysiological research. Berger (1929) described changes in rhythm depending on intellectual work in his report on the first EEG recordings in humans. The finding that the pattern and degree of cortical activity is modified by various psychological and physiological states corroborates these results (Davis et al., 1936). Hebb (1949) stated that the consequence of a sensory event must be influenced by existing activity, as the brain is continuously active and all excitation must be superimposed on already existing excitation. Thus, in order to predict the state of a neural network, it is necessary to know its recent history. This observation was supported by empirical data, which have shown that the excitability of the auditory cortex varies periodically (Lindsley, 1952). This finding implies that knowledge of the oscillatory nature of local excitability helps to predict the cortical response to a given stimulus. The idea that the cortical state prior to stimulation influences the outcome of stimulation has gained widespread attention and support over the last decade (e.g., Jensen & Mazaheri, 2010; see Lange et al., 2014 for a review). Modulations of amplitude and phase of oscillatory neural activity impact how the brain processes stimuli and thus shape perception and behavior. However, thus far, little is known about the mechanisms influencing multisensory integration.

Neural oscillations influence stimulus processing

Electrophysiological research employing unisensory experimental paradigms indicates that alpha band power and phase influence visual perception (Van Dijk et al.,

2008; Busch et al., 2009; Iemi et al., 2016). Similarly, beta band power and phase influence tactile perception (Lange et al., 2011; Baumgarten et al., 2015). Likewise, ongoing cortical activity influences the effect of neurostimulation, as shown for the influence of alpha band power on phosphene perception (Romei et al., 2010). Cortical beta band power and phase as well as corticospinal synchronization also influence the amplitude of motor evoked potentials (MEP, Schulz et al., 2013; Keil et al., 2014a, **Study 6; Figure 6**). However, it is not yet known whether ongoing oscillatory activity represents specific cortical states and how these states might arise (VanRullen, 2016).

