

Beta-band oscillations — signalling the status quo?

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In this review, we consider the potential functional role of beta-band oscillations, which at present is not yet well understood. We discuss evidence from recent studies on top-down mechanisms involved in cognitive processing, on the motor system and on the pathophysiology of movement disorders that suggest a unifying hypothesis: beta-band activity seems related to the maintenance of the current sensorimotor or cognitive state. We hypothesize that beta oscillations and/or coupling in the beta-band are expressed more strongly if the maintenance of the status quo is intended or predicted, than if a change is expected. Moreover, we suggest that pathological enhancement of beta-band activity is likely to result in an abnormal persistence of the status quo and a deterioration of flexible behavioural and cognitive control.

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Introduction

Evidence has accumulated in the past two decades strongly suggesting that oscillatory signals subserve important functions both in the developing and in the mature brain [1–12]. In general terms, oscillations are important because they provide an effective means to control the timing of neuronal firing. Thereby, they can temporally coordinate the information transfer across brain regions and support spike-timing dependent plasticity [3–6]. Ongoing intrinsic and event-related oscillations are usually categorized into five frequency bands: delta (0.5–3.5 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz) and gamma (>30 Hz). An important but unresolved question is whether these different frequencies subserve distinct physiological roles and whether specific perceptual, sensorimotor or cognitive operations can be assigned to them.

The frequency range that has captured most attention in recent years is probably the gamma-band. The available data demonstrate that changes in amplitude or coherence of gamma-band oscillations relate to a broad range of processes, including feature integration, stimulus selection, attention, multisensory and sensorimotor integration, movement preparation, memory formation and even conscious awareness [1,2,4,6,9–12]. Likewise, oscillatory activity in the other frequency bands has been related to a variety of brain states and functions. Delta is the predominant frequency during deep sleep, and this frequency range is associated with learning, motivational processes and the brain reward system [9,13]. Activity in the theta-band has been linked to working memory functions, emotional arousal and fear conditioning [7,9]. The prominent alpha-band responses, which have been discovered in the human EEG by Hans Berger in the late 1920s, have been suggested to reflect cortical operations during the awake resting-state in the absence of sensory inputs. More recent theories have proposed that alpha-band oscillations may also relate to the disengagement of task-irrelevant brain areas, as well as working memory function and short-term-memory retention [8]. Although classically considered as being related to sensorimotor functions [14], the functional role of beta-band oscillations at present seems to be least understood. It is this frequency range that we will discuss in the following, focussing on recent experimental data that may cast new light on its potential functions. In the remainder of this review, beta-band activity will be denoted as ‘BBA’.

Lack of unifying hypotheses

The findings briefly summarized above indicate that it may be difficult to associate cognitive functions in a unique and direct way with oscillatory activity in a single frequency band and, conversely, that it is unlikely that a given frequency band subserves a single cognitive function in the brain. Major unifying hypotheses regarding the physiological origins and functional relevance of the different frequency ranges are still lacking, although suggestions have been made. A well-established fact is that oscillations of different frequencies reflect global state changes of the brain. Fast rhythms indicate states of enhanced arousal that are apparently distinguished by specific and spatially fine-grained interaction patterns. States of low arousal, such as deep sleep or anaesthesia, in contrast, are characterized by spatially less specific, global synchronization of slow oscillations [13,15]. It has also been proposed that differences in oscillation frequencies might reflect variations in local circuit and cellular properties, giving rise to different frequency tuning properties of the microcircuits [16]. This hypothesis has been

tested in a recent study where TMS-induced oscillations were investigated for a set of brain regions, showing a predominance of alpha-band activity in occipital regions, of BBA in parietal cortex and of gamma-band activity in frontal cortex [16]. An alternative hypothesis predicts that oscillations in different frequency ranges might enable dynamic interactions across neural populations as different spatial scales. On the basis of modelling studies, it has been suggested that slower oscillations (e.g. BBA) may support functional coupling of neurons over much larger distances than fast (e.g. gamma-band) oscillations [17], because the maximal conduction delays that are still compatible with synchrony are directly related to the cycle length of the oscillations.

