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Attentional Activation in Corticothalamic Loops of the Visual System

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All sensory information in mammals, except for smell, arrives at the cerebral cortex via the thalamus (Jones, 2001, 2007). However, far from being a simple relay, thalamic sensory nuclei receive much more reentrant cortical connections than ascending peripheral ones (Rouiller & Welker, 2000). These thalamocortical loops have been implicated in numerous cognitive functions (Briggs & Usrey, 2008; Saalmann & Kastner, 2009, 2011), including attention (Rees, 2009; Wróbel, 2000), perceptual grouping (Robertson, 2003; Ward et al., 2002; Wilke at al., 2010), and general consciousness (Dehaene & Changeux, 2011; Llinas et al., 1998; Ward, 2011). It is also widely accepted that the momentary state of the neuronal network modifies stimulus information processing (Anderson et al., 2000; Arieli et al., 1996; Briggs & Usrey, 2007; Wróbel & Kublik, 2000) and that the resulting response variability (initially attributed to "noise") might represent one of the foundations of brain function (Bernasconi et al., 2011). The factors governing such variability across different processing states are under intensive investigations (Saalmann & Kastner, 2011; Sherman, 2005) and are not yet fully understood. Much is already known about gross state transitions, such as between sleep and wakefulness (Steriade, 1997), but in order to understand the mechanisms underlying various brain functions it is necessary to investigate subtle, rapid natural state transitions evoked during behavioral/cognitive tests in awake animals (i.e., Bekisz & Wróbel, 1993; Buschman & Miller, 2007; Sobolewski et al., 2010). Proper performance in these tasks is critically dependent on the neuromodulatory actions of brainstem nuclei (Buhl et al., 1998; Roopun et al., 2010; Soma et al., 2012; Steriade et al., 1991; Wróbel & Kublik, 2000; see Harris & Thiele, 2011, for review) and the dynamic neural mechanisms utilized during processing of information within the neuronal network. The purpose of this chapter is to shed light on how different attentive demands reconfigure the functional arrangement of the corticothalamic network of the visual system.

VISUAL THALAMIC RELAYS, THEIR POSTULATED FUNCTIONS, AND STATE MODULATION

In mammals visual information arrives at the thalamus via its two largest afferent pathways. Signals in the retinogeniculate pathway reach the dorsal lateral geniculate nucleus (dLGN), directly from the retina and in turn project further to area 17 of the visual cortex. In the retinotectal pathway retinal signals arrive at the thalamus lateral posterior pulvinar complex (LP-P) of the cat and pulvinar complex of the monkey indirectly (via the superior colliculus), where they project further to higher-order visual cortical areas.

The retinogeniculocortical pathway contains three separate streams conveyed by morphologically and functionally different neurons. The first of them (X in the cat/P in the monkey) provides maximum acuity for detailed vision. The second (Y/M) is chiefly involved in motion detection and processing of high temporal and low spatial frequencies. The function of the third stream (W/K) appears to be involved in heterogeneous functions (Sherman, 2009) and is beyond the scope of this chapter. Most of the retinogeniculate axons of the two latter streams branch to innervate midbrain targets implicated in eye movements, pupillary control, and other functions. Among them the superior colliculus provides a link to the LP-P/pulvinar (Chalupa, 1991; Garey, Dreher, & Robinson, 1991). The function of the dLGN in processing visual information is well documented; however, the role of the LP-P/pulvinar relay is less clear, although many findings suggest an involvement in attention (Baluch & Itti, 2011; Chalupa, 1991; Saalmann & Kastner, 2009; Shipp, 2004) and active vision (Noudoost et al., 2010; Wurtz et al., 2011).

Visual thalamic nuclei project to the primary cortex, albeit in parallel streams, and the LP-P sends additional projections to higher-order visual areas (Berman & Wurtz, 2010; Sherman, 2009; Symonds et al., 1981; Wurtz et al., 2011). Ascending output projections from primary to higher visual areas are less separated than previously thought (Casagrande, 1994), but some cortical areas in the ventral visual stream are predominantly innervated by X/P input and dorsal areas by Y/M input (Nassi & Callaway, 2006; Waleszczyk et al., 2004). Nevertheless, the cortical areas of the ventral stream (like area 21a in the cat and area V4 in the monkey) are functionally specialized for processing of form and pattern information, whereas dorsal stream areas are specialized for analyses of motion and spatial relationships (Casagrande & Xu, 2004; Waleszczyk et al., 2004).

