TICS 1595 No. of Pages 13 ARTICLE IN PRESS

Trends in Cognitive Sciences

CellPress

Review

Perceptual Cycles

Rufin VanRullen[1,2,*]

Brain function involves oscillations at various frequencies. This could imply that perception and cognition operate periodically, as a succession of cycles mirroring the underlying oscillations. This age-old notion of discrete perception has resurfaced in recent years, fueled by advances in neuroscientific techniques. Contrary to earlier views of discrete perception as a unitary sampling rhythm, contemporary evidence points not to one but several rhythms of perception that may depend on sensory modality, task, stimulus properties, or brain region. In vision, for example, a sensory alpha rhythm (~10 Hz) may coexist with at least one more rhythm performing attentional sampling at around 7 Hz. How these multiple periodic functions are orchestrated, and how internal sampling rhythms coordinate with overt sampling behavior, remain open questions.

Trends

Brain rhythms not only modulate but also drive perception, resulting in striking illusions of flicker and reverberation.

Recently popularized single-trial analyses of electrophysiological signals can be used to probe the causal influence of spontaneous brain states (such as the phase of oscillatory cycles) on perception.

Spectral analyses applied to ‘high temporal resolution’ behavioral measurements reveal behavioral, perceptual and attentional oscillations.

The partiality to the ‘standard’ oscillatory nomenclature (delta, theta, alpha, beta, gamma) and the community's fixation on specific rhythms (alpha, gamma) are becoming less prominent. As a result, perceptual rhythms are found in a wide range of frequencies (so far, often restricted to below 15 Hz).

Alpha (~10 Hz) and theta (~7 Hz) are the most commonly reported frequencies for perceptual cycles.

Is Perception Discrete or Continuous?

Philosophers, psychologists and neuroscientists have long questioned whether the apparently continuous stream of our mental experience could in fact rely on a disjoint series of discrete ‘moments’ of experience [1] (a more detailed history is given in [2]) similar to the disjoint snapshots of a movie or video clip. My colleague Christof Koch and I evaluated this question more than 13 years ago in the same journal, tentatively concluding that, although hard evidence was clearly lacking at the time, **discrete perception** (see Glossary) could not be simply ruled out [3]. Since then, owing in part to important advances in experimental recording and data analysis techniques, a large body of literature (surveyed comprehensively in [2]) has surfaced in support of the discrete view. The present review synthesizes these recent developments.

The idea of discrete perception has often been linked to the brain rhythms that can be recorded in various **frequency** bands and at multiple scales, from single-neuron studies to whole-brain techniques such as **electroencephalography** (EEG) and **magnetoencephalography** (MEG). Neuroscientific evidence accumulated over more than a century has clearly established that these rhythms play a crucial role in sensory, cognitive, and motor mechanisms (e.g., [4] for review). Logically, then, our sensory, cognitive, and motor processing abilities should be expected to fluctuate rhythmically: within each oscillatory cycle of a functionally important brain rhythm, there should be a **phase** that is more appropriate and one less appropriate for the neural process under consideration (if only because oscillations of the local field-potential modulate neural firing probability [5,6]). In short, brain rhythms produce **perceptual cycles**. This unavoidable consequence of the very existence of brain rhythms, which can be coined **rhythmic perception** (or, equivalently, cyclic or periodic perception) (Figure 1A,C,E), has long been disregarded; but a flurry of recent findings (described below) leave little doubt that many aspects of human perception and cognition do fluctuate rhythmically.

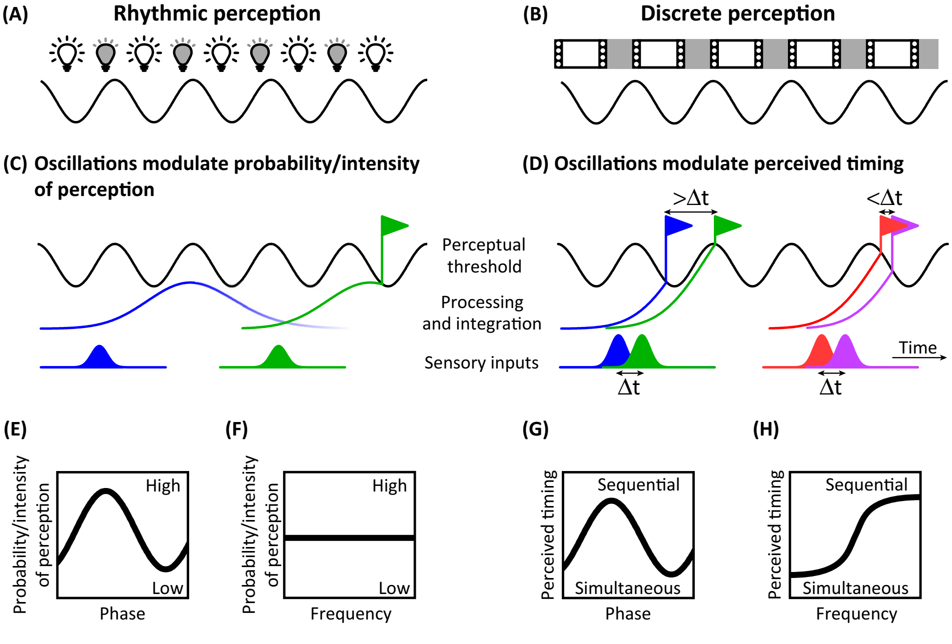
Rhythmic versus Discrete Perception

At first sight, it might be argued that rhythmic modulations of perception do not truly equate discrete perception (Figure 1A,B). A genuine discretization would imply that sensory and mental events are chunked into distinct epochs, with nothing in-between (Figure 1B); within each epoch, the passage of time is not directly experienced–only across epochs (note: this does not preclude encoding, within each epoch, a static representation of time-dependent sensory

[1]Centre National de la Recherche Scientifique (CNRS), Unité Mixte de Recherche 5549, Faculté de Médecine Purpan, Toulouse, France
[2]Université de Toulouse, Centre de Recherche Cerveau et Cognition, Université Paul Sabatier, Toulouse, France

*Correspondence:
rufin.vanrullen@cerco.ups-tlse.fr
(R. VanRullen).

http://dx.doi.org/10.1016/j.tics.2016.07.006



Trends in Cognitive Sciences

Figure 1. Rhythmic and Discrete Perception. (A) The notion of rhythmic perception (also referred to as cyclic or periodic perception) implies that a particular phase of each oscillatory cycle gives rise to more efficient neuronal, sensory, perceptual, or cognitive processing (illustrated here by the brighter light bulbs), whereas the same process is less efficient at the opposite phase (dimmer light bulbs). (B) Discrete perception further entails that neuronal, sensory, perceptual, or cognitive events are separated into discrete epochs (like the snapshots of a video clip, depicted here above the oscillation). Events that are not perceived in one snapshot are deferred to the next. Therefore, oscillatory cycles modulate the temporal parsing of perceptual events. (C,D) One example illustration (among many other alternatives) of a brain rhythm modulating sensory perception. Sensory inputs are processed and integrated with a given latency and time-constant, including exponential decay. A brain rhythm is assumed here to modulate the threshold of perception (similar results are obtained when the rhythm affects the processing/integration stage). (C) For two identical weak sensory inputs, integration may or may not reach perceptual threshold, depending on the phase of stimulus presentation. (D) Stronger sensory inputs consistently reach perceptual threshold, but at slightly different times. Thus, two pairs of sensory events separated by the same time interval (Δt) can reach threshold with an extended (>Δt) or compressed (<Δt) interval, depending on the phase of stimulus presentation. In this illustration a simple rhythmic modulation of neuronal processing thus results in a periodic modulation of both the probability/intensity of perception (C,E), in other words ‘rhythmic perception’, and of perceived timing or temporal parsing (D,G), in other words ‘discrete perception’. The two notions, therefore, can easily be reconciled. Although oscillatory phase modulates both perceptual variables (E,G), the frequency of the critical brain rhythm is only expected to modulate perceived timing (H): for a given interval Δt, slower or faster modulation frequency (within the natural range of fluctuation of the relevant brain rhythm) will favor simultaneous or sequential percepts, respectively. (F) Threshold-level sensory inputs have a similar probability of crossing perceptual threshold, regardless of the modulation frequency (assuming the time-constant of integration and decay remains small compared to the oscillatory period).

attributes such as visual motion or flicker, auditory pitch, etc.). Discretization does not necessarily entail that events occurring in-between two epochs are lost to perception, but rather that events that are processed too late for one **snapshot** should be deferred until the next. In other words, discrete perception would seem to require a cyclic fluctuation not merely of perceptual responsiveness (i.e., rhythmic perception), but of the very *temporal structure* of perception (i.e., **temporal parsing**) [7]: two events occurring in rapid succession at one phase of the critical rhythm may fall into a single snapshot, and hence be experienced together, while at the opposite phase the same two events could be split into successive snapshots, and experienced sequentially (Figure 1G).

