

# Is perception discrete or continuous?

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**How does conscious perception evolve following stimulus presentation? The idea that perception relies on discrete processing epochs has been often considered, but never widely accepted. The alternative, a continuous translation of the external world into explicit perception, although more intuitive and subjectively appealing, cannot satisfactorily account for a large body of psychophysical data. Cortical and thalamocortical oscillations in different frequency bands could provide a neuronal basis for such discrete processes, but are rarely analyzed in this context. This article reconciles the unduly abandoned topic of discrete perception with current views and advances in neuroscience.**

In the quest for the neuronal correlates of consciousness, time is an important but often ignored variable: *when* percepts arise is probably as fundamental a question as *where* they do. How do percepts and their neural representations evolve over time, both when the outside world is standing still or when it is abruptly changing, such as during an eye movement? Do we experience the world as a continuous signal or as a discrete sequence of events, like the snapshots of a Multimedia Component camera? Although the subjectively seamless nature of our experience would suggest that the relevant underlying neuronal representations evolve continuously, this is not the only possibility. Conscious perception might well be constant within a snapshot of variable duration.

The idea of discrete perception was already considered, but quickly discarded by William James [1]. It faced a renewal during the 20th century with the expansion of the cinematograph – an obvious technological metaphor. The most influential modern version of this discrete sampling hypothesis is the ‘perceptual moment’ theory of Stroud [2]. The popularity of this topic peaked around 50 years ago, and has declined continuously since. We review the psychological evidence for discrete visual perception and advocate that, although definitive experimental evidence is still lacking, the case is not at all closed. We will see that oscillations in different frequency bands could serve as a neural substrate for such processes.

## Psychophysical evidence for discrete processes in visual perception

The concept of ‘discrete perception’ should not be confounded with that of an integration period (Box 1): whereas the latter only determines the temporal resolution of perception, the former is intrinsically linked to the process of perception

itself. Discrete perception implies that two distinct events will be judged as simultaneous or sequential depending not only on the time interval between them, but also on their temporal relationship to some intrinsic discrete neuronal process. Historically, many psychological observations have been related to such discrete processes [2–4].

### *Apparent simultaneity and temporal numerosity*

There is a certain minimal interstimulus interval for which two successive events are consistently perceived as simultaneous: one can think of them as occurring within a single discrete ‘epoch’ of processing time. This interval depends on stimulus conditions and has been estimated to be around 20–50 ms [5,6]. When the stimulus (composed of many distinct visual events, for example, 8 flashing lights) is repeated in cycles of less than 125 ms periodicity, all stimuli within one cycle are reported as occurring together, regardless of the specific time differences between them [7]. When the frequency of visual stimulation is varied, subjective reports of the number of elements presented in a cycle reach a ceiling at an effective rate of ~10–12 item/s [8]. Similar experiments using dichoptic stimulation have demonstrated that this phenomenon occurs following binocular fusion, that is, at a later stage than V1 and is thus not due to peripheral limitations [9,10]. Overall, these studies are compatible with the idea of a discrete perceptual ‘frame’ of ~100 ms or less within which stimuli would be grouped and subjectively interpreted as a single event. Of course, this does not preclude the existence of specialized neural circuitry that resolves effective time differences at the (sub)millisecond level in motion, auditory localization and other modalities.

### *Periodicity in reaction time*

Close inspection of reaction-time histograms reveals periodicities at intervals of ~100 ms [11] and 25 ms [8]. These could occur if some stimuli arriving too late to be processed in one particular discrete epoch were deferred to the next. Note that this would only become apparent in reaction time histograms if the length or the onset of these discrete epochs was dependent on stimulus presentation. Some studies find that the length of this periodic interval is task-dependent, with an average of ~25 ms [12]. We will later return to the apparent discrepancy between the duration of these periodicities in behavior versus perceptual simultaneity judgement.

