Trends in
Neurosciences

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Opinion

Decoding the rhythmic representation and communication of visual contents

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Rhythmic neural activity is considered essential for adaptively modulating responses in the visual system. In this opinion article we posit that visual brain rhythms also serve a key function in the representation and communication of visual contents. Collating a set of recent studies that used multivariate decoding methods on rhythmic brain signals, we highlight such rhythmic content representations in visual perception, imagery, and prediction. We argue that characterizing representations across frequency bands allows researchers to elegantly disentangle content transfer in feedforward and feedback directions. We further propose that alpha dynamics are central to content-specific feedback propagation in the visual system. We conclude that considering rhythmic content codes is pivotal for understanding information coding in vision and beyond.

Highlights

Rhythmic activity is considered critical for modulating responses in the visual system.

Herein we propose that neural rhythms serve another fundamental function: the representation and communication of visual contents.

We discuss a set of recent multivariate decoding studies on visual perception, imagery, and prediction that demonstrate such rhythmic content representations. These studies highlight how rhythmic content representations untangle feedforward and feedback information flows in the visual system, with alpha rhythms emerging as carriers of stimulus-specific feedback information.

We outline how the study of rhythmic content representations may yield important insights into how visual contents are represented, transformed, and communicated in the human brain.

A content-specific look at visual brain rhythms

Neural activity in the cortex varies in rhythmic ways. Rhythmic brain dynamics are observed across different characteristic timescales, and they are present across brain regions and species [1]. However, their role in neural coding is debated. Current accounts range from brain rhythms forming the very fundamentals of cortical communication to being somewhat epiphenomenal [2]. To better gauge the importance of brain rhythms for cortical processing, there is a need to assess how information is encoded in neural rhythms, and how this rhythmic coding supports the efficient representation and communication of information in the brain.

In this opinion article we posit that recent advances in decoding techniques invite a reassessment of the role of neural rhythms in cortical processing dynamics. We argue that reading out the contents encoded in neural rhythms enables researchers to investigate how content-specific information is encoded, transformed, and communicated, opening a new window into the inner workings of the brain. Our focus will be primarily on the human visual system, as a case in point for outlining the notions at hand. We collate a set of studies using multivariate pattern analyses, which demonstrate that visual stimulus attributes are encoded in rhythmic neural response patterns. Synthesizing studies from perception, imagery, and prediction, we show that the direction of signal propagation in the visual cortex is related to differential representations of visual contents across neural rhythms: feedforward propagation is related to representations in transient broadband responses and high-frequency gamma rhythms, while feedback propagation is related to representations in low-frequency rhythms, and most prominently the alpha rhythm. We further show that studying the contents of brain rhythms can illuminate neural representations that might elude investigation when only considering broadband signals.

The role of rhythmic activity in the visual system

One of the major tenets in the study of brain rhythms is that they shine a light on the dynamic exchange of information across neural populations, thereby yielding unique insights into neural communication.

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This rhythmic information transfer is also considered critical for the neural analysis of visual inputs. In the visual system, processing has classically been conceptualized as a hierarchical reconstruction of external stimuli. In this view, information is analyzed in increasingly complex ways along a hierarchically convergent feedforward cascade [3]. This classical view aligns, for instance, with neuroimaging studies that show a hierarchical emergence of face, object, or scene representations across space and time [4,5]. Beyond the prominent feedforward response, however, there is abundant top-down connectivity in the visual system, from local recurrence to interregional feedback [6–8].

Neural oscillations are thought to have an important function in mediating this dynamic exchange of visual information. For instance, cortical rhythms are associated with the coordination of attentional allocation [9–12] and the binding of complementary features into coherent objects [13–15] (although the latter is debated [16]). Further, the state of prestimulus oscillations determines the efficiency and the perceptual outcome of subsequent stimulus processing [17–20]. Perception itself is also rhythmic: the efficiency of visual processing varies periodically across time [21–25]. Together, these studies suggest that visual rhythms serve a critical role in orchestrating information coding.