Rhythmic and discrete perception may thus seem like qualitatively distinct phenomena. However, any periodic modulation of sensory neural processes will result in distortions of perceived

Glossary

Apparent motion: retrospective formation of a continuous motion percept, based on discrete shifts of stimulus position. This process, dependent on attention, could contribute to the stability of visual experience despite rhythmic sampling.

Blinking spotlight: the periodicity of attention processes turns the classic ‘spotlight’ of attention into a ‘blinking spotlight’ that can rhythmically sample a single location, or rapidly switch between multiple targets.

Discrete perception: an ‘extreme’ form of rhythmic perception that temporally structures perceptual events into disjoint epochs (or frames or snapshots). Discrete perception can be defined as a rhythmicity of temporal parsing.

Electroencephalography/ magnetoencephalography (EEG/MEG): recording techniques providing a real-time view of large-scale brain activity, and at a sufficient temporal resolution to measure oscillations at 40 Hz or higher.

Entrainment: a process by which brain oscillations follow a rhythmic temporal structure present in the sensory environment. Entrainment can be opposed to spontaneous oscillations that reflect the inherent rhythmic organization of perception.

Frequency: the rate of repetition of a brain oscillation, in cycles per second or Hz.

Impulse response function: the average brain response to a unitary increase of sensory input intensity (e.g., luminance). Oscillatory impulse response functions can produce perceptual reverberation phenomena.

Perceptual cycle: the consequence of rhythmic perception is to produce perceptual cycles, in other words oscillatory cycles whose phase directly influences perceptual abilities (also called epochs, frames, or snapshots in the context of discrete perception)

Phase: instantaneous position of a brain oscillation along its oscillatory cycle, expressed in radians (circular variable). By convention, the oscillatory peak corresponds to zero phase and the trough to a phase of π radians.

Rhythmic perception: sampling or processing of sensory inputs that is rhythmically modulated following the phase of one or more brain rhythms timing that actually resemble a discrete temporal framing (Figure 1D). In other words, the distinction between rhythmic and discrete perception is essentially a matter of degree, and all perceptual periodicities are in fact germane to the question of discrete perception. Nonetheless, we will later pay special attention to those perceptual cycles that specifically modulate temporal parsing and the timing of perceptual experience because these could be considered a more extreme case, or a more direct demonstration, of discrete perception.

Nature of Evidence for Perceptual Cycles

Brain rhythms occur at multiple frequencies, and therefore their perceptual consequences–the perceptual cycles–should display similar periodicities. This logic forces us to abandon the chimera of a unitary central sampling rhythm simultaneously affecting all aspects of perceptual experience, as postulated by early proponents of the discrete perception theory (who often placed the critical frequency in the 'alpha' range, around 10 Hz) [1]. Multiple perceptual cycles could in fact coexist in distinct brain networks, with different periodicities.

By the same logic, any of the thousands of experiments relating brain rhythms to sensory perception could be taken as indirect evidence for perceptual cycles. We focus here instead on the most direct experimental data, leaving aside reports of correlations between perception and brain rhythm amplitude, phase–amplitude coupling between rhythms, phase coherence between electrodes or brain regions, and the above-mentioned local coupling between rhythmic phase and neuronal firing [5,6]. Only a link between perception [or at least, large-scale markers of perception such as MEG, EEG, or blood oxygen level-dependent (BOLD) responses] and oscillatory phase *per se* (Figure 1E,G) and, in some situations, oscillatory frequency (Figure 1F,H), constitutes direct evidence for rhythmic perception. Similarly, we do not consider studies where the perceptual periodicity is driven (or 'entrained') by an obvious periodicity in the stimulus itself, emphasizing instead the intrinsic rhythmicity of perceptual processes. These strict constraints, while excluding a large number of potentially relevant studies, can be satisfied by four general classes of experimental evidence for perceptual cycles, listed below.

Phase-Dependent Perception and Behavior

The most straightforward prediction of rhythmic perception is that the outcome of sensory processing should depend on the exact phase of the critical rhythm at around the time of stimulus presentation (Figure 1A,C,E). With modern computers, this prediction can readily be tested, via single-trial analysis of electrophysiological recordings, by comparing the pre-stimulus phases of otherwise identical trials producing one or the other perceptual outcome. This paradigm of choice (examined in more detail in Box 1) has been employed repeatedly in recent years to probe perceptual periodicities [8].

Box 1. Key Paradigm: Phase Dependence of Perception

Several recent studies have investigated the relationship between pre-stimulus oscillatory phase and perceptual performance–an essential prediction of the rhythmic perception framework. Although some researchers have elected to focus on a specific, *a priori* defined frequency (e.g., 10 Hz), our lab (among others) has pursued an unbiased approach, testing the phase-dependence of a given perceptual function for any measurable oscillatory frequency (and of course, appropriately correcting for multiple statistical comparisons). Figure I depicts a joint analysis of 10 distinct datasets testing the rhythmicity of very different visual perception tasks (involving threshold detection [10], threshold detection with attentional manipulation [12], transcranial magnetic stimulation (TMS) phosphene detection [13], visual search [23], saccadic execution [19], saccadic remapping [21], temporal parsing as measured by the flash-lag effect [26] or by a temporal reversal illusion [28], top-down influence of predictions and expectations [33,34]. The compilation of datasets reveals highly significant modulations of perceptual outcome by pre-stimulus EEG phase in a restricted range of frequencies (5–15 Hz). Such modulations imply that, for several visual functions, there is a succession of 'good' phases (at which the function is more efficient, eventually leading to an optimal perceptual outcome) and 'bad' phases (at which the function is less efficient, eventually leading to suboptimal perception); this cyclic alternation is already visible in spontaneous EEG oscillations, before the stimulus is even shown. In other words, several visual functions operate periodically, as an ongoing succession of 'perceptual cycles'.

(also called cyclic or periodic perception)

Snapshot: in the context of discrete perception, a perceptual cycle can be understood as a 'snapshot' (or an epoch, or frame), the temporal unit of perceptual experience. All events and attributes within a snapshot are experienced as simultaneous (including temporally defined attributes such as visual motion, flicker, or auditory pitch).

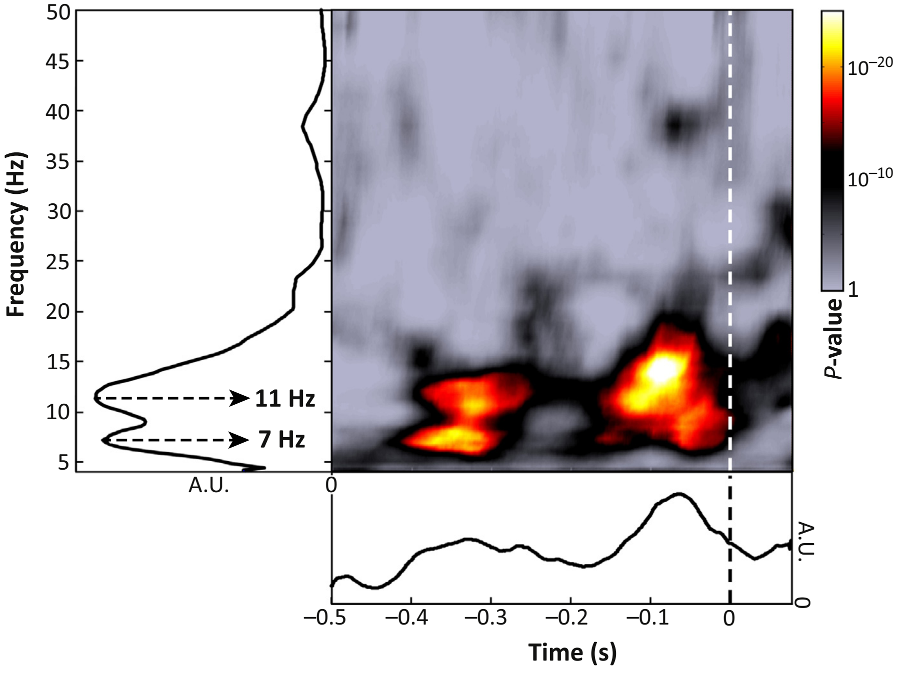
Temporal aliasing: erroneous interpretation of the direction of a periodically evolving stimulus by a system performing discrete sampling. Aliasing occurs when the rate of the periodic stimulus exceeds the Nyquist frequency (the theoretical sampling limit) of the system.