### *Periodicity in visual threshold*

Visual thresholds themselves were found to oscillate, with a period of ~25 ms [13]. This means that the postulated

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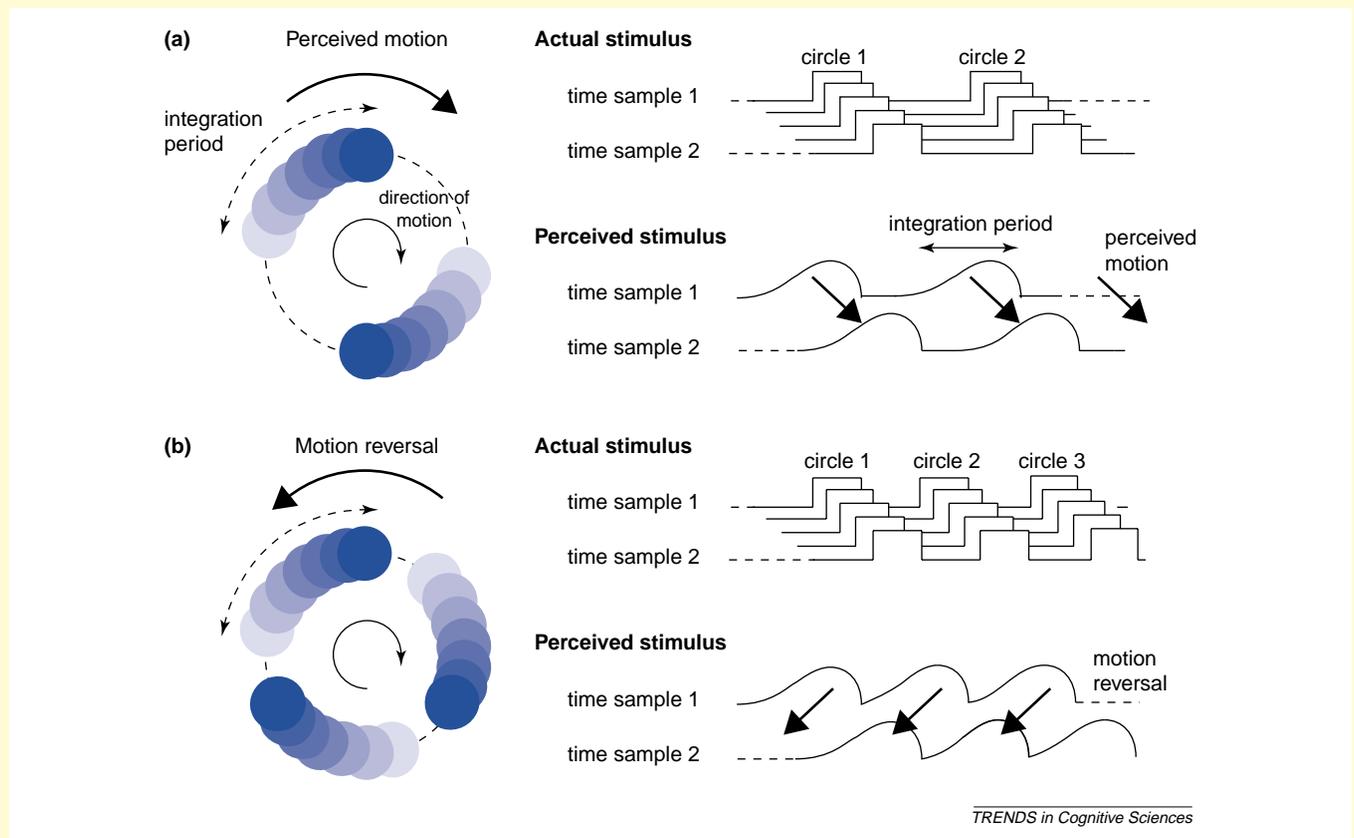
### Box 1. Concept definition: discrete perception versus integration period

An integration period can be considered as a low-pass filtering of the input signal, which could take place at different levels of the visual system [14]. This 'blurring' along a particular feature dimension, characteristic of an integration period, can occur regardless of how the visual system actually processes sequences of events (i.e. in a continuous versus discrete fashion).

In Fig 1, an integration period can thus explain why the movement of the disks appears 'blurred'. However, some form of discrete sampling process can be invoked to account for the occasional motion reversal seen when the alternation rate is increased. This phenomenon, also called the 'wagon wheel illusion,'

is particularly obvious in Multimedia Component because of their discrete sampling at 24 images/s. Remarkably, it can also be observed in broad daylight [17]. This could be taken to imply that the visual system represents continuous events as a sequence of discrete perceptual 'snapshots' [53].

