# Decoding the contents of visual brain rhythms

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## Abstract

In this Opinion, we argue for a reevaluation of the functions of rhythmic activity in visual cortex. We posit that the application of decoding methods to rhythmic signals reveals a new role for brain rhythms in encoding and communicating visual contents. By collating recent studies from visual perception, imagery and prediction, we demonstrate how brain rhythms serve a key function in representing visual contents. We further argue that characterizing representations across frequency bands allows researchers to elegantly disentangle content transfer in feedforward and feedback directions and 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.

## Keywords
Neural oscillations, Multivariate pattern analysis, Electrophysiology (EEG, MEG), Object recognition, Visual processing, Cortical feedback

## Highlights

- We claim that neural rhythms serve a fundamental function in vision: the representation of visual contents.
- We collate a set of recent multivariate decoding studies on visual perception, imagery, and predictions that demonstrate such rhythmic content representations.
- We argue that rhythmic content representations are useful for untangling feedforward and feedback information flows in the visual system.
- In particular, alpha rhythms emerge as carriers of stimulus-specific feedback information across the visual system.
- We posit that the study of rhythmic content representations will yield important new 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 cortex varies in rhythmic ways. Rhythmic brain dynamics are observed across different characteristic timescales, and they are present across brain regions and even species [1]. However, their role in neural coding is controversially debated. Current accounts range from brain rhythms forming the very fundamentals of cortical communication to being somewhat epiphenomenal (see [2]). To better gauge the importance of brain rhythms for cortical processing, we 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, we posit that recent advances in decoding techniques enable us to reassess the role of neural rhythms in cortical processing dynamics. We argue that reading out the contents encoded in neural rhythms allows researchers to investigate how content-specific information is encoded, transformed, and communicated in the visual system, opening a new window into the inner workings of the human visual system. To support this claim, we collate a set of studies that used multivariate analysis methods to uncover how attributes of the visual stimulus are encoded in neural rhythms and highlight the merits of such approaches for understanding information propagation across visual brain networks. Based on these studies, we argue that brain rhythms in visual cortex carry the very contents of our perception and further highlight 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.

This rhythmic cortico-cortical 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. On this view, information is analyzed in increasingly complex ways along a hierarchically convergent feedforward cascade [3]. This classical view of visual processing aligns well 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 inter-regional 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]. Further, the state of prestimulus oscillations determines the efficiency and the perceptual outcome of subsequent stimulus processing [16–19]. Perception itself is also rhythmic: the efficiency of visual processing varies periodically across time [20–24]. 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 if visual rhythms are also important for coding stimulus information. In the following, we show that visual rhythms indeed 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 in visual neuroscience has altered the research landscape by allowing us to read out the very contents of neural codes and thereby delineate how stimuli are organized across representational spaces in the brain [25,26]. The application of such multivariate techniques to time-resolved neural data (from EEG, MEG, ECoG, or single-cell recordings) has equipped researchers with a toolkit to examine how visual contents are encoded in visual brain dynamics with high temporal precision. Methods like neural decoding [27,28] and representational similarity analysis (RSA) [29] have led to critical advances in our understanding of how visual content representations emerge and change through time [4,5,30], and how they are altered under different viewing conditions and task demands [31,32]. While these methods were by and large used to study time-varying representations in broadband responses, they can equally be applied to rhythmic neural signals to understand whether information about the visual world is represented in rhythmic codes (Fig. 1).