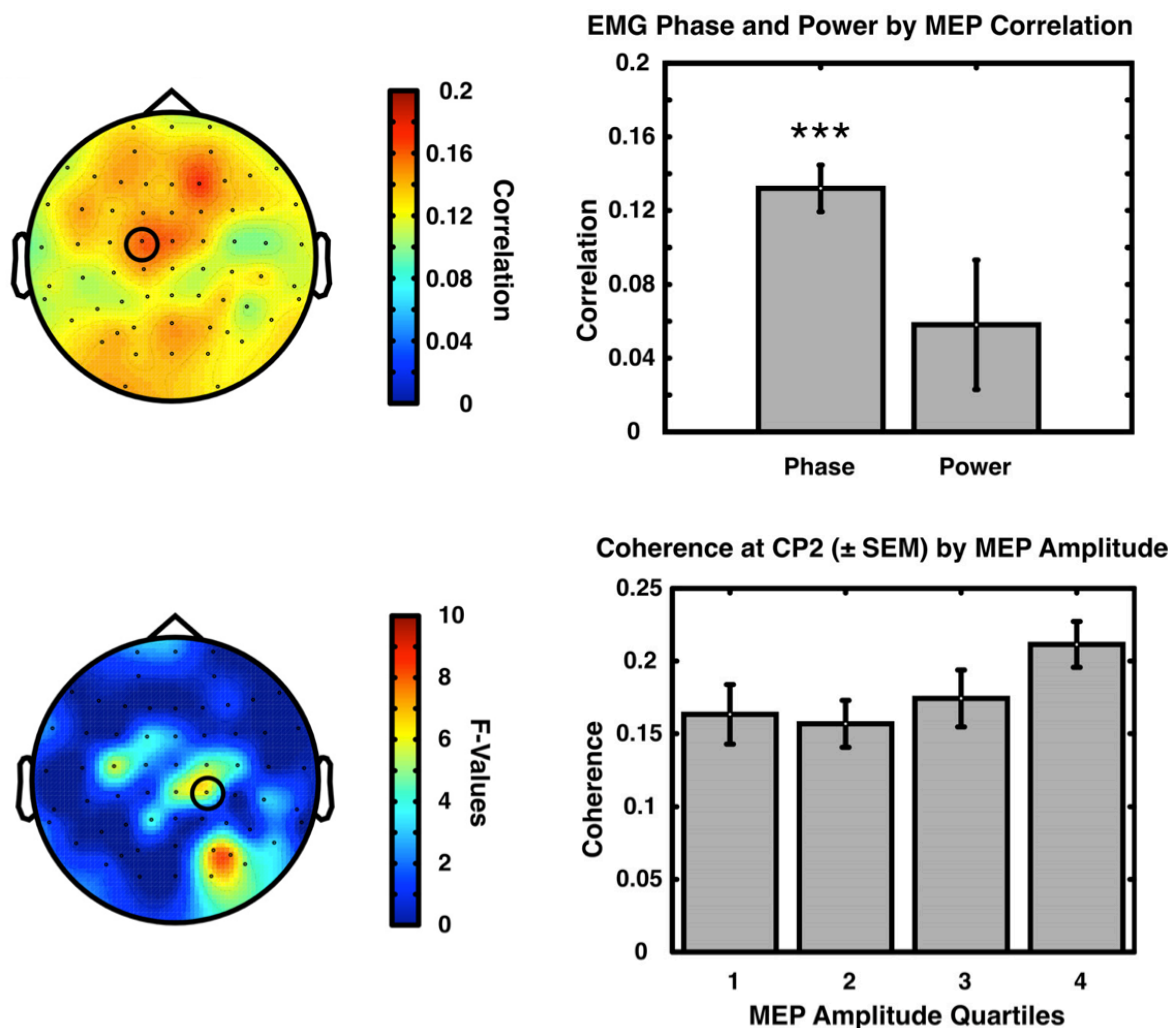


Figure 6: Cortical beta band phase and corticospinal beta band coherence influence the amplitude of TMS-evoked MEPs. **Top:** The influence of beta band phase over somatosensory cortex on MEP amplitudes. **Bottom:** The linear relationship between corticospinal coherence and MEP amplitudes. Adapted from Keil et al., 2014a.

Of particular relevance for the question of whether oscillatory activity represents specific cortical states is the finding that ongoing neural oscillations not only influence

unisensory stimulus processing, but also shape multisensory integration and perception. Hipp et al. (2011) investigated neural coherence in the audiovisual bounce-pass paradigm. In this paradigm, two moving vertical bars approach each other, overlap and diverge again (Sekuler et al., 1997). At the point of overlap, a sound is presented, which results in a bistable percept in which the bars either pass each other or bounce off each other. Hipp et al. (2011) found that increased coherence in two cortical networks predicts an integrated audiovisual percept. Gamma band coherence marked a network encompassing parietal and temporal cortical areas. Besides, beta band coherence characterized a second network spanning frontal, parietal, temporal and occipital cortical areas. Similarly, Keil et al. (2012) found increased beta band power in the STG, precuneus and right frontal cortex prior to an integrated audiovisual percept in an MEG study using audiovisual speech stimuli eliciting the McGurk illusion (McGurk and MacDonald, 1976). The authors also found a beta band functional connectivity network, involving temporal, occipital and frontal areas, predicting perception. Another MEG study by the same authors obtained similar results for incongruent audiovisual stimuli eliciting the SIFI (Keil et al., 2014b). Again, increased beta band power in the STG preceded an integrated audiovisual percept, resulting in a multisensory illusion. Moreover, alpha band and beta band functional connectivity in a network spanning temporal, parietal and frontal areas differentiated between illusory and non-illusory percepts. Interestingly, beta band functional connectivity between STG and primary auditory cortex predicted perception on a single trial level, with increased connectivity fostering illusions. Using a visuotactile adaptation of the SIFI, Lange et al. (2013a) found that cortical activity prior to stimulus onset predicts perception. In this study, reduced alpha band power in visual cortical areas and increased gamma band power in parietal and temporal cortical areas preceded a tactile induced flash illusion. Together, these findings suggest that increased excitability in primary sensory areas, enhanced local activity in multisensory cortical areas, and increased functional connectivity within distributed cortical networks foster multisensory integration. A recent study using the SIFI further highlighted the role of low-frequency oscillations for the shaping of audiovisual perception (Cecere et al., 2015). The authors found a correlation between the individual alpha band frequency (IAF) and SIFI illusion rate, which indicates that alpha band oscillations provide a temporal window in which the cross-modal influence could induce an illusion. Underscoring the causal role of low-frequency oscillations for cross-modal influence, Cecere et al. (2015) showed that modulating the individual alpha

band frequency via TDCS could modulate the probability of an illusion perception. A recent EEG-study could replicate this finding (Keil et al., in press, **Study 7**). Importantly, this study localized this effect to the calcarine sulcus, underscoring the role of excitability in primary sensory areas, which presumably determines windows of opportunity for cross-modal influence (**Figure 7**). In summary, local cortical activity and activity within functional connectivity networks fluctuate, and these fluctuations affect multisensory integration and perception. Thus, oscillatory activity likely represents cortical states that predict multisensory integration and perception.