Importantly, the activity of both thalamic relay nuclei can be modulated powerfully by stream-specific corticothalamic feedback from layer 6 (figure 24.1) (Briggs & Usrey, 2009a; Vanduffel, Tootell, & Orban, 2000; Wróbel et al., 2007). The LP-P complex receives additional recurrent projections from layer 5 of many cortical areas (distinct from modulatory corticothalamic feedback) whose ultrastructure suggests a strong synaptic weight (Guillery, 1995; Huppe-Gourgues et al., 2006). Such corticofugal connections, present in various sensory modalities of mammalian brains, inspired Sherman and Guillery (2002) to put forward a hypothesis dividing thalamic relays into first-order and higher-order types and describing the function of thalamic relays by the source and nature of their strongest input (the driver). In this context first-order thalamic nuclei (such as dLGN) would be predicted to transmit peripheral signals to the primary cortex (e.g., V1), and higher-order nuclei (e.g., LP-P) would process ascending traffic between the cortices (figure 24.1; compare Theyel, Llano, & Sherman, 2010). Note that driving fibers projecting to higher-order centers are paralleled with reciprocally directed modulatory feedback pathways at each level of processing (Harris & Thiele, 2011; Sherman & Guillery, 2002). In support of this hypothesis an increasing number of studies have demonstrated that the complex functions of the thalamus, including the first and higher-order type relays, affect the nature of information relayed in a manner that reflects behavioral state, including attention (Sherman, 2009; Sobolewski et al., 2010, 2011b).

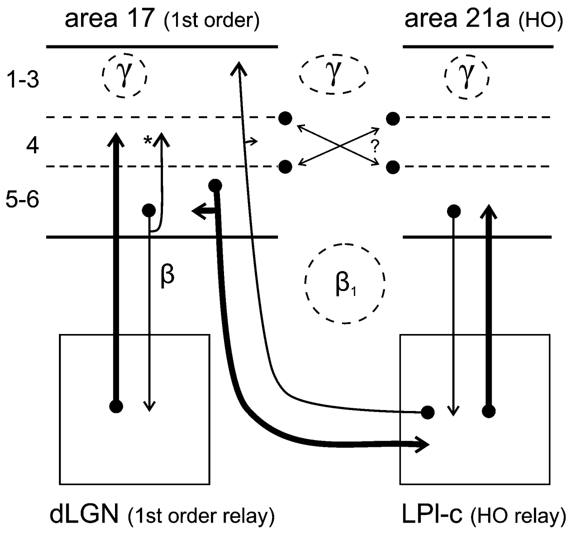

Figure 24.1 Schematic diagram showing connections between first- and higher-order relays in the cat visual system. The dLGN (a first-order thalamic relay, left) represents the relay of retinal information to area 17 (first-order cortical area, homologue to V1). The LPl-c (right), a part of the higher-order relay (LP-P), relays information from layer 5 of area 17 to the higher-order cortical area 21a (homologue to V4). The driver inputs (thick lines) show the postulated route of thalamocortico-thalamocortical communication, which involves afferent input to a primary cortex, a projection from its layer 5 to a higher-order thalamic relay and from there to higher-order cortical areas. All these relay centers receive parallel modulatory feedbacks from higher levels (thin lines). The question mark indicates direct corticocortical projections where the function, drive, or modulation is not known. dLGN, dorsal lateral geniculate nucleus; LPl-c, caudal part of the lateral zone of the LP-P, lateral posterior–pulvinar complex; HO, higher order; β, β1, γ, putative circuits with characteristic resonance frequencies as outlined in the text. The asterisk indicates one of the intracortical modulatory feedbacks; see text for details.

RESONANCE FREQUENCIES IN CORTICOTHALAMIC LOOPS

Alpha and Gamma Bands

The rich network of reentrant corticothalamic loops (figure 24.1) generates oscillations of different frequencies related to its architecture and the properties of the neurons involved (Wróbel, Hedström, & Lindström, 1998; for reviews see Steriade, 2000; Wang, 2010). Indeed, over the years recordings in humans and experimental animals have shown that alpha rhythm (8–12 Hz) is associated with an idle state of sensory networks, and attention reduces the amplitude of this oscillation (Bollimunta et al., 2011; Hanslmayer et al., 2007; Kelly, Gomez-Ramirez, & Foxe, 2009; Sauseng et al., 2005; Snyder & Foxe, 2010; Sobolewski et al., 2011a; Worden, 2000). In contrast, it is well documented that enhanced attention is accompanied by increased amplitude and/or synchrony of gamma rhythms (30–60 Hz) in many visual centers (Doesburg et al., 2008; Fries et al., 2001; Gregoriou et al., 2009; Ray et al., 2008; Taylor et al., 2005. See also topical reviews: Deco & Thiele, 2009; Engel, Fries, & Singer, 2001; Fries, 2009; Harris &