This critical role of rhythmic activity in visual processing prompts the question of whether visual rhythms are also important for coding stimulus information. In the following, we show that visual rhythms represent information about the contents of vision, from basic visual shapes to real-world objects and complex scenes.

Content representations in visual rhythms

The advent of multivariate analysis methods has transformed visual neuroscience by allowing researchers to read out the contents of neural codes and thereby delineate how stimuli are organized across representational spaces in the brain [26,27]. The application of such multivariate techniques to time-resolved neural data – from electroencephalography (EEG), magnetoencephalography (MEG), electrocorticography (ECoG), or single-cell recordings – has enabled researchers to examine how visual contents are encoded in visual brain dynamics with high temporal precision. Methods such as neural decoding [28,29] and representational similarity analysis (RSA) [30] have led to critical advances in our understanding of how visual content representations emerge and change through time [4,5,31], and how they are altered under different viewing conditions and task demands [32,33]. While these methods were by and large used to study time-varying representations in evoked broadband responses, they can also be applied to rhythmic neural signals to understand whether information about the visual world is represented in rhythmic codes (Figure 1).

Studies using multivariate pattern analyses have demonstrated that stimulus information can be read out from rhythmic neural signals. Both attributes of basic visual stimuli like gratings [34] or letters [35] and complex stimuli like objects, faces, and scenes [36–41] can be decoded from rhythmic responses in different frequency bands, including high frequencies in the gamma range (30–100 Hz) and lower frequencies in the theta (4–7 Hz), alpha (8–13 Hz) and beta (14–29 Hz) ranges. Whereas broadband gamma is classically thought to carry visual feature information [14,42,43], these studies suggest that visual representations are encoded in a broad range of brain rhythms. Particularly high-level representations of more naturalistic stimuli seem to rely strongly on low-frequency rhythms [37,38,41], with stimulus information sometimes expressed in the power of an oscillation, and sometimes in its phase, likely reflecting different component processes [41,44]. Representations in the power and phase of different rhythms may not operate independently from one another. For instance, the phase of theta rhythms is coupled to the power of gamma rhythms [45–47]. It has also been shown that the phase of low-frequency oscillations is coupled with neural spiking activity [48,49]. Such dependencies