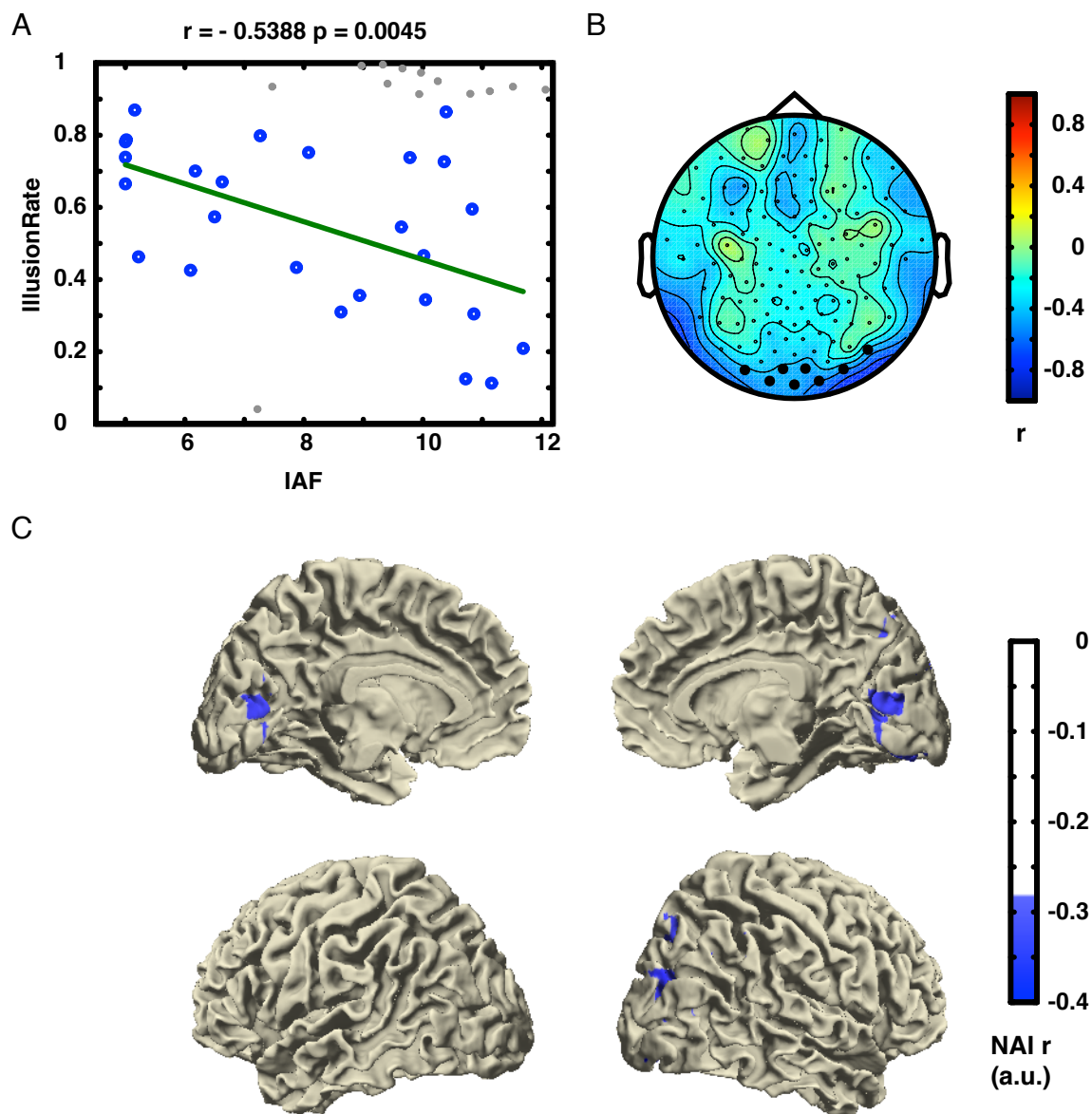


Figure 7: Correlation between the individual alpha band frequency and the SIFI illusion rate. (A) The IAF is negatively correlated with the SIFI illusion rate, indicating that a lower IAF with longer phase duration facilitates audiovisual integration. (B)

Statistical analysis revealed one occipital cluster of eight electrodes for the negative correlation between the IAF and the SIFI illusion rate. (C) Source analysis indicated the calcarine sulcus as the likely source of the correlation between IAF and SIFI illusion rate. Adapted from Keil et al., in press.