Thiele, 2011). These centers include the primary visual cortex and dLGN, where gamma activity increases in power and becomes synchronized during attention (Briggs & Usrey, 2009a; Bekisz & Wróbel, 1999; Steriade et al., 1991).

Two Beta Frequencies Characterize Distinct Corticothalamocortical Loops

The attentional enhancement related to beta-band (12–30 Hz) activity has remained relatively less studied (reviewed in Engel & Fries, 2010; Saalmann & Kastner, 2011; Wróbel, 2000). Experiments on cats (Bekisz & Wróbel, 1993; Wróbel et al., 1994, 2007; Wróbel, Bekisz, & Waleszczyk, 1994) provided data supporting the hypothesis that beta-band activity plays an important role in both overt and covert attention processes in numerous thalamic (dLGN, LP-P) and cortical (area 17, 18, and various parts of suprasylvian cortex) regions of the visual system (figure 24.2A–E). This hypothesis was based on the finding that beta-band power increased during the anticipatory period of a visual spatial differentiation task only in trials resulting in correct responses (figure 24.2C). Additionally, it was shown that attentional demands increase corticothalamic synchronization of beta oscillations between structures representing consecutive visual processing levels (i.e., dLGN and area 17—Bekisz & Wróbel, 1999, 2003; or area 17, LP-P, and suprasylvian sulcus—Wróbel et al. 2007; shown in figures 24.1 and 24.2F).

