11 Oscillatory Activity and Multisensory Processing

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Why does food lose its taste when your nose is stuffed up? Why do turn signals attract the drivers' attention more when clicking sounds are simultaneously presented? Why are we better at hearing speech in noisy environments when we see the lip movements of the speaker? These are all questions of interest for researchers in the areas of multisensory information processing. Although the scientific study of multisensory integration on the behavioral level has been pursued since psychology became an experimental discipline, the precise neural mechanisms underlying multisensory integration, particularly in the human brain, are to date not well understood. The application of modern techniques and analysis strategies now allows us to uncover the finer details of how the various sensory inputs that continuously enter our nervous system are merged to become coherent multisensory percepts. In this chapter, we summarize and discuss recent studies that suggest that synchronized oscillatory brain activity may be a crucial mechanism for multisensory processing.

Traditionally, multisensory integration processes have been considered to take place automatically in a hierarchical manner by progressive convergence of pathways in regions of the association cortex such as the superior temporal sulcus (STS) (Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004; Calvert, 2001; Noesselt et al., 2007) and in specialized subcortical regions such as the superior colliculus (SC) (Stein & Meredith, 1993). Interestingly, the collicular multisensory response patterns were similar in awake and anesthetized animals, which supported the original view that higher cognitive processes are not a prerequisite for multisensory processes (Wallace, Meredith, & Stein, 1998). The assumption that multisensory integration can occur automatically is also supported by behavioral studies, which showed that multisensory interactions were not affected by the voluntary directing of attention (Bertelson, Vroomen, De Gelder, & Driver, 2000).

Recently, numerous authors have suggested that a pure convergence model might not be sufficient to account for all aspects of multisensory processing (Ghazanfar & Schroeder, 2006; Kayser & Logothetis,

2007; Lakatos et al., 2009; Senkowski, Schneider, Foxe, & Engel, 2008). First, multimodal interactions and modulation already occur in primary sensory cortices, a result that is difficult to reconcile with the hierarchical convergence model. Second, a convergence scenario does not appear flexible enough to allow for rapid recombination of multisensory signals into completely novel percepts. Third, a hierarchical convergence model does not explain how low-level information about objects can remain accessible, because the high-level representation is noncompositional and does not explicitly make reference to elementary features. Therefore, an alternative account for multisensory processing has been emerging, where multisensory integration is achieved by flexible synchronization of oscillatory signals (Kayser & Logothetis, 2009; Senkowski et al., 2008). In this chapter we first outline the relevance of synchronized oscillatory activity for a number of cortical processes such as sensory information processing, attentional selection, and working memory and then provide an overview on recent studies supporting the notion that synchrony in neuronal populations is important for multisensory integration. Finally, we pinpoint open questions and future research directions in the emerging field of multisensory processing and oscillatory activity.

ROLE OF OSCILLATORY RESPONSES FOR CORTICAL PROCESSING

In general, two types of stimulus-related oscillatory responses can be distinguished. *Evoked* oscillatory activity is strictly phase-locked and time-locked to the onset of an event. Accordingly, this activity remains present in the average event-related potential waveform. *Induced* activity comprises oscillatory responses that are stimulus related but not phase-locked to the onset of an event. Oscillatory activity patterns in the dog and monkey brain had already been observed decades before the first reports of alpha-band (8–12 Hz) activity in the human electroencephalogram (EEG); the first EEG data from humans and previous findings from animal

studies are summarized in Berger (1929). Of particular relevance in human EEG studies was the observation of ongoing alpha activity that changed with the subject's behavior. Most prominently, alpha activity is strongly reduced when subjects open their eyes after they have been closed, suggesting that oscillatory activity is related to the physiological state of a person. Following the groundbreaking research on ongoing synchronized activity on human EEG activity by Berger (1929), more recent studies, primarily in animals, showed that oscillatory activity is indeed a ubiquitous property of neuronal populations (Buzsaki & Draguhn, 2004; Engel, König, Kreiter, Schillen, & Singer, 1992; Hutcheon & Yarom, 2000). Moreover, the strength of neural response synchronization, in particular at frequencies in the gamma-band (> 30 Hz), was shown to be functionally relevant for sensory information processing (Singer, 1993; Singer & Gray, 1995). Although this latter subject is not without controversy (e.g., Shadlen & Movshon, 1999), there is increasing consensus that understanding of neural synchronization mechanisms is crucial for our understanding of brain functions (Buzsaki & Draguhn, 2004; Engel, Fries, & Singer, 2001; Schroeder & Lakatos, 2008). Meanwhile, there is direct evidence from in vivo studies that the mutual influences among neuronal groups depend on the phase relationships of oscillatory activity patterns (Fries, 2005; Womelsdorf et al., 2007).

Beyond sensory processing, neural synchronization mechanisms have also been linked to more complex, higher-level cognitive functions (Engel, Fries, König, Brecht, & Singer, 1999; Engel & Singer, 2001). There is ample evidence from animal and human studies that gamma-band synchrony is related to attentional selection (Bauer, Oostenveld, Peeters, & Fries, 2006; Engel et al., 2001; Fries, Reynolds, Rorie, & Desimone, 2001; Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Womelsdorf, Fries, Mitra, & Desimone, 2006). A key role of gamma-band activity (GBA) in higher cortical processes might be the top-down matching of incoming information with expected inputs (Engel et al., 2001) and contents of working memory (Herrmann, Munk, & Engel, 2004). For instance, the presentation of visual objects for which subjects have a memory trace leads to higher evoked GBA than does the presentation of objects that do not match stored memory contents (Herrmann, Lenz, Junge, Busch, & Maess, 2004). Likewise, oscillatory activity in the other frequency bands has been related to a variety of brain states and functions. Delta (about 1–3 Hz) is the predominant frequency during deep sleep, and this frequency range is associated with learning, motivational processes, and

the brain reward system (Knyazev, 2007; Steriade, McCormick, & Sejnowski, 1993). Activity in the theta-band (4–7 Hz) has been linked to working memory functions, emotional arousal, and fear conditioning (Jensen & Lisman, 2005; Knyazev, 2007). Oscillatory signals in the beta-band (13–30 Hz) have classically been considered to be related to sensorimotor functions, but additional hypotheses on their possible relation to cognitive functions have been discussed recently (Engel & Fries, 2010). Taken together, these studies provide strong evidence for an involvement of oscillatory activity in numerous sensory and cognitive processes.

