Cortical oscillations and sensory predictions

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Many theories of perception are anchored in the central notion that the brain continuously updates an internal model of the world to infer the probable causes of sensory events. In this framework, the brain needs not only to predict the causes of sensory input, but also when they are most likely to happen. In this article, we review the neurophysiological bases of sensory predictions of ''what' (predictive coding) and 'when' (predictive timing), with an emphasis on low-level oscillatory mechanisms. We argue that neural rhythms offer distinct and adapted computational solutions to predicting 'what' is going to happen in the sensory environment and 'when'.

Cortical oscillations and sensory predictive mechanisms

Our sensory environment is full of regularities, for example, repetitive stimuli and contexts, which we use to predict future events. A popular hypothesis is that the brain hosts internalized representations of the world from which it predicts "what" happens in the sensory environment [1]. This theory, referred to as 'predictive coding', assumes that the brain infers the most likely causes of sensory events, which are often not directly accessible to the senses [2]. Predictive coding is classically implemented using the Bayesian framework, which assumes that the causes of inputs are retrieved from probabilistic computations [1,3–6]. The theory and its current implementation imply that predictions are internal representations of 'what' causes sensory events.

In everyday life, as for instance in speech communication [7], not only the nature but also the timing of events is of prime importance [8,9]. Even though the brain likely generates predictions about "what" and 'when' simultaneously, a recent stream of studies suggests that the underlying neurophysiological mechanisms might be distinct. Slow cortical oscillations can tune brain activity to rhythmic events and optimize signal selection, suggesting that 'predictive timing' may involve specific computations on specific timescales [10]. Temporal predictions are partly based on the perception of statistical regularities in physical stimuli at a high level, for example, semantics (e.g., the train passes every day at 5pm). However, for organizing predictive timing at shorter timescales (e.g., a syllable lasts on average 200 ms), the dynamics of cortical oscillations at the low-level of sensory processing represents an interesting complementary means.

Cortical oscillations are involved in many perceptual and cognitive operations [11–13] and are traditionally invoked as a tool that fosters flexible communication between synchronized distant neuronal populations [14]. The view that they could additionally be instrumental in predictive processing has recently received extensive experimental support (for a review, see [15]). In this article, we integrate predictive coding and predictive timing hypotheses into a common framework relying on cortical oscillations, arguing that neural rhythms offer distinct and adapted computational solutions to predicting 'what' and 'when'.

Predicting 'when': oscillation-based predictive timing

Predicting with accuracy 'when' the next event is going to happen implies having internalized the regularity of events [8]. This would be a difficult task if events presented themselves in random temporal sequences. Most meaningful stimuli, however, show strong regularities. Biological signals exhibit quasi-periodic modulations, which makes them very predictable in time. When these stimuli are produced by living entities, they reflect their properties, in particular the fact that neuronal activity is often periodic. Biological signals hence align with slow endogenous cortical activity [16] and their resonance with neocortical delta-theta oscillations represents a plausible way to automate predictive timing at a low processing level [18].

Glossary

Predictive coding: the idea that the brain generates hypotheses about the possible causes of forthcoming sensory events and that these hypotheses are compared with incoming sensory information. The difference between top-down expectation and incoming sensory inputs, that is, prediction error, is propagated forward throughout the cortical hierarchy.
Predictive timing (temporal expectations): an extension of the notion of predictive coding to the exploitation of temporal regularities (such as a beat) or associative contingencies (for instance, temporal relation between two inputs) to infer the occurrence of future sensory events.
Top-down processing: efferent neural operations that convey the internal goals or states of the observer. This notion generally includes different cognitive processes, such as attention and expectations (Box 1).
Neural oscillations: neurophysiological electromagnetic signals [from Local Field Potentials (LFP), electroencephalographic (EEG) and magnetoencephalographic recordings (MEG)] that reflect coherent neuronal population behavior at different spatial scales. These signals have been labeled as a function of their frequency from human surface EEG: delta (2–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12– 30 Hz), and gamma bands (30–100 Hz). The mechanistic properties of oscillations are computationally interesting as a means of explaining various aspects of perception and cognition, for example, long-distance communication across brain regions, unification of various attributes of the same object, segmentation of the sensory input, memory etc.