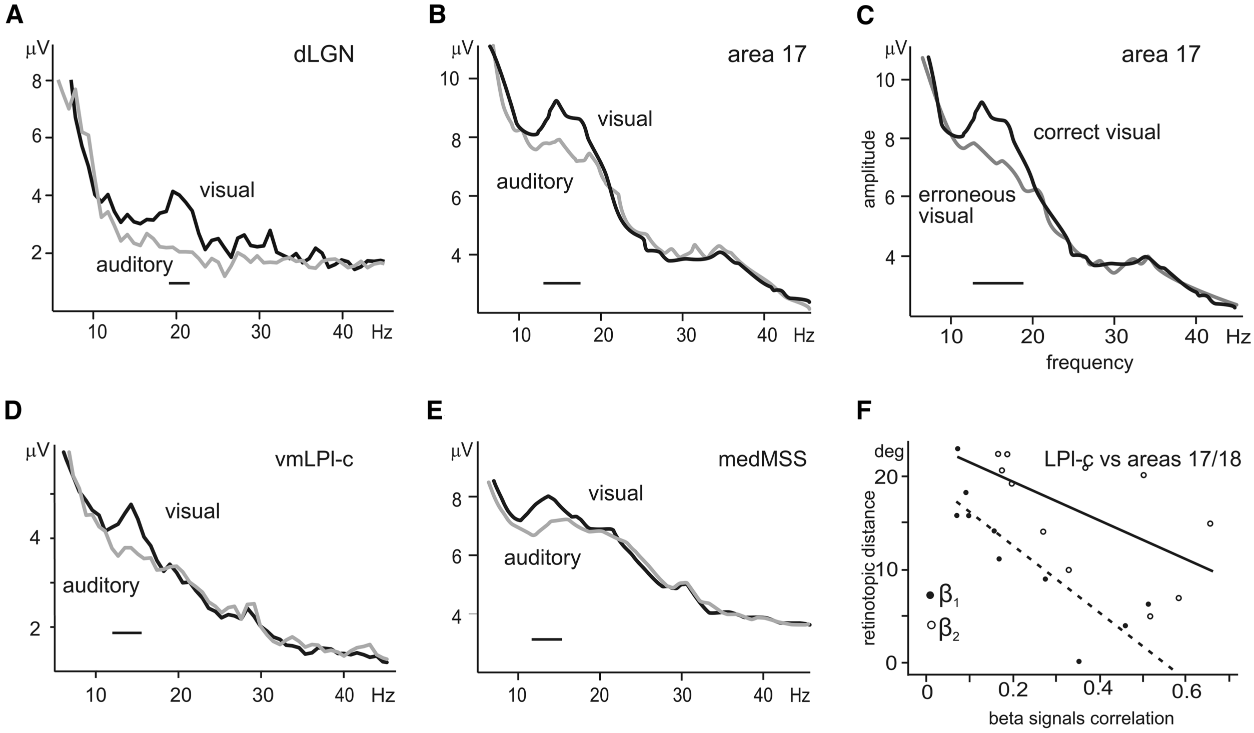

FIGURE 24.2 Beta activity in the visual centers of the cat performing a spatial differentiation task with visual and auditory cues increases during the anticipatory period of the visual trials (adapted from Wróbel et al., 2007). Mean FFT amplitude (example ordinate labeled in C) spectra (in frequency units, abscissa labeled in C) for individual cortical sites in dLGN (A), area 17 (B), vmLPl-c, the ventromedial part of the lateral zone of the LP-P complex (D), medMSS, medial part of middle suprasylvian sulcus (E) of a cat attentively expecting visual (black lines) or auditory (gray lines) target stimuli. The FFTs shown correspond to recordings during the stimulus-free time interval between cessation of either modality cue and onset of the appropriate target stimuli. Averages were taken only from trials that ended with correct behavioral responses. (C) FFT spectra averaged from visual trials ending with a correct response (black line) are compared with those ending with an incorrect conditional response (gray). Short lines above the horizontal axes denote significantly different frequency ranges between the spectra ($p < 0.01$). Note that, in these examples, activity in vmLPl-c, cortical areas 17, and medMSS was enhanced during visual trials in the low beta-frequency range (beta 1), but, at the same time, dlLPl-c, dorsolateral part of the lateral zone of the LP-P complex, and areas 18 and latMSS, lateral part of middle suprasylvian sulcus, recordings exhibited larger amplitudes in higher, beta 2 frequencies (not shown). See text for further details. (F) Beta synchronization depends on the retinotopic distance between cortical and LPl-c recording sites. The signals recorded from correlated pairs were filtered at beta 1 (12–19 Hz) and beta 2 (17–25 Hz) ranges, respectively. Pearson's correlation within the beta 1 pairs, –0.851 ($p = 0.002$); and within beta 2 pairs, –0.603 ($p = 0.05$).

To further define a putative functional role of the higher-order corticothalamocortical pathway in visual processing, Wróbel et al. (2007) analyzed attention-related changes of local field potentials recorded from the LP-P complex and interconnected primary and higher-order cortical visual areas in the cat. Among the latter the suprasylvian region (encompassing the higher-order visual areas) was chosen because of its strong interconnections with the LP-P (Garey, Dreher, & Robinson, 1991; Huppe-Gourgues et al., 2006; Payne & Lomber, 2003) and its involvement in visually guided behavior (Kiefer et al., 1989; Ouellette et al., 2004; Rudolph & Pasternak, 1996). It was observed that solely during visual, but not auditory, anticipatory attentive tasks, the amplitude of beta activity increased in signals recorded from the caudal part of the lateral zone of the LP-P (LPl-c), cortical areas 17 and 18, and the complex located at the middle suprasylvian sulcus (MSS) extending to area 21a (compare figure 24.2, panels B–E). Ventromedial and dorsolateral subregions of LPl-c were distinguished based on the occurrence of attentionally related beta activity of low (12–18 Hz; beta 1) and high (18–25 Hz; beta 2) frequencies, respectively. A selective increase of beta 1 power was observed in the medial bank of the MSS and area 21a, whereas cortical area 18 and the lateral bank of the MSS were activated in the high, beta 2 range. Area 17 exhibited attentional activation in the whole beta range. Phase-correlation analysis revealed that two distinct corticothalamic systems were synchronized by the beta activity of different frequencies. Beta 1 was associated with cortical area 17, ventromedial region of LPl-c, and regions extending to area 21a (and most probably represents the ventral stream), and beta 2 involved area 18 and the dorsolateral LPl-c (regions belonging to the dorsal stream).