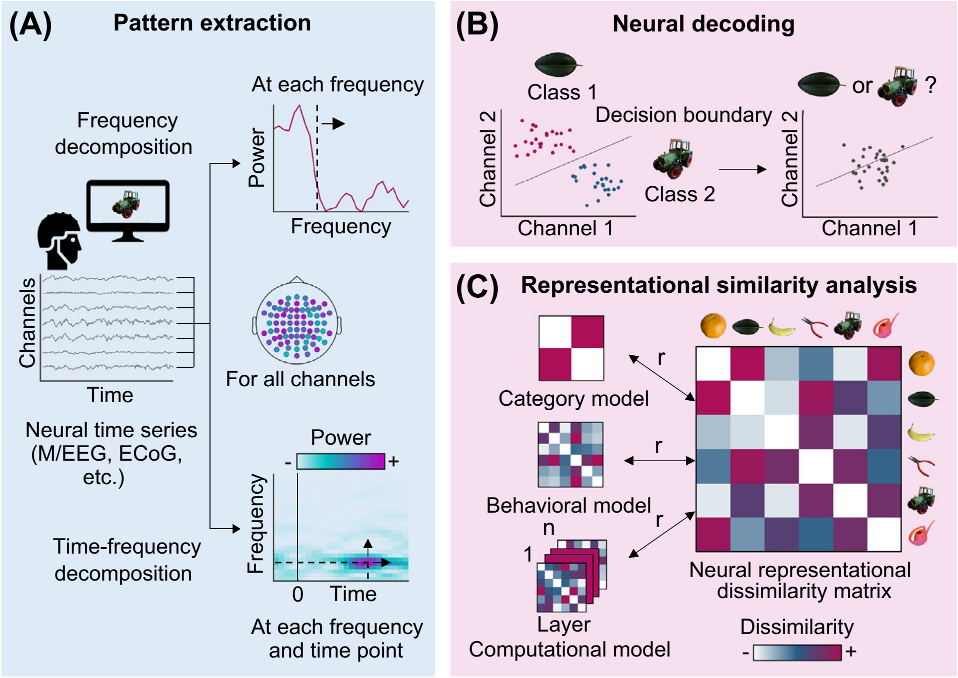

Figure 1. Unveiling content coding in neural rhythms with multivariate analyses. (A) Time-varying responses to a set of visual stimuli – from electroencephalography (EEG), magnetoencephalography (MEG), or intracranial recordings – are decomposed into a set of frequencies of interest, either for an entire time period of interest (upper path, resulting in spectral response patterns) or across time (lower path, resulting in time–frequency response patterns). (B) In neural decoding analyses, classifiers are trained on frequency-resolved patterns across channels to predict the presented stimulus. The resulting classification accuracy serves as a measure of content separability in a given neural frequency. (C) In representational similarity analysis (RSA), the representational organization across a set of stimuli is characterized by calculating the pairwise distances between frequency-resolved response patterns, yielding representational dissimilarity matrices (RDMs). These RDMs can then be related (e.g., via correlation) to model RDMs such as categorical RDMs, behavioral rating RDMs, or computational model RDMs. The resulting correlations between neural and model RDMs show how well the representational organization emerging in a given neural frequency relates to the model of interest. Stimulus photos by the authors, for illustrative purposes.

among neural rhythms may influence how visual content representations emerge across these rhythms. Moreover, rather than being static, rhythmic responses may dynamically change across the lifespan and in brain disorders (Box 1).

Together, this multifaceted picture raises the fundamental question of whether representations emerging in different frequency bands serve dissociable functions. In the following, we take a closer look at how brain rhythms differ in the visual information they represent, and which function this differential coding serves. We particularly showcase how rhythmic representations reveal the dynamic exchange of information across the visual system. We highlight three domains in which content decoding from visual rhythms has yielded significant new insights into the dynamics of information processing: the interplay of feedforward and feedback signals during visual perception, the internal generation of visual representations, and the prediction of upcoming visual information.

Feedforward and feedback flows during visual perception

Feedback connectivity is widespread in the visual system and is considered crucial for efficient visual processing [7,50]. The importance of visual feedback and its co-occurrence with feedforward connectivity prompts the question of how feedforward and feedback signals are

Box 1. Alterations of rhythmic representations across the lifespan and in neurodevelopmental disorders

Brain rhythms change across development. In the visual domain, oscillations recorded over human occipital cortex progressively change from slower theta rhythms to faster alpha rhythms [91]. Decoding methods, which have only rarely been applied to developmental data [92], can help trace the evolution of visual codes through these different stages of maturation in brain rhythms. A recent study using decoding methods on EEG data acquired from infants and adults highlights that the representation of visual contents in these rhythms similarly matures across development [93]: an initial coding of visual object information in theta rhythms in 6- to 8-month-old infants develops into a coding in alpha and beta rhythms in adults. These findings highlight different modes of cortical processing across development. They may be interpreted as a stronger reliance on feedforward processing in the theta frequency range in infants that is overshadowed by prominent feedback processes in the alpha/beta range [51] in adults. Alternatively, infants may recruit memory systems, associated with theta rhythms [94], more strongly when viewing objects, supporting the formation of visual memory representations early in life [95,96]. Multivariate analyses of rhythmic brain data can also be used to answer how visual representations change across the lifespan. Visual brain rhythms also undergo systematic alterations in old age [97,98]. Characterizing how these alterations relate to differences in visual content coding in the aging brain [99] will provide new insights into how older adults parse the world differently from younger adults. Finally, autism spectrum disorder, a neurodevelopmental disorder, is characterized by alterations in visual gamma and beta rhythms, likely indexing characteristic differences in perceptual organization [100,101]. Understanding how such alterations in rhythmic activity relate to the coding of visual contents in these rhythms opens new avenues for understanding the neuro-functional underpinnings of the visual correlates of neurodevelopmental disorders.

exchanged across the cortical hierarchy. One proposal is that these information flows are routed along different oscillatory channels [42,47]: according to this view, the feedforward analysis of visual inputs is mediated by high-frequency gamma oscillations [39,51,52], whereas feedback processes are mediated by low-frequency oscillations in the alpha and beta range [51–54]. These feedforward- and feedback-related rhythms are further separated across cortical layers [54,55], creating a spectral and spatial signature that allows for efficient multiplexing of visual counterstreams.