A number of intriguing hypotheses have also been suggested on how oscillations may interact across different frequencies. It has been proposed that nesting of theta and beta/gamma oscillations may provide a mechanism for sequential encoding of processed items in working memory and for retrieval from long-term memory [7,18]. Direct evidence for such a mechanism has been obtained in a recent study in awake monkeys [19^{••}]. During sleep, slow oscillations seem to support memory consolidation by synchronizing thalamo-cortical spindles and hippocampal sharp wave-ripples, thus promoting a transfer of re-activated information between hippocampus and neocortex [20]. Furthermore, it has been proposed that nesting of fast and slow oscillations may facilitate cross-modal interaction between sensory channels that process information on different time scales [21]. Although all these hypotheses seem highly interesting and partly supported by experimental evidence, we do not yet have a coherent picture on why the brain oscillates at such a diverse range of frequencies and how these different oscillatory processes functionally complement each other.

Beta-band oscillations in motor control

Regarding the beta-band, many classical observations have linked this rhythm to motor functions. Numerous studies have provided evidence that BBA is particularly pronounced during steady contractions, is attenuated by voluntary movements and greatest during holding periods following movements [22–28]. During the preparation and execution of movements, BBA is actually replaced by faster rhythms in the gamma-band (e.g. [29,30^{••}]). Notably, BBA is also inhibited by motor imagery [31], a finding that is widely exploited in the design of brain–computer interfaces [32,33]. This characteristic relation between BBA and steady-state contractions is observed in all parts of the motor system, including motor and premotor cortex, the basal ganglia, the cerebellum and also in the peripheral motor units [22,34]. Owing to its prominent occurrence at rest, it has been proposed early on that BBA may correspond to an ‘idling rhythm’ in the motor system [14].

However, recent work motivates an alternative hypothesis regarding the physiological relevance of BBA. Rather than reflecting a mere lack of movement, BBA may be a signature of an active process that promotes the existing motor set whilst compromising neuronal processing of new movements [35–37,38^{••}]. A number of studies have attempted to directly test this hypothesis in healthy subjects. Gilbertson *et al.* [35] demonstrated that spontaneous enhancements of BBA are associated with impairment in movement performance, showing that voluntary movements triggered during periods of enhanced BBA are slowed. A study by Androulidakis *et al.* [36] provides evidence that corrective responses during a visually controlled postural task are more effective during periods of BBA, suggesting that the effect of beta synchrony in motor cortex may be the maintenance of steady-state force output. Recently, Pogosyan *et al.* [38^{••}] attempted to test the role of BBA by a manipulative approach. They used transcranial alternating-current stimulation to entrain motor cortex to a 20 Hz rhythm whilst subjects performed a visuomotor tracking task. The results show that, whilst reaction times were not affected, the subject’s voluntary movements were decreased in velocity. Supportive evidence also comes from a study by Swann *et al.* [39^{••}] who show that successful stop trial performance in a Go/NoGo-task is related to enhanced BBA in inferior frontal cortex and that the response-related beta-band power decrease in primary motor cortex is less strong for stop trials. Importantly, the frontal BBA effect observed in this study corresponds to a genuine enhancement, which is compatible with the suggestion of an ‘active-akinetic’ process. A weaker beta-band power decrease for NoGo-trials has also been reported by Wheaton *et al.* [40]. An enhanced BBA rebound has been observed following motor errors, which has also been interpreted as a signature of increased response inhibition [41].

Taken together, these data are compatible with the hypothesis that BBA may signal the tendency of the sensorimotor system to maintain the status quo. An interesting suggestion in this context is that BBA may allow the more efficient processing of feedback (e.g. proprioceptive signals) that is required for monitoring the status quo and recalibrating the sensorimotor system [22]. This is also supported by recent analyses of directed interactions (Granger causality) between somatosensory, motor and parietal cortices in monkeys showing that somatosensory cortex is a dominant source of information flow in the beta band [42,43]. In addition, there is evidence that BBA can modulate processing of stimuli in somatosensory cortex [44].