Temporal parsing: the determination of temporal relations between events (simultaneity, asynchrony, temporal order). Discrete perception can be defined as a rhythmicity of temporal parsing.

Trailing effect: a form of stroboscopic perception caused by some recreational and prescription drugs. Moving objects are perceived together with a series of multiple discrete 'copies' of the object, trailing in their wake. Trailing could happen either because the drugs drive our normally subliminal brain oscillations above the perceptual threshold, or because they inhibit the neural mechanisms that normally serve to conceal the perceptual cycles.

It is interesting to note that the spectral profile of perceptual cycles across the 10 studies presents two well-separated peaks at frequencies of 7 Hz and 11 Hz. Neither the type of visual functions investigated (see Table S1 in the supplemental information online) nor the scalp topography of the phase effects (not shown here) reveal a clear-cut dichotomy between periodicities found at 7 Hz versus 11 Hz. There is, however, an emerging pattern in that many studies reporting periodicities around 7 Hz (theta-band) tend to involve visual attention and engage frontocentral electrodes [10,12,21,23,26], whereas those reporting cycles around 11 Hz (alpha-band) often implicate occipital channels, and might thus relate more directly to sensory aspects of visual perception [13,19,21,33]. Nonetheless, this distinction between a ~11 Hz (alpha-band) peripheral or sensory sampling rhythm and a ~7 Hz (theta-band) central or attentional sampling rhythm remains speculative (see Outstanding Questions).

Although measuring and interpreting the phase dependence of perception can be fraught with technical challenges [2,8,127], this paradigm constitutes one of the most solid sources of evidence for rhythmic perception.



Trends in Cognitive Sciences

Figure I. Compilation of 10 Independent EEG Studies of Phase-Dependent Perception from Our Laboratory. All studies had in common: 9–18 observers; a randomized inter-stimulus interval, guaranteeing unpredictable stimulus onset and an overall uniform distribution of pre-stimulus EEG oscillatory phases across trials; between 4000 and 75 000 trials overall; an identical stimulus on each trial, but variable perceptual outcome, as reported by the observer. This dependent perceptual variable came from a different task in each study. In each study statistical analysis involved a comparison of EEG phase distributions between trials yielding distinct perceptual outcomes, separately for every timepoint around stimulus onset (marked by time 0) and for every oscillatory frequency. The 10 studies were combined using Fisher's method. Significant effects in the time–frequency map imply that one phase of the EEG oscillation tended to favor one perceptual outcome, whereas the opposite phase was associated with the alternative outcome. A consistent pattern is present at frequencies between 5 and 15 Hz (left, mean spectral profile across the pre-stimulus period), with a maximum immediately before stimulus onset (bottom, mean timecourse across frequencies). Furthermore, the spectral profile presents two individual peaks at frequencies of 7 and 11 Hz. Abbreviation: A.U., arbitrary units.

In the visual domain, the pre-stimulus phase of brain oscillations at various frequencies has been related to trial-by-trial fluctuations in threshold-level perception [9–16], supra-threshold perception as measured by reaction times [17–19], oculomotor functions such as saccadic execution [19,20] and saccadic remapping [21], attention and visual search [12,22–25], temporal parsing [7,26–30], decision-making [31], top-down influence of predictions and expectations [32–34] and short-term memory [35–39]. Not surprisingly therefore, large-scale physiological markers of perceptual processing such as event-related potentials (ERPs) [18,40,41], stimulus-evoked BOLD responses [42], and fMRI network connectivity between areas [15] have also been shown to depend on oscillatory phase at (or immediately before) the time of visual stimulus onset.

In these diverse studies, the rhythmic frequencies that cyclically modulated perception ranged from 1 to 30 Hz, with many studies reporting modulations at around 7 or 10 Hz (Box 1), but without any apparent logic relating frequency to perceptual or cognitive function (a complete list of experimental studies of perceptual cycles and the corresponding frequencies is presented in Table S1 in the supplemental information online). The amount of trial-by-trial perceptual variability explained by changes in oscillatory phase was consistently small–on the order of 10–20%. While this modulation is clearly not all-or-none, the omnipresent noise in threshold-level decision mechanisms and in single-trial electrophysiological measurements must be factored in. The real amount of performance modulation along the perceptual cycle, therefore, remains unknown.

Frequency-Dependent Perception

Contrary to fluctuations in oscillatory phase, changes in the exact frequency of a critical oscillation (measured across trials, or across observers) need not always influence perceptual abilities (Figure 1E–H). The frequency/perception relationship is most direct, however, when the perceptual function under study involves temporal parsing (Figure 1H). Indeed, a frequency change of the critical brain rhythm is equivalent to a change in the ‘frame rate’ of discrete perception (to employ again the video clip metaphor). This should logically result in a commensurable change in temporal parsing performance, in other words, an improvement or decrement in temporal resolution. As predicted, the peak frequency of the alpha rhythm was found to correlate with two-flash simultaneity judgments, both across [43,44] and within subjects [44]. Slower alpha rhythms were associated with poorer temporal resolution, as if the less-frequent perceptual ‘frames’ made the two successive flashes more likely to wind up in the same frame, and thus be perceived as simultaneous.

Behavioral Oscillations

Electrophysiology is not the only tool that can be used to probe perceptual rhythms: behavioral and psychophysical measurements can also be employed [45]. The first reports of oscillations in perceptual accuracy (e.g., detection threshold) and reaction time date back to the 1960s [46–50], with effects being found principally in the ‘alpha’ frequency range but also at higher frequencies, all the way to 100 Hz. These periodicities were taken to reflect the underlying rhythms of perception, under the necessary assumption that these perceptual cycles could be ‘reset’ by the onset of the visual stimulus. Over the past few years this approach has been successfully applied in several behavioral studies. In their simplest form, these studies employ two separate stimuli, one to reset the (postulated) perceptual oscillation and serving as a temporal reference, and another to probe the state of this perceptual oscillation by measuring perceptual accuracy (or reaction time) at various times after the reference. A key aspect of these paradigms is the need to sample perception with relatively high temporal resolution, in other words using a large set of reference-probe temporal intervals. The behavioral performance time-course can then be analyzed through spectral methods that are traditionally reserved for electrophysiological signals.

Using variations of this method, several researchers have recently measured behavioral periodicities in visual attention [51–56]. Some of these studies were consistent with previous reports of rhythmic attentional sampling at around 7 Hz [12,57], while others reported lower periodicities, around 3–4 Hz [51,52,54,56], possibly because a 7 Hz attentional rhythm was focusing alternately on multiple locations (Box 2: Rhythmic Attention). Similar studies based on behavioral oscillations have also revealed periodicities in visual object and scene recognition processes [58,59].

Box 2. Rhythmic Attention

An increasing number of studies demonstrate that visual attention is an intrinsically rhythmic process [128]. That is, even when observers are instructed to continuously sustain attention to a single location, the focus of attention appears to wax and wane rhythmically, a so-called **blinking spotlight** [57] (Figure IA). Although much evidence in humans points to a ~7 Hz attentional sampling rhythm [12,23–25,51,52,57,129,130] (together with one report of attentional exploration at around 26 Hz in monkeys [22]), several authors have reported lower periodicities, around 3–4 Hz [51,52,54,56]. To reconcile the two findings it has been argued that in the latter studies the display and task instructions, either explicitly or implicitly, could have encouraged the possibility of dividing attention between two objects or locations [128]. If attention does operate periodically, it could then have focused on each object or location during alternate cycles (Figure IB), with the result that the periodicity measured at any one location would actually be one half of the ~7 Hz intrinsic rhythm of attention. Compatible with this interpretation, recent studies have found a proportional decrease of attentional temporal resolution [131] and temporal aliasing frequency [132] (i.e., the continuous wagon-wheel illusion; see Figure 2D in main text) when attention went from a single target to multiple targets. In short, the reported 3–4 Hz periodicities could remain consistent with a major mode of attention sampling at around 7 Hz [57,128]. This rhythmicity confers a useful functional flexibility to the attention system: depending on the situation, the same system can sample a single location, or rapidly scan multiple items (Figure I), as postulated for example by standard theories of 'sequential attention' in visual search [23].