Feedforward signals in the gamma frequency range have been linked to stimulus information that emerges during early visual processing [34,36,39]. They do so in a hierarchical manner that corresponds to the feature extraction cascade in deep neural networks (DNNs) [39], suggesting a correspondence between computational models of the feedforward processing cascade and neural gamma rhythms. For feedback-related visual rhythms, the situation is less clear. Do they encode stimulus information, too?

As discussed earlier, some studies have reported representations of visual contents in low-frequency rhythms [37,38,41], which have been linked to cortical feedback propagation. First evidence for these content-specific codes reflecting feedback signals comes from studies investigating neural representations from simple to complex visual features, where complex feature representations are often assumed to arise from recurrent processing. With increasing feature complexity, representations indeed emerged later and in lower frequencies (Figure 2A): whereas simpler stimulus properties (captured by early layers of visual DNNs) are encoded across a broad frequency range, spanning theta to gamma rhythms, more high-level stimulus properties (captured by late DNN features and semantic neural networks) are coded later in time and more prominently in theta, alpha, and beta rhythms [37,41], suggesting that they arise from recurrent and feedback connections among neuronal ensembles in high-level visual cortex. When cortical feedback is disrupted by effective backward masking, object representations in later alpha and beta power (after around 400 ms of processing) are less pronounced, suggesting a direct link between cortical recurrence and alpha and beta frequencies [44].

Compelling evidence for differential neural coding in feedforward- and feedback-related rhythms is offered by a recent study on spatial integration of dynamic and naturalistic stimuli [56]. This study featured natural videos presented to the left and right visual hemifields, in a coherent and