Cognitive states and stimulus processing

We are constantly exposed to a vast amount of information from various external and internal sources. However, not all of this information is equally relevant at any given time. Cognitive control mechanisms, such as attention and expectations enable us to prioritize processing of certain information. Thus, these mechanisms can exert top-down influence on cortical processes and perception (Picton and Hillyard, 1974; Lange, 2013c; Gregoriou et al., 2015). The prefrontal cortex has been closely associated with different cognitive control mechanisms (Miller and Cohen, 2001). Two recent electrophysiological studies in humans have highlighted the role of top-down control in visual perception and the importance of frontal and parietal cortical areas (Marshall et al., 2015; Samaha et al., 2015). The role attention plays in multisensory integration is still a matter of debate (Hartcher-O'Brien et al., 2016). Notably, recent findings indicate that attention modulates cortical activity and multisensory integration (Schroeder and Lakatos, 2009; Cavanagh and Frank, 2014).

Predictions and Expectations

In multisensory paradigms, shifting attention towards one sensory modality – known as intersensory attention – as well as shifting attention in space or towards specific stimulus features is reflected in changes in local neural oscillations (Foxye and Snyder, 2011). In a study using visuotactile stimulation, Bauer et al. (2012) found that attention modulates modality-specific frequencies, with alpha band power modulations over the occipital cortex and beta band power modulations over the somatosensory cortex. Moreover, task demands modulate neural oscillations. In an EEG study, Göschl et al. (2015) compared neural oscillations in a visuotactile target detection task and a visuotactile congruence evaluation task. The authors found that alpha band and beta band power are concurrently modulated in the premotor cortex, somatosensory cortex, and supramarginal gyrus, depending on the current task. These findings are in agreement with the “gating-by-inhibition” hypothesis, which posits that oscillatory activity in the alpha band provides an inhibitory mechanism that reduces the processing capacities of a cortical area (Jensen and Mazaheri, 2010). More specifically, task-

irrelevant cortical areas are inhibited to optimize performance in active cortical areas. In line with this hypothesis, Göschl et al. (2015) suggested that their findings of suppressed alpha band and beta band power indicate a higher engagement of cortical areas associated with visuotactile integration in the more demanding detection task. In another recent study, in which intersensory attention and temporal predictions were manipulated simultaneously and EEG data were analyzed in source space, Pomper et al. (2015, **Study 8**) observed similar task- and modality-specific modulations of alpha band and beta band power. The authors found that intersensory attention reduced alpha band and beta band power in the primary visual cortex when subjects attended to visual stimuli. In addition, beta band power in the primary somatosensory cortex was reduced when subjects attended to tactile stimuli. Furthermore, temporal predictions were reflected in beta and delta band modulations in motor and somatosensory cortex. In a follow-up analysis, Keil et al. (2016a, **Study 1**) showed that intersensory attention modulates an alpha band functional connectivity network, encompassing visual, somatosensory and inferior parietal areas. Moreover, temporal predictions modulate a beta band functional connectivity network, involving visual, parietal and frontal areas. Interestingly, both attention mechanisms modulated a common theta band functional connectivity network, spanning frontal and parietal cortical areas (**Figure 8**). The authors interpreted their finding as evidence for two distinct modes of attention in multisensory processing: a bottom-up driven, automatic mode and a deliberate mode requiring top-down control. A previous study also reported a theta band power increase following incongruent audiovisual speech processing (Keil et al., 2012). Frontal theta band activity has been most prominently associated with cognitive control and mismatch or error processing (Keil et al., 2010; Cavanagh and Frank, 2014). Hence, the enhancement of frontal theta band power for incongruent audiovisual speech likely reflects cross-modal prediction error processing. In summary, top-down processes, such as attention and predictions, modulate local cortical activity and functional connectivity networks, thereby orchestrating the integration of multisensory stimuli. Importantly, temporal predictions and intersensory attention can have opposing effects on stimulus-evoked activity (Keil et al., 2017, **Study 9**). Furthermore, selectively attending to one constituent of a multisensory stimulus modulates local neural oscillations, depending on the attended stimulus constituent. Finally, predicting stimulus onset across sensory modalities modulates a global beta band network, presumably reflecting top-down temporal orienting.