These observations suggest that the LPl-c belongs to the wide corticothalamic attentional system, which is functionally segregated by distinct, and each retinotopically specific (figure 24.2F), streams of beta activity (Wróbel et al., 2007). This hypothesis on the functional organization of the cat LP-P is remarkably similar to that proposed by Shipp (2004) for the monkey pulvinar complex based on anatomical connections and retinotopic mapping. Shipp proposed that the primate pulvinar complex, regardless of internal anatomical boundaries, might be divided into two functional parts, which are used by separate corticothalamocortical loops matching reciprocal ventral and dorsal pathways of cortical processing of visual information. Both findings provide functional and anatomical support for the involvement of the pulvinar complex of cats and monkeys in attentional modulation of visual information processing (Olshausen, Anderson, & Van Essen, 1993; Saalmann & Kastner, 2009, 2011; Sherman & Guillery, 2002; Wilke et al., 2010).

Buschman and Miller (2007) recently demonstrated a positive correlation between beta-band power and visual attention in frontal and parietal cortices of the monkey. Importantly, they also found that synchrony between frontal and parietal areas during a paradigm involving top-down (anticipatory) attention was stronger in lower frequencies (beta) and during bottom-up (stimulus-evoked) attention synchrony in higher frequencies (gamma dominated). A spatially selective increase of attentional beta EEG activity during stimulus expectancy period was also found in humans (Basile et al., 2007; Kamiński et al., 2011; Siegel et al., 2008), and a very recent study indicates that the deterioration of attention observed in elderly subjects correlates with changes in beta-band activity (Gola et al., 2011). Similarly, Hanslmayer et al. (2007) demonstrated that brief visual stimuli were perceived by subjects only when preceded by periods of increased phase coupling in both beta and gamma EEG bands. Finally, in a magnetoencephalographic study, Gross et al. (2004) showed that long-range beta-band phase synchronization was a significant indicator of performance in an attentional blink task.

PUTATIVE MECHANISMS OF ATTENTIONAL ENHANCEMENT

The two mechanisms postulated for the neuronal correlates of attention have assumed either biased competition between neuronal ensembles (by increasing the firing rate of neurons encoding the attended stimulus features and decreasing the unattended [Reddy, Kanwisher, & VanRullen, 2009]) or synchronization of their firing by high-frequency oscillations (Fries et al., 2001; Gray et al., 1989; see Harris & Thiele, 2011, for review). Although the two phenomena are independent (Buehlmann & Deco, 2008), they can influence each other. Thus, intrinsic, cellular, and field oscillations during attentive states might self-regulate specific firing generated within the sensory system, as hypothesized by several investigators (for reviews see Schroeder & Lakatos, 2009; Wang, 2010; Ward, 2011; Wróbel, 2000). The long-range, top-down attentional signals may additionally influence the amplitude and phase of synchronous activities in the same frequency range or across different frequencies (Engel, Fries, & Singer, 2001; Kopell et al., 2000; Saalmann, Pigarev, & Vidyasagar, 2007; Siegel, Donner, & Engel, 2012). These descending signals spread to sensory systems from parietal and prefrontal cortical areas (Moore, 2006), and the coherence between them is modulated by attention (Siegel et al., 2008). Note that the flow of activity in these corticocortical circuits may exhibit directionality as shown for beta 2 rhythms between association and primary auditory cortices (Roopun et al., 2010) and between the primary visual cortex and dLGN for the whole beta range (figure 24.1) (Bekisz & Wróbel, 1993; Wróbel, Bekisz, & Waleszczyk, 1994). The reverberatory circuit dynamics in the long- and short-range circuits might also generate location-specific, self-sustained persistent activity (Siegel et al., 2008; Siegel, Donner, & Engel, 2012; Wang, 2010). In general it is widely accepted that enhancement of gamma oscillations often accompanies bottom-up attentional control of stimulus features (Fries et al., 2001; Lima, Singer, & Neuenschwander, 2011; but compare Chalk et al., 2010) and that beta-band activity is involved in top-down attentional signaling (Buschman & Miller, 2007; Gross et al., 2004; see Wang, 2010, for review).