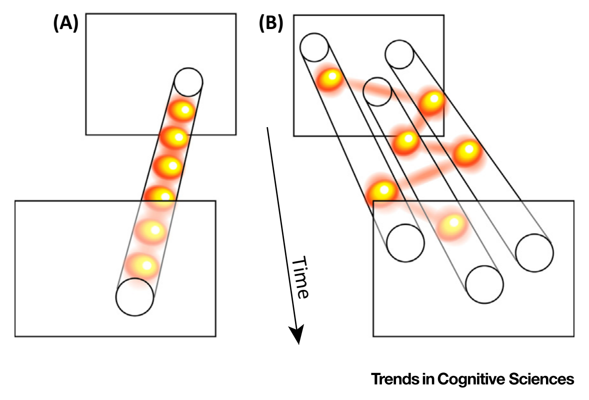


Figure I. Relating Discrete Perception with Sequential Attention. (A) A sensory process that periodically samples a single visual input illustrates the concept of discrete perception. (B) A sensory process that serially samples three simultaneously presented visual stimuli demonstrates the notion of a sequential attention spotlight. Both types of periodic psychological operations (A,B) could actually reflect a common oscillatory neuronal process. According to this view, the spotlight of attention is intrinsically rhythmic, which gives it both the ability to rapidly scan multiple objects and to discretely sample a single source (the yellow balls linked by red lines illustrate successive attentional samples).

Illusory Flicker, Reverberation, and Aliasing

Do oscillations merely modulate perception, or can they also have a driving influence–that is, can perceptual cycles produce novel illusory percepts? Several visual illusions have recently been related to cyclic perceptual fluctuations at around the alpha frequency (Figure 2). In the 'flickering wheel illusion' (Figure 2A), the center of a static radial pattern (a wheel) viewed in the periphery appears to flicker regularly around 10 Hz; the moments of intense illusory flicker correspond to increased EEG alpha amplitude [60]. In the 'triple-flash illusion' (Figure 2C), two brief light pulses separated by about 100 ms are often perceived as a succession of three flashes [61]. This phenomenon is explained by the superposition of two oscillatory **impulse response functions**, one for each stimulus flash: when the delay between flashes matches the period of the oscillation, the superposition results in an enhancement of a later part of the oscillation that would normally be damped; when this enhancement crosses the threshold of perception, a third flash is erroneously perceived. The triple-flash illusion is therefore a form of perceptual reverberation [62]. Compatible with this interpretation, visual impulse response functions (measured by cross-correlating random or 'white noise' luminance stimulation sequences with concurrent EEG responses) were found to oscillate at 10 Hz for several cycles, sometimes for more than 1s, and were therefore dubbed 'perceptual echoes' [63]. Because of these echoes, a stimulus undergoing a random sequence of luminance fluctuations can be erroneously perceived as

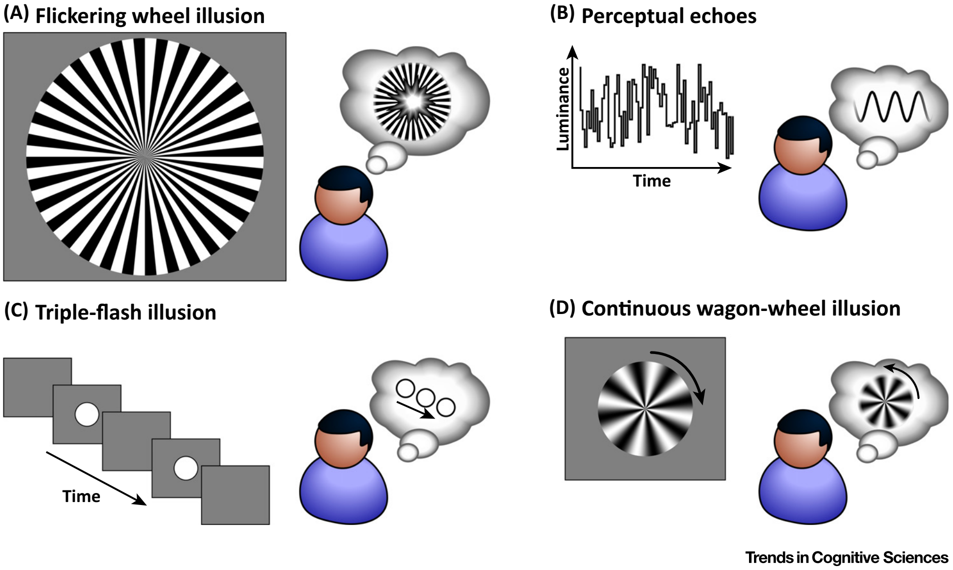


Figure 2. Illusory Phenomena Produced by Perceptual Cycles. (A) In the flickering wheel illusion, the center of a static wheel made up of 30–40 spokes appears to flicker regularly at a rate around 10 Hz, especially when the eyes move around the stimulus (as happens for example when reading this legend, or when visually exploring different parts of the figure). This flicker is linked to increased EEG alpha amplitude, suggesting that the illusion is a direct perceptual manifestation of the internal alpha rhythm. (B) A visual stimulus undergoing a random sequence of rapidly changing luminance values (white noise) is erroneously experienced as a regularly flickering 10 Hz stimulus. This effect could be caused by oscillatory impulse response functions (so-called ‘perceptual echoes’) and reverberation phenomena. (C) In the triple-flash illusion, two flashes separated by approximately 100 ms are experienced as three successive flashes. The illusory 3rd flash could also be caused by reverberation of oscillatory responses to the first two (real) flashes. (D) A moving periodic stimulus sampled by a discrete system (e.g., a movie camera) can be perceived as if it moved backwards, because of temporal aliasing. Under specific conditions, reversed motion can also be perceived with a moving stimulus that is perfectly continuous (such as a physically rotating wheel in broad daylight). The temporal aliasing causing this ‘continuous wagon-wheel illusion’ may be due to periodic sampling occurring in the brain. Experimental work has placed the frequency of this sampling at around 13 Hz.

regularly flickering around 10 Hz (Figure 2B). Furthermore, the period of perceptual echoes is correlated, across individuals, with the two-flash delay that is most likely to produce a triple-flash illusory percept [62].

The discovery of such long-lasting perceptual echoes lends further support to the notion that perception is cyclic. However, this time the perceptual cycles are not seen in spontaneous oscillations of the pre-stimulus period, in other words as a periodically fluctuating readiness to process future incoming stimuli (Box 1), but instead during stimulus processing itself, while the random luminance sequence is physically unfolding on the screen. Importantly, the existence of long-lasting correlations between stimulus information and brain responses indicates that perceptual cycles are not independent entities (as would be the snapshots of a camera): visual information is shared or ‘carried over’ between successive cycles. Arguably, this could be part of the brain's strategy to conceal the discreteness of its operations, and stitch together a continuous sensory experience from a sequence of rhythmically sampled inputs.

Another process with the ability to link information across successive perceptual cycles is **apparent motion**, by which sudden stimulus displacements are retrospectively perceived as continuous motion. This linkage process is under attentional control [64], and there is now robust evidence that attention operates periodically (Box 2). As a result, **temporal aliasing** can happen when such a rhythmic apparent motion system is faced with a stimulus in periodic motion, such as a rotating wheel: at specific rotation rates the wheel is erroneously interpreted as rotating backwards. This ‘wagon-wheel illusion’ is often seen in movies as a result of the periodic sampling of video cameras. However, it has also been reported under continuous conditions of illumination, for example when directly viewing a rotating wheel in daylight (Figure 2D) [65,66]. In this case, the postulated aliasing can only originate from rhythmic sampling in the visual system of the observer. Psychophysical and electrophysiological experiments have identified the rate of this sampling to be around 13 Hz [67–70], and its likely source in right parietal brain regions [71,72], known for their involvement in attentional processes. Although other accounts of the illusion that do not presuppose discrete perception are still being debated [73–80], this temporal aliasing illusion could constitute a prime demonstration of discrete perception.

Why Does the World Seem Continuous?

The perceptual cycles are not usually experienced in daily life–the world appears mostly continuous to us, except for the odd reverberation illusion (Figure 2A–C). The mechanisms responsible for this normal sense of continuity are unknown, but, as explained above, are likely to include apparent motion as well as the potential ‘echoing’ of visual information across successive cycles. What happens when these safeguard mechanisms fail? There are very few reported cases of akinetopsia, or patients incapable of perceiving motion who experience the world as a series of disjointed still snapshots [81]; in these patients the impaired sense of apparent motion is thus accompanied by a damaged sense of perceptual continuity. More common is the **trailing effect**, a vivid case of stroboscopic perception at a rate of around 15 Hz that is experienced after ingestion of particular recreational drugs (such as LSD) or prescription drugs (including several antidepressants) [82]. Trailing can be understood as another example of illusory perception produced by reverberation in the visual system (similar to Figure 2A–C). Nevertheless, it might also reveal what the world would look like if the perceptual cycles suddenly became accessible to consciousness.