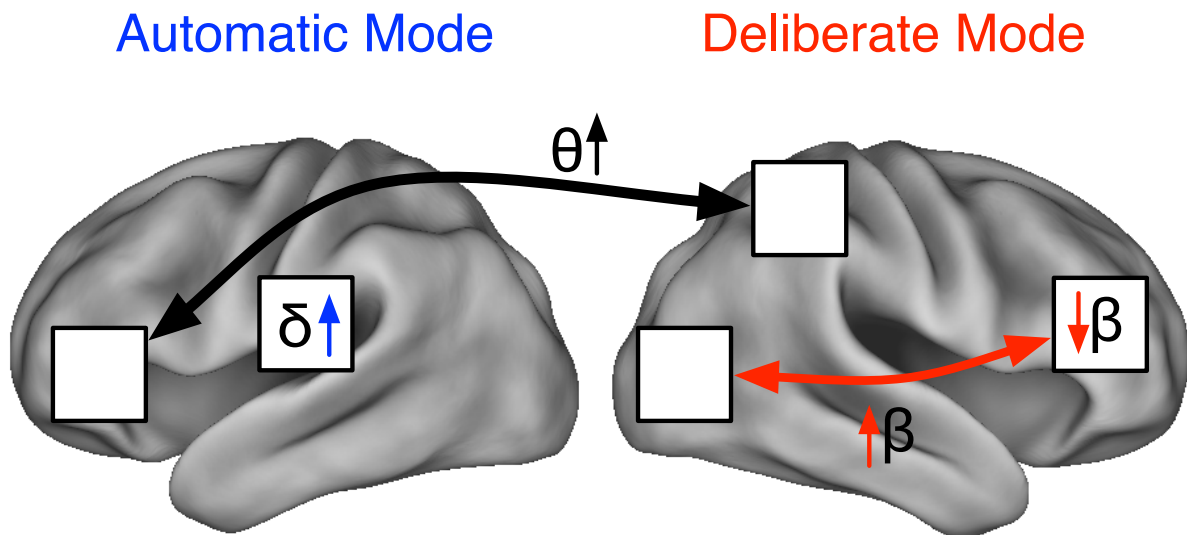


Figure 8: Two distinct modes of attention in multisensory processing. The automatic mode (**left**) is driven by bottom-up sensory input. Here, stimulus regularities induce delta-band oscillations. The deliberate mode (**right**) is governed by top down cognitive influence. Here, beta band functional connectivity relays this influence. The dynamic switching between the attention modes based on task demands is reflected in theta band functional connectivity between frontal, parietal and sensory cortical areas. Adapted from Keil et al., 2016a.

Aberrant oscillations and perception

Cognitive impairments and impaired sensory processing are core symptoms in psychiatric disorders such as autism or schizophrenia (Senkowski and Gallinat, 2015). Importantly, these impairments might be related to aberrant neural oscillations (Uhlhaas and Singer, 2015). For example, it has been proposed that aberrant gating of irrelevant sensory input contributes to cognitive impairments in schizophrenia (Patterson et al., 2008; Bob et al., 2014). This sensory gating deficit is reflected in aberrant neural oscillations in the alpha and gamma band, and these atypical oscillations in turn are related to positive and negative symptoms in schizophrenia (Keil et al., 2016, **Study 2**).

In addition to impaired unisensory stimulus processing and cognitive deficits, altered multisensory processing has also been observed in psychiatric disorders such as schizophrenia and autism (Baum et al., 2015; Tseng et al., 2015). A recent study compared processing of the McGurk illusion in patients with schizophrenia and healthy control participants (Roa Romero et al., 2016a). While no group difference was found in the early processing stage of the McGurk illusion, the late processing stage, which was reflected in frontal alpha band modulations, was impaired in the patient group.

Supporting the role of alpha band suppression for audiovisual integration, the authors also found a negative correlation between frontal alpha band modulations with the McGurk illusion rate. A further study focused on cross-modal predictions in audiovisual speech processing in schizophrenia (Roa Romero et al., 2016b). This study indicated that audiovisual incongruence detection is reflected in enhanced early evoked responses. Moreover, the authors found that cross-modal prediction error processing involves frontal theta band oscillations, and that this process is impaired in schizophrenia. In a recent study examining the SIFI in patients suffering from schizophrenia and healthy control participants, Balz et al. (2016b) also found altered multisensory processing in schizophrenia. Similar to the aberrant cross-modal generation of predictions, the authors reported that multisensory processing deficits in schizophrenia are reflected in altered beta and gamma band oscillations. Taken together, these findings indicate that multisensory processing deficits are related to aberrant local neural oscillations. New developments in integrative research approaches focusing on local cortical processes and functional connectivity networks in healthy individuals and clinical populations will allow for a deeper understanding of the interplay between bottom-up and top-down processes during multisensory perception.