Interestingly, a recent study in behaving rats and mice showed cross-frequency coupling between theta-band activity in hippocampus and GBA in cortical areas, including somatosensory cortex and frontal cortex (Sirota et al., 2008). Thus, cross-frequency coupling may be functionally relevant for learning and memory functions, which is in line with the observation that interactions across frequency bands are important for memory consolidation during sleep (Maquet, 2001). The significance of cross-frequency interactions for higher cortical functions has been demonstrated by Lakatos and co-workers (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). This study shows that delta-band activity is crucial for attentional selection in experimental setups with predictable stimulation (e.g., fixed interstimulus intervals). When stimuli were relevant, the phase of delta-band activity was reset so that high-excitability phases tended to coincide with the attended inputs. Phase resetting refers to a shift of the phase of ongoing neural oscillations because of an event, which can lead to phase locking (i.e., a constant phase relationship to an event is maintained across trials) or to increased phase coherence (i.e., two oscillatory signals have a constant relationship between the phases of the two signals) with other oscillatory responses. This alignment to high-excitability delta-band phases was accompanied by an increase in GBA power (Lakatos et al., 2008).

In summary, the available data largely support the notion that synchronized oscillatory activity plays an important role for various cortical operations, such as feature integration, perception, attentional selection, and working memory. Of particular relevance for several of these functions is activity in the gamma-band (Engel et al., 2001; Fries, 2009). Additionally, it is becoming increasingly clear that cross-frequency interactions may be important for sensory information processing. Because neural synchronization is related to integrative processes within and across cortical regions,

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it is likely that it may also be relevant for the processing of sensory information across modalities.

ROLE OF NEURAL SYNCHRONIZATION IN MULTISENSORY PROCESSING

If synchronization does support multisensory integration, several hypothetical scenarios seem possible regarding the interaction of "early" and higher-order regions (figure 11.1). These scenarios comprise changes of neural synchrony within brain areas as well as changes in the interplay between the various structures. One scenario of how neural synchronization could be crucial for multisensory integration involves modulations within or interplay between sensory areas (figure 11.1A). Another scenario involves changes in neural synchronization in multisensory association areas (figure 11.1B). Furthermore, it is possible that multisensory interactions through neural synchronization are reflected in an interplay between sensory cortices and multisensory association areas (figure 11.1C). Changes in neural synchronization could also occur between multisensory association structures and higher frontal areas (figure 11.1D). Most likely, at least for real-world scenarios, neural synchronization during multisensory integration occurs in a complex manner involving a cortical network of frontal areas, sensory cortices, and temporoparietal areas (figure 11.1E). In addition, it is also likely that neural synchronization during multisensory processing includes subcortical structures such as the thalamic nuclei (figure 11.1F). In the sections that follow, we describe the most relevant findings on the role of oscillatory responses during multisensory processing that are in line with these different scenarios. Thus far, the majority of studies on multisensory integration and neural synchronization have used EEG and magnetoencephalography (MEG). Because these methods allow only limited conclusions about the structures underlying multisensory interactions, we assigned findings of the EEG and MEG studies to the most likely scenarios.

Dynamic Interactions within and between Sensory Areas

The last decade has seen a strong increase in studies suggesting that multisensory interactions occur in areas that were classically considered to be unisensory in function (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Schroeder & Foxe, 2005). A detailed review of multisensory interactions in low-level sensory processing areas is presented by James et al. in
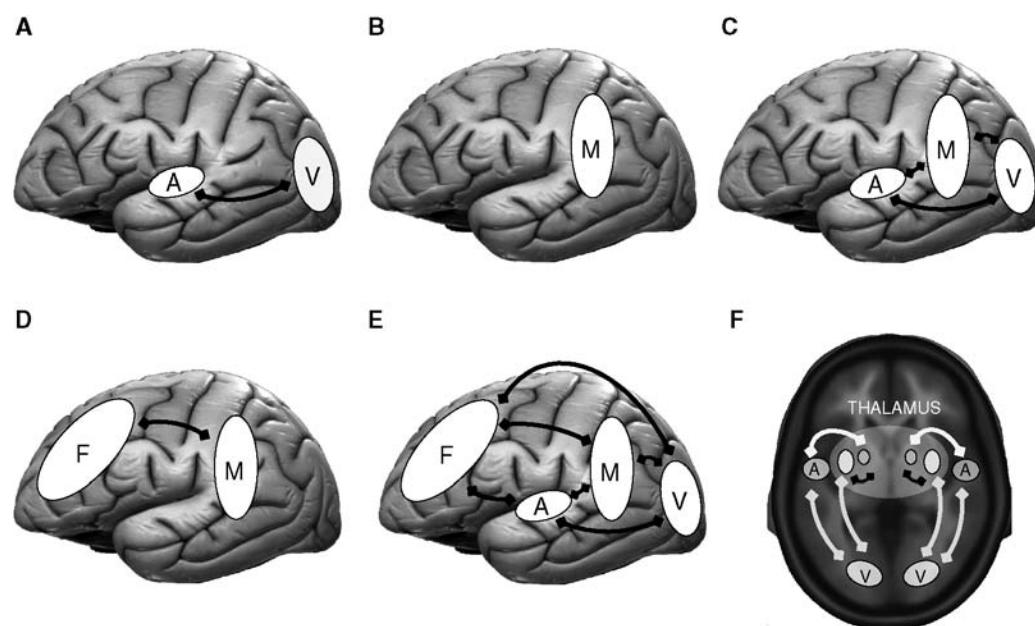