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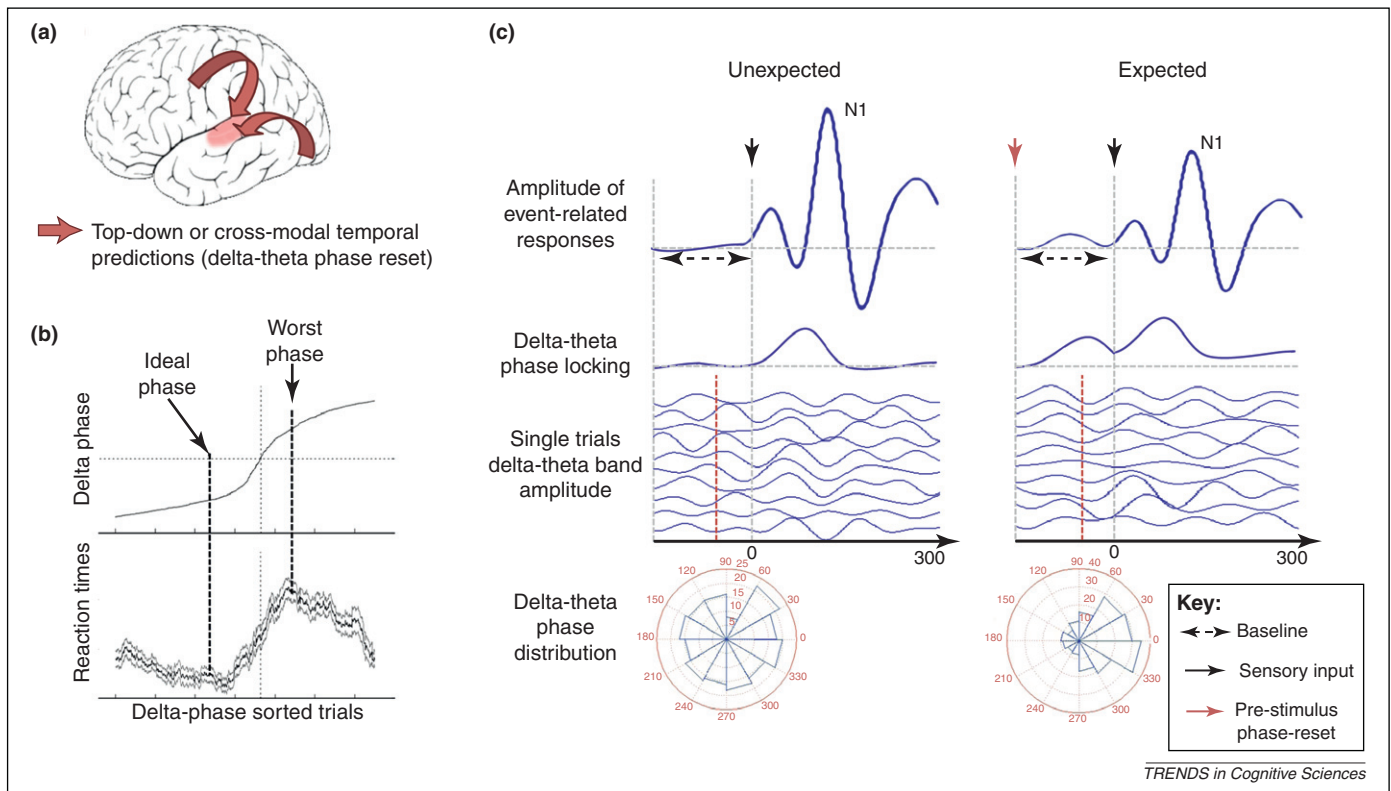
Figure 1. Predictive sensory facilitation using low frequency oscillations. **(a)** Temporal predictive signals modulate auditory processing by resetting the phase of slow ongoing oscillations. Temporal signals can be endogenously generated or triggered by exogenous signals (e.g., cross-modal). **(b)** The phase-alignment of delta-band oscillations modulates sensory processing and related behavioral responses. If appropriately timed, phase-reset aligns stimulus and the ideal phase of delta oscillations, so that reaction times become faster[20,21] panel (b) adapted from [21]. In the absence of such a phase reset or if stimuli occur in a non-ideal phase, behavioral responses are suppressed or slowed down. **(c)** When the timing of a sound is correctly anticipated (right panel), a decrease in evoked auditory responses (N1) is observed [22,23]. This schematic compares the amplitude of an event-related response (N1, averaged across 10 trials) to unexpected (left panel) and expected (right panel) auditory stimuli. Because evoked responses [event-related potentials (ERPs) and event-related fields (ERFs)] are correlated with the phase-locking of (delta-theta) ongoing oscillations [84], their amplitude depends on the pre-stimulus phase distribution across trials. When a stimulus is anticipated (via the generation of cross-modal or rhythmic predictions), delta-theta phase-reset precedes stimulus onset, which gives rise to a response (ERPs, ERFs) to predicted stimuli of lower magnitude (right panel) relative to when phase-locking is only elicited by the stimulus onset (left panel). This mechanism could control the dampening of evoked responses for anticipated stimuli. It suggests that predictive timing could operate by controlling pre-stimulus delta-theta momentary phase.

Predictive timing and delta-theta oscillations

We define predictive timing as the process by which uncertainty about 'when' events are likely to occur is minimized in order to facilitate their processing and detection [8,18,19]. At the neurophysiological level, anticipating sensory events resets the phase of slow, delta-theta (2-8 Hz) activity before the stimulus occurs (Figure 1a). The predictive alignment of delta-theta oscillations in an ideal excitability phase speeds up stimulus detection (Figure 1b) [20,21]. Furthermore, when stimuli are implicitly expected based on their temporal regularity, early sensory responses are reduced (Figure 1c) [22,23]. The magnitude of neural responses, however, depends on whether temporal predictions are tested in the presence or absence of explicit attention to the nature or location of those events (Box 1 and [24–27]). Attention interacts with predictive timing and increases (rather than dampens) neural responses to stimuli that fall into its focus [10,20]. Responses are presumably dampened when predictable features should receive as little processing as possible to liberate resources for more relevant and challenging processing steps (i.e. semantic processing, integration) or on sensory oddities. Predictive timing likely arises from a low-level mechanism of neural entrainment by rhythmic stimulation [28]. For instance, in the presence of a fast speaker, the auditory cortex first adapts by increasing the rate of spikes [29] and oscillations. In a second step, entrained oscillations may become predictive by creating periodic temporal windows that higher-order regions can rely upon to read out the encoded information. Ghitza and collaborators [30] demonstrated that the bottleneck for speech decoding lies in the regularity of the delay left for the higher order readout rather than in the quality of the encoded sensory signal [31]. Predictive timing by oscillatory entrainment presumably suffices to account for the delay with which one adapts to speaker rates, as well as for the accuracy of such adaptation [32]. Such a low-level, stimulus-driven mechanism is not only modulated by attention, but also by the sensorimotor loop (Box 2; see [33], for a review) and other sensory systems.

