

A guideline for linking brain wave findings to the various aspects of discrete perception

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Abstract

Brain waves, determined by electrical and magnetic brain recordings (e.g., EEG and MEG), and fluctuating behavioral responses, determined by response time or accuracy measures, are frequently taken to support discrete perception. For example, it has been proposed that humans experience only one conscious percept per brain wave (e.g., during one alpha cycle). However, the proposed link between brain waves and discrete perception is typically rather vague. More importantly, there are many models and aspects of discrete perception and it is often not apparent in what theoretical framework brain wave findings are interpreted and to what specific aspects of discrete perception they relate. Here, we review different approaches to discrete perception and highlight issues with particular interpretations. We then discuss how certain findings on brain waves may relate to certain aspects of discrete perception. The main purpose of this meta-contribution is to give a short overview of discrete models of perception and to illustrate the need to make explicit what aspects of discrete theories are addressed by what aspects of brain wave findings.

KEYWORDS

brain rhythms, consciousness, discrete perception, EEG, temporal structure

1 | INTRODUCTION

In experiments on apparent motion, two static discs are presented at different locations with a delay of up to a few hundred milliseconds. Instead of two static disks, a single moving stimulus is perceived. Clearly, the vivid motion percept from the first to the second disk cannot occur before the second disk is presented. This and similar phenomena have been taken as evidence that stimuli are not perceived immediately but substantially

delayed, that is, well beyond the standard neural transmission times.

There are two possibilities to account for these facts: Either conscious perception is continuous (i.e., we are conscious at each moment in time) but substantially delayed and convoluted, or it is discrete (i.e., we are not conscious at each moment in time). Continuous models face considerable problems (Herzog et al., 2016, 2020; for a recent controversy on continuous vs. discrete consciousness, see Fekete et al., 2018; Doerig et al., 2019).

Abbreviations: EEG, electroencephalography; MEG, magnetoencephalography; TMS, transcranial magnetic stimulation.

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For example, explanations of apparent motion within a continuous framework are confronted with surplus content (Dainton, 2018), also called the too-many-percepts-problem (Herzog et al., 2020). Continuous models predict an initial percept of the first disk, then motion, and finally a percept of the second disk. However, humans perceive only one moving disk. Discrete models avoid the generation of too many percepts by suggesting that humans are not conscious at each moment of time.

We here take discrete perception for granted but wonder to what extent brain waves may be linked to specific aspects of discrete perception.