Note that there exist several differences between this illusion in broad daylight and its cinematographic cousin [17]. For example, the percept of the wheel cannot be brought to a stop under continuous light. The troubling fact remains that motion reversals are difficult to explain without assuming a discrete processing component acting during, or before, the perception of motion.



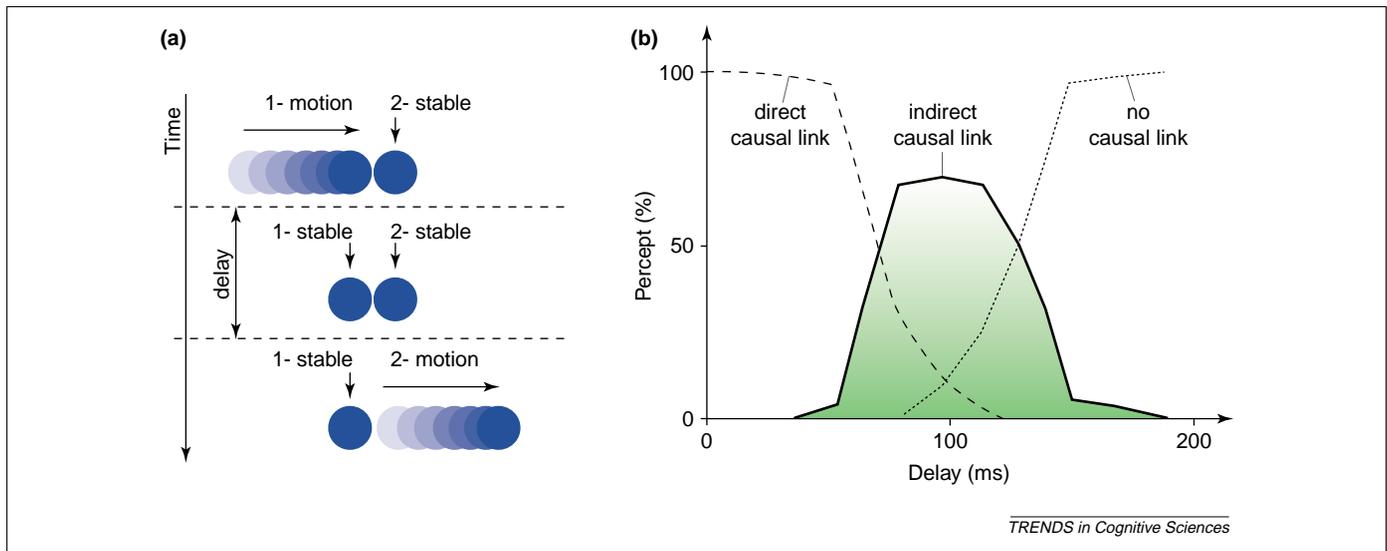
**Fig. 1.** The wagon-wheel illusion under continuous light. An integration period implies that the appearance of an object along a particular feature dimension can be 'blurred' if the relevant stimulus attribute is changing faster than the duration of the integration period. In the schematic illustrations on the left, circles rotating faster than a certain speed will appear to leave a trace behind them: their spatial location is not perceived at a single point in time, but as the result of a temporal integration period. This 'blurring' could occur in both a discrete or a continuous processing framework. On the other hand, the existence of perceived motion reversals at certain critical alternation rates (b) can be taken to imply that spatial location (or potentially, other stimulus attributes such as motion) is sampled in a discrete manner. When the stimulus alternation rate increases, either by increasing the rotation speed or by introducing additional stimuli (as done between a and b), the most likely interpretation of the circular motion that has occurred between two consecutive (and discrete) time samples can become the opposite of the actual direction of motion: a motion reversal is perceived.

discrete mechanism could be perceptual by nature, and take place before central or motor decision stages.

#### Perceived causality

A moving disk reaches another one and pauses for a certain delay, before the second disk starts moving itself. As a function of the intervening delay, the *qualitative* perception of causality between these two events changes, rather abruptly every 70 ms (see Fig. 1): for delays under 70 ms, the first event appears to directly cause the second; between 70 and 140 ms, the first event now seems to cause the second in an 'indirect' way; after 140 ms, the two events appear independent [3].