Interestingly, BBA in the motor system does also reflect anticipatory processes. Several studies have shown that BBA can change depending on the expectancy of a forthcoming event. In awake cats engaged in a visuomotor task, enhanced beta-band synchrony occurs in the entire

dorsal pathway when the animals expect the upcoming of a predicted sensory event [45]. In the human brain, lateralized changes in BBA in motor and premotor cortex reflect a decision about an upcoming action already several seconds before it is executed [30^{••}]. If human subjects predict that the likelihood for executing a motor response decreases, beta-band cortico-spinal coherence increases [29]. Cortico-spinal coherence in the beta-band has also been shown to increase when subjects are warned of an imminent postural disturbance that they have to counteract [37]. These studies indicate that BBA may be specifically related to mechanisms that maintain the status quo. This raises the interesting question whether BBA may be related to signalling maintenance of the status quo also during other processes beyond the domain of motor control.

Beta-band oscillations and cognitive processes

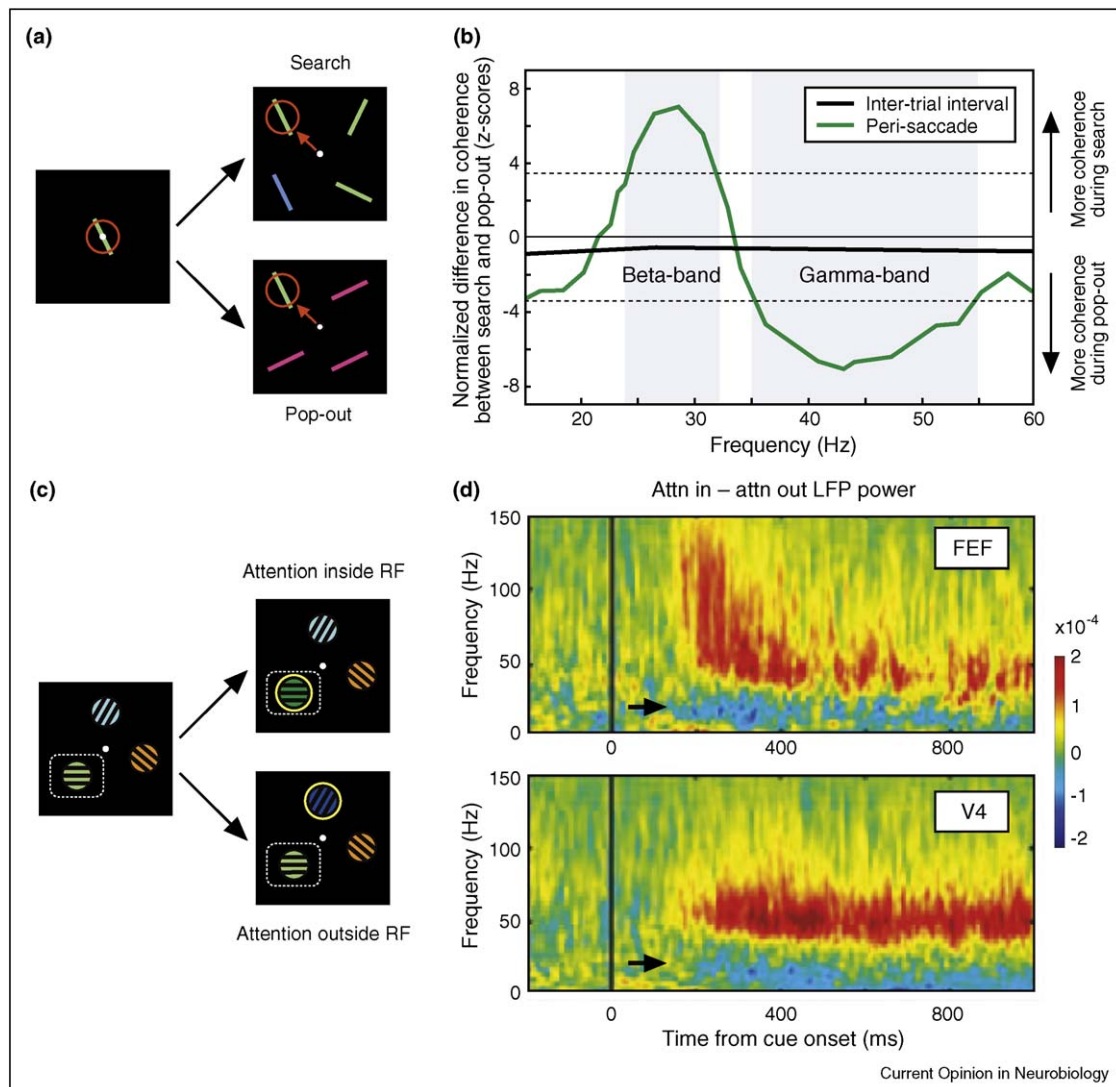
If BBA would have a similar function in non-motor circuits, one would predict an unchanged level of BBA if there is no change in the cognitive or perceptual set, an elevation if the system has to actively maintain the current cognitive set and a decrease if the current setting is disrupted because a novel, or unexpected event occurs. Thus, for instance, tasks involving a strong endogenous, top-down component should be associated with high BBA, whereas one should observe a decrease of BBA in paradigms where the behavioural response of the subject is largely determined by exogenous, bottom-up factors.