How enhanced synchrony may support selective attention has also been investigated in several modeling studies. A pronounced attention-specific rate enhancement of neuronal activity based on gamma synchronization between sensory and executive cortical areas was reproduced by Ardid, Wang, and Compte (2010). Buia and Tiesinga (2008) postulated that feedforward and recurrent cortical interneurons in area V4 are responsible for setting gamma and beta rhythms according to attentional demands. Grossberg and Versace (2008) investigated a thalamocortical model in which gamma synchronization between various brain regions supported visual attention and learning, whereas a mismatch in synchronization led to inhibition of learning and instead initiated beta oscillations in the deep cortical layers. Similarly, the large multineuronal model of the mammalian thalamocortical sensory system spontaneously exhibited interregional beta oscillation, preferably in basket cells of layer 5, which in turn generated strong local gamma rhythms (Izhikevich & Edelman, 2008). Thus, these modeling results provide additional support for the idea that long-range beta and gamma oscillations might be used in the process of distributing attentional signals in sensory systems, and the local gamma oscillations would be utilized for columnar processing.

Modulation by Feedback Pathways

The idea that descending feedback pathways are involved in attention processing is not new (Adrian, 1953; Hernandez-Peon, 1966). Because of the complicated organization of the interlaminar and corticocortical connections (Douglas & Martin, 2004; Ferster & Lindström, 1983), this was first investigated in corticothalamic pathways of the visual system (Lindström & Wróbel, 1990; Wróbel et al., 2007). It is now widely agreed that the descending projections from layer 6 of the visual cortex play a modulatory role in the transmission of retinal information through the dLGN (Sherman, 2005). One putative function of this feedback loop is optimization of the selective segmentation of visual features (Sillito & Jones, 2003). A second possibility is that the loop provides a gain regulatory mechanism (Lindström & Wróbel, 1990; Livingstone & Hubel, 1981; Saalmann & Kastner, 2009; Waleszczyk, Bekisz, & Wróbel, 2005) that could be utilized during attentive visual processing (Bekisz & Wróbel, 1993; Wróbel, 2000).

It was originally proposed that the corticogeniculate projection from layer 6 might form a positive neuronal amplifier and, together with its perigeniculate (PGN) recurrent inhibitory counterpart, be used in attention control (figure 24.3A) (Ahlsén, Lindström, & Lo, 1985). Using intracellular recording techniques, Lindström and Wróbel (1990) showed that corticogeniculate synapses have a built-in frequency potentiation mechanism that reaches optimal (i.e., approximately three times enhancement of EPSPs and below an epileptic threshold at about 50 Hz) values at the beta frequency (figure 24.3B). Based on this observation it was proposed that beta-frequency activity transmitted in bursts via the corticogeniculate modulatory pathway would depolarize geniculate cells for a hundred to several hundred milliseconds (figure 24.3B) and therefore increase the input–output gain of the geniculate relay (figure 24.3C) (Lindström & Wróbel, 1990; Wróbel, Bekisz, & Waleszczyk, 1994). Accordingly, it was recently found that the amplitude of potentials evoked by chiasm stimulation in the primary visual cortex of attending cats increased in synchrony with beta bursts, suggesting a greater number of neurons involved in the population spike due to the lowered threshold in depolarized dLGN cells (figure 24.3E, F) (A. Wróbel, M. Bekisz, W. Bogdan, A. Ghazaryan, unpublished results). Note that, in parallel, spatially specific inhibitory feedback is reduced as the cortically induced increase of geniculate activity was found to be accompanied by a decrease of firing of PGN recurrent inhibitory interneurons (see figure 7 of Wróbel, 2000; Funke & Eysel, 1998; McAlonan, Cavanaugh, & Wurtz, 2008; Waleszczyk, Bekisz, & Wróbel, 2005).

It is plausible to postulate that a similar gain regulatory mechanism may exist in all processing levels of the visual system, thereby enabling each higher center to enhance the activity of its predecessor. Such a mechanism certainly applies for the feedback collaterals of axons of layer 6 cells, which, despite dLGN targets, also