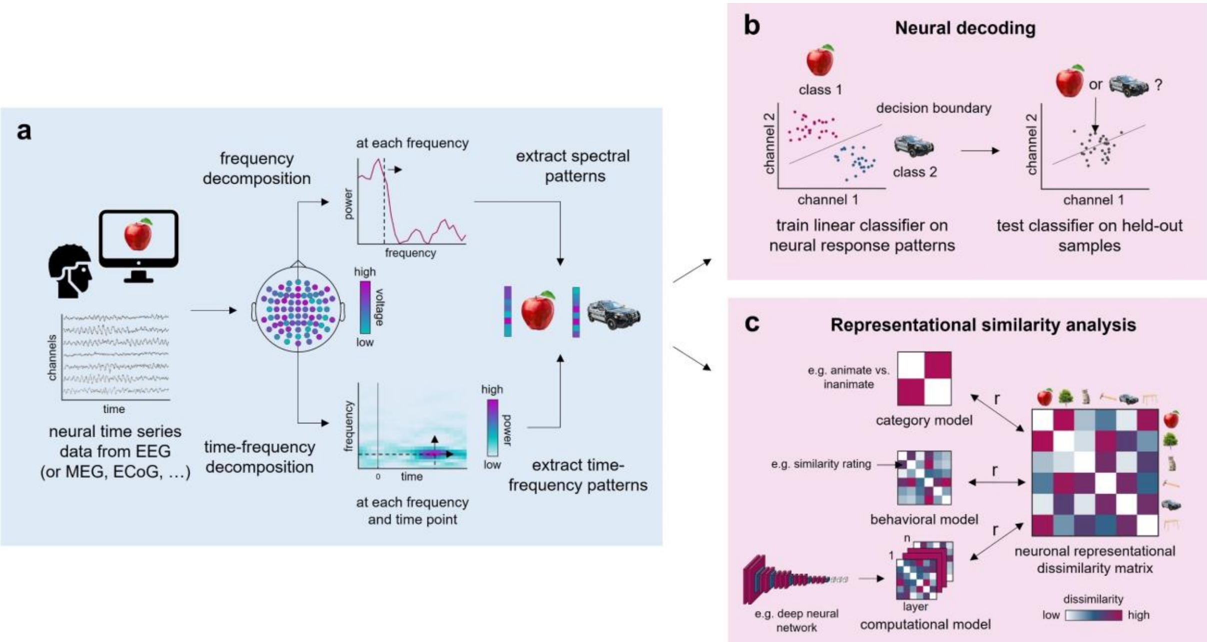


***Figure 1. Unveiling content coding in neural rhythms with multivariate analyses.*** ***a)*** *Time-varying responses to a set of visual stimuli (from EEG, MEG, or intracranial recordings) are decomposed into a set of frequencies of interest, either for an entire time period of interest (upper path, 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.*

By applying multivariate analysis methods, researchers have demonstrated that stimulus information can be read out from rhythmic neural signals. Recent studies show that both attributes of basic visual stimuli like gratings [33] or letters [34] as well as complex stimuli like objects, faces, and scenes [35–40] can be decoded from rhythmic responses in different frequency bands, including both high frequencies in the gamma range (30–100Hz) and lower frequencies in the theta (4–7Hz), alpha (8–13Hz) and beta (14–29Hz) range. Whereas broadband gamma is classically thought to carry visual feature information [14,41,42], these studies instead 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 [36,37,40], with stimulus information sometimes expressed in the power of an oscillation, and sometimes in its phase, likely reflecting different component processes [40,43]. Furthermore, rather than being static, these rhythmic features may dynamically change across the lifespan and in brain disorders (see Box 1).

Together, this multifaceted picture raises the question of whether different brain rhythms encode similar visual information, or whether there are systematic differences. In the following, we take a closer look at how brain rhythms encode different types of visual information, and which function this rhythmic coding serves. We showcase that the study of rhythmic representations reveals the dynamic exchange of information across the visual system. We highlight three domains in which the decoding of the content of 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 considered crucial for efficient visual processing [7,44]. The importance of visual feedback and its cooccurrence with feedforward connectivity prompts the question of how feedforward and feedback signals are exchanged across the cortical hierarchy. One proposal is that these information flows are routed along different oscillatory channels [41,45]: On this view, the feedforward analysis of visual inputs is mediated by high-frequency gamma oscillations [38,46,47], whereas feedback processes are mediated by low-frequency oscillations in the alpha and beta range [46–49]. These feedforward- and feedback-related rhythms are further separated across cortical layers [49,50], creating a spectral and spatial signature that allows for efficient multiplexing of visual counterstreams.

Feedforward signals in the gamma frequency range have been shown to encode stimulus information that emerges during early visual processing [33,35,38]. They do so in a hierarchical manner that corresponds to the hierarchical feature extraction cascade of a feedforward deep neural network (DNN) [38], 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?