FIGURE 11.1 Hypothetical scenarios on the role of neural synchronization for multisensory processing. Using the case of audiovisual interactions, six possible scenarios, which are not mutually exclusive, of how neural synchronization may be involved in multisensory integration are illustrated (see text for details). The connecting lines (black or white) denote interplay or modulations in neural synchronization between the respective structures. Abbreviations: A, auditory cortex; V, visual cortex; M, higher-order multisensory regions; F, prefrontal cortex. (Brain image reproduced with permission from http/:www.joelertola. com. Redrawn from Senkowski et al., 2008.)

chapter 12 in this section. Research in both animals and humans now suggests that oscillatory responses may play an important role for multisensory processing in lower-tier areas.

Microelectrode recordings and analysis of laminar current source density in primary auditory cortex of awake macaques provide compelling evidence for an involvement of oscillatory activity in early multisensory processes (Kayser, Petkov, & Logothetis, 2008; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007). Lakatos et al. (2007) examined the effect of median nerve stimulation on auditory responses in primary auditory cortex and observed an enhancement of delta-, theta-, and gamma-band responses. Moreover, their analysis showed that this effect was, at least in part, caused by a phase resetting of auditory oscillations by the somatosensory inputs. Another striking observation in the same study was that systematic variation of the relative temporal synchrony between somatosensory and auditory inputs leads to multisensory response enhancements at intervals corresponding to the cycle length of gamma-, theta-, and delta-band oscillations (see Naue, Rach, Strüber, Huster, Zaehle, Körner, Herrmann 2011, for a similar finding in a recent human EEG study). By contrast, for intermediate delays, the paired stimulus response was smaller than the responses to auditory stimuli alone. Additional support for phase resetting as a potential mechanism of multimodal interaction comes from a study that focused on sensory information processing in the auditory cortex of monkeys (Kayser et al., 2008). Using auditory and visual stimuli while recording in the auditory core and belt regions of awake behaving monkeys, Kayser et al. (2008) found both enhancement and suppression of single-unit and field potential responses. Interestingly, the presentation of visual stimuli modulated the phase angle of alpha- and theta-band activity in the auditory cortex. Together, these findings suggest that phase modulation of oscillatory activity in primary sensory areas may be an important neuronal mechanism contributing to multisensory processing.

Additional evidence for the assumption that oscillatory activity in sensory areas is linked to multisensory processing stems from a human EEG study that focused on the effects of stimulus onset asynchrony on the evoked GBA to audiovisual inputs. In their study, Senkowski, Talsma, et al. (2007) presented subjects with a continuous stream of auditory-only, visual-only, and bimodal audiovisual stimuli while occasional targets had to be detected in the auditory or the visual modality (figure 11.2). The bimodal stimuli were presented with asynchronies between the auditory and visual inputs ranging from –125 to +125 msec. For simultaneously presented audiovisual inputs, the evoked GBA triggered by auditory inputs was enhanced compared to the GBA evoked by unisensory auditory stimuli. In line with previous single-cell recording studies in the SC (Meredith, Nemitz, & Stein, 1987), this suggests that multisensory inputs are optimally integrated when the sensory constituents are in exact or near temporal synchrony. The mediofrontal topography and the short latency (50–80 msec) of this effect indicated an involvement of auditory areas. In the same study, the evoked GBA to simultaneously presented audiovisual stimuli triggered by visual inputs was enhanced compared to the evoked GBA to unisensory visual inputs (figure 11.2). This early effect (60–100 msec) spread over the occipital scalp, suggesting an involvement of visual cortical areas. Taken together, these studies suggest that stimulus-driven factors, like the relative temporal synchrony between the different unisensory constituents of a multisensory stimulus, influence multisensory processing through neural synchronization in sensory areas.

Further studies corroborate the role of neural synchronization across sensory areas in multisensory processing by demonstrating a relation to perception or behavior. In an MEG study, Kaiser et al. (2006) examined neural synchronization during the McGurk illusion (this illusion is detailed by Beauchamp in the chapter 10 in this section). The authors showed that the illusory perception of auditory input induced by simultaneously presented visual stimuli is reflected in enhanced GBA over visual areas. Moreover, an enhanced GBA over occipital areas was also found for illusory trials compared to nonillusory trials in the double-flash illusion, whereby a single flash that is accompanied by two tones is often perceived as two flashes (Bhattacharya, Shams, & Shimojo, 2002; Mishra, Martinez, Sejnowski, & Hillyard, 2007). Of particular interest are also the results from a visuotactile matching study that focused on long-range synchronization between visual and somatosensory regions (Hummel & Gerloff, 2005). In experimental blocks in which subjects performed well compared to blocks in which they performed poorly, an enhancement of phase coherence in the alpha-band between occipital and lateral central EEG channels was observed. This suggests that mutual interplay between visual and sensorimotor cortex is relevant for the multisensory matching of semantically meaningful information.