Periodicities Across Modalities

Although a majority of rhythmic perception studies have focused on the visual system (as we have, so far in this review), there are many corresponding reports of perceptual cycles in other sensory modalities. In the tactile domain, for example, EEG oscillatory phase at around 10 Hz was found to modulate the detection of threshold-level somatosensory stimuli [83]. MEG oscillatory phase at around 14 Hz also influenced temporal parsing of two successive tactile stimuli [84].

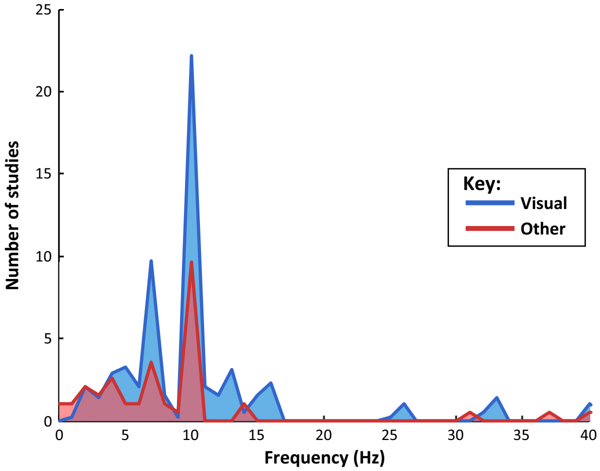
The investigation of perceptual cycles in the auditory domain is a more complex matter (see [2,85] for in-depth discussion). Auditory perception seems to be intimately linked to brain rhythms, via the notion of oscillatory **entrainment** [86–95]. However, there are far fewer reports of spontaneous periodicities occurring in the absence of a driving rhythm in the auditory environment. Those few existing studies suggest that spontaneous perceptual rhythms are more likely to affect higher-level auditory properties (e.g., speech content, auditory source identity, or stream segregation [96], voice recognition), whose neural representation evolves more slowly than the highly time-sensitive basic auditory features and processes (e.g., tone pitch, intensity, inter-aural differences) [97–108]. The frequencies of reported spontaneous auditory periodicities cover a wide range, from 1 Hz to more than 40 Hz, including several observations around 10 Hz (Table S1).

Several recent demonstrations of perceptual periodicities cannot easily be classified as visual, auditory, or tactile, because they actually engage two of these modalities. These cross-modal findings involve a stimulus in one modality resetting the phase of brain rhythms, and thus the accompanying perceptual rhythmicity, in another. For example, a sound can reset the phase of visual cortex rhythms [109–111]; in turn, the sound-reset visual rhythm causes behavioral oscillations in saccadic reaction times [112,113] and threshold-level visual detection performance [114]. Accordingly, the temporal window of the sound-induced double-flash illusion (in which two sounds paired with a single flash cause the illusory perception of a double-flash) was recently shown to correlate with individual EEG alpha (~10 Hz) frequency [115]. The phase of EEG alpha oscillations was also found to modulate an equivalent cross-modal illusion in which two tactile stimuli produce the illusory perception of a visual double-flash (even though, again, only a single flash is actually presented) [116]. Auditory rhythms from 1 to 40 Hz can also be reset by stimuli in the tactile [117] or visual modalities [106,109,118–120]. Finally, sensory periodicities, at least in the visual domain, appear to be synchronized not only with sensory events in other modalities but also with motor events–in other words, with action. This sensorimotor synchronization is the likely origin of 3–7 Hz behavioral oscillations found in visual detection around the time of a hand [121,122] or eye movement [30,123].

All these studies are listed in Table S1, organized by sensory modality, nature of experimental evidence, and the observed periodic frequencies. Figure 3 summarizes this entire body of literature as a spectral distribution of reported perceptual cycles, separately for visual studies and studies in other modalities (including cross-modal ones). Aside from the total number of studies, which is obviously greater in vision, the spectral distributions have similar shapes, with a primary peak at 10 Hz and a secondary one around 7 Hz. This indicates that similar neural mechanisms could support perceptual cycles in distinct modalities. As developed in Box 1, one could tentatively assign ~10 Hz (alpha) cycles to sensory periodicities, while ~7 Hz (theta) rhythms may contribute to higher-level, attentional cycles (see also Box 2). However, it must be emphasized that careful consideration of Table S1 does not (as yet) uphold any strict taxonomy linking specific frequencies to specific functional processes (see Box 3: Current Limitations).

Is Temporal Parsing a Rhythmic Process?

Perceptual cycles were shown to affect nearly all aspects of perception and cognition. Their influence on temporal parsing mechanisms, however, is of special theoretical importance because it more directly supports the notion of discrete as opposed to rhythmic perception



Trends in Cognitive Sciences

Figure 3. Spectral Distribution of Published Experimental Studies Reporting Perceptual Cycles in the Visual (Blue) and Non-Visual (Red) Modalities (the Latter Including Tactile and Auditory as well as Cross-Modal Studies). Each study is only counted once; when a study reports multiple distinct periodicities, the corresponding frequencies are given a proportionally lower weight in the histogram. The area under each histogram is thus equal to the number of studies in each class. Although the total number of studies in the visual domain (n = 61) clearly exceeds those in other domains (n = 28), the shapes of the two frequency profiles are not significantly different. Note that this conclusion remains true when all studies measuring a visual rhythm (influenced by stimulation in other modalities) are discarded from the list of cross-modal periodicities.

Box 3. Current Limitations

Effect Size and Negative Results

The large number of recent studies demonstrating perceptual cycles does not imply that such evidence is easy to obtain. Most reported effects are subtle (often a small percent of behavioral or perceptual variability). The apparent surge in positive findings could thus reflect, in part, recent improvements in signal processing and statistical analysis methods. It is still unknown whether this small effect size is a technical limitation of experimental paradigms (e.g., owing to measurement noise) or a true reflection of the meager contribution of these periodicities to the overall perceptual experience. In addition, although only a handful of negative findings have been explicitly reported [133,134], it is notoriously difficult to appreciate the number of unpublished negative results–the so-called 'file drawer' effect.

Low-Frequency Bias

Although brain oscillations are found at all frequencies up to at least 100 Hz [4], perceptual cycles appear to be limited to lower frequencies (<15 Hz). This bias could be technical: for example, the frequency range of behavioral oscillations is often constrained below 20 Hz by the limited number of trials, while the signal-to-noise ratio of EEG and MEG declines rapidly with frequency. By contrast, some cycles of neural information processing might well exist at higher frequencies, but it could be argued that, if this rate exceeds the temporal resolution of the perceptual system, the ensuing perceptual consequences would simply not occur.

Scarcity of Physiological Data

Invasive recordings in animals constitute, so far, only a minimal fraction of the available evidence (less than 10%; see Table S1 in the supplemental information online). Nevertheless, only these techniques enjoy a spatiotemporal resolution sufficient to resolve the origins of perceptual cycles. Physiological studies could also help to elucidate the potential existence of higher-frequency cycles, as well as other important questions: does every sensory area produce a perceptual periodicity at its own rhythm? What about different hierarchical levels in the same sensory system [135]? Are thalamocortical loops an important source of periodicity?

Functional Advantages?

It is not immediately apparent how perception would benefit from a periodic temporal organization. Oscillations could create temporal windows that favor communication between neurons [136,137]. Rhythmic framing also permits using the nested temporal structure, within each oscillatory cycle, as a means to encode other, non-temporal stimulus dimensions [138–140]. Concentrating neuronal resources at specific moments in time could also be energy-efficient. Finally, it might be that brain oscillations and the associated perceptual rhythms confer no specific advantage to sensory perception, but instead arise as a consequence of satisfying physiological and anatomical constraints. It might simply be impossible (or at least, needlessly complicated) for the brain to operate without such (wanted or unwanted) periodicities.

(Figure 1). Although this issue remained undecided for many years [3,7,124], recent evidence has accumulated for cyclic temporal parsing in vision. Parsing performance was affected by ongoing MEG and EEG phase around the alpha frequency range [26–30], and by within- and between-observer changes in the exact frequency of the alpha rhythm [43,44]. Behavioral oscillations of temporal parsing were also reported between 3 and 12 Hz [30,125]. Thus, at least in the visual modality, perception may well be discrete after all [3] (so far, only one corresponding report exists in the tactile domain around 14 Hz [84], and one in the auditory domain at around 40 Hz [126]).