The presence of stimulus-related information in low-frequency oscillations for complex visual stimuli [36,37,40] indeed suggests that properties of the stimulus are encoded in feedback-related rhythms. This stimulus encoding is orchestrated in a feature- and frequency-specific manner (Fig. 2a): Whereas simpler visual 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 [36,40], 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 400ms of processing) are less pronounced, suggesting a direct link between cortical recurrence to alpha and beta frequencies [43].

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 [51]. This study featured natural videos presented to the left and right visual hemifields, in a coherent and incoherent way (Fig. 2b). 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 [52]. Combining the EEG data with fMRI recordings in a fusion analysis [53], 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 [51]. 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 cortex. 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 provide a new window into the mechanisms that govern information exchange in the visual brain.

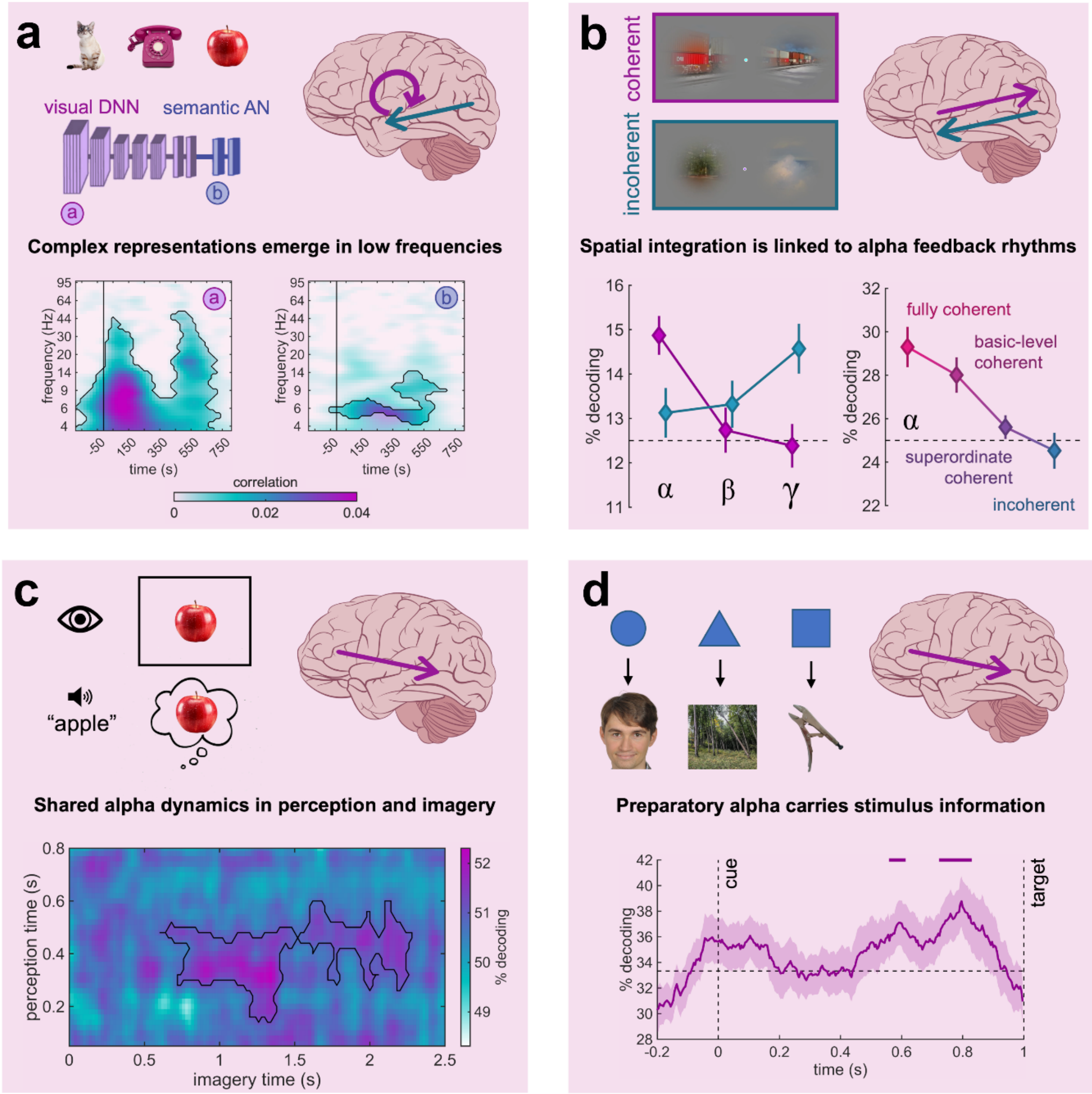


***Figure 2. Rhythmic representations in the visual system reveal feedforward and feedback propagation. a)*** *Rhythmic content codes dissociate simple and complex feature processing. Simple features (captured by early layers of a visual DNN) correspond to rhythmic activity in a broad frequency spectrum. Complex features (captured by a semantic artificial network, AN, appended to the DNN) correspond to delayed alpha and theta rhythms, suggesting an involvement of recurrent processing in high-level visual cortex. Data reproduced from* [36]. ***b)*** *Rhythmic content codes index integration-related feedback. When natural videos are presented in coherent ways, they are decodable from feedback-related alpha dynamics, whereas incoherent videos are decodable from feedforward-related gamma (left). This integration-related shift to alpha-frequency feedback is more pronounced when the content in videos matches categorically (from basic to superordinate level; right). Data reproduced from Chen* [51,52]. ***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 re-activation of visual contents during imagery. Data reproduced from* [54]*.* ***d)*** *Preparatory alpha activity is content-specific. When participants are symbolically cued for an upcoming categorical object target, alpha dynamics prior to target onset discriminate between the expected object categories, suggesting that alpha mediates content-specific preparatory representations. Data reproduced from* [55]*.*

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. Here, multivariate approaches have allowed us to gain new insights into how the brain employs rhythmic codes to reactivate representations of visual contents.

Univariate changes in alpha rhythms have been established as a common correlate of visual imagery by numerous studies spanning multiple decades (e.g. [56–58]). Current multivariate work demonstrates that they may in fact play a crucial role as carriers of visual contents during the formation of mental images [54,59,60]. These studies further showcase how assessing representations in rhythmic activity can unveil insights that may elude investigation when only considering broadband responses.