In summary, the studies described above are compatible with the hypothesis that amplitude and phase modulation of oscillatory activity are crucial for multisensory processing within and between sensory areas. Moreover, these studies suggest that oscillatory responses in
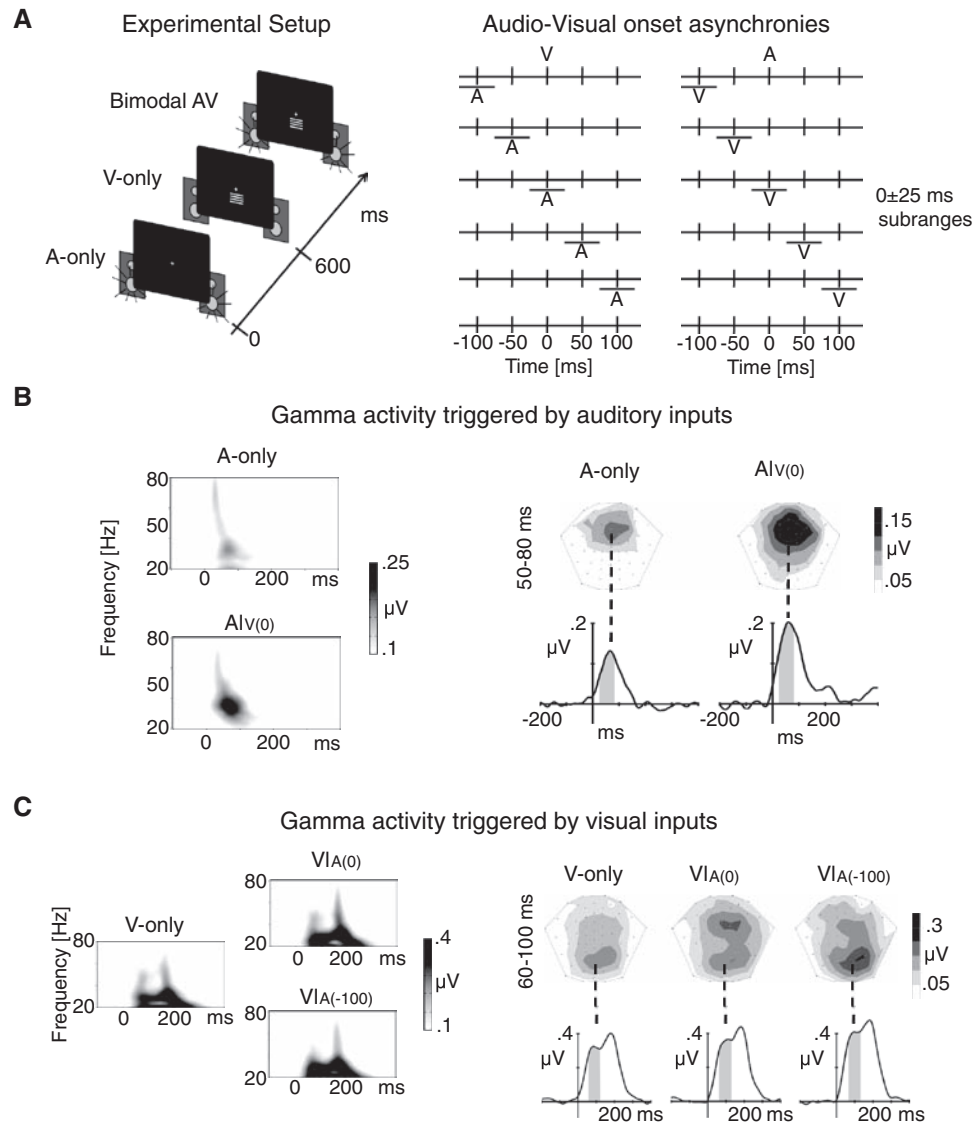
FIGURE 11.2   Early evoked EEG gamma activity reflects relative onset asynchrony of auditory and visual components of multi-sensory audiovisual stimuli. (A) Left panel: The experimental setup. A continuous randomized stream of unisensory auditory, unisensory visual, or multisensory audiovisual stimuli was presented, while subjects were instructed to detect occasional targets either in the auditory or visual modality. Right panel: Auditory and visual inputs were presented with stimulus onset asynchronies ranging between –125 to +125 msec, and five ±25-msec subranges of asynchrony were extracted for the analysis of multisensory integration effects in evoked GBA (see main text for further details). (B) Evoked EEG gamma-band responses triggered by *auditory* inputs were enhanced for synchronously presented audiovisual inputs [A|V(0)] compared to auditory-only stimuli (left panel shows time-frequency planes of a mediofrontal scalp channel). The short latency (around 50 ms) and the mediofrontal topography of this effect suggest an involvement of auditory areas. Note that due to the tangential orientation (relative to the head surface) of the dipolar fields generated in auditory cortical areas on the superior temporal plane, early auditory responses in the EEG are typically picked up at the central and mediofrontal scalp. (C) Enhanced EEG gamma-band activity triggered by *visual* inputs was found for simultaneously presented audiovisual inputs [A|V(0)] and when auditory inputs preceded visual ones by 100 msec [A|V(–100)] compared to visual-only stimuli (left panel) shows time-frequency planes of a channel located over the occipital regions. The topography of this effect suggests an involvement of areas in the visual cortex. Note that the two peaks in gamma activity represent on- and offset responses to visual inputs, which had a duration of 100 msec. (Modified from Senkowski, Talsma, et al., 2007.)

sensory areas reflect stimulus-driven as well as perceptually relevant multisensory integrative processing.