Arguably, many of the above observations (e.g. apparent simultaneity, temporal numerosity) can theoretically be explained by a temporal integration mechanism acting as a 'low-pass filter' on the visual input [14]. Conceptually equivalent hypotheses have been considered under the names of 'moving average' [3], 'travelling moment' [15] or 'sensory persistence' [16]. However, it is also clear that several of these findings (e.g. observations of reaction time or visual threshold periodicities) cannot easily be accounted for by such mechanisms. In particular, the observation that reversals of perceived motion direction (the 'wagon wheel' illusion; see Box 1) can be perceived in continuous light [17] can be interpreted as evidence for a



**Fig. 1. Discrete effects in causality perception.** (a) Disk 1 moves towards disk 2 and stops. After a certain delay, disk 2 starts moving in the same direction, away from disk 1. (b) The associated percept of causality changes abruptly as a function of the intervening delay. Below 70 ms, stimulus 1 appears to directly set stimulus 2 in motion (dashed line, direct causal link). For delays between 70 and 140 ms, the causal link is still apparent, but more indirect, as if the two stimuli would 'stick' together for a short period of time (solid line, indirect causal link). After ~140 ms, the apparent causal link (dotted line) vanishes. (Adapted from [3].)

discrete sampling process (although this interpretation remains controversial).

There appears to be no valid reason, apart from the usual fluctuations of interest in any scientific community, why the question of discrete perception was abandoned. We recognize, however, that single-cell electrophysiology, the current gold standard of brain science, has yet to clearly reveal such mechanisms.

If such processes exist in the brain, they are unlikely to be implemented by a strictly synchronous clock as in today's computers. Instead, as emphasized already by Stroud [2], their period will be variable, depending on stimulus contrast and saliency, attention and task requirements. Their onset or phase will depend on stimulus-induced reset (e.g. flashing the image) and eye movements. Furthermore, perceived motion might well involve different process durations as perceived color, just as the duration of auditory, tactile or olfactory percepts might differ from visual ones. Although not the only possible explanation, oscillatory brain rhythms constitute a viable candidate to implement such discrete processes.

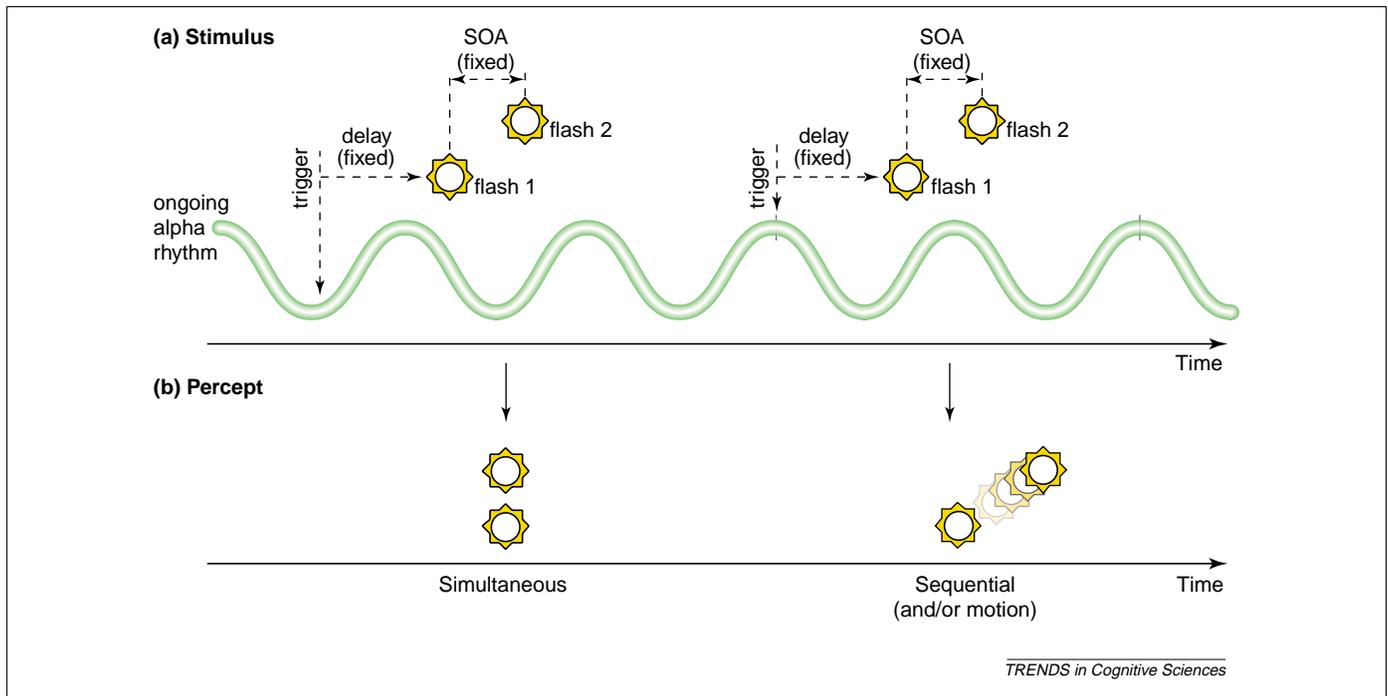
### Discrete perception and brain rhythms