Concluding Remarks and Future Directions

The inventory of findings presented here suggests that the study of discrete perception has recently switched gears. After conceding that there might not exist a single common sampling rhythm affecting all of our perceptions, but instead many simultaneous rhythms that periodically modulate various perceptual and cognitive functions in distinct modalities at independent rates, one begins to see perceptual rhythms (almost) everywhere (see, however, Box 3). The frequencies of these periodicities are very diverse, but with clear peaks at 10 Hz and 7 Hz (Box 1 and Figure 3), which can be tentatively ascribed to sensory and attentional sampling rhythms, respectively. Importantly, periodicities are also found to affect temporal parsing mechanisms, supporting a more 'extreme' version of discrete perception in which the temporal continuity of

Outstanding Questions

Can we define a taxonomy of perceptual cycles? Current evidence does not support the notion that each rhythmic frequency could be associated with a well-defined brain function, and vice versa. We may need many more datapoints until the correct picture emerges: a taxonomy of perceptual rhythms relating each brain function to a specific periodicity, with a well-defined frequency, and involving a particular network of brain regions.

How are distinct cycles coordinated? The fact that rhythmic perception occurs concurrently for multiple sensory and cognitive processes, with potentially distinct phases and frequencies, poses a serious problem for any communication between these processes (and for communication with motor outputs that may also present intrinsic periodicities): perceptual cycles need to synchronize their 'best' phase for optimal transmission. How this coordination is achieved remains a key question for the future.

How do perceptual cycles relate to overt sampling? Perceptual cycles can be thought of as an inward or covert form of perceptual sampling, one that the brain operates on its own inner states. However, in addition, sensory information is also sampled overtly (e.g., by saccades and microsaccades, by sniffing, and whisking in rodents), and this type of movement behavior can often display temporal rhythmicity. Intrinsic sensory periodicities and overt sampling rhythms also need to coordinate their cycles for optimal performance. An intriguing possibility is that ~7 Hz attentional cycles evolved from oculomotor sampling rhythms at 3–4 Hz: by directing the samples to internal neural representations rather than external stimuli, metabolic costs of overt movements are spared, and exploration can operate faster (here, at twice the rate).

Do perceptual cycles have spatial dimensions? Perceptual cycles are not necessarily spatially uniform. An alternative, for example, would be that the sampling phase propagates smoothly across space, as in a traveling wave. Most existing experiments were designed to investigate temporal dynamics, and ignored this spatial dimension.

experience itself is chopped up in successive frames or snapshots. This conclusion brings up a host of further questions (see Outstanding Questions) that should keep this field lively for the foreseeable future.

Acknowledgments

The work described was funded by an European Research Council Consolidator Grant 614244 (P-CYCLES). I am indebted to past and present members of my lab for helping me, directly or indirectly, to put together an extensive list of bibliographic references. In addition, I wish to thank Leila Reddy for detailed comments on the manuscript.

Supplemental Information

Supplemental information related to this article can be found online at http://dx.doi.org/10.1016/j.tics.2016.07.006.

References

1. Stroud, J.M. (1956) The fine structure of psychological time. In *Information Theory in Psychology* (Quastler, H., ed.), pp. 174–205, Free Press
2. VanRullen, R. (2016) Perceptual Rhythms. In *Stevens Handbook of Experimental Psychology* (Serences, J., ed.), Wiley (in press)
3. VanRullen, R. and Koch, C. (2003) Is perception discrete or continuous? *Trends Cogn. Sci.* 7, 207–213
4. Buzsáki, G. (2006) *Rhythms of the Brain,* Oxford University Press
5. McLelland, D. and Paulsen, O. (2009) Neuronal oscillations and the rate-to-phase transform: mechanism, model and mutual information. *J. Physiol.* 587, 769–785
6. Haegens, S. *et al.* (2011) Alpha-oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. U.S.A.* 108, 19377–19382
7. Varela, F.J. *et al.* (1981) Perceptual framing and cortical alpha rhythm. *Neuropsychologia* 19, 675–686
8. VanRullen, R. *et al.* (2011) Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Frontiers in Perception Science* 2, 1–9
9. Nunn, C.M. and Osselton, J.W. (1974) The influence of the EEG alpha rhythm on the perception of visual stimuli. *Psychophysiology* 11, 294–303
10. Busch, N.A. *et al.* (2009) The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci.* 29, 7869–7876
11. Mathewson, K.E. *et al.* (2009) To see or not to see: prestimulus alpha phase predicts visual awareness. *J. Neurosci.* 29, 2725–2732
12. Busch, N.A. and VanRullen, R. (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc. Natl. Acad. Sci. U.S.A.* 107, 16048–16053
13. Dugué, L. *et al.* (2011) The phase of ongoing oscillations mediates the causal relation between brain excitation and visual perception. *J. Neurosci.* 31, 11889–11893
14. Fiebelkorn, I.C. *et al.* (2013) Cortical cross-frequency coupling predicts perceptual outcomes. *Neuroimage* 69, 126–137
15. Hanslmayr, S. *et al.* (2013) Prestimulus oscillatory phase at 7 Hz gates cortical information flow and visual perception. *Curr. Biol.* 23, 2273–2278
16. Manasseh, G. *et al.* (2013) Retinal and post-retinal contributions to the quantum efficiency of the human eye revealed by electrical neuroimaging. *Frontiers in Psychology* 4
17. Callaway, E.I. and Yeager, C.L. (1960) Relationship between reaction time and electroencephalographic alpha phase. *Science* 132, 1765–1766
18. Dustman, R.E. and Beck, E.C. (1965) Phase of alpha brain waves, reaction time and visually evoked potentials. *Electroencephalogr Clin. Neurophysiol.* 18, 433–440
19. Drewes, J. and VanRullen, R. (2011) This is the rhythm of your eyes: the phase of ongoing electroencephalogram oscillations modulates saccadic reaction time. *J. Neurosci.* 31, 4698–4708
20. Hamm, J.P. *et al.* (2012) Pre-cue fronto-occipital alpha phase and distributed cortical oscillations predict failures of cognitive control. *J. Neurosci.* 32, 7034–7041
21. McLelland, D. *et al.* (2016) The phase of ongoing EEG oscillations predicts the amplitude of peri-saccadic mislocalization. *Sci. Rep.* 6, 29335
22. Buschman, T.J. and Miller, E.K. (2009) Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations. *Neuron* 63, 386–396
23. Dugué, L. *et al.* (2015) Theta oscillations modulate attentional search performance periodically. *J. Cogn. Neurosci.* 27, 945–958
24. Landau, A.N. *et al.* (2015) Distributed attention is implemented through theta-rhythmic gamma modulation. *Curr. Biol.* 25, 2332–2337
25. Voloh, B. *et al.* (2015) Theta–gamma coordination between anterior cingulate and prefrontal cortex indexes correct attention shifts. *Proc. Natl. Acad. Sci. U.S.A.* 112, 8457–8462
26. Chakravarthi, R. and VanRullen, R. (2012) Conscious updating is a rhythmic process. *Proc. Natl. Acad. Sci.U.S.A.* 109, 10599–10604
27. Cravo, A.M. *et al.* (2015) Visual causality judgments correlate with the phase of alpha oscillations. *J. Cogn. Neurosci.* 27, 1887–1894
28. Inyutina, M. *et al.* (2015) Who wins the race for consciousness? Ask the phase of ongoing ~7 Hz oscillations. *J. Vis.* 15, 569
29. Milton, A. and Pleydell-Pearce, C.W. (2016) The phase of pre-stimulus alpha oscillations influences the visual perception of stimulus timing. *Neuroimage* 133, 53–61
30. Wutz, A. *et al.* (2016) Temporal integration windows in neural processing and perception aligned to saccadic eye movements. *Curr. Biol.* 26, 1659–1668
31. Wyart, V. *et al.* (2012) Rhythmic fluctuations in evidence accumulation during decision making in the human brain. *Neuron* 76, 847–858
32. Samaha, J. *et al.* (2015) Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proc. Natl. Acad. Sci. U.S.A.* 112, 8439–8444
33. Sherman, M.T. *et al.* (2016) Rhythmic influence of top-down perceptual priors in the phase of pre-stimulus occipital alpha oscillations. *J. Cog. Neuroscience* 28, 1318–1330
34. Han, B. and VanRullen, R. (2016) The rhythms of predictive coding: pre-stimulus oscillatory phase modulates the influence of shape perception on luminance judgments. *bioRxiv* Published online June 29, 2016. http://dx.doi.org/10.1101/061309
35. Siegel, M. *et al.* (2009) Phase-dependent neuronal coding of objects in short-term memory. *Proc. Natl. Acad. Sci. U.S.A.* 106, 21341–21346
36. Fuentemilla, L. *et al.* (2010) Theta-coupled periodic replay in working memory. *Curr. Biol.* 20, 606–612
37. Bonnefond, M. and Jensen, O. (2012) Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Curr. Biol.* 22, 1969–1974
38. Myers, N.E. *et al.* (2014) Oscillatory brain state predicts variability in working memory. *J. Neurosci.* 34, 7735–7743
39. Leszczynski, M. *et al.* (2015) Rhythmic working memory activation in the human hippocampus. *Cell Rep.* 13, 1272–1282