An integrative model for the role of neural oscillations in conscious multisensory perception

From the empirical evidence reviewed above, three distinct elements of multisensory integration become evident: (i) the influence of cognitive processes, (ii) the influence of cortical states, and (iii) the correlates of integration and perception (**Figure 9**). Multisensory integration and perception requires the concerted activity in primary sensory, e.g. primary auditory and visual areas, multisensory, e.g. the superior temporal gyrus, and frontal cortical areas. Moreover, this coordinated activity is reflected in different coexisting rhythms of neural oscillations.

The first element, the cognitive states prior to stimulus onset, describes the influence of cognitive processes such as attention, expectations and predictions on local neural oscillations in primary sensory areas as well as the functional connectivity between these areas (**Figure 9, right**). Attention modulates alpha and beta band power in primary sensory areas, whereas expectations influence modality-unspecific power in

frontal and parietal cortical areas (Pomper et al., 2015). The influence of top-down cognitive control is transferred via theta band functional connectivity to multisensory and primary sensory cortical areas (Keil et al., 2016)a.

The second element describes ongoing fluctuations in local cortical activity and functional connectivity networks prior to stimulus onset (**Figure 9, middle**). Ongoing cortical activity in primary sensory and multisensory areas as well as the functional connectivity between these areas influences how an upcoming stimulus will be processed. Local alpha, beta and gamma band activity in primary sensory areas index inhibition and excitability (Jensen and Mazaheri, 2010). Increased local beta band activity in multisensory areas predicts multisensory integration. Moreover, functional connectivity between primary sensory areas and multisensory areas in the alpha and beta band might index a functional network, which promotes multisensory integration by integration or segregation of unisensory stimuli (Lange et al., 2014).

The third element, the neural correlates of multisensory integration and perception, summarizes the mechanisms following stimulus presentation and during stimulus processing (**Figure 9, right**). Cortical activity within one primary sensory area can influence activity in a second primary sensory area. These cross-modal influences are transferred via low-frequency neural oscillations in the delta and theta bands. Importantly, the activity within primary sensory areas and the interactions between these areas do not necessarily result in an integrated, conscious percept, but can for example lead to changes in perceptual sensitivity in one sensory modality. Multisensory information integration into an integrated, conscious percept is reflected in gamma band power in sensory and multisensory cortical areas. This corresponds to the classical feed forward integration model of multisensory information (Meredith and Stein, 1993). Finally, feed-forward and feedback information regarding expectations and predictions is transferred between frontal and multisensory cortical areas (Arnal and Giraud, 2012). This information transfer presumably relies on long-range functional connectivity in the beta band.

Here, I propose an integrative network model that attempts to bring together the three major elements of multisensory integration (**Figure 9**). In this model, sensory input is initially processed in primary sensory areas and subsequently transferred to multisensory and higher-order cortical areas. Fluctuations within primary sensory and

multisensory areas, as well as the functional connectivity between these areas influence the processing of the upcoming sensory input. Cognitive processes shape local activity and functional connectivity within and between primary sensory, multisensory and frontal cortical areas. In psychiatric disorders, such as autism or schizophrenia, the coordination of neural oscillations within and between cortical areas is presumably disrupted. This results in aberrant stimulus processing and multisensory integration in these disorders.