Dynamic Interactions Involving Multisensory Association Areas

A frequently described region linked to multisensory integration is the STS (Beauchamp, Argall, et al., 2004; Calvert, 2001; Noesselt et al., 2007). Both animal and human studies suggest that oscillatory responses in the STS play an important role for multisensory processing. While recording local field potentials (LFPs) in STS during the presentation of dynamic faces and voices, Chandrasekaran and Ghazanfar (2009) observed enhancements of alpha- and gamma-band activity for multisensory compared to combined unisensory responses. Across the different stimulation conditions the most robust multisensory integration effects in oscillatory responses were obtained in the gamma-band. In addition, a recent MEG study showed that synchronized oscillatory responses may be crucial for the integration of facial expressions and voices in STS (Hagan et al., 2009). Using source modeling of oscillatory activity, the authors found multisensory interactions evoked by static faces and voices expressing fear in broadband frequency responses (3–80 Hz), which were localized to STS, regions of cingulate cortex, and superior frontal gyrus (figure 11.3). This shows that neuronal synchronization reflects the integration of emotionally congruent visual and auditory speech inputs in STS. Further support for the role of neural synchronization in STS stems from two multisensory priming studies in which a linear beamforming approach was used (Schneider, Debener, Oostenveld, & Engel, 2008; Schneider, Lorenz, Senkowski, & Engel, 2011). The beamforming approach is frequently applied to reconstruct the cortical sources underlying oscillatory responses in the EEG and MEG (Gross et al., 2001; van Veen, van Drongelen, Yuchtman, & Suzuki, 1997). Because of the high temporal resolution of the EEG and MEG, this approach makes it possible to estimate the cortical regions underlying oscillatory responses in the time-frequency domain. Schneider and co-workers observed that semantic congruency in visual-to-auditory object presentations (Schneider et al., 2008) and haptic-to-auditory stimulation (Schneider et al., 2011) is reflected by enhanced GBA in regions of STS. The results of the former study are illustrated in figure 11.4.

Evidence for the notion that oscillatory responses may be also involved in the interaction between different multisensory association areas stems from an earlier EEG study on multisensory processes in which coherence patterns during the presentation of auditory and