When physical stimuli reach the brain through several senses, their processing is facilitated by cross-modal mechanisms. Visual and somatosensory inputs, for instance, induce fast responses in the auditory cortex [34,35], which act as temporal priors by resetting low-frequency activity [17,36,37]. This reset, as in the unimodal situation described above, aligns neuronal excitability to expected sound modulations, which fosters the extraction of the most relevant acoustic cues in the auditory stream [17,38,39]. This is typically 'what' happens in noisy environments, when

Box 1. Distinct top-down modulations by attention and expectation

Attention and expectation are generally thought of as a single mechanism that enhances detection and facilitates recognition (for reviews, see [25,27]). However, they operate in a distinct fashion on neuronal populations and modulate responses in opposite directions: attention increases neural responses to attended stimuli, whereas expectations reduce responses to expected stimuli. This dissociation presumably signifies that, although attention prioritizes sensory processing as a function of input relevance for goal-directed behavior, expectations exploit the prior probability of events, that is, they constrain the interpretation of incoming inputs [25,87]. This distinction makes it possible to (i) sort out the data showing that predictions modulate cortical oscillations and ii) unify the findings for predicting 'what' and 'when'.

In the context of predicting 'what' (or 'where'), the distinction between attention and expectation is grounded on experimental neuroimaging [24–26] and behavioral [87] data. Quantitative models describe the relative effects of expectations and attention on neural responses (Figure I). Electrophysiological data demonstrate that attention increases neural excitability (gamma-band activity) [88,89]. On the other hand, if a stimulus is expected, gamma-band activity decreases [75,76], reflecting fulfilled expectations. Because gamma-band activity covaries with metabolic demands [90,91], and in line with Kok *et al.* [26], we propose that there should be a similar interaction of attention and expectations in gamma-band activity when predicting the content of events.

Predicting 'when' is generally thought to rely on temporal attention, which controls time periods of maximal excitability [10]. Accordingly, the magnitude of delta and gamma oscillations increases when rhythmic stimuli are in the focus of attention, which boosts evoked responses and stimulus salience [20,92]. Conversely, temporal expectations are encoded in the phase of pre-stimulus delta oscillations, which align as a function of the temporal probability of a sensory event [21,93]. Prestimulus phase alignment is a possible cause of reduced evoked responses under temporal expectations (Figure 1c). In sum, behavioral relevance (attention) and prior probability (expectation) of a sensory signal might modulate sensory processing in a dissociable way: whereas attention globally gains neural entrainment and reduces internal noise, temporal expectations control the momentary phase of low frequency oscillations, biasing the baseline of signal selective populations [94]. Whether attention and expectation induce reverse effects on oscillatory patterns in predictive timing remains to be tested using dedicated experimental designs that orthogonalize these two factors Figure I.
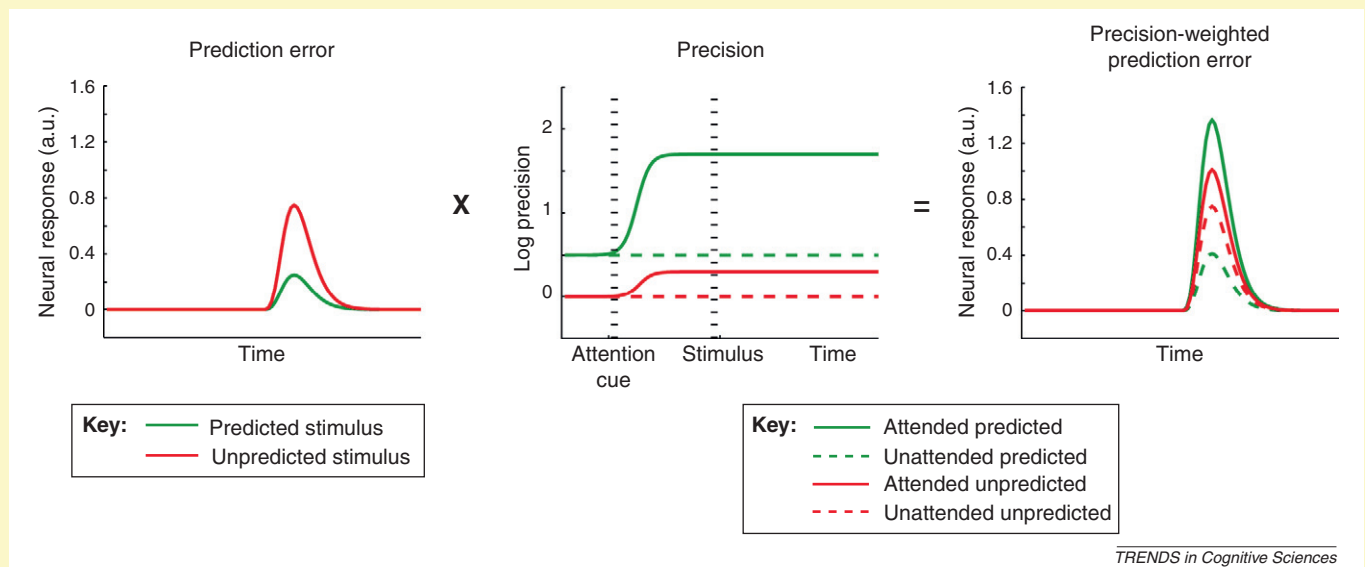
Figure I. Schematic illustration of the interplay between attention and prediction and related amplitude-modulation of neural activity. Whereas prediction errors reflect the extent to which a stimulus differs from the observer's prediction, the magnitude of prediction error-related neural effects is modulated by attention. According to this model, the activity of neuronal populations that compute the difference between top-down predictions and incoming input (error units; see also Figure 3) depends on whether the stimulus is presented in the focus of attention or not. This predicts how neural responses (i.e., prediction errors, as indexed by bold and gamma activity; expressed in arbitrary units, a.u.) are weighted as a function of prediction precision. Adapted from [26].