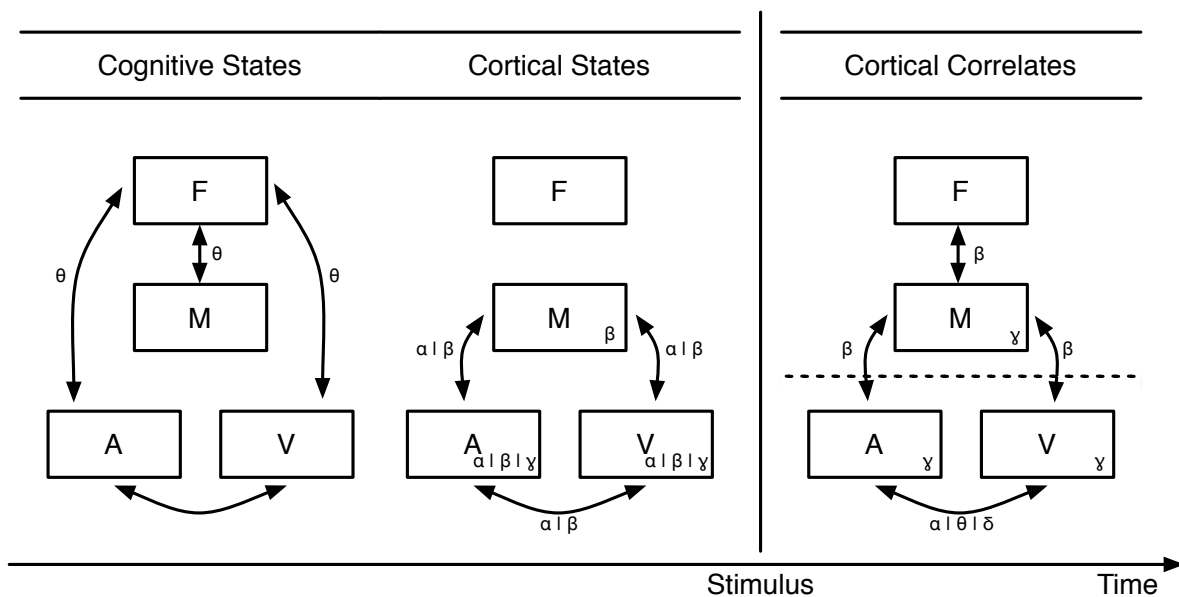


Figure 9: Integrative model for multisensory processing in local nodes and functional connectivity networks. Neural oscillations in different frequency bands reflect distinct mechanisms underlying multisensory processing. Primary sensory (e.g. auditory [A] and visual [V]), multisensory [M] and higher order frontal [F] cortical areas are involved in multisensory integration and perception. **Left:** Cognitive states influence task- and modality dependent local neural oscillations in primary sensory and multisensory cortical areas as well as functional connectivity between these areas via top-down theta band functional connectivity. **Middle:** Cortical states **prior to** stimulus onset influence multisensory perception. Local alpha, beta and gamma band power reflect excitability in primary sensory areas. Beta band power in multisensory cortical areas and alpha and beta band functional connectivity between primary sensory and multisensory cortical areas influence multisensory integration. **Right:** Neural processes **during** stimulus processing. The dashed line symbolizes the threshold to a conscious integrated percept. Low-frequency neural oscillations mediate cross-modal influences between primary sensory areas. Multisensory information integration into a conscious percept is reflected in gamma band power in sensory and multisensory cortical areas. Feed-forward and feedback information regarding expectations and predictions is transferred between frontal and multisensory cortical areas in the beta band. Capital letters indicate exemplary cortical areas (auditory [A], visual [V], multisensory [M] and higher order frontal [F] areas) and small greek letters indicate frequency bands (δ = delta, θ = theta, α = alpha, β = beta and γ = gamma bands).

Outlook and future directions

As summarized above, the hypothesis that synchronous neural oscillations play a prominent role in unisensory and multisensory processing has received substantial support. Moreover, local oscillations and functional connectivity reflect bottom-up as well as top-down processing during multisensory integration. The integrative model for the role of neural oscillations in conscious multisensory perception involves three distinct elements (**Figure 9**). This model allows the formulation of predictions for various multisensory integration scenarios and accordingly, many potential future research directions. According to the model, multisensory perception requires joint activity of primary sensory and higher-order cortical areas, whereas simple cross-modal influence can occur directly between sensory cortices. Furthermore, the various processing steps underlying multisensory perception are reflected in distinct, coexisting spectral signatures. Also, the processing of congruent and incongruent multisensory information requires different processing steps, especially if incongruent information needs to be resolved into a coherent percept or predictions need to be updated following violations.

An interesting open question is whether these information-processing steps act simultaneously or whether they are engaged sequentially. Hence, the temporal cascade of activity in primary sensory and higher-order cortical areas during multisensory perception should be investigated in further detail. Recent findings lend support to the idea of temporally orchestrated steps including predictions, cross-modal comparison and multisensory integration (Lange et al., 2014; Roa Romero et al., 2015). In future research, data from intracranial recordings in humans, with high temporal resolution and broad spatial coverage, could help to shed new light on these questions (e.g., Mercier et al., 2015; Schepers et al., 2015). Multisensory electrophysiological studies have often used statistical comparisons between two distinct perceptual categories. Correlating the qualia of multisensory perception with neural activity in single trials would allow a more direct link between cortical states to cognitive processes. Thus, an approach formulated to correlate near-threshold visual perception and cortical activity (Chaumon & Busch, 2014) should be extended to multisensory perception.