#### *Frequency and phase dependence of behavioral variables*

From the early days of perception research, these postulated discrete psychological phenomena have been linked to brain oscillations, in particular the alpha rhythm [18,19], in the 8–12 Hz frequency range. Studies relating behavioral periodicities to the EEG alpha rhythm have been more or less successful [19], depending on the particular aspect of the EEG under consideration. There is, in general, a consistent relationship between the frequency of the alpha rhythm and that of the behavioral variable, be it reaction time (the higher the frequency, the faster the reaction time [20]) or simultaneity judgment (the period of the alpha rhythm and the maximal inter-stimulus interval for perceived simultaneity are highly

correlated [5]). On the other hand, experiments investigating the relation between reaction time and the *phase* of the alpha rhythm (assuming that RT is preferentially generated at certain particular phases of the oscillations) have generally failed to show any effect larger than ~10 ms [21], that is, much smaller than one would predict if alpha oscillations were responsible for the variability in reaction time. However, periodicities in RT are often found to be much faster than 100 ms (the normal period of the alpha rhythm), and this might be because another rhythm with ~25 ms periodicity is affecting motor decisions and behavior [8,12]: its frequency of 40 Hz lies in the 'gamma' band. More to the point, it was later realized that reaction time and temporal order judgment are relatively independent measures of perception, the former being easily accounted for by automatic thresholding processes, whereas the latter could depend on the peak of the evoked neural response [22,23]. Under this account, the effect of presenting a stimulus at different phases of the alpha rhythm should exert maximum influence on judgments of order or simultaneity, rather than on reaction time. Indeed, Varela *et al.* [24,25] found that presenting two flashes of light with always the same SOA, but at different phases of the ongoing alpha rhythm could induce dramatic changes in their perception (Fig. 2): when at one particular phase they would be judged as simultaneous, at the opposite phase they were perceived as sequential. This result, if adequately replicated, would be a particularly clear demonstration that discrete components in visual perception can be tightly related to brain oscillations<sup>†</sup>.

<sup>†</sup> **Note added in proof** The authors would like to indicate that their own recent attempt to replicate this result in 10 subjects using at least 600 trials per subject was unsuccessful: no significant correlation was found between the phase of alpha activity and stimulus perception on a trial-by-trial basis. A similar negative result was obtained independently by D. Eagleman (personal communication).



**Fig. 2. Perception and alpha phase.** The perception of a given physical event can be influenced by the phase of the ongoing alpha EEG cycle at which this event takes place. For phases separated by  $180^\circ$ , the perception of two successive flashes goes from 'sequential' to 'simultaneous'. (Adapted from [24,25].)

### Slow versus fast rhythms

There appears to be a functional dissociation between periodicities in the alpha band (8–12 Hz), related to judgments involving explicit perception, and those in the gamma band (30–60 Hz), more directly correlated to behavior and reaction times. This idea is consistent with the relatively long time frames usually involved in explicit perception [26,27]. Although the alpha rhythm remained for a long time the most popular in neuroscience, there was a turnaround  $\sim 15$  years ago: much interest is now focused on gamma-band oscillations. This might in part be because single-cell cortical recordings in anesthetized and alert cats and monkeys reveal activity in the gamma band more often than at lower frequencies. Since the work of Gray *et al.* [28], and Eckhorn *et al.* [29], there is ample evidence that oscillations and correlations of neuronal activities in the gamma band play some role in perception, attention, cognition and behavior [30,31]. With hindsight, it is possible that both slow rhythms (not only alpha, but also theta, i.e. 4–8 Hz [32]) and fast rhythms, as well as their interactions, have a role to play in perception [33,34], and restricting research efforts to only one frequency band might well conceal the bigger picture.