40. Jansen, B.H. and Brandt, M.E. (1991) The effect of the phase of prestimulus alpha activity on the averaged visual evoked response. *Electroencephalogr Clin. Neurophysiol.* 80, 241–250
41. Gruber, W.R. *et al.* (2014) Alpha phase, temporal attention, and the generation of early event related potentials. *Neuroimage* 103, 119–129
42. Scheeringa, R. *et al.* (2011) Modulation of visually evoked cortical fMRI responses by phase of ongoing occipital alpha oscillations. *J. Neurosci.* 31, 3813–3820
43. Kristofferson, A.B. (1967) Successiveness discrimination as a two-state, quantal process. *Science* 158, 1337–1339
44. Samaha, J. and Postle, B.R. (2015) The speed of alpha-band oscillations predicts the temporal resolution of visual perception. *Curr. Biol.* 25, 2985–2990
45. VanRullen, R. and Dubois, J. (2011) The psychophysics of brain rhythms. *Front Psychol.* 2, 203
46. Venables, P.H. (1960) Periodicity in reaction time. *Brit. J. Psychol.* 51, 37–43
47. Latour, P.L. (1967) Evidence of internal clocks in the human operator. *Acta Psychol.* 27, 341–348
48. Harter, M.R. and White, C.T. (1968) Periodicity within reaction time distributions and electromyograms. *Q. J. Exp. Psychol.* 20, 157–166
49. Poppel, E. and Logothetis, N. (1986) Neuronal oscillations in the human brain. Discontinuous initiations of pursuit eye movements indicate a 30-Hz temporal framework for visual information processing. *Naturwissenschaften* 73, 267–268
50. Dehaene, S. (1993) Temporal oscillations in human perception. *Psychol. Sci.* 4, 264–270
51. Landau, A.N. and Fries, P. (2012) Attention samples stimuli rhythmically. *Curr. Biol.* 22, 1000–1004
52. Fiebelkorn, I.C. *et al.* (2013) Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr. Biol.* 23, 2553–2558
53. Dugué, L. and VanRullen, R. (2014) The dynamics of attentional sampling during visual search revealed by Fourier analysis of periodic noise interference. *J. Vis.* 14, 11
54. Song, K. *et al.* (2014) Behavioral oscillations in attention: rhythmic alpha pulses mediated through theta band. *J. Neurosci.* 34, 4837–4844
55. Dugué, L. *et al.* (2015) Attention searches nonuniformly in space and in time. *Proc. Nat. Acad. Sci.* 112, 15214–15219
56. Huang, Y. *et al.* (2015) Behavioral oscillation in priming: competing perceptual predictions conveyed in alternating theta-band rhythms. *J. Vis.* 15, 1246
57. VanRullen, R. *et al.* (2007) The blinking spotlight of attention. *Proc. Natl. Acad. Sci. U.S.A.* 104, 19204–19209
58. Blais, C. *et al.* (2013) Human visual processing oscillates: evidence from a classification image technique. *Cognition* 128, 353–362
59. Drewes, J. *et al.* (2015) Dense sampling reveals behavioral oscillations in rapid visual categorization. *Sci. Rep.* 5, 16290
60. Sokoliuk, R. and VanRullen, R. (2013) The fickering wheel illusion: when alpha rhythms make a static wheel flicker. *J. Neurosci.* 33, 13498–13504
61. Bowen, R.W. (1989) Two pulses seen as three flashes: a superposition analysis. *Vision Res.* 29, 409–417
62. Gulbinaite, R. *et al.* (2016) Something out of nothing: the role of alpha-frequency reverberation in the triple-flash illusion. *F1000Research* 5–1781 http://dx.doi.org/10.7490/f1000research.1112669.1
63. VanRullen, R. and Macdonald, J.S.P. (2012) Perceptual echoes at 10 Hz in the human brain. *Curr. Biol.* 22, 995–999
64. Cavanagh, P. and Mather, G. (1989) Motion: the long and short of it. *Spat. Vis.* 4, 103–129
65. Schouten, J.F. (1967) Subjective stroboscopy and a model of visual movement detectors. In *Models for the Perception of Speech and Visual Form* (Wathen-Dunn, I., ed.), pp. 44–45, MIT Press
66. Purves, D. *et al.* (1996) The wagon wheel illusion in movies and reality. *Proc. Natl. Acad. Sci. U.S.A.* 93, 3693–3697
67. Simpson, W.A. *et al.* (2005) Illusory percepts of moving patterns due to discrete temporal sampling. *Neurosci. Lett.* 375, 23–27
68. VanRullen, R. *et al.* (2005) Attention-driven discrete sampling of motion perception. *Proc. Natl. Acad. Sci. U.S.A.* 102, 5291–5296
69. VanRullen, R. *et al.* (2006) The continuous wagon wheel illusion is associated with changes in electroencephalogram power at approximately 13 Hz. *J. Neurosci.* 26, 502–507
70. Piantoni, G. *et al.* (2010) Beta oscillations correlate with the probability of perceiving rivalrous visual stimuli. *J. Vis.* 10, 18
71. VanRullen, R. *et al.* (2008) The continuous wagon wheel illusion and the ‘when’ pathway of the right parietal lobe: a repetitive transcranial magnetic stimulation study. *PLoS ONE* 3, e2911
72. Reddy, L. *et al.* (2011) Neural correlates of the continuous wagon wheel illusion: a functional MRI study. *Hum. Brain Mapp.* 32, 163–170
73. Kline, K. *et al.* (2004) Illusory motion reversal is caused by rivalry, not by perceptual snapshots of the visual field. *Vision Res.* 44, 2653–2658
74. Andrews, T. *et al.* (2005) The wheel keeps turning: reply to Holcombe *et al*. *Trends Cogn. Sci.* 9, 561
75. Holcombe, A.O. *et al.* (2005) Illusory motion reversal in tune with motion detectors. *Trends Cogn. Sci.* 9, 559–560
76. VanRullen, R. (2006) The continuous wagon wheel illusion is object-based. *Vision Res.* 46, 4091–4095
77. VanRullen, R. (2007) The continuous wagon wheel illusion depends on, but is not identical to neuronal adaptation. *Vision Res.* 47, 2143–2149
78. Holcombe, A.O. and Seizova-Cajic, T. (2008) Illusory motion reversals from unambiguous motion with visual, proprioceptive, and tactile stimuli. *Vision Res.* 48, 1743–1757
79. Kline, K. and Eagleman, D.M. (2008) Evidence against the temporal subsampling account of illusory motion reversal. *J. Vis.* 8, 11–15
80. VanRullen, R. *et al.* (2010) A motion illusion revealing the temporally discrete nature of awareness. In *Space and Time in Perception and Action* (Nijhawan, R., ed.), pp. 521–535, Cambridge University Press
81. Zeki, S. (1991) Cerebral akinetopsia (visual motion blindness). A review. *Brain* 114, 811–824
82. Dubois, J. and VanRullen, R. (2011) Visual trails: do the doors of perception open periodically? *PLoS Biol.* 9, e1001056
83. Ai, L. and Ro, T. (2014) The phase of prestimulus alpha oscillations affects tactile perception. *J. Neurophysiol.* 111, 1300–1307
84. Baumgarten, T.J. *et al.* (2015) Beta oscillations define discrete perceptual cycles in the somatosensory domain. *Proc. Natl. Acad. Sci. U.S.A.* 112, 12187–12192
85. VanRullen, R. *et al.* (2014) On the cyclic nature of perception in vision versus audition. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 369, 20130214
86. Large, E.W. and Jones, M.R. (1999) The dynamics of attending: how people track time-varying events. *Psychol. Rev.* 106, 119–159
87. Lakatos, P. *et al.* (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320, 110–113
88. Ghitza, O. (2011) Linking speech perception and neurophysiology: speech decoding guided by cascaded oscillators locked to the input rhythm. *Front. Psychol.* 2, 130
89. Giraud, A.L. and Poeppel, D. (2012) Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.* 15, 511–517
90. Gross, J. *et al.* (2013) Speech rhythms and multiplexed oscillatory sensory coding in the human brain. *PLoS Biol.* 11, e1001752
91. Henry, M.J. *et al.* (2014) Entrained neural oscillations in multiple frequency bands comodulate behavior. *Proc. Natl. Acad. Sci. U. S.A.* 111, 14935–14940
92. Hickok, G. *et al.* (2015) The rhythm of perception: entrainment to acoustic rhythms induces subsequent perceptual oscillation. *Psychol. Sci.* 26, 1006–1013
93. Kayser, C. *et al.* (2015) Rhythmic auditory cortex activity at multiple timescales shapes stimulus-response gain and background firing. *J. Neurosci.* 35, 7750–7762