In the last decade it has been established that multisensory integration is a highly malleable process that can be influenced by cues and distractors, and can be affected by

mental disorders like autism or schizophrenia. In multisensory experiments, cross-modal influence can vary on a trial-by-trial basis. Thus, perception can be shifted to the integration or segregation of sensory streams. Until now, however, it has never been systematically examined how manipulating cognitive states, e.g. by attentional or emotional load, influences multisensory integration. A recent series of experiments showed that occipital alpha band power is increased during cognitively and emotionally demanding visual imagery, suggesting that cognitive states modulate local cortical processing (Bartsch et al., 2015). In future research, the role of emotions and prior experiences for conscious perception should be explored. This question encompasses experiments with healthy participants as well as experiments with patients suffering from psychiatric disorders. For the latter, the main question is how learning experiences, traumatic experiences or chronic stress, or pathological changes in the brain influence cortical activity and conscious perception. Furthermore, cortical stimulation techniques (e.g. TMS or tDCS) could be used to experimentally control cortical states in order to more directly examine the causal relationship between neural oscillations and conscious multisensory perception.

Taken together, the current work summarizes accumulating evidence for the electrophysiological signatures of conscious multisensory perception. It will be a long and exciting endeavor to uncover all facets of the functional fingerprints of neural oscillations for multisensory processing and perception.

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Appendix

List of published empirical articles of the studies used in this work. Copies of the articles will not be included due to copyright concerns.

Study 1: Keil, J., Pomper, U., Senkowski, D., 2016. Distinct patterns of local oscillatory activity and functional connectivity underlie intersensory attention and temporal prediction. *Cortex* 74, 277–288.

<https://doi.org/10.1016/j.cortex.2015.10.023>

Study 2: Keil, J., Roa Romero, Y., Balz, J., Henjes, M., Senkowski, D., 2016. Positive and Negative Symptoms in Schizophrenia Relate to Distinct Oscillatory Signatures of Sensory Gating. *Frontiers in Human Neuroscience* 10, 639.

<https://doi.org/10.3389/fnhum.2016.00104>

Study 3: Krebber, M., Harwood, J., Spitzer, B., Keil, J., Senkowski, D., 2015.
Visuotactile motion congruence enhances gamma-band activity in visual and somatosensory cortices. *NeuroImage* 117, 160–169.
<https://doi.org/10.1016/j.neuroimage.2015.05.056>

Study 4: Balz, J., Keil, J., Romero, Y.R., Mекle, R., Schubert, F., Aydin, S., Ittermann, B., Gallinat, J., Senkowski, D., 2016a. GABA concentration in superior temporal sulcus predicts gamma power and perception in the sound-induced flash illusion. NeuroImage 125, 724–730.

<https://doi.org/10.1016/j.neuroimage.2015.10.087>

Study 5: Roa Romero, Y., Senkowski, D., Keil, J., 2015. Early and late beta-band power reflect audiovisual perception in the McGurk illusion. J Neurophysiol 113, 2342–2350. <https://doi.org/10.1152/jn.00783.2014>

Study 6: Keil, J., Timm, J., SanMiguel, I., Schulz, H., Obleser, J., Schonwiesner, M., 2014. Cortical brain states and corticospinal synchronization influence TMS-evoked motor potentials. J Neurophysiol 111, 513–519.

<https://doi.org/10.1152/jn.00387.2013>

Study 7: Keil, J., Senkowski, D. (2017). Individual Alpha Frequency Relates to the Sound-Induced Flash Illusion. *Multisensory Research* 30(6), 565–578.

<https://doi.org/10.1163/22134808-00002572>

Study 8: Pomper, U., Keil, J., Foxe, J.J., Senkowski, D., 2015. Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices. Hum Brain Mapp 36, 3246–3259.

<https://doi.org/10.1002/hbm.22845>

Study 9: Keil, J., Pomper, U., Feuerbach, N., Senkowski, D., 2017. Temporal orienting precedes intersensory attention and has opposing effects on early evoked brain activity. *NeuroImage* 148, 230–239.

<https://doi.org/10.1016/j.neuroimage.2017.01.039>