listeners automatically resort to orofacial movements to understand an interlocutor [40]. In such a situation, the amount of visual information (visual predictiveness) is reflected in delta-theta oscillation phase-locking [41], which likely causes the cross-modal acceleration of early auditory responses [41–44]. Importantly, temporal facilitation by cross-modal input does not appear to rely on the ecological validity (i.e., the congruence of visual and auditory associations [41,42]), but only requires that visual stimuli precede sounds by about 50 to 150 milliseconds [36]. The fact that this predictive mechanism is both rapid and non-supervised argues for its automaticity and non-semantic nature. Accordingly, cross-modal delta-theta phase reset is proposed to be driven either by the non-specific thalamus [10,17] or from a direct, cortico-cortical route from visual to auditory cortices [34,41].

Predictive timing and alpha and beta oscillations
Temporal predictions of event occurrence have been associated with a desynchronization of oscillations in the alpha (8-12 Hz) band at the expected onset of the predicted stimulus [45,46]. Moreover, for temporally unpredictable stimuli, neural and perceptual responses are modulated by the phase of alpha oscillations at which stimulation occurs [47,48]. Oscillations in the alpha band are generally viewed as an active inhibitory mechanism that gates sensory information processing as a function of cognitive relevance [49]. The specific role of delta-theta oscillations in this context is less clear. How alpha- and delta-theta-band oscillations functionally interact during predictive timing of visual events remains to be elucidated.

Beta oscillations might additionally contribute to predictive timing (Box 2). They are traditionally associated

Box 2. Active inference by motor systems in predictive timing

Internal predictive model theories provide a unifying standpoint about perception and action. In these theories, internal models make it possible to infer either (i) forthcoming sensory input or (ii) the sensory consequences of an action. When experimentally tested, both types of inference are associated with reduced evoked responses relative to responses to unexpected sensory inputs [22,95]. In the context of action, response reduction relies on efference copies propagating from motor to sensory cortices [95]. During speech production, such efference copies suppress auditory responses specifically in the high (80-100 Hz) gamma band [96]. Efference copies could also serve to anticipate externally generated sensory inputs [97], as the motor system is recruited during passive listening of rhythmic streams, including speech [16], even when attention is directed away from this stimulus [52]. The motor system appears to actively contribute to predicting the timing of rhythmic events by controlling neural excitability. This notion is consistent with the contingent negative variation, a slow electrophysiological component generated in motor regions during predictive timing [98], and supported by coupled delta and beta activity in sensorimotor systems [53,56] during predictive timing. A causal link between sensory and motor delta/beta activity during predictive timing remains to be addressed using appropriate methods, for instance by applying Granger causality measures to simultaneous motor and sensory recordings during beat perception.

with motor functions [50,51] and their role in sensory predictive timing is denoted by the fact that they can track the expected timing of beats [52,55] (Figure 2). Whereas stimulus-driven beta-desynchronization is transient and does not depend on stimulus rate, the post-inhibitory resynchronization of beta activity (beta rebound) follows the rate of the beat, such that beta activity peaks when the next expected event occurs [52]. Interestingly, the omission of an expected sound induces a larger beta rebound (following an increase of gamma-band response) [54], which possibly reflects the correction of temporal inferences (Figure 2). Note that, in this specific case, prediction errors are related to the violation of both 'what' and 'when' expectations (see next section). Finally, the phase of delta-theta oscillations when anticipating a stimulus is also

coupled with beta-power modulations in sensorimotor systems [53,56]. Beta oscillations could hence cooperate with low-frequency activity in top-down modulation of ongoing activity in sensory regions during predictive timing.

In sum, predictive timing operates by organizing low and mid-frequency oscillations (in the delta-theta and beta ranges) and by dissolving activity in the alpha band. Although delta-theta oscillations are primarily entrained by mere stimulus regularity, higher-order predictive mechanisms actively strengthen this entrainment by coordinating the coupling between delta-theta and beta oscillations [56]. Whether stimulus-driven delta-theta activity is amplified by endogenous beta oscillations that originate in the motor system remains to be directly addressed. At any rate, the fact that they interact during temporal expectations [53,56] supports a functional cooperation between these oscillations in predictive timing.