Indeed, there seems to be substantial evidence matching this prediction. On the one hand, it has been established in a large number of studies on sensory processing that in task settings which are largely stimulus-driven and have only a weak endogenous, top-down component, the appearance of a new sensory stimulus causes a decrease in BBA and, typically, an increase in the power of gamma-band oscillations (for review, see e.g. [4,12]). On the other hand, a number of recent studies suggest that interactions in the beta-band predominate in tasks that strongly involve endogenous top-down processes. To this end, the most extreme case is probably provided by the processing of ambiguous stimuli where the percept is fully determined by endogenous factors, whereas stimulus features do not deliver any task-relevant information. Interestingly, several recent studies of bistable perception in humans show a specific association of BBA with endogenously triggered perceptual changes [46,47[•]]. Similarly, a recent study in awake monkeys has shown that endogenously driven choices in a search task are accompanied by higher BBA compared to stimulus-instructed decisions [48[•]]. In the same vein, one can predict that mental imagery of sensory events should be associated with enhanced BBA, a hypothesis that has not yet been tested experimentally.

A number of recent studies have observed an association of BBA with attentional top-down processing. In this respect, two recent studies by Buschman and Miller are of particular interest [49^{••},50[•]]. The authors trained monkeys to detect a target amongst a set of distractors in either a pop-out or a serial search regime (Figure 1a). Analysis of coherence between frontal and parietal signals revealed that interactions occurred predominantly in the beta-band during search, that is, in the condition involving a strong endogenous top-down processing component (Figure 1b). In contrast, coupling was more prominent in the gamma-band in the pop-out condition, where performance primarily depended on the saliency of the target stimulus [49^{••}]. What these studies suggest is that endogenously driven top-down attention is associated with large-scale communication in lower frequency bands, whereas coupling occurs at higher frequencies when bottom-up signals need to be conveyed, a suggestion that has also been made earlier based on a study in cats [51]. In line with this conclusion, several studies have also linked BBA to target stimulus processing in the attentional blink paradigm, a setting where the saliency of the target to be detected is intentionally kept low [52–54].

An open question is why other studies on attention have not observed the same BBA effects (e.g. [55,56^{••}]). One important factor seems to be the cortical layer in which recordings are performed. Buffalo and coworkers (EA Buffalo, P Fries, R Desimone, abstract in *Soc Neurosci Abstr* 2004, 717.6) found stimulus-induced gamma in awake monkey areas V1, V2 and V4 exclusively in superficial layers. By contrast, deep layers showed stimulus-induced oscillations not in the gamma-band, but exclusively in an alpha-band to beta-band range (a preliminary report of this is contained in [57]). In addition, it seems possible that different cortical areas exhibit different profiles of spectral modulation during attentional processing. This is suggested by a recent study of attention-related oscillatory activity in humans [58^{••}] where BBA was shown to be decreased in frontal cortex, but increased in early visual cortex and nearly unchanged in parietal cortex. Beyond layer or areal specificity, differences in the attention paradigms employed might play a role. The studies by Fries *et al.* [55] and Gregoriou *et al.* [56^{••}] observed enhanced gamma-band activity and gamma-band coherence, respectively, for neural assemblies processing the attended stimulus (Figure 1c,d). Whilst these studies did not explicitly address changes in the beta-band, the data seem to indicate that BBA and beta-band coherence were stronger for the non-attended stimulus. We speculate that the apparent discrepancy to the studies by Buschman and Miller [49^{••},50[•]] may relate to the fact that in the studies by Fries *et al.* [55] and Gregoriou *et al.* [56^{••}], monkeys always predicted a change for the task-relevant attended stimulus, whereas in the former, the content of the task-relevant prediction was that of a matching, unchanged stimulus.