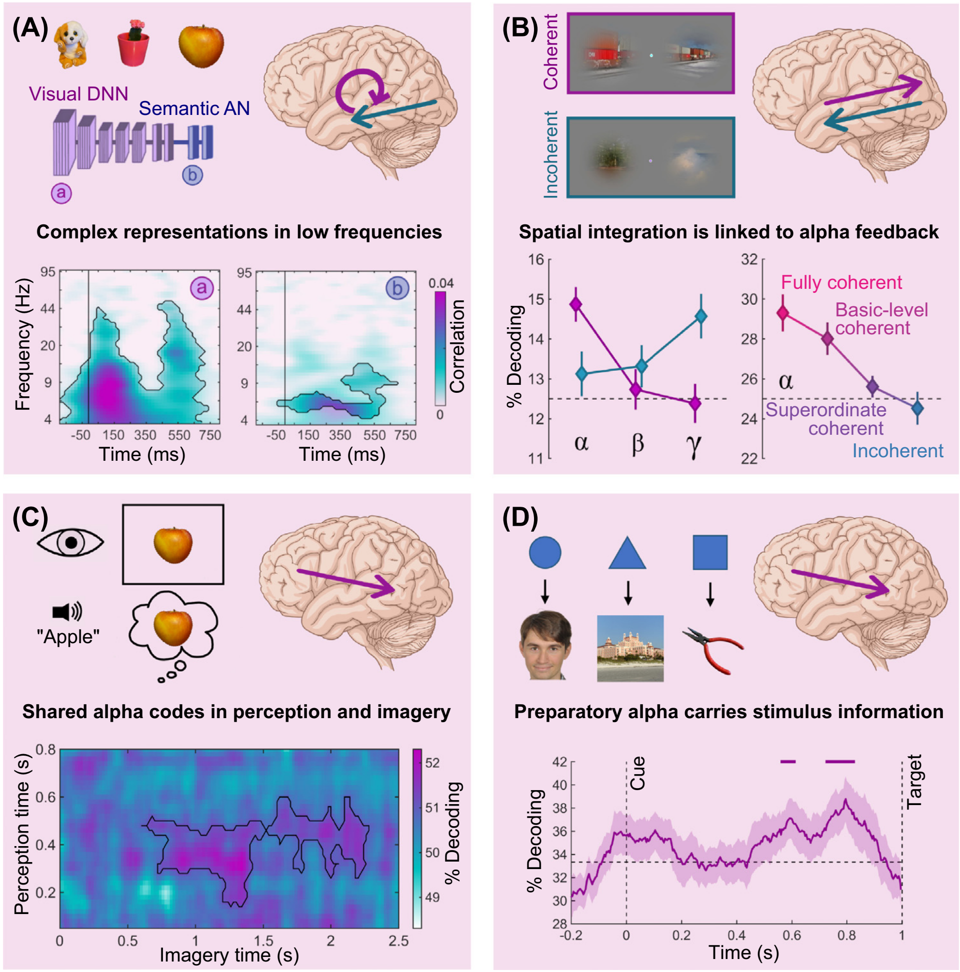

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Figure 2. Rhythmic representations in the visual system reveal feedforward and feedback propagation. (A) Rhythmic content codes dissociate simple and complex feature processing. Simple features – captured by early layers of a visual deep neural network (DNN) – correspond to activity in a broad frequency spectrum. Complex features – captured by a semantic artificial network (AN) appended to the DNN – correspond to delayed alpha and theta rhythms, suggesting an involvement of higher-level recurrent processing. Data reproduced from [37] (©2018 by the Massachusetts Institute of Technology; all rights reserved). (B) Rhythmic content codes index integration-related feedback. When coherent (i.e., matching) parts of natural videos are presented across hemifields, they are decodable from feedback-related alpha activity, whereas incoherent videos are decodable from feedforward-related gamma activity (left). The integration-related coding in alpha rhythms is most pronounced when coherent parts of the same video are shown (right) and decreases from videos coherent on the basic level (two videos of flying birds) to videos coherent on the superordinate level (two videos of animals) and incoherent videos (two videos from different superordinate categories). Data reproduced from [56,57]. (C) Alpha rhythms track the contents of mental imagery. Visual objects are cross-classified between perception and imagery from alpha power patterns, suggesting that top-down alpha dynamics mediate the reactivation of visual contents during imagery. Data reproduced from [63]. (D) Preparatory alpha activity is content-specific. When participants are cued for an upcoming categorical object target, alpha dynamics prior to target onset discriminate between the expected categories, suggesting that alpha mediates content-specific preparatory representations. Data reproduced from [71]. Stimulus photos by the authors, for illustrative purposes.

incoherent way (Figure 2B). In the coherent condition, corresponding parts of the same video were presented across hemifields, affording integration into a single percept. This integration may be guided by top-down signals that inform the correct binding of features across space and time. In the coherent condition, by contrast, different videos were presented across hemifields, which do not afford integration. When the videos were presented incoherently, stimulus information was decodable from feedforward-related gamma activity. By contrast, when the videos were presented coherently, stimulus information could be decoded from alpha activity. This feedback-related code is specifically conveyed by oscillatory power, rather than phase, and the relative strength of representations in the alpha dynamics is modulated by the similarity of the contents that require integration [57]. Combining the EEG data with functional magnetic resonance imaging (fMRI) recordings in a fusion analysis [58], where representations were mapped across frequency bands and brain space using RSA, the representations of coherent stimuli in the alpha band were spatially linked to early visual cortex [56]. This finding shows that the spatial integration of visual information recruits top-down activity in the alpha frequency range, that carries visual content information upstream to the earliest visual processing stages in the cortex. A more recent study further demonstrates that shifts from feedforward-related to feedback-related rhythms co-vary with phenomenological integration [59]: when the same, ambiguous input is represented in alpha dynamics it is perceived as coherent, whereas when it is represented in gamma rhythms it is perceived as incoherent.

More generally, these findings further illustrate the potential of decoding information from rhythmic brain signals for separating the contents of feedforward and feedback information flows: the dynamic shift between feedforward and feedback processing was not observed when the same analyses were performed on evoked broadband responses. This demonstrates that when combined with fMRI recordings, multivariate analyses of rhythmic brain data can provide a new window into the mechanisms that govern information exchange in the visual brain.