First evidence of a new functional role of alpha rhythms in imagery was provided by Xie and colleagues [54], who asked participants to view images of objects and mentally imagine them in separate tasks. 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 (Fig. 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 [59].

Another recent study [60] 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. 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 the 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. These findings thus showcase the unique insights about visual representations that can be gained by studying how neural representations emerge in rhythmic activity patterns.

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

**Preparatory visual representations**

In the continuous stream of our daily visual input, the appearance of a stimulus is frequently predictable 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 [61].

One process by which the visual system achieves this is preparatory attention [62]. 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 [63,64]. The involvement of alpha and beta rhythms in feedback propagation prompts the question if these rhythms are involved in the formation of content-specific preparatory templates.

First evidence for a connection between brain rhythms and preparatory representations comes from an EEG study that contrasted visual search for motion- and color-defined targets [65]: 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 recent EEG study employed multivariate decoding to provide deeper insights into what is coded in these alpha rhythms [55]. Here, participants were cued to expect a face, scene, or tool in the upcoming trial. Critically, alpha activity in a preparatory phase between cue and stimulus differentiated between the upcoming stimulus categories (Fig. 2d), indicating that alpha rhythms encode preparatory attentional templates suitable for guiding the analysis of subsequent matching inputs. Notably, these alpha dynamics contained more sustained content representations that emerged closer to the appearance of the stimulus than those in evoked broadband responses [66], suggesting that the contents transported in alpha rhythms induce the critical preparatory states.

Similar results were found in a recent MEG study that tested whether neural expectations manifest in preparatory alpha rhythms [67]. The authors employed auditory cues to indicate the likely appearance of a specific visual shape in a shape discrimination task. In this task, pre-stimulus alpha power patterns represented information about the shape that is likely to appear. These 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, showing that the preparatory alpha rhythms indeed code the visual shape of the stimulus.

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 [68,69]: Predictions that traverse from higher to lower level of the visual hierarchy – mediated by feedback-related alpha activity [49] – guide the visual analysis of upcoming inputs, thereby reducing prediction error in the visual system.