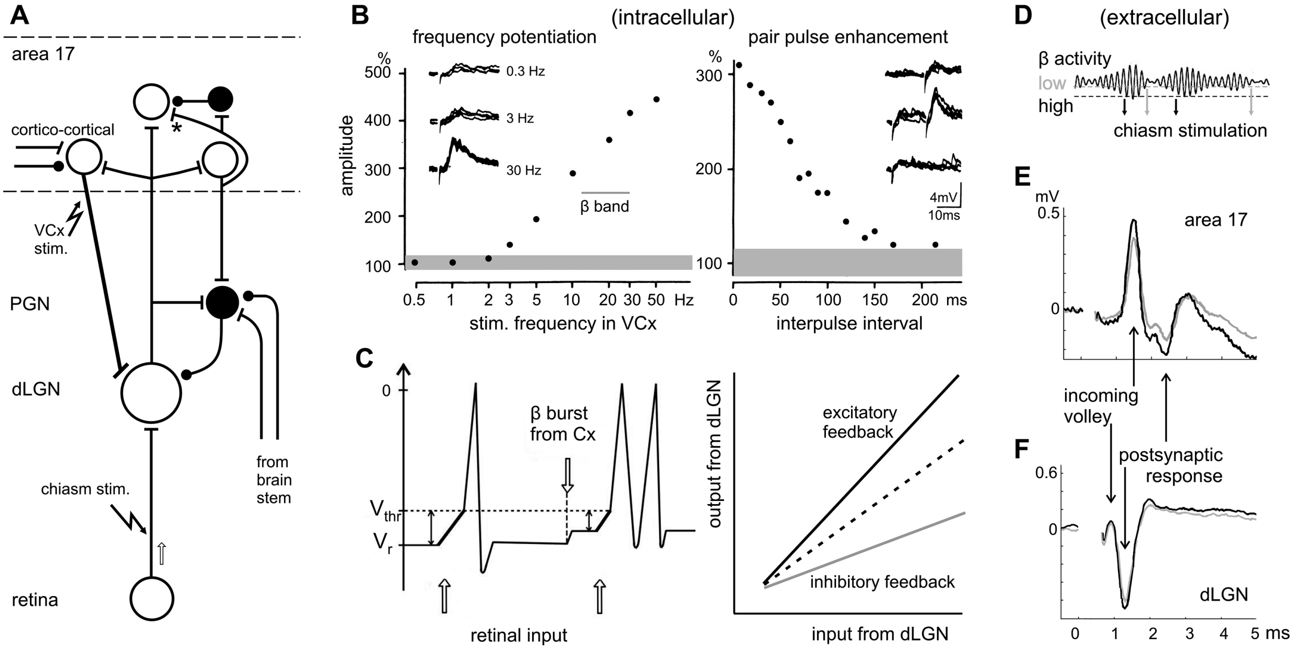

FIGURE 24.3
The mechanism of gain modulation by recurrent projections from layer 6 cortical cells and PGN (perigeniculate) interneurons in the cat dLGN. (A) Principal dLGN cells monosynaptically excite layer 6 corticogeniculate cells and in turn receive from them modulatory feedback projection (Ahlsén, Lindström, & Lo, 1985). They also send excitatory collaterals to cells in layer 4, the main cortical targets of dLGN fibers, and this synapse (*) also has a pronounced frequency sensitivity (Ferster & Lindström, 1985). Thus, layer 6 cells can influence visual input to the cortex by a combined positive feedback–feedforward action onto the main input neurons in layer 4 of the cortex. To maintain stability in such a system it is probably necessary to keep the resting gain low, which is controlled by the other branch of the recurrent pathway projecting to the PGN, which is also under brainstem control (the ascending modulation of principal dLGN cells is not shown). During visual attention, on the other hand, the gain in the dLGN should be increased in order to significantly influence input to the cortex. This is achieved by frequency enhancement at corticothalamic synapses. On the other hand the intracortical inhibitory loop secures similar balanced activity at layer 4 by a divisive gain modulation (Chance, Abbott, & Reyes, 2002). (B) Frequency enhancement and paired pulse enhancement of corticogeniculate EPSPs in a dLGN principal cell recorded in vivo from an anaesthetized animal (from Lindström & Wróbel, 1990). The EPSPs were evoked by cortical stimulation (as shown in A), and the recorded cell was hyperpolarized to the reversal level for the recurrent IPSP. The left plot shows the mean amplitude of maximally enhanced EPSPs at different frequencies expressed as a percentage of the mean amplitude at 1 Hz. The right plot shows the mean amplitude of the second EPSP in a paired pulse test, expressed as a percentage of the unconditioned test response for increasing interpulse interval. The hatched fields represent the mean test levels' SEM. Calibration bars refer to both sets of representative EPSPs. (C) The left plot shows the scheme of enhancement of principal dLGN cell activity in response to the same retinal input after depolarization evoked by beta burst activity at the corticogeniculate synapse. On the right is shown the input–output function for dLGN principal cells with and without the recurrent circuits operating. (D–F) Recordings from a cat during an anticipatory attention test. (D) Each chiasm stimulation (as shown in A) was triggered at a time when beta-filtered local field potential in the visual cortex reached the arbitrarily set low or high thresholds. (E, F) Evoked potentials were recorded after the lowest beta activity during the auditory task (gray lines) or the highest beta activity during the visual task (black lines). Note the increased postsynaptic wave of dLGN potential and increased amplitudes of the population spike and postsynaptic wave in cortical recordings. VCx, primary visual cortex; PGN, perigeniculate nucleus; dLGN, dorsal lateral geniculate nucleus; stim, electrical stimulation; (intracellular) recordings applies for B and C, and (extracellular) for D–F.