Together, these studies highlight how content-specific rhythmic representations orchestrate feedforward and feedback dynamics during visual perception. We next discuss how the decoding of visual representations in brain rhythms provides new avenues for understanding the internal generation of visual representations in the complete absence of feedforward input.

Internally generated visual representations

Mental imagery is an ideal testbed for studying the top-down generation of visual representations. Multivariate analysis approaches help gain new insights into how the brain employs rhythmic codes to reactivate representations of visual contents during imagery.

Univariate changes in alpha rhythms have been established as a common correlate of visual imagery by numerous studies spanning multiple decades (e.g., [60–62]). Current multivariate work demonstrates that they may in fact play a crucial role as carriers of visual contents during the formation of mental images [63–65]. These studies further showcase how assessing representations in rhythmic activity can unveil insights that may elude investigation when considering only broadband responses.

Evidence of a new functional role of alpha rhythms in imagery was provided in a study in which participants were asked to view images of objects and mentally imagine them in separate tasks [63]. Employing cross-decoding on rhythmic power patterns, the authors found shared representations between imagery and perception exclusively in the alpha frequency band (but not in broadband responses), suggesting that cortical alpha activity mediates the top-down reactivation of perceptual contents during imagery (Figure 2C). Using RSA, they further showed that these shared representations could be best explained by high-level visual features in late layers of a DNN trained for object classification, suggesting that these alpha rhythms carry information about complex visual object features. More recently, converging results were obtained for scene imagery, where a shared code between perception and imagery was solely observed in alpha rhythms [64].

Another recent study [65] investigating self-generated and cue-induced mental imagery of simple line orientations provides further evidence for a link between alpha rhythms and the top-down reactivation of visual representations. During cue-induced imagery, participants imagined line orientations associated with a previously learned cue, whereas during self-generated imagery they chose which orientation to imagine on every trial. Cue-induced imagined line orientations were represented less prominently in broadband responses, but more prominently in posterior alpha activity in the EEG and in the early visual cortex in fMRI, suggesting a link between alpha rhythms and the reactivation of low-level visual representations through top-down connectivity. By contrast, self-induced imagery was encoded less strongly in alpha activity, but more strongly in broadband responses, and showed enhanced representations only in frontal regions. These differences may be explained by a reduced vividness in self-generated images or an engagement of different cognitive processes that results in less reliance on rhythmic visual codes during self-generated imagery.

In sum, recent studies show that alpha rhythms carry imagined visual contents of differing levels of complexity (ranging from line orientations to objects and entire scenes). These rhythmic representations occur under conditions that recruit early visual cortex regions, suggesting that they enable top-down reactivation of imagined visual contents that can even extend to the lowest levels of the visual hierarchy. Interestingly, across the highlighted studies, many critical effects were found in rhythmic power patterns but were weaker or absent in evoked broadband responses.

Next, we consider how content-specific rhythmic feedback not only contributes to immediate perception or imagery, but also allows the visual system to actively prepare for expected future inputs.

Preparatory visual representations

In real-world vision, the appearance of a stimulus can often be predicted in advance. Harnessing this predictable nature of visual inputs is considered critical for adaptive natural behavior, as it allows the brain to prepare for upcoming stimuli before they even occur [66].

One process by which the visual system achieves this is preparatory attention [67]. If a target stimulus can be expected before its appearance, stimulus-specific features are pre-activated. For example, in visual search, the category of the search target (one of two letters, or a person versus a car) is decodable from preparatory fMRI activity [68,69]. The involvement of alpha and beta rhythms in feedback propagation prompts the question of whether these rhythms are involved in the formation of content-specific preparatory templates.