Figure 1



Relation of BBA to top-down processing. **(a)** and **(b)** BBA is enhanced during visual search in monkeys [49**]. **(a)** The animals were trained to match a target to a sample stimulus (left) in two different task settings. In one setting, the target (highlighted by the red circle) was embedded in an array of distractors that differed in both colour and orientation, thus creating a 'pop-out' condition in which the target's salience automatically drew attention to it. In the other setting, detection of the target was more difficult, because it matched some of the distractors in either orientation or colour. Thus, monkeys had to search the target based on the remembered feature combination. **(b)** Analysis of coherence between local field potentials recorded from parietal and frontal cortex, respectively, during the two task settings. During both 'search' and 'pop-out', an increase in frontoparietal coherence was observed. Interestingly, the coherence increase differed between the two tasks in a frequency-specific manner. Whilst the 'pop-out' was associated with a higher increase of gamma-band coherence, the coupling was stronger in the beta-band for the 'search' condition. The dashed lines indicate significance levels. Panels (a) and (b) modified with permission from [49**]. **(c)** and **(d)** Enhancement of gamma-band activity during visual change detection in the monkey [56**]. **(c)** Animals had to attend one of three grating stimuli and detect a change in the target stimulus (highlighted by the yellow circle). One of the stimuli was placed into the receptive field (dashed outline) of the recorded cells. Since attention was directed to different stimuli on different trials, processing of the stimulus overlaying the receptive fields could be compared with attention and without attention, respectively. **(d)** Time-frequency plots of the attention-related change (i.e. difference 'attention inside' minus 'attention outside' the receptive fields) in local field potential oscillations in the frontal eye field (FEF) and area V4. In both regions, there is an increase in gamma-band activity if the recorded cells are involved in attentional processing of the stimulus change. However, if attention is shifted to a different location and, hence, there is no ensuing change in the stimulus within the receptive fields of the recorded cells, BBA is enhanced (indicated by the arrow in both panels). Panels (c) and (d) modified with permission from [56**].

On the basis of these considerations, we propose that the enhancement or decrease of BBA may relate not only to the involvement of top-down processing, but also to the *contents* of the top-down signal: BBA may be enhanced if

the status quo is given priority over new signals (and potential new signals are deemed distractive), whereas gamma-band activity may predominate if changes in the stimulus are expected. If this hypothesis holds true, then

BBA should also specifically be modulated during delay-periods where the cognitive set has to be maintained following a cue. Indeed, there is evidence for elevation of BBA in the delay phase of working memory tasks where subjects had to detect a matching stimulus [19^{••},59–62]. Similarly, a recent study on visual motion detection showed a specific relation of BBA to the subject's ability to accumulate sensory information during a demanding visual search [63].

Pathophysiological role of beta-band activity

If indeed BBA signals, or promotes, a low likelihood of imminent change in the sensorimotor set, then one would hypothesize that pathological exacerbation of BBA or beta-band coherence should result in abnormally strong inhibition of behavioural and cognitive changes. Strong support for this hypothesis is provided by studies in movement disorders such as Parkinson's disease (PD) [34,64–66]. Clear evidence for a movement-prohibitive role of BBA comes from recordings in human subcortical structures that are carried out during stereotactic operations for the treatment of PD [67]. The therapeutic goal of the surgery is to implant electrodes for chronic deep brain stimulation (DBS) in basal ganglia structures such as the internal segment of the globus pallidus or the subthalamic nucleus, which is typically targeted today in PD patients. The surgical approach opens up the possibility to record neural signals from the target structures and to test the presence of oscillatory activity and its coherence with EEG and EMG signals during motor tasks in the patients.