A Experimental Setup

Neutral Bimodal AV

Fear V-only

Neutral A-only

Neutral V-only

Fear A-only

Fear Bimodal AV

Time

B Supra-additive responses in broadband power

Fear: AV < A+V

Superior temporal gyrus

R R R

R L R L R L
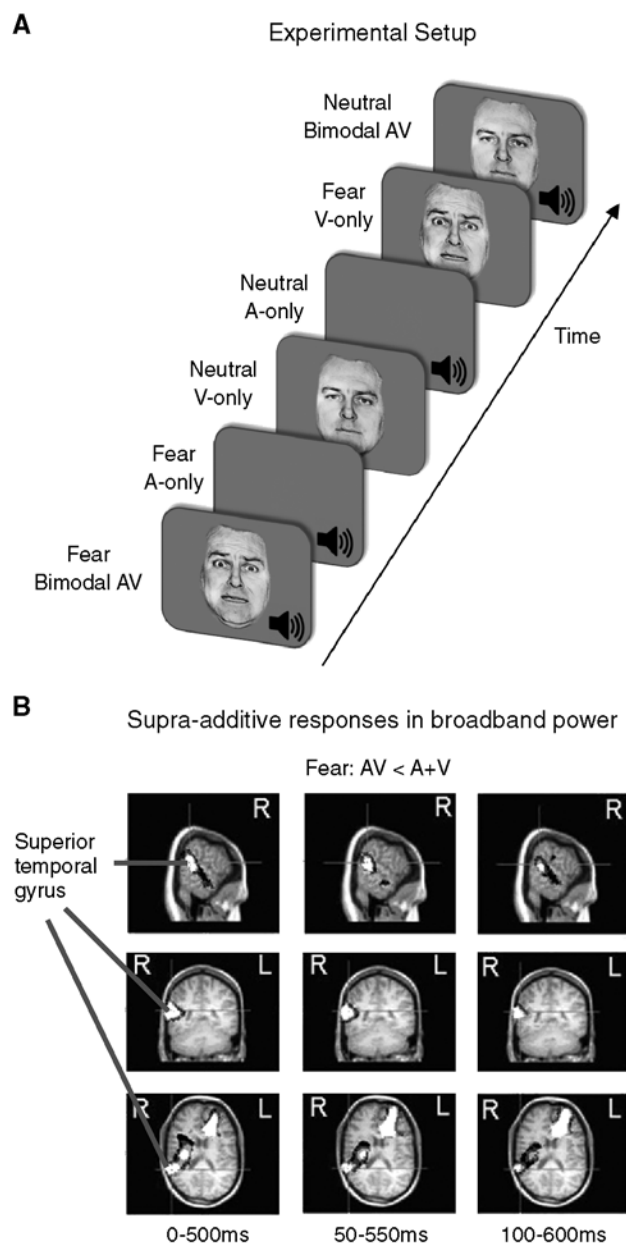
R L R L R L

0–500ms   50–550ms   100–600ms

FIGURE 11.3   Multisensory integration of facial and vocal emotion is reflected in supra-additive broadband MEG responses in the right superior temporal sulcus. (A) A continuous stream of faces (V-only), voices (A-only), and faces plus voices (bimodal AV) was presented while MEG responses were monitored. Faces and voices had either a neutral or a fearful expression. (B) The linear beam-forming approach was applied to estimate the sources underlying oscillatory response patterns, and statistical parametric maps were generated from the supra-additive comparison (i.e., AV < A+V) of broadband power (3–80 Hz) changes after stimulation onset. Within the first 600 msec a supra-additive response pattern emerged in the superior temporal sulcus for the fearful expression stimuli (see illustration). By contrast, no significant interactions were observed for neutral expressions (not shown). This suggests that emotional content mediates the integration of faces and voices in the superior temporal sulcus. (Modified from Hagan et al., 2009.)
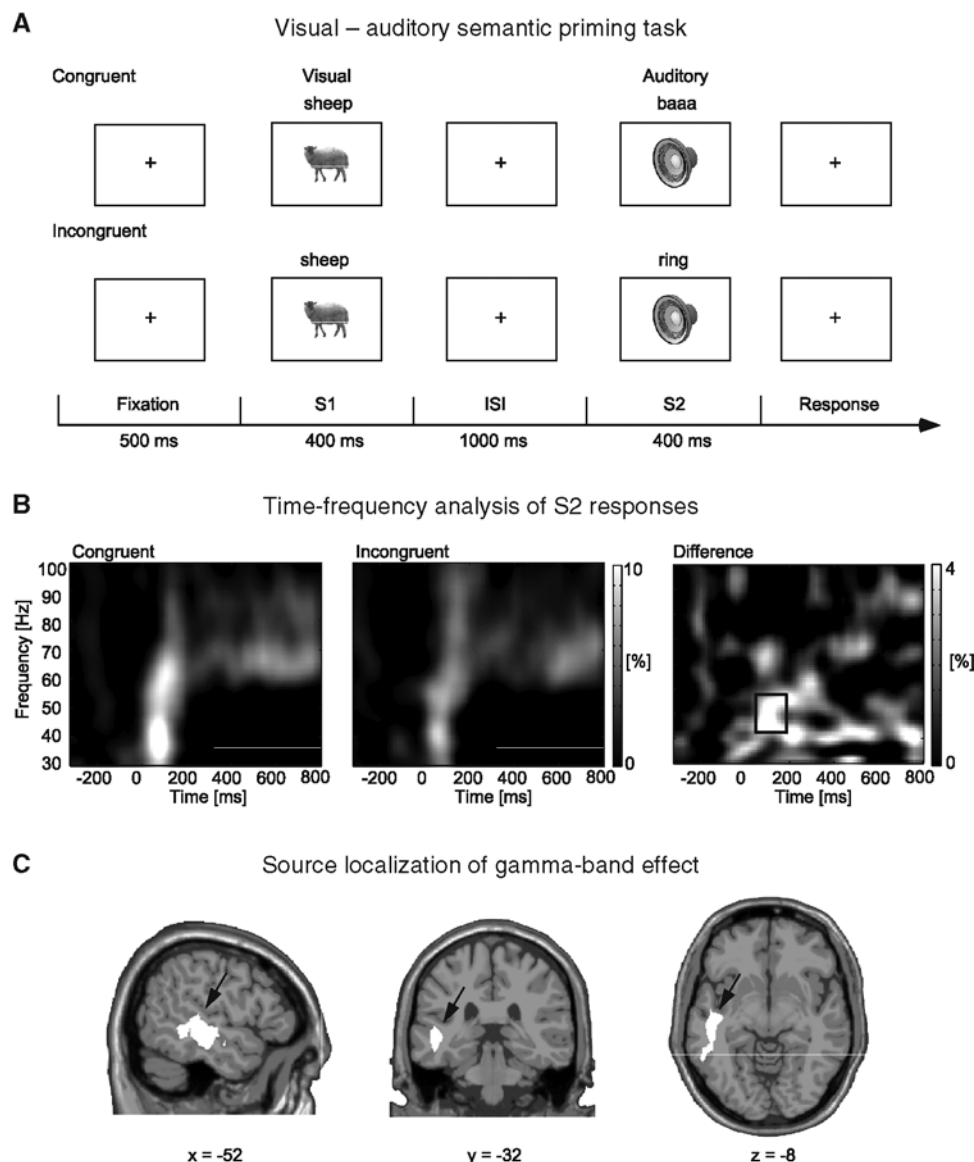
FIGURE 11.4   Enhanced gamma-band activity during semantic multisensory matching. (A) Semantically congruent and incongruent objects were presented in a visual-to-auditory (S1-S2) priming paradigm. (B) GBA in response to auditory S2 target stimuli was enhanced following congruent compared to incongruent stimuli. The square in the right panel indicates a time-frequency window where the GBA difference was significant. (C) Source localization of GBA (40–50 Hz) between 120 and 180 msec after auditory stimulus onset using the method of linear beam forming (threshold at $z = 2.56$). Differences between the congruent and incongruent conditions are prominent in the left medial temporal gyrus (BA 21) (arrow). This suggests that the enhanced GBA reflects multisensory semantic matching processes in the lateral temporal cortex. (Modified from Schneider et al., 2008.)

visual objects names, as well as pictures of objects, were presented under condition of passive stimulation (von Stein, Rappelsberger, Sarnthein, & Petsche, 1999). The authors observed an increase of coherence in the beta-band between temporal and parietal electrode sites that was commonly found for all three presentation types (pictorial presentation and spoken and written words). They suggested that coherent activity in this frequency range is important for the integration of meaningful semantic inputs in a modality-independent network comprising association structures in temporal and parietal cortices. Collectively, these findings suggest a crucial role of neural synchronization for multimodal processing within and between multisensory association areas.

Three recent studies in monkeys addressed whether neural synchronization may also serve to link multisensory processing between STS and primary auditory

areas during integrative multisensory processing (Ghazanfar, Chandrasekaran, & Logothetis, 2008; Kayser & Logothetis, 2009; Maier, Chandrasekaran, & Ghazanfar, 2008). One of these studies examined the effects of audiovisual looming signals on neural oscillations in the two regions (Maier et al., 2008). The main finding of this study was enhanced coherence in the gamma-band between STS and primary auditory cortex for coherent looming signals (across modalities) compared to unimodal or receding motion inputs. In a similar vein, enhanced gamma-band coherence between STS and auditory cortex also occurred for the integration of dynamic faces and voices in the second study (Ghazanfar et al., 2008). The third study investigated directed interactions between auditory cortex and multisensory integration sites in the STS during the processing of dynamic naturalistic audiovisual clips (Kayser & Logothetis, 2009). The authors observed interactions directed from STS to the auditory cortex at higher frequency ranges (>20 Hz), whereas feed-forward interactions from auditory cortex to STS were reflected in lower-frequency beta-band activity. These findings demonstrate that activity in different frequency bands may relate to different aspects of information transfer in the dynamic interplay between STS and auditory cortex during multisensory processing.

Taken together, the available data provide strong evidence that oscillatory responses in the gamma-band and in lower frequency ranges are important for multimodal integration in association regions such as STS. Moreover, neural synchronization seems to be crucial for the interaction between multisensory cortices and primary sensory regions in multisensory processing.