This problem is accentuated by the fact that many current brain activity recording, processing and analysis techniques are not optimally designed to explore these issues and tend instead to minimize their effects (Box 2). Essentially, this could mean that largely discrete phenomena escape experimental study. The widespread use of more sophisticated analysis techniques (e.g. Makeig *et al.* [35]) will facilitate the discovery of discrete processes, in particular if they involve more than one frequency band, or if their duration is variable from trial to trial (see Box 2).

In what follows, we suggest one potential mechanism by which interactions between oscillations at different frequencies could support discrete perception.

### Multiplexing representations

Based partly on the usual observation of cortical oscillations in the hippocampus, and partly on the set size effects on RT (a constant increase of  $\sim 25$  ms per 'to-be-remembered' item) obtained during short-term memory tasks [36], Lisman and Idiart [37] proposed that cortical oscillations at two distinct frequencies could be used to simultaneously maintain several items in short-term memory (Fig. 3). The slow waves (4–12 Hz) would define the span of memory, on which the fast waves (30–60 Hz) would inscribe the memories themselves. Depending on the particular ratio between the slow and fast wave frequencies, up to seven items could be 'multiplexed' in this manner. In analogy with FM radio, the slow wave acts as the carrier frequency, the fast wave as the actual signal.

A similar mechanism could account for visual perception and the structure of neuronal representations. Slow and fast waves are both common in the visual pathway (thalamus and visual cortex), although 'slow' waves are more frequently recorded in the alpha than in the theta range, which might constitute a functional difference between memory and perceptual systems. Alpha waves tend to be more global, travelling throughout cortex, with well-defined phase lags between distinct areas [38], whereas gamma waves generally correspond to more localized neuronal processes, involving neuronal populations within one [39,40], or occasionally a few cortical areas [41,42]. As we will see, this fits well with the idea that slow waves would constitute the 'context', and fast waves the 'content' of neuronal representations [43,44].

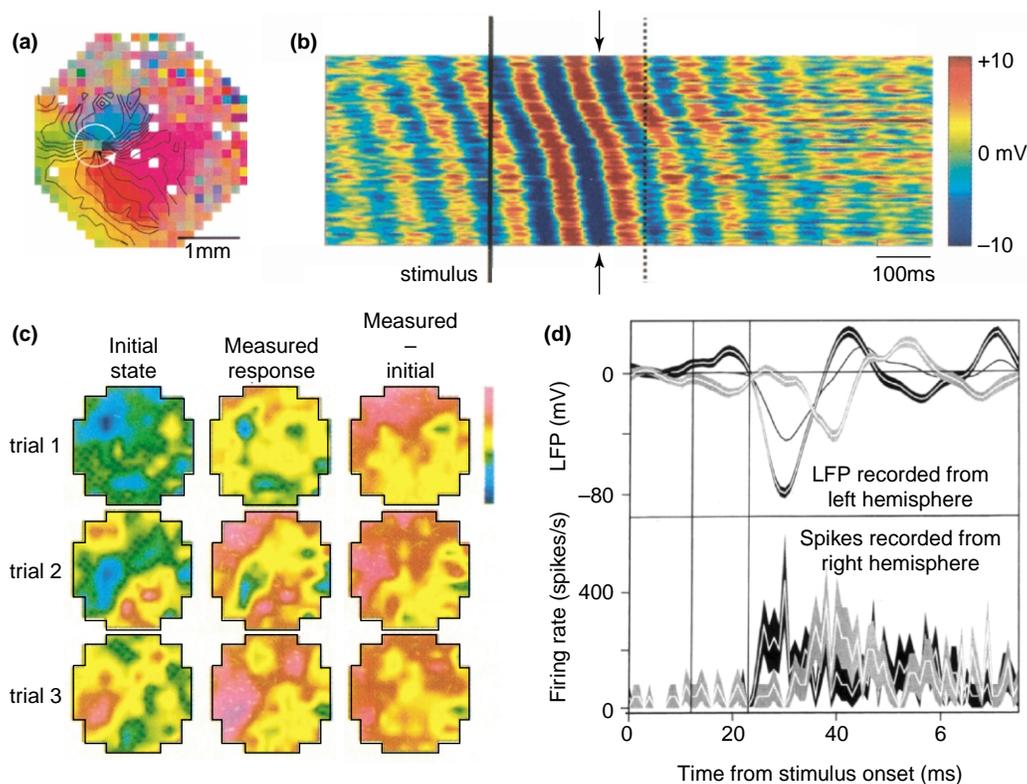
## Box 2. Are current techniques appropriate?