innervate input cortical neurons in layer 4 of the visual cortex (figure 24.1) (Ferster & Lindström, 1985). Interestingly, Briggs and Usrey (2009b) found recently that average gamma activity is higher among output cells of layer 6 as compared to the input neurons in layer 4, as measured in alert monkeys. This may be due to the gain regulatory mechanism utilizing prominent beta activity as observed in layer 6 in this experiment. The balanced excitatory and inhibitory barrage from layer 6 (marked by the asterisk in figure 24.3A) may result in a divisive gain modulation of layer 4 neuronal responses (Chance, Abbott, & Reyes, 2002) with a resulting decrease of their population firing rate (Olsen et al., 2012) and spatially specific increase of the stimulus processing stream (figure 24.3C).

Further research is needed to support generalization of the hypothesis that frequency potentiation in the beta frequency range serves as a gain enhancer in all modulatory feedback pathways (delineated by thin lines in figure 24.1) during processes of visual attention.

GENERAL SUMMARY INCLUDING THE ROLE OF CROSS-FREQUENCY COHERENCE IN COGNITION

In recent years the complex relations between different frequency bands and their functional meanings for corticothalamic systems have been intensively investigated. As outlined in this chapter many recent findings have provided a new framework for understanding many neural mechanisms supporting attentional processes and other cognitive functions (Benchenane, Tiesinga, & Battaglia, 2011; Fan et al., 2007; Grossberg & Versace, 2008; Kopell et al., 2010; Siegel et al., 2008; Steriade, 2006; Wilke, Mueller, & Leopold, 2009).

An increasing amount of data converge in favor of the hypothesis that a top-down covert attentional mechanism is supported by beta oscillation and synchronization (Buschman & Miller, 2007; Gross et al., 2004; Saalmann, Pigarev, & Vidyasagar, 2007). Beta-band oscillations are recorded predominantly in infragranular cortical layers, whereas gamma-band oscillations dominate in supragranular layers (Buffalo, Fries, & Desimone, 2004; Buhl, Tamas, & Fisahn, 1998; Maier et al., 2010; Roopun et al., 2006). Anatomical findings match the physiology: upper layers send rich afferent horizontal connections to higher visual areas (Binzegger, Douglas, & Martin, 2004); the latter mediate feedback projections originating in deep layers to the lower areas as well as to subcortical brain structures (Douglas & Martin, 2004). Thus, beta oscillations originating in deep layers may be especially involved in long-distance signaling along feedback, corticothalamocortical pathways (figure 24.1) (Sherman & Guillery, 2002; see also model by Grossberg & Versace, 2008), whereas gamma oscillations would support local and strong monosynaptic interareal cortical coherence (figure 24.1) (for reviews, see Donner & Siegel, 2011; von Stein & Sarnthein, 2000).

The hypothesis proposed in this chapter is based on the assumption that beta-frequency activity causes subthreshold depolarizations within the regions of visual system selected by attentional requirements. These depolarizations are produced by a frequency potentiation mechanism at the synaptic level of the feedback modulatory pathways and result in lower thresholds within the required ensemble of neurons (Lindström & Wróbel, 1990; Wróbel, 2000; Wróbel et al., 2007; compare figures 24.1 and 24.3B, C). This would evoke an activation state (attention) allowing for synchronization of higher-frequency activities in local networks (Briggs & Usrey, 2009b; Buschman & Miller, 2010; Lakatos et al., 2008; Steriade, Amzica, & Contreras, 1996) and could be utilized during putative feature-binding processes (Bibbig, Traub, & Whittington, 2002; Eckhorn et al., 1988; Gray et al., 1989). In favor of this hypothesis recordings from the cat dLGN and visual cortex have shown that attention-related bursts of beta activity tend to correlate in time with gamma bursts (Bekisz & Wróbel, 1999).

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