In a series of studies, Brown and coworkers investigated task-dependent and dopamine-dependent changes of neural coherence between cortex and basal ganglia structures [68–72]. They investigated shifts in the frequency range of coherence when the patient was under different states of medication or in different behavioural states. Measurements without medication showed that, in the akinetic 'Off' state, coherence between the basal ganglia and cortex is dominated by tremor frequencies and frequencies in the beta-band. Interestingly, treatment with the dopamine precursor levodopa reduced BBA and resulted in a new coherence peak at 70 Hz in the gamma-band [68] (Figure 2a). Essentially similar observations on the frequencies of oscillatory activity and their modulation by dopaminergic agonists have been made in a rat model of PD [71]. The functional importance of oscillatory activity has also been investigated by testing the modulation of coherence before and during voluntary movement. In the 'Off' state, beta-band coherence was decreased during movement preparation and execution, whereas in the 'On' state (i.e. after levodopa treatment), gamma-coherence was enhanced in relation to the movement [69]. In the patients, a clear relation between BBA and suppression of movement has been observed. In a Go–NoGo paradigm, a relative increase of BBA has been

found when patients had to suppress a cued movement [70]. A recent study has quantified directed interactions between cortex and basal ganglia as a function of dopaminergic medication and movement in patients. The data suggest a predominance of information flow from cortex to the basal ganglia in the beta-band in the 'Off' state, which gives way to a bidirectional gamma-band coupling pattern in the 'On' state of the patients [72] (Figure 2b).

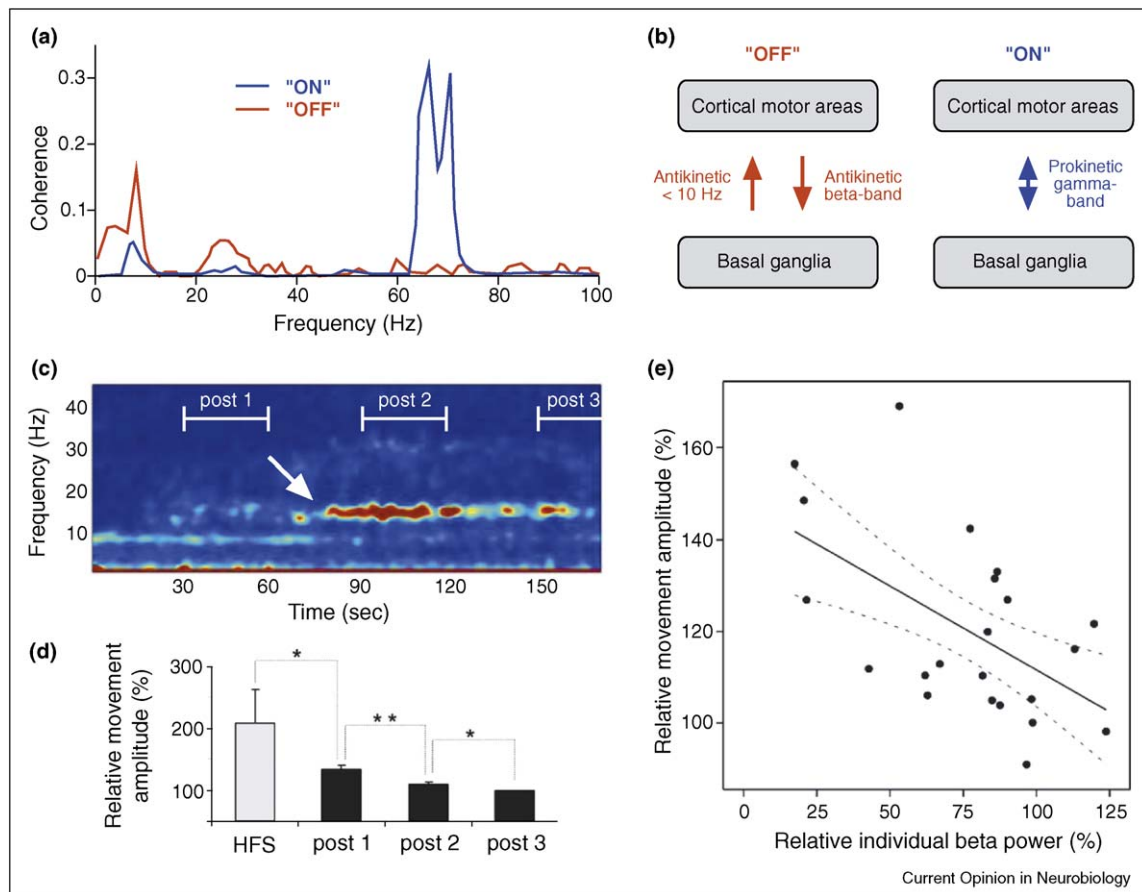
Of key importance are observations on the effect of electrical stimulation through the surgically implanted electrodes. For therapeutic DBS, chronic high-frequency stimulation at pulse rates around 130 Hz is typically applied in the patients. Physiological evidence from studies in monkeys has shown that DBS effectively entrains neurons in the target structure to the electrical stimulation pattern [73]. An early study demonstrated that analysis of BBA can be used to predict the clinical effect of DBS. Electrical stimulation at those sites where beta-band coherence was highest with the EEG and the contralateral EMG turned out to yield the best amelioration of Parkinsonian symptoms [74]. In line with the assumption of a causal relation between BBA and the akinesia or bradykinesia observed in PD, subsequent studies demonstrated that DBS leads to a reduction of BBA and to an improvement of movement capabilities in the patients [75,76^{••},77] (Figure 2c–e). A very interesting aspect of DBS is that also the effects of lower stimulation frequencies can be probed. Systematic exploration of a broad range of frequencies showed that, indeed, bradykinesia is enhanced specifically by beta-band stimulation, whereas it is ameliorated by stimulation at frequencies above 30 Hz [78,79].