If perception is indeed discrete, with a tight relationship between perception and/or behavior and brain oscillations, how could experimentation have failed to reveal these phenomena?

Most current studies are designed in a way that, unfortunately, avoids the issues that we put forward in this article. Records of brain activity are generally averaged over hundreds of repeated trials or more, to eliminate fluctuations in ongoing activity (the 'noise') that are not correlated with stimulus presentation. Eye-movements that could trigger new cycles, are usually prevented. Post-stimulus time histograms (PSTHs) from single-cell or multi-unit recordings, as well as 'visually evoked potentials' (VEPs) from 'local field potentials' (LFPs) or EEG, which represent the majority of today's data on neuronal activity, are all based on this averaging principle. In addition, it is current practice in the calculation of VEPs to exclude all trials that display significant activity in the alpha band [54], assumed to reflect cortical 'idling' [55]. It is therefore no surprise that the discrete processes reviewed here could have escaped experimental observation.

Figure 1 illustrates a few recent examples of techniques that open new avenues of exploration: trial-per-trial EEG analysis can reveal stimulus-induced phase resets [35,56]; trial-per-trial optical imaging exhibits ongoing activity and stimulus-induced travelling waves [57], and when analyzed together with single-cell recordings [58–59], can reveal the organizational principles of cortical areas. The correlation between aspects of LFPs (e.g. their phase) and of single-cell activity (e.g. firing latency) can also demonstrate properties that would be concealed in regular PSTHs [60].

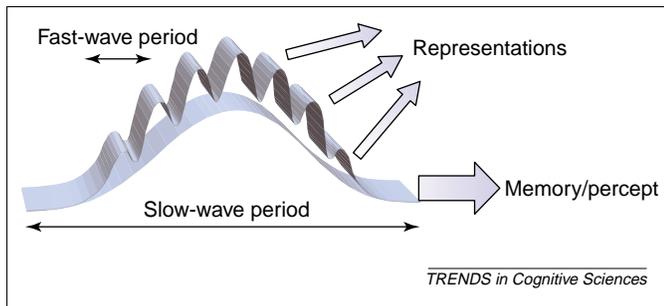
All these studies point to a fundamental aspect of brain activity: the importance of ongoing (or so-called 'spontaneous') activity for neuronal processing. Once ongoing activity is taken into account, the apparent variability of neuronal response, classically attributed to high neuronal noise, is greatly reduced. Thus, if not only evoked neuronal firing is considered, but also ongoing, potentially subthreshold activities, as well as the interactions between the two, the brain processes underlying perception might finally lie within our grasp.



**Fig. 1.** Advances in understanding of cortical processing by the use of alternative recording and analysis techniques. (a) Optical imaging of visual cortex reveals waves of stimulus-induced rhythmic activity in different frequency bands, that can take the form of translating or rotating wave fronts (shown here at 18 Hz, turtle cortex). Phase is color-coded, with thin black lines marking equal phases separated by 12 degrees. Note that the phase gradients (white circular arrow) never exceed  $2\pi$ , meaning that each location within the wave can be associated with a unique phase (from [57]). (b) A stimulus-induced phase reset of the ongoing alpha activity, illustrated by the non-uniform distribution of phases between the arrows, can account for a large portion of the N1 visual-evoked potential in human subjects, which is classically interpreted as the collective activation at a particular moment in time of specific brain areas. Each horizontal line corresponds to one trial, with the color representing the amplitude of the band-passed EEG (only the 10% of trials with maximal alpha amplitude in the period 0–293 ms post-stimulus are represented, sorted by relative phase; from [35]). (c) Optical imaging of cat visual cortex in 3 repeated trials with identical stimulus conditions. The initial state (activity immediately before response onset) displays high trial-to-trial variability, as does the measured response 28 ms later. The difference between the two, however, is much more reproducible. Thus, visual cortex actually behaves as a deterministic rather than noisy processing device, once the ongoing activity is taken into account (from [58]). (d) Similarly, local field potentials (LFPs) from cat primary visual cortex, which represent ongoing subthreshold activity at a particular recording site, can strongly affect neuronal firing in another recording site from the opposite hemisphere. Here, firing latency was found to depend on the sign (i.e. the phase of gamma oscillations, positive and negative represented respectively by black and gray curves) of the LFPs 20 ms before response onset. (Reproduced with permission from [60].)