Multisensory Processing and Neural Synchrony in Higher Cortical Regions

Support for the scenario that oscillatory activity in higher cortical regions is important for multisensory integration stems from an EEG study on the bimodal redundant target effect (Senkowski, Molholm, Gomez-Ramirez, & Foxe, 2006). The bimodal redundant target effect is detailed by Murray et al., chapter 13, in this volume. In line with previous observations (Miller, 1982), Senkowski et al. (2006) found that bimodal redundant targets are processed faster than the corresponding unisensory targets. Moreover, the facilitation of response speed for multisensory compared to unisensory inputs is reflected by enhanced evoked beta-band responses over frontal, central, and occipital electrode sites. Interestingly, the strongest beta-band responses were observed over right frontal scalp, indicating an involvement of frontal brain areas. Moreover, across

trials and across participants, this enhancement predicted the response facilitation for bimodal redundant targets, indicating that evoked beta-band responses reflect behaviorally relevant aspects of multisensory processing.

The role of oscillatory activity for multisensory processes was also shown in a tactile-to-visual cueing paradigm (Trenner et al., 2008). For tactile inputs that served as cues compared to tactile stimuli that did not serve as cues, enhanced prefrontal gamma-band responses were observed, which may reflect multisensory spatial attention or expectation across sensory modalities. Further evidence for the assumption that GBA in higher cortical regions is linked to multisensory processing stems from a MEG study on the McGurk effect (Kaiser, Hertrich, Ackermann, Mathiak, & Lutzenberger, 2005). In addition to the above-described effects on GBA over occipital areas in the same study (Kaiser et al., 2006), an enhanced GBA in epochs where a visual deviant within a continuous stream of multisensory audiovisual speech stimuli induced an illusory auditory percept was found over posterior parietal cortex and inferior frontal cortex. Interestingly, the topography of the frontal effect was comparable with the topography of a GBA enhancement obtained in an auditory mismatch study (Kaiser, Lutzenberger, Ackermann, & Birbaumer, 2002). This suggests that the GBA effect in the McGurk illusion study may represent a perceived auditory pattern change caused by the visual lip movement. In sum, these studies are compatible with the hypothesis that multisensory processes can involve neural synchronization in higher cortical areas.

Changes in neural coherence with higher cortical areas are presumably also involved in cases where top-down processes, such as attention, influence multisensory integration. Recently, Lakatos et al. (2009) addressed how supramodal attention affects phase-resetting mechanisms caused by sensory inputs from one modality on the neural responses in primary sensory areas of another modality. Oscillatory activity was simultaneously measured in primary auditory and primary visual cortex while unisensory visual and unisensory auditory inputs were presented in random order, and monkeys attended to one designated modality in which they had to detect occasional target stimuli. The main finding of this study was that sensory inputs in one modality (e.g., visual) were associated with a modulation of local cortical excitability expressed by a phase reset of ongoing oscillatory activity in primary sensory areas of the other modality (e.g., primary auditory cortex). Notably, this phase-resetting mechanism was found only for attended but not for unattended

sensory inputs. Along the same lines, a previous EEG study in humans showed higher phase locking of GBA for spatially attended compared to spatially unattended multisensory inputs (Senkowski, Talsma, Herrmann, & Woldorff, 2005). This suggests that attention plays an important role in multimodal processing.

Interplay among Sensory Cortices, Multisensory Association Areas, Higher Cortical Regions, and Subcortical Structures

Most likely, at least for real-world scenarios, multisensory processes involve complex interplay among various cortical regions, including sensory cortices, multisensory association cortices, higher-order cortical areas, and subcortical structures such as the thalamus (figure 11.1). To date, most of the evidence for the involvement of such complex multisensory networks in humans derives from studies using functional magnetic resonance imaging (fMRI) (Beauchamp, Lee, Argall, & Martin, 2004; Bushara et al., 2003; Calvert, 2001; Hein et al., 2007). Investigating multisensory processing during a bistable percept of visual motion ("bounce" vs. "pass"), Bushara et al. (2003) observed a widely distributed network of cortical and subcortical structures when comparing physically identical audiovisual stimuli that are perceptually bound to multisensory inputs with stimuli that are perceptually unbound. A widely distributed network of cortical and subcortical structures was also found during the detection of auditory-visual stimulus onset asynchrony (Bushara, Grafman, & Hallett, 2001). Another fMRI study demonstrated that spatial attention to audiovisual speech stimuli modulates neural activity in both cortical and subcortical regions, including STS, striate and extrastriate visual areas, and SC (Fairhall & Macaluso, 2009). In a recent EEG study using the same paradigm as Bushara et al. (2003), specific coherence changes relating to the bistable percept were observed in a network involving the frontal eye fields, parietal cortex, and sensory areas (Hipp, Engel, & Siegel, 2011). Taken together, these studies suggest that multisensory processes involve various cortical and subcortical structures (Ghazanfar & Schroeder, 2006) and that at least some of these processes can be modulated by complex cognitive functions such as attentional selection (Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010).

Although there is increasing evidence for the existence of a widespread multisensory network in the mammalian brain, the precise neural mechanisms by which multimodal information is coded and transferred across widespread cortical and subcortical areas during multisensory integration are not well understood.

There are no studies that have yet explicitly examined the complex interplay among cortical and subcortical structures, as schematically depicted in figures 11.1E and 11.1F, in terms of functional connectivity measures.