Taken together, these studies clearly support the notion that an abnormal enhancement of slow oscillations, resulting from dopamine depletion, disrupts normal motor function. By contrast, gamma-band rhythms seem to be important for the organization of normal voluntary movement, as indicated by the emergence of these fast oscillations in the 'On' state, and by the prokinetic effects of DBS at these frequencies or higher harmonics. As mentioned above, BBA promotes maintenance of the current motor set already in normal subjects. PD patients present the case that pathological enhancement of BBA may, in the extreme, result in a near complete inability to modify their status quo.

Conclusions: a putative functional role

In this review, we have considered the potential role of different frequency bands observed in neural oscillatory activity, with specific focus on the beta-band that currently still seems to be least well understood in terms of its functional significance. Converging evidence from recent studies in the motor system, on the pathophysiology of movement disorders and on top-down mechanisms involved in cognitive and perceptual processing suggests

Figure 2



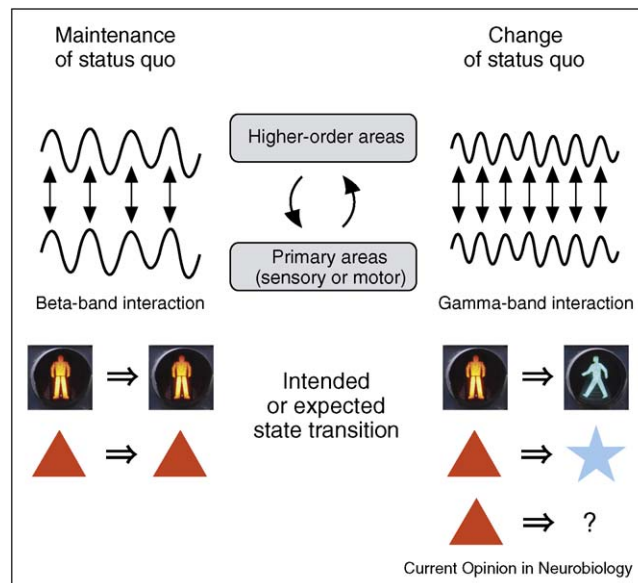
BBA and motor system pathophysiology. **(a)** and **(b)** Oscillatory coupling between cortex and basal ganglia in PD. **(a)** Coherence of oscillatory signals between cortex and basal ganglia in a PD patient off medication ('Off', red trace) and after reinstitution of levodopa ('On', blue trace). In the 'Off', coupling is dominated by tremor-related frequencies below 10 Hz and by BBA. In the 'On' state, strong coupling in the gamma-band appears. **(b)** Schematic summary of the interactions between cortex and basal ganglia observed in PD patients. Panels **(a)** and **(b)** modified with permission from [65]. **(c)** and **(d)** High-frequency stimulation through the DBS electrode influences both BBA and motor performance in PD patients. **(c)** Time-frequency plot of power changes in signals recorded from the subthalamic nucleus after high-frequency stimulation (HFS). HFS was applied between -200 and 0 s. BBA activity (white arrow) was completely suppressed for about 30 s and then slowly returned over the following 30-40 s. The amplitude of hand movements performed by the patient was tested between -30 and 0 s, as well as in three subsequent 30 s intervals labelled 'post 1', 'post 2' and 'post 3'. **(d)** Average movement amplitude (10 patients) in the 4 tested epochs, expressed relative to the movement amplitude in epoch 'post 3'. The amplitude was highest during HFS and showed a significant stepwise decrease over time after the end of HFS. **(e)** Scatter plot showing the anticorrelation of individual pre-movement BBA and movement amplitude. The plot includes data from epochs 'post 1' and 'post 2' which are expressed relative to the data from 'post 3'. Panels **(c-e)** modified with permission from [76**].