Initial evidence for a connection between brain rhythms and preparatory representations came from EEG results contrasting visual search for motion- and color-defined targets [70]: search for motion-defined targets increased alpha activity over dorsal motion-selective visual cortex, whereas search for color-defined targets increased alpha activity over ventral color-selective regions. A more recent EEG study employed multivariate decoding to provide deeper insights into what is coded in these alpha rhythms [71]. Here, participants were cued to expect a face, scene, or tool in the upcoming trial. Alpha activity in a preparatory phase between cue and stimulus differentiated between the upcoming stimulus categories (Figure 2D), indicating that alpha rhythms encode preparatory attentional templates suitable for guiding the analysis of subsequent matching inputs. Notably, these alpha dynamics contained sustained content representations that emerged closer to the appearance of the stimulus than those in evoked broadband responses [72], suggesting that the contents transported in alpha rhythms induce critical preparatory states.

Complementary results were found in a recent MEG study that tested whether neural expectations are expressed in alpha rhythms [73]. The authors employed auditory cues to indicate the likely appearance of a specific visual shape in a shape discrimination task. To test whether preparatory representations generalized from the preparatory period in the experiment to an independent shape 'localizer', where the shapes were presented outside of the task context, the authors performed cross-decoding analysis on MEG response patterns. They found that cross-decoding performance fluctuated with a 10 Hz rhythm, suggesting an alpha-rhythmic activation of preparatory shape representations.

Together, these studies highlight that pre-stimulus alpha activity encodes the contents of probable future stimuli. These results can be interpreted in the context of predictive processing theories [74,75]: predictions that traverse from higher to lower levels of the visual hierarchy – mediated by feedback-related alpha activity [54] – guide the visual analysis of upcoming inputs, thereby reducing prediction error in the visual system.

Concluding remarks

In this opinion article we have argued that recent results from multivariate decoding studies call for reassessing the functional role of visual brain rhythms: rhythmic activity may play a critical role in enabling content-specific information transfer across the visual system.

By collating a set of recent studies from complementary domains of vision research (perception, imagery, and prediction), we showed that the frequency in which rhythmic content representations are encoded enables researchers to infer the direction of content-specific information flows in visual cortex: feedforward information transport is mediated by evoked broadband signals and high-frequency gamma rhythms, whereas content propagation in the feedback direction is mediated by lower-frequency rhythms, predominantly in the alpha frequency range. Critically, the visual information encoded in neural rhythms is often distinct from the information encoded in evoked broadband signals. The study of rhythmic activations thus opens a unique window into feedforward and feedback information flows in the visual system.

A notable finding across the different lines of research reviewed here is that alpha rhythms emerge as a key driver in propagating visual feedback information. This is in line with theories and empirical findings that suggest a prominent role of low-frequency alpha and beta rhythms in transmitting visual feedback [51–54], but also suggests a functional dissociation between alpha and beta rhythms [76]. While alpha rhythms carry stimulus-specific information, beta rhythms may also fulfill other purposes in the top-down regulation of visual information [77]. Differences between alpha and beta rhythms may also emerge as a function of beta activity operating in transient bursts rather than in sustained rhythms [78], and by alpha and beta bursts fulfilling different functional roles [79].

The prominent involvement of alpha rhythms in content-specific feedback prompts a re-evaluation of the functional relevance of alpha dynamics in visual cortex (Box 2). The studies we reviewed show that alpha rhythms mediate content-specific feedback propagation across a range of stimuli and tasks, and they highlight that such feedback-related representations are often found exclusively in alpha activity. Yet the current evidence for alpha rhythms being necessary for content representations to emerge is largely correlational. Future studies should probe the causal role of alpha rhythms in representing visual contents. Such studies could entrain – or disrupt – alpha rhythms through rhythmic visual stimulation [80,81] or neurostimulation [82,83] and quantify effects on the perception and neural representation of visual contents.

Outstanding questions

Brain rhythms are often nested: for instance, when the power of one rhythm is coupled to the phase of another. Is such coupling also reflected in content-specific codes, where information contained in the power of one rhythm varies given the phase of another, or vice versa?

How do visual representations across brain rhythms vary as a function of task demands? Attentional mechanisms have been linked to neural rhythms, but it remains to be tested how attended and unattended visual information is differently encoded in these rhythms.

More generally, it has been proposed that overarching brain states are characterized by a relative dominance of feedforward or feedback processing. Are these brain states linked to enhanced low- or high-frequency coding in the visual system?