Predicting 'what': a hypothetical oscillatory framework for predictive coding

How the brain predicts 'what' is going to happen in its sensory environment has been extensively discussed at a theoretical level [25]. According to predictive coding and other popular theories of perception (analysis-by-synthesis, generative models) [1,57–61], the brain uses available information continuously to predict forthcoming events and reduce sensory uncertainty. While doing so, it presumably exploits the errors made when predicting events to update internal representations that serve as templates, or so-called 'models', for predictions. This theory is parsimonious and conveniently accounts for many psychophysical and neurophysiological facts (mismatch negativity, priming effects, repetition suppression) [1]. Yet, it insufficiently specifies how local neural computations are implemented at neurophysiological and biophysical levels. Whereas investigating the timing of neural events is easy to do even from human scalp recordings, exploring concepts such as internal models requires access to fine-grained spatial resolution. Evidence that the major computation at each
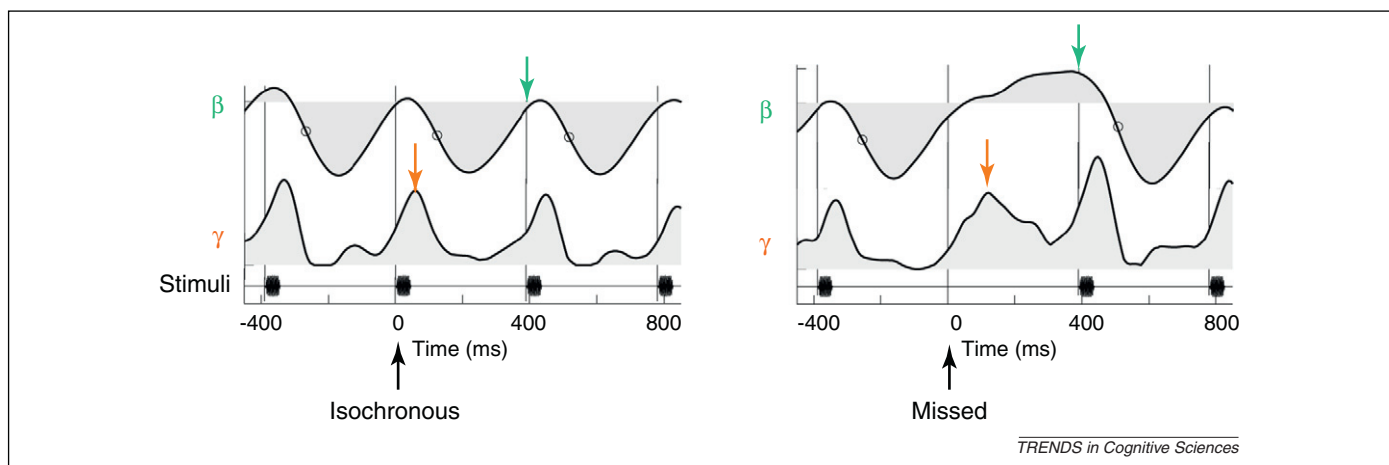

Figure 2. Beta and gamma oscillatory patterns during predictive timing. Event-related changes in gamma- (28-48 Hz) and beta-band (15-20 Hz) auditory activity are measured during the perception of an isochronous sequence of tones without (left panel) or with omission of one sound (right panel). Gamma- and beta-band activities fluctuate in opposite phase (left panel). Whereas gamma power is maximal after the presentation of the sound, beta activity is suppressed and resynchronizes later so that beta power is maximal when the next expected sound occurs. Of note, the alignment of beta resynchronization with sensory events adapts to the rate of the stimulation [52], which indicates their role in anticipating the timing of future events. When a sound is omitted (right panel), gamma-band response is larger and followed by an increased beta rebound. Omission constitutes a violation of expectations that induces prediction error-related responses primarily in the gamma band followed by an increased beta rebound. Adapted from [54].

Box 3. Asymmetric hierarchical message-passing reflected in beta and gamma oscillations

It has recently been proposed that the beta band carries descending information, whereas the main vector of ascending information is the gamma band [12]. The hypothesis of asymmetric hierarchical message-passing reflected in beta and gamma oscillations is roughly consistent with their laminar expression. On the one hand, *in vitro* and *in vivo* recordings show that gamma activity is prominently generated in superficial layers 2/3 of the cortex, whereas beta oscillations are largely found in deep 5/6 layers [65,78,99–101]. On the other hand, feed-forward projections originate in superficial layers and contact layer IV of the next hierarchical stage [85], whereas feed-back connections project from deep layers to the lower stage superficial layers (Figure I). Even though hierarchical cortical connectivity is presumably much more complex than this scheme, a growing amount of evidence supports such a simplification.

