CellPress

Review

Perceptual Cycles

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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

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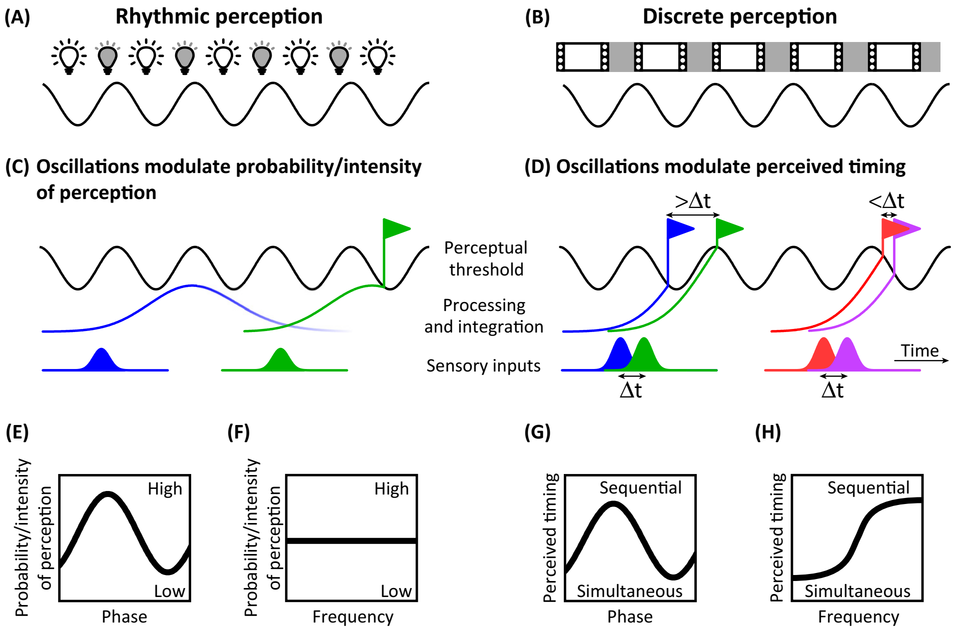

Figure 1. Rhythmic and Discrete Perception. (A) The notion of rhythmic perception (also referred to as cyclic or periodic perception) implies that a particular phase of each oscillatory cycle gives rise to more efficient neuronal, sensory, perceptual, or cognitive processing (illustrated here by the 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