**Concluding remarks**

In this Opinion, we argued that decoding the contents of visual rhythms allows us to reassess the function of these rhythms and specifically how they enable information transfer of visual contents 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 specifically mediated by lower-frequency rhythms, predominantly in the alpha frequency range. Critically, the visual information encoded in neural rhythms is distinct from the information encoded in evoked broadband signals, suggesting that studying rhythmic activations is particularly fruitful for enabling a targeted parcellation of feedforward and feedback information flows in the visual system.

A remarkable finding across the different lines of research reviewed here is that alpha rhythms emerged 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 [46–49]. This also suggests a functional dissociation between alpha and beta feedback rhythms [70], where alpha rhythms carry stimulus-specific information, whereas beta rhythms may also fulfill other purposes in the top-down regulation of visual information [71]. The prominent involvement of alpha in content-specific feedback prompts a reevaluation of the functional relevance of alpha dynamics in visual cortex (see Box 2).

Rhythmic representations also play a critical role in mediating other visual functions like attention [9,11,12] or visual working memory [72,73], and the control of visual representations via prefrontal circuits [74,75]. How contents are represented in these rhythms and how these representations interact with visual representations during perception needs to be explored in future research. The study of visual content representations may also prove very fruitful in understanding visual information coding across overarching brain states [76], traits of individual observers [77], and pathological alterations of vision [78]. For a more detailed look into possible future directions, see the 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. The insights gained in this way may transform the way we think about brain rhythms and their functions.

**Outstanding questions**

- How do visual representations across brain rhythms vary as a function of task demands? Attentional mechanisms have been linked to neural rhythms before, but it remains to be tested how visual information is differently encoded in these rhythms as a function of task. More generally, it has been proposed that there are overarching brain states that are defined by emphasized feedforward or feedback processing. Are these brain states fundamentally 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 other brain systems. For instance, the prefrontal cortex also responds rhythmically to visual stimuli, yet its rhythms are dominated by task-related demands. Such prefrontal representations can indeed control processing in visual cortex through specific rhythmic channels. How they influence the

representation of visual contents in neural rhythms remains an exciting question for future study.

- Relatedly, rhythmic visual representations during perception may interact with concurrent rhythmic representations in visual memory. For instance, representations in visual working memory are also encoded in a rhythmic fashion. How do rhythms that mediate visual processing and rhythms that fulfill memory-related functions 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 traits such as the ability to efficiently categorize or attend to visual information, related to specific tradeoffs between representations in feedforward- and feedback-related rhythms? Are they also characteristic of disorders that are linked to imbalances in feedforward and feedback processing like autism or schizophrenia?

**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 occipital cortex progressively change from slower theta rhythms to faster alpha rhythms [79]. Decoding the contents of visual rhythms, which has only rarely been employed on developmental data [80], can help trace the evolution of visual codes through these different stages of maturation in brain rhythms. A recent study [81] 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: 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 [46] in adults. Alternatively, infants may recruit memory systems, associated with theta rhythms [82], more strongly when viewing objects, supporting the formation of visual memory representations early in life [83,84]. 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 [85,86]. Characterizing how these alterations relate to differences in visual content coding in the aging brain [87] 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 [88,89]. 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 characteristic visual correlates of neurodevelopmental disorders.

**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. Alpha rhythms are classically considered a neural correlate of idling [90], suppression [91,92], or visual memory [72,93], seemingly at odds with a role of alpha in visual feedback propagation. Newer proposals also ascribe a more active role in cortical communication to alpha oscillations [45,94–96], including the encoding of stimulus information [97,98]. On such a 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 frequencies actively encoding stimulus information [98,99]. Another possibility is that stimulus coding in alpha relates to the initiation of stimulus-specific activity propagation through travelling waves of neural activity, which have been shown to spread across the cortex in alpha rhythms [100]. Such travelling 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 mainly suggest that content-specific feedback in the alpha band primarily manifests in variations of oscillatory power, that is the amplitude of alpha rhythms carries stimulus information. Some studies, however, also find stimulus-specific information in alpha phase [36,40,43]. How the representations in power and phase differ functionally and under which task conditions representations shift between power- and phase-based codes is currently unclear.

## Declaration of interests

The authors declare no conflicts of interest.

## Acknowledgements

We would like 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.

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