These anatomofunctional data have not yet been explicitly connected to predictive coding. Recent findings, however, support the view that prediction errors are propagated forward on a gamma frequency channel from superficial cortical layers to deep layers of the next stage, while predictions are propagated backward on a beta frequency channel from deep cortical layers to superficial layers of the lower stage (Figure 3) [74,99,102]. A model by Roopun *et al.* [101] suggests that beta could be generated by the concatenation of faster activity in superficial and deep layers. As a consequence, feed-forward message-passing could be interrupted and redirected backwards (Figure I). This scheme is hypothetical and should be tested experimentally. It implies that feed-forward and feedback propagation on distinct frequency channels is not simultaneous (multiplexing), but is characterized by alternation of gamma-forward dominant and beta-backward dominant phases.
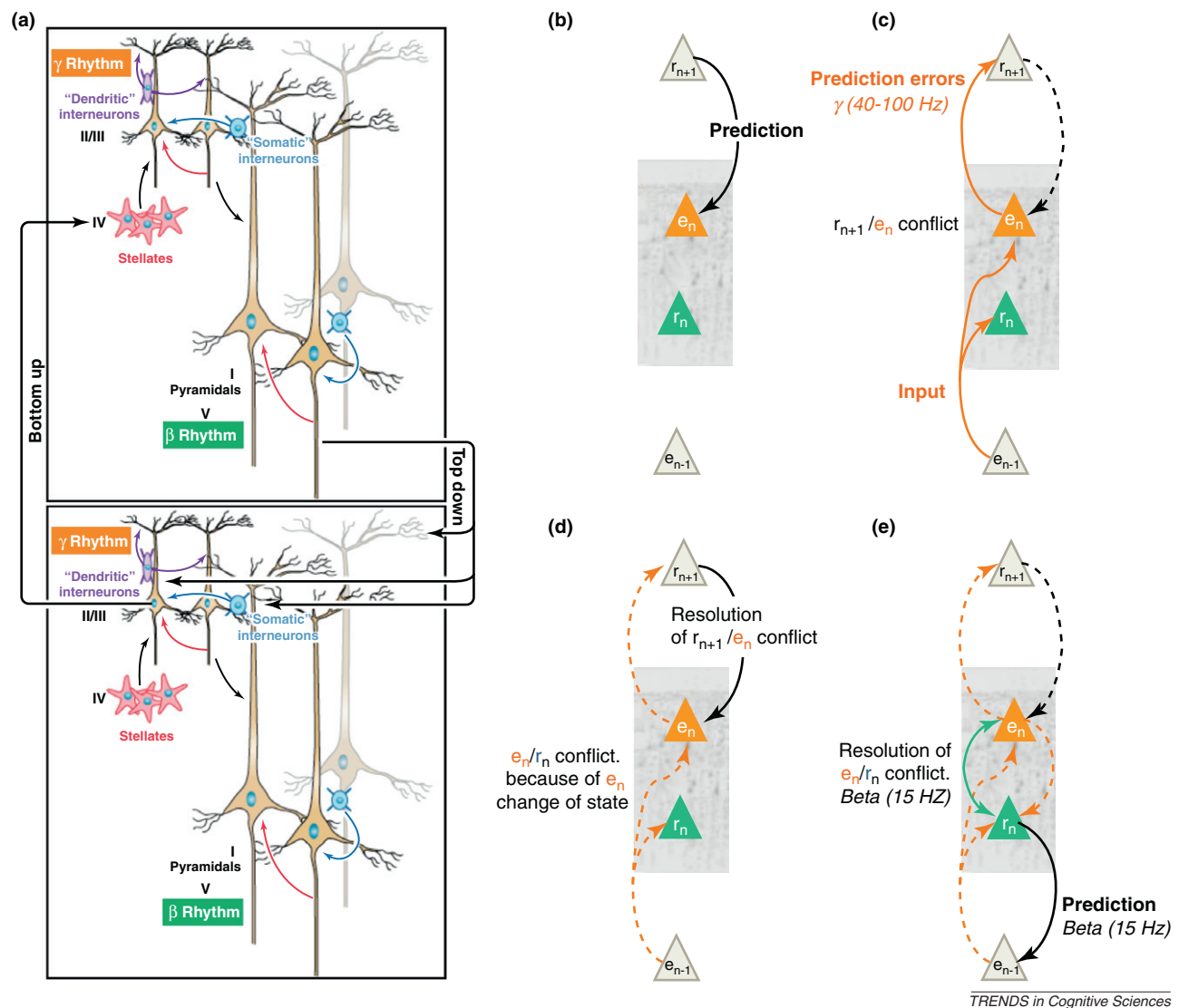
Figure I. A model of sensory information message-passing between hierarchical cortical levels. (a) The left panel reproduces a schematic from Wang [12] depicting a reciprocally connected loop between two hierarchical levels. Neuronal populations situated in superficial layers generate synchronous oscillations in the gamma range that propagate information to deep-layer neuronal populations of the level above, which in turn generate oscillations in the beta range. Gamma oscillations are involved in forward propagation of sensory information, whereas beta oscillations are involved in top-down signaling and presumably control lower-level gamma activity. The right panel extends the Wang's model to predictive coding. The model assumes two functional categories of neuronal units: Error units (e) and Representational units (r), respectively sitting in superficial and deep layers of the cortex [1,85,86]. According to predictive coding and recent *in vitro* and *in vivo* data, prediction error is propagated forward from e_n to r_{n+1} units using a gamma-frequency channel, whereas top-down predictions are conveyed backward from r_n to e_{n-1} units through a beta-frequency channel. (b) Priors conveyed by the higher level constrain the possible state of e_n units. (c) In the case of an invalid prediction with regard to the incoming input, prediction error is computed in e_n units and propagated to the level above using a gamma frequency channel. The generation of gamma activity is associated with competitive spiking between neural assemblies [78]. (d) The generation of new predictions from r_{n+1} units reduces prediction error in e_n units that change their state accordingly, which induces a new conflict with r_n units. (e) The transition to a beta regime (see text) results in the formation of another stable neuronal assembly [78,100,101], which generates new predictions in r_n units that are propagated to lower sensory levels on a beta channel.

processing stage consists in comparing descending and ascending signals in such a way that residual error is propagated forward is currently scarce. The understanding of computations at a very local level hence remains a challenging endeavor [62]. Recent work, however, suggests that cortical oscillations could be used in directional message-passing [12,63–65]. This view offers a novel putative neurophysiological substrate of the operations required by predictive coding (Box 3).