94. Zoefel, B. and VanRullen, R. (2015) Selective perceptual phase entrainment to speech rhythm in the absence of spectral energy fluctuations. *J. Neurosci.* 35, 1954–1964

95. Zoefel, B. and VanRullen, R. (2015) EEG oscillations entrain their phase to high-level features of speech sound. *Neuroimage* 124, 16–23

96. Zion-Golumbic, E.M. *et al.* (2013) Mechanisms underlying selective neuronal tracking of attended speech at a 'cocktail party'. *Neuron* 77, 980–991

97. Rice, D.M. and Hagstrom, E.C. (1989) Some evidence in support of a relationship between human auditory signal-detection performance and the phase of the alpha cycle. *Percept. Mot. Skills* 69, 451–457

98. Haig, A.R. and Gordon, E. (1998) EEG alpha phase at stimulus onset significantly affects the amplitude of the P3 ERP component. *Int. J. Neurosci.* 93, 101–115

99. Barry, R.J. *et al.* (2004) Event-related potentials in the auditory oddball as a function of EEG alpha phase at stimulus onset. *Clin. Neurophysiol.* 115, 2593–2601

100. İlhan, B. and VanRullen, R. (2012) No counterpart of visual perceptual echoes in the auditory system. *PLoS ONE* 7, e49287

101. Ng, B.S. *et al.* (2012) A precluding but not ensuring role of entrained low-frequency oscillations for auditory perception. *J. Neurosci.* 32, 12268–12276

102. Zoefel, B. and Heil, P. (2013) Detection of near-threshold sounds is independent of EEG phase in common frequency bands. *Front. Psychol.* 4, 262

103. Fontolan, L. *et al.* (2014) The contribution of frequency-specific activity to hierarchical information processing in the human auditory cortex. *Nat. Commun.* 5, 4694

104. Arnal, L.H. *et al.* (2015) Delta–beta coupled oscillations underlie temporal prediction accuracy. *Cereb. Cortex* 25, 3077–3085

105. Strauss, A. *et al.* (2015) Alpha phase determines successful lexical decision in noise. *J. Neurosci.* 35, 3256–3262

106. Ten Oever, S. *et al.* (2015) Increased stimulus expectancy triggers low-frequency phase reset during restricted vigilance. *J. Cogn. Neurosci.* 27, 1811–1822

107. Zoefel, B. *et al.* (2015) The ability of the auditory system to cope with temporal subsampling depends on the hierarchical level of processing. *Neuroreport* 26, 773–778

108. Kayser, S.J. *et al.* (2016) Prestimulus influences on auditory perception from sensory representations and decision processes. *Proc. Natl. Acad. Sci. U.S.A.* 113, 4842–4847

109. Lakatos, P. *et al.* (2009) The leading sense: supramodal control of neurophysiological context by attention. *Neuron* 64, 419–430

110. Romei, V. *et al.* (2012) Sounds reset rhythms of visual cortex and corresponding human visual perception. *Curr. Biol.* 22, 807–813

111. Mercier, M.R. *et al.* (2013) Auditory-driven phase reset in visual cortex: human electrocorticography reveals mechanisms of early multisensory integration. *Neuroimage* 79, 19–29

112. Diederich, A. *et al.* (2012) Saccadic reaction times to audiovisual stimuli show effects of oscillatory phase reset. *PLoS ONE* 7, e44910

113. Diederich, A. *et al.* (2014) Fronto-central theta oscillations are related to oscillations in saccadic response times (SRT): an EEG and behavioral data analysis. *PLoS ONE* 9, e112974

114. Fiebelkorn, I.C. *et al.* (2011) Ready, set, reset: stimulus-locked periodicity in behavioral performance demonstrates the consequences of cross-sensory phase reset. *J. Neurosci.* 31, 9971–9981

115. Cecere, R. *et al.* (2015) Individual differences in alpha frequency drive crossmodal illusory perception. *Curr. Biol.* 25, 231–235

116. van Erp, J.B. *et al.* (2014) Pre- and post-stimulus EEG patterns associated with the touch-induced illusory flash. *Neurosci. Lett.* 562, 79–84

117. Lakatos, P. *et al.* (2007) Neuronal oscillations and multisensory interaction in primary auditory cortex. *Neuron* 53, 279–292

118. Kayser, C. *et al.* (2008) Visual modulation of neurons in auditory cortex. *Cereb. Cortex* 18, 1560–1574

119. Mercier, M.R. *et al.* (2015) Neuro-oscillatory phase alignment drives speeded multisensory response times: an electro-corticographic investigation. *J. Neurosci.* 35, 8546–8557

120. Perrodin, C. *et al.* (2015) Natural asynchronies in audiovisual communication signals regulate neuronal multisensory interactions in voice-sensitive cortex. *Proc. Natl. Acad. Sci. U.S.A.* 112, 273–278

121. Tomassini, A. *et al.* (2015) Rhythmic oscillations of visual contrast sensitivity synchronized with action. *J. Neurosci.* 35, 7019–7029

122. Benedetto, A. *et al.* (2016) Rhythmic modulation of visual contrast discrimination triggered by action. *Proc. R. Soc. Lond B Biol. Sci.* 283, 20160692

123. Hogendoorn, H. (2016) Voluntary saccadic eye movements ride the attentional rhythm. *J. Cogn. Neurosci.* Published online May 31, 2106. http://dx.doi.org/10.1162/jocn_a_00986

124. Gho, M. and Varela, F.J. (1988) A quantitative assessment of the dependency of the visual temporal frame upon the cortical rhythm. *J. Physiol.* 83, 95–101

125. Morand, S. *et al.* (2015) Temporal framing in apparent motion perception cycles with a 12 Hz (alpha) rhythm. *J. Vis.* 15, 588

126. Baltus, A. and Herrmann, C.S. (2015) Auditory temporal resolution is linked to resonance frequency of the auditory cortex. *Int. J. Psychophysiol.* 98, 1–7

127. VanRullen, R. (2016) How to evaluate phase differences between trial groups in ongoing electrophysiological signals. *bioRxiv* Published online June 29, 2016. http://dx.doi.org/10.1101/061283

128. VanRullen, R. (2013) Visual attention: a rhythmic process? *Curr. Biol.* 23, R1110–R1112

129. Dugué, L. *et al.* (2015) Attention searches nonuniformly in space and in time. *Proc. Natl. Acad. Sci. U.S.A.* 112, 15214–15219

130. Dugué, L. *et al.* (2016) Attention reorients periodically. *Curr. Biol.* 26, 1595–1601

131. Holcombe, A.O. and Chen, W.Y. (2013) Splitting attention reduces temporal resolution from 7 Hz for tracking one object to <3 Hz when tracking three. *J. Vis.* 13, 12

132. Macdonald, J.S. *et al.* (2014) Attentional sampling of multiple wagon wheels. *Atten. Percept. Psychophys.* 76, 64–72

133. Walsh, E.G. (1952) Visual reaction time and the alpha-rhythm, an investigation of a scanning hypothesis. *J. Physiol.* 118, 500–508

134. Bompas, A. *et al.* (2015) The contribution of pre-stimulus neural oscillatory activity to spontaneous response time variability. *Neuroimage* 107, 34–45

135. Rosanova, M. *et al.* (2009) Natural frequencies of human corticothalamic circuits. *J. Neurosci.* 29, 7679–7685

136. Varela, F.J. *et al.* (2001) The brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2, 229–239

137. Fries, P. (2015) Rhythms for cognition: communication through coherence. *Neuron* 88, 220–235

138. Lisman, J. (2005) The theta/gamma discrete phase code occurring during the hippocampal phase precession may be a more general brain coding scheme. *Hippocampus* 15, 913–922

139. VanRullen, R. *et al.* (2005) Spike times make sense. *Trends Neurosci.* 28, 1–4

140. Jensen, O. *et al.* (2012) An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends Cogn. Sci.* 16, 200–206