The systems involved in the generation and maintenance of slow and fast waves are actively studied [45]. Whereas slow waves could originate in dedicated neuronal populations of the thalamus (e.g. reticular and relay nuclei), fast waves can also be entrained by intrinsic

cortical generators. In the thalamus, two sub-populations of neurons exist. The non-specific network or 'matrix' [46] is a distributed neuronal network occupying the entire thalamus, and connected with virtually all sensory and motor cortices. In association with the reticular nucleus, it



**Fig. 3. Multiplexing representations.** Each period of the fast wave rhythm (gamma-band, i.e. 30–60 Hz) underlies a specific representation. It is superimposed on a slower rhythm (alpha- or theta-band, 4–12 Hz) that effectively multiplexes visual representations. This model was proposed by Lisman and Idiart [37] to account for reaction time increases in the Sternberg memory task [36]. The same mechanisms could be invoked to explain how the interactions between slow and fast neuronal rhythms participate in shaping visual perception: the fast wave representations would constitute the contents of each discrete snapshot, the entire percept being mediated by the slow waves.

could be capable of supporting oscillations in the alpha range, the global coherence of which could, in turn, be modulated by cortical feedback [47]. The specific networks or ‘core’ are neuronal subpopulations present in various sensory nuclei of the thalamus (e.g. LGN) and having reciprocal connections restricted to the corresponding cortical regions. These loops could maintain fast thalamo-cortical waves of activity [40,43]. Note that thalamocortical gamma rhythms have been found to correlate with the time frames involved in various sensory discrimination tasks [48]. Together, the ‘matrix’ and ‘core’ thalamocortical networks could thus support global and local orchestration of brain activities [43], implementing a multiplexing scheme as proposed here.

In practice, how would such a scheme relate to psychological data on visual perception? As in the case of short-term memory multiplexing described above, the ratio between slow and fast frequencies will define the span of the system. Here, because the slow wave is generally more likely to lie in the alpha than in the theta range, the expected capacity limit is around 4 items during each explicit percept, a value identical to the most recent psychological estimate of the number of visual objects that can be seen ‘at a glance’ [49]. To account for the large difference between time frames involved in explicit simultaneity or order judgments (~100 ms) and in RTs (~25 ms), one need only assume that each fast wave representation can directly trigger motor behavior, but that only the entire slow wave (and its contents) is made available at once to explicit perception. This dissociation would imply that a great deal of our motor behavior actually occurs a few tens of ms before we even know what triggered it (a form of ‘zombie’ behavior [50]), a surprising prediction which has actually been confirmed in laboratory conditions [51,52]. Finally, in this context, ‘serial’ visual search would correspond to a situation where each stimulus in an array must be encoded in a separate fast wave representation, and the average time taken to trigger a response thus increases with the number of objects in the scene; by comparison, ‘pop-out’ would imply that more objects do not delay the encoding of the target to a later fast wave representation.

## Conclusion

The backbone and originality of our argument rests on the idea that the temporal evolution of perception can provide a constrained framework to investigate the computations leading to awareness. If perception is discrete, and this remains to be clearly demonstrated, then one or more intrinsic neuronal mechanisms must reflect this organization, that is, must be global (i.e. able to link distinct areas or brain regions; this, however, has been disputed, e.g. [27]), quasi-periodic (i.e. possess at least an active and inactive phase) and flexible (i.e. dynamically adapt their period and amplitude to external and internal constraints).

It seems surprising that such a fundamental question as whether conscious perception occurs in discrete batches or continuously has not been definitely answered one way or another. The trend toward simultaneously recording from hundreds of neurons in animals free to move their eyes or otherwise explore their environment represents a very encouraging development that—together with EEG analysis coupled to new computational tools (Box 2), and behavioral measures of subjective perception—should finally inform us about these outstanding questions.

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