Predictive coding and gamma oscillations

Gamma-band oscillations (>30 Hz) do not underpin a unitary function. They accompany a wide variety of cognitive processes, such as feature integration, stimulus selection, attention, multisensory, and sensorimotor integration [11,15,66,67]. They admittedly signal local cortical processes, in particular the encoding of stimulus properties in sensory cortices [68]. Herrmann and colleagues proposed that gamma activity is implicated in the assessment of sensory predictions and suggested that gamma-band activity depends on the match between expectations and bottom-up input [69]. Other experimental paradigms incidentally support the implication of gamma oscillations in the evaluation of predictions. Mismatch negativity (MMN) and other violations of expectations are generally associated with an increase of gamma-band activity and changes of gamma topography [70–73]. Gamma activity also scales with prediction errors stemming from the

violation of cross-modal expectations [74]. Paradigms that manipulate sensory expectations demonstrate that this effect is reversed when predictions are fulfilled, that is, the amplitude of evoked gamma-band activity is reduced when a repetition (or an omission) of the stimulus is correctly anticipated (Figure 3a and b) [75,76]. On the other hand, unexpected omissions of predicted events constitute an interesting experimental tool to examine situations where expectations do not coincide with bottom-up input and hence cannot be fulfilled (Figure 3d) [77]. In such situations, omissions induce an increase in gamma-band activity (Figure 2) [54,55]. Altogether, experimental data concur to suggest that gamma activity is modulated as a function of sensory surprise and, among its other possible functions, is used to signal unexpected information, that is, prediction error.

Predictive coding and beta oscillations

Interestingly, error-related effects also reveal modulations in the beta band, yet gamma and beta oscillations behave differently during external stimulation: gamma activity increases, whereas beta oscillations are first suppressed (or desynchronized) and then resynchronized (beta rebound, see Figure 2) [50]. When explicit expectations are violated, the beta rebound is determined by the magnitude of earlier gamma enhancement [70]. As mentioned above, the omission of a sound in an isochronous sequence also induces an increase in gamma-band activity followed by a
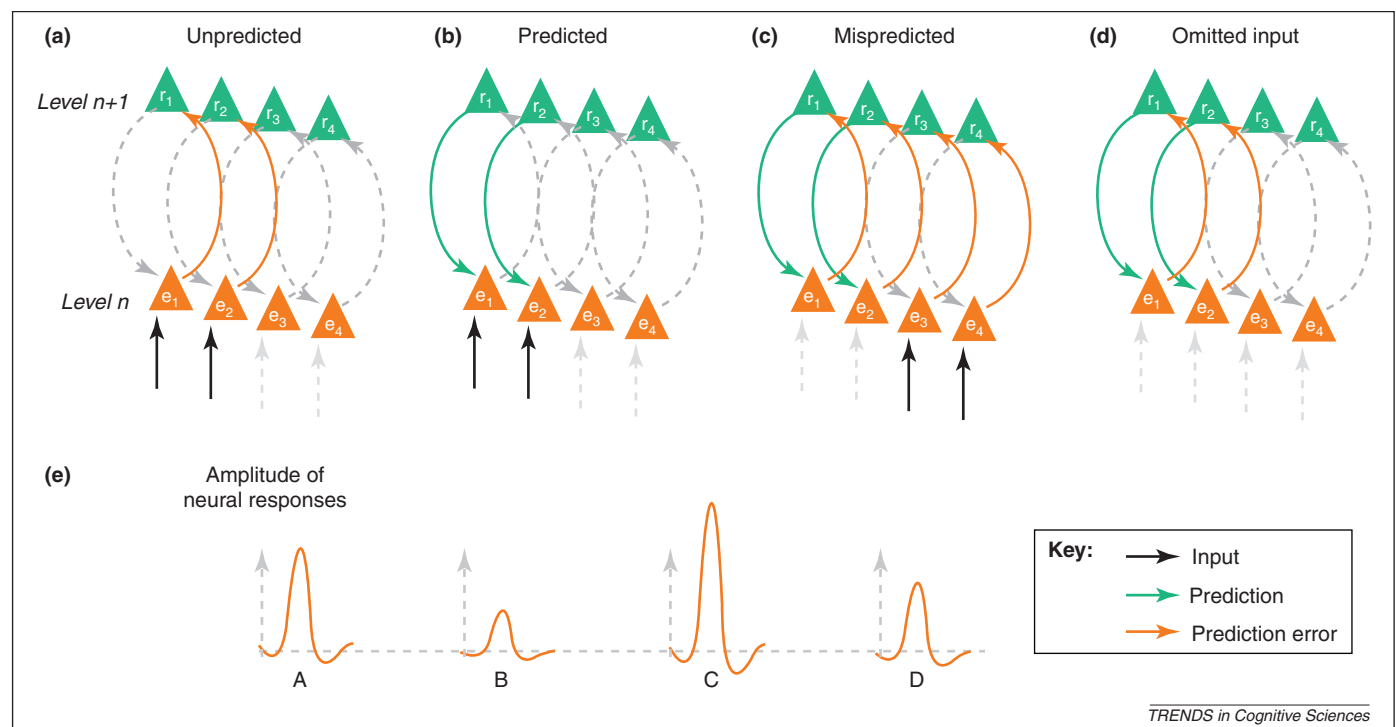
Figure 3. Predictive coding architecture and quantitative predictions about neurophysiological evoked responses. Predictive coding suggests that feed-forward information, that is, prediction error (orange arrows), reflects the difference between top-down prediction (green arrows) and forward input (black arrows). This schematic illustrates the message-passing of forward information between two hierarchical levels (level *n* and level *n+1*). Distinct neuronal populations (each constituted of 4 neuronal units) are represented: representation units (r) situated in deep layers of the *level n+1* encode expectations about possible inputs, whereas error units (e) are situated in superficial layers of the level *n* and receive sensory input from lower levels [1,85,86]. The information that propagates forward from each e unit reflects the difference between prediction and input. The amplitude of neural response represented in the lower part reflects the sum of these units' residual errors. **(a)** Response to an unpredicted stimulus: the amount of received and propagated information is unchanged. **(b)** Response to correctly anticipated stimulus: the prediction is consistent with incoming information and the prediction error is minimized. **(c)** Response to incorrectly predicted stimulus: the prediction error reflects the activity of preactivated units that do not receive any input (e units 1 and 2) and non-preactivated units that receive an input (e units 3 and 4). **(d)** Endogenous response to an unexpected omission: prediction error is generated by pre-activated units (e units 1 and 2) that do not receive any input. **(e)** Quantitative predictions about the amplitude of evoked responses as a function of residual error.