a potentially unifying hypothesis regarding the functional role of BBA. In the motor system, BBA apparently relates to maintenance of the current motor set. On the perceptual-cognitive side, BBA seems associated with a continuation of the cognitive set and the dominance of endogenous top-down influences that override the effect of potentially novel, or unexpected, external events. We propose that both aspects are closely linked: what this evidence suggests is that BBA is related to imposing a maintenance of the sensorimotor set during the next processing step or, in a nutshell, to *signalling the status quo*. We hypothesize that BBA and/or coupling in the beta-band are expressed more strongly if the maintenance of the status quo is intended or predicted, than if a change

is expected (Figure 3). As demonstrated by the pathophysiological alteration of oscillatory activity in PD, abnormal enhancement of BBA is likely to result in an abnormal persistence of the status quo and a deterioration of flexible behavioural and cognitive control.

Evidently, many aspects of this hypothesis require further investigation. One of the important unresolved questions is why, in mechanistic terms, BBA promotes maintenance of the current sensorimotor set. Although it seems reasonable to assume that oscillations in different frequency bands may modulate spike timing and neural information transfer at different time scales, it is unclear through which mechanisms slower oscillations would actually

Figure 3



Schematic summary of the hypothesis proposed. We suggest that BBA may have a similar functional role in both sensory and motor circuits. (Left) Maintenance of the status quo seems associated with beta-band interactions in networks involving both early and higher order cortical areas. BBA may signal that the sensorimotor system is primed to keep the current state like, for example in situations where there is still a 'NoGo' sign at the traffic light or where the sensory stimulus is not expected to change (bottom). (Right) In contrast, gamma-band interactions seem to predominate if the sensorimotor system is ready to process novel information, for example when a 'Go' signal is expected, a change in a sensory stimulus, or if an unknown novel stimulus is expected to occur (bottom). In these cases, gamma-band activity may signal the readiness to change the status quo.

block, or slow down, changes of the status quo. Along the same line, it is an open question how abnormal beta-band coherence in PD patients actually arises from the dopamine depletion, and why excessive BBA in the basal ganglia causes bradykinesia. Resolving these issues would also require a better understanding on how oscillatory processes with different carrier frequencies (e.g. beta and gamma) involved in top-down and bottom-up processing might actually interact. At present, it is unclear how such processes involving different frequencies might compete or match and how the results of their interaction might be read by downstream neural assemblies. It would therefore also be interesting to directly test the effects of top-down prediction of change or no change in the cognitive set, respectively, in a single experiment.

A number of implications of our hypothesis might be of potential interest for further experimental testing. As discussed above, the effects of enhancement of BBA through artificial stimulation have already been tested in the motor system. Likewise, the effects of changes of BBA on cognitive processes should be investigated in a manipulative approach. For instance, artificial entrainment of neural circuits with beta-band frequencies should increase the threshold for and slow down the responses to novel unexpected stimuli. Along the same line, it would be interesting to test the relationship between mental, or cognitive, disorders and altered BBA. Our hypothesis predicts that, for instance, psychopathologic conditions

involving strong predominance of endogenous top-down processing such as, for example episodes of compulsive thought (in patients with obsessive-compulsive disorder) should be associated with high BBA. Finally, our hypothesis would predict that resting-state networks [80] should be distinguished by prominent BBA and beta-band coupling, since the default mode of brain function constitutes a state which seems distinguished by low expectation of ensuing change in the sensorimotor set.

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- of outstanding interest

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