OPEN QUESTIONS AND FUTURE RESEARCH DIRECTIONS

The available data provide evidence in support of the hypothesis that neural synchronization may serve an important role in multisensory processing. The most robust findings are power modulations of oscillatory responses that correspond to the degree of multisensory interactions. Cross-sensory power modulations have been found directly from single-cell or LFP recordings in cortical areas (Chandrasekaran & Ghazanfar, 2009; Kayser et al., 2008; Lakatos et al., 2007) as well as in more global-scale EEG and MEG studies (e.g., Kaiser et al., 2006; Senkowski, Gomez-Ramirez, et al., 2007; Senkowski, Schneider, Tandler, & Engel, 2009; Senkowski, Talsma, et al. 2007). In addition, an increasing number of studies showed that phase-resetting mechanisms in various frequency bands and across cortical regions are linked to multisensory processes (e.g., Kayser & Logothetis, 2009; Lakatos et al., 2009). Evidence for changes of neural coherence related to multisensory processing is still sparse. Although the findings described above suggest an involvement of oscillatory activity in multisensory processing, the scenarios illustrated in figure 11.1 require further experimental testing. There are several lines of research that are promising for improving our understanding of the role of oscillatory activity in multisensory processing.

One promising research direction for human EEG and MEG studies lies in the examination of neural coherence of oscillatory activity and cross-frequency interactions during multisensory integration. Ideally, such interactions should be analyzed in anatomical source space (Gross et al., 2001; Van Veen et al., 1997), but, currently, the study of neural synchronization mechanisms in source space using source estimation approaches (see above) still represents a major methodological challenge (see Siegel et al., 2008, and Hipp et al., 2011 for examples of source coherence analyses). In a similar vein, cross-frequency interactions after unisensory visual stimulation have been shown to be crucial for cognitive functions such as working memory processes (Sauseng et al., 2009). Thus far, there are no human studies on cross-frequency interactions during multisensory processing.

Another interesting research account is the study of multisensory processing in clinical conditions where

impairments in multimodal integration are found, such as schizophrenia or autism. The investigation of multisensory processes and oscillatory activity in patients with schizophrenia is interesting at least for two reasons. First, behavioral studies consistently show multisensory processing deficits in patients with schizophrenia (e.g., de Jong, Hodiamont, Van den Stock, & de Gelder, 2009; Ross et al., 2007). Second, schizophrenia has been frequently associated with abnormal neural synchronization in high-frequency EEG activity (Gallinat, Winterer, Herrmann, & Senkowski, 2004; Uhlhaas & Singer, 2006). Another psychiatric disorder in which multisensory processing deficits are assumed is autism (Oberman & Ramachandran, 2008). There is evidence for impaired oscillatory activity after visual stimulation in autism (Brown, Gruber, Boucher, Rippon, & Brock, 2005; Grice et al., 2001), which has led some authors to hypothesize general disordered neural connectivity in autism (Brock, Brown, Boucher, & Rippon, 2002; Rippon, Brock, Brown, & Boucher, 2007). If neural synchronization, as proposed here, were indeed a crucial mechanism for integrative multisensory processing, one would expect to find impaired oscillatory activity during multimodal integration in autism. Abnormal synchronization across brain areas might also play a role in synesthesia, in which excessively strong multisensory coherence may occur that would not only modulate processing in unimodal regions but actually drive sensory neurons even in the absence of a proper stimulus. Future studies of oscillatory activity in clinical conditions in which multisensory interactions can be shown to be impaired might lead to a better understanding of the neural mechanisms underlying these conditions.

A third research line that is promising to deliver new insights regarding the role of oscillatory activity for multisensory processing comprises the examination of intracranial data from epileptic patients. Using intracranial recordings from multiple depth electrodes implanted in the temporal lobe of epileptic patients, Besle et al. (2008) reported multisensory interactions during audiovisual speech processing in intracranial ERPs. Future studies may focus on multisensory interactions in oscillatory responses obtained from human intracranial EEG recordings. A main advantage of intracranial studies is the much higher signal-to-noise ratio and the more localized nature of the recorded oscillatory responses. Compared to invasive studies in animals, intracranial human studies also provide better access to examination of higher cognitive processing of semantically meaningful multisensory information.

With relation to improving the spatial acuity for the investigation of neural synchronization during multisensory processing, study designs using combined EEG and functional MRI may also be promising (Debener, Ullsperger, Siegel, & Engel, 2006). The sluggishness and the low temporal resolution (within the framework of seconds) of the blood-oxygen-level dependence (BOLD) response obtained in fMRI studies is not suitable for examining neural synchronization in frequency ranges that seem to be crucial for multisensory processing (about 0.5–120 Hz). Thus, fMRI studies alone can hardly contribute to the question of how oscillatory responses are linked to the dynamic interplay among cortical regions during multisensory integration. Of special interest are studies that showed significant correlations between oscillatory responses, primarily in the gamma-band, and the BOLD response (Goense & Logothetis, 2008; Niessing et al., 2005). Therefore, the high spatial acuity of the BOLD response may be used to define landmarks for the source estimation of synchronized oscillatory responses during multisensory processing obtained in combined fMRI-EEG studies.

Finally, major breakthroughs for our understanding of the role of neural synchronization in multisensory processing can be also expected from animal studies using newly developed multisite recording channel arrays, which allow the simultaneous recordings of neural activity across large areas of the brain (Rubehn, Bosman, Oostenveld, Fries, & Stieglitz, 2009). Of particular interest in future animal studies will be to investigate neural synchronization mechanisms during multisensory processing among sensory areas, multisensory regions, and thalamic nuclei. The majority of studies described above comprised noninvasive EEG and MEG measures of neuronal activity in humans. Considering the extreme complexity of interactions in neural populations, these studies provide valuable information about multisensory integration on a rather macroscopic scale. In addition, noninvasive studies also may not allow reliable conclusions about neural processing in subcortical structures. We believe that future LFP and single-neuron recording studies in animals will provide more accurate information about the temporospatial dynamics underlying multisensory integration in cortical and subcortical networks. These studies may also focus on the question of how cognitive processes influence multisensory interactions in oscillatory responses.

In summary, the studies reviewed above provide evidence for the notion that oscillatory activity plays a crucial role in multisensory processing. We believe that the study of oscillatory activity and of dynamic functional coupling will lead to major improvements in our understanding of the neuronal mechanisms underlying multisensory integration.

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