larger beta rebound (Figure 2) [54,55]. On the whole, these observations imply that beta activity signals processing steps downstream from prediction error generation.

Whereas predicting 'when' predominantly involves low-frequency oscillations, predicting 'what' points to a combined role of gamma and beta oscillations. Computational studies suggest that beta and gamma rhythms could reflect distinct aspects of neuronal population synchronization during sensory processing. Although ongoing input usually prompts the formation of neuronal assemblies at gamma rhythms, the emergence of a beta rhythm changes these assemblies into new patterns via a rebound from inhibition [78]. In addition, beta and gamma oscillations could underlie the flow of information in opposite directions, that is, forward vs. backward (Box 3; see [12], for a review). Along the lines of predictive coding, this suggests that prediction errors could be propagated in a feed-forward manner, mainly using the gamma frequency channel, whereas predictions (and their revisions) could be transmitted 'backward' using mainly the beta channel [12,65,79].

That beta activity increases before the occurrence of an expected event [52] potentially reflects the mobilization of neuronal populations under predictive signals [80]. To what extent such top-down signals are content-specific remains unclear. Yet, a strong argument for the 'what' nature of such predictive mechanisms is that post-stimulus beta rebound increases in sensory regions when the content of predictions is violated [74]. Beta oscillations may hence be exploited to predictively synchronize relevant neuronal populations that encode expected sensory inputs. If the input is correctly anticipated, evoked gamma activity could be limited to the population 'pre-synchronized' by beta oscillations (Figure 3b). Conversely, if the neuronal population recruited by sensory stimulation differs from the pre-activated one, the number of units recruited would have to extend to the not pre-activated ones (Figure 3b), resulting in a larger neural response due to an increase in the overall gamma activity proportional to prediction error (e.g., a spatial mismatch).

Combining predictive timing and coding in the oscillatory framework: the example of speech processing

In this article, we have presented two means the brain may use to predict its sensory environment. Predictive timing uses the temporal regularities of sensory input to minimize the sensory processing of events that do not require extensive processing, which frees cognitive resources for higher-order cognitive processes. The most compelling example is probably that of speech comprehension. Continuous speech perception results from cortical sequencing into segments or units that most likely do not receive full processing, but only sufficient processing of their most salient parts [7]. Severely time-compressed speech can remain intelligible, provided enough processing time follows each speech unit [30]. Processing focused on the salient parts of speech (onset of syllables) likely relies on predictive timing and a plausible role of oscillations in this mechanism is not only to align neuronal excitability with important speech cues, but also to suppress the less important parts in order to free processing time [10]. Because predictive timing is

largely based on stimulus-induced regularities, it is (in part at least) a non-supervised computational process that minimally depends on the validity of predictions. When an expected event falls out the expected temporal window, it receives reduced processing [20]. If, conversely, an unexpected event (oddball) falls within the expected window (as, for instance, in MMN paradigms), then the 'predicting what' scheme applies, whereby the response reflects the mismatch between expectation and input. Whereas slow delta-theta oscillations are mostly involved in setting temporal windows of sensory integration due to predictive mechanical entrainment, beta oscillations are involved in both the rhythmic modulation of sensory sampling [52,54,55] and in top-down transmission of content specific predictions [50].

In summary, implicit temporal predictions could periodically modulate the overall activity of sensory cortices with a relatively weak functional specificity to facilitate sensory processing, regardless of the informational content of forthcoming information. Furthermore, when targeting specific neuronal populations, top-down signals could provide content-related priors. These two mechanisms are complementary at the computational level. Whereas predictive timing temporally aligns neuronal excitability by controlling the momentary phase of low-frequency oscillations relative to incoming stimuli, predictive coding targets neuronal populations specific to the representational content of forthcoming stimuli. The combination of these two types of mechanisms is again ideally illustrated by speech processing. Speech comprehension has long been argued to rely on cohort models where each heard word preactivates a pool of other words with the same onset, until it reaches a point where the word is uniquely identified [81,82]. This model assumes that cognitive resources are used at the lexical level, where predictions are formed. Gagnepain and collaborators [83] recently demonstrated, however, that the predictive mechanisms in word comprehension involve segmental rather than lexical predictions, meaning that each segment is likely used to predict the next. Computationally, this observation supports the view that auditory cortex (i) samples speech into segments using mechanisms that make them predictable in time and (ii) that a representation of these segments is used to test specific predictions in a recurrent, predictable fashion.

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