Rhythmic representations in the visual system are likely to interact with rhythms in the prefrontal cortex, which responds rhythmically to visual stimuli in a task-driven way. How do prefrontal rhythms influence content representation in visual rhythms?

Relatedly, representations in visual working memory are also encoded in a rhythmic fashion. How do perception- and memory-related rhythms differ in the visual system, and how do they interact when the contents of perception and memory are similar and thus compete for representation?

How does coding in neural rhythms relate to the traits of individuals? Are individual differences in the ability to categorize or attend to visual information related to tradeoffs between representations in feedforward- and feedback-related rhythms?

Are rhythmic representations altered in conditions that are linked to imbalances in feedforward and feedback processing, such as schizophrenia or autism spectrum disorder?

Box 2. Alpha rhythms and content-specific feedback

The finding that alpha rhythms are consistently involved in representing the contents of cortical feedback invites a reconceptualization of the functional role of alpha activity. Alpha rhythms are classically considered a neural correlate of 'idling' [102], suppression [103,104], or visual memory [84,105], seemingly at odds with a role of alpha activity in visual feedback propagation. Newer proposals also ascribe a more active role in cortical communication to alpha oscillations [47,106–108], including the encoding of stimulus information [109,110]. In this view, stimulus-specific feedback propagation may oscillate in an alpha rhythm, allowing the classification of stimulus information from patterns of alpha activity. The active role of alpha rhythms in feedback propagation could be reconciled with other functions of alpha when two discernable visual alpha rhythms are assumed, with lower-frequency alpha rhythms primarily subserving suppression and higher-frequency rhythms actively encoding stimulus information [110,111]. Another possibility is that stimulus coding in alpha relates to the initiation of stimulus-specific activity propagation through traveling waves of neural activity, which have been shown to spread across the cortex in alpha rhythms [112]. Such traveling waves may modulate neural excitability in alpha rhythms in a stimulus-specific way, giving rise to stimulus-specific patterns in the alpha frequency band. The majority of studies collated here suggest that content-specific feedback in the alpha band primarily manifests in variations of oscillatory power, suggesting that the amplitude of alpha rhythms carries stimulus information. Some studies, however, also find stimulus-specific information in alpha phase [37,41,44]. It is currently unclear how the representations in power and phase differ functionally and under which task conditions representations shift between power- and phase-based codes. Content-specific feedback in alpha rhythms likely varies across tasks, with different neural sources and targets for the feedback and different features carried by feedback as a function of the task demands. Studies often only highlight one of these aspects, such as where the feedback signals are headed, or which features they represent. More studies are thus needed that combine a spectral and spatial mapping of feedback-related content representations with computational models suitable for characterizing these representations.

Rhythmic representations also play a critical role in mediating other visual functions such as attention [9,11,12] or visual working memory [84,85], and the control of visual representations via prefrontal circuits [86,87]. How contents are represented in these rhythms, and how these representations interact with visual representations during perception, need to be explored in future research. The study of visual content representations may also prove fruitful in understanding visual information coding across overarching brain states [88], traits of individual observers [89], and pathological alterations of vision [90] (see Outstanding questions).

To conclude, we argue that the study of visual content codes in rhythmic brain dynamics provides a new window into the formation and dynamic exchange of representations in the visual system. Such insights may transform the way we think about brain rhythms and their functions.

Acknowledgments

We would like to thank Micha Engeser for providing feedback on our manuscript. R.M.C. is supported by the Deutsche Forschungsgemeinschaft (DFG; grant CI241/3-1) and by a European Research Council (ERC) Starting Grant (CRACK, ERC-2018-STG 803370). D.K. is supported by the DFG (grants SFB/TRR135, project number 222641018; KA4683/5-1, project number 518483074; KA4683/6-1, project number 536053998), 'The Adaptive Mind', funded by the Excellence Program of the Hessian Ministry of Higher Education, Science, Research and Art, and an ERC Starting Grant (PEP, ERC-2022-STG 101076057). Views and opinions expressed are those of the authors only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them.

Declaration of interests

The authors declare no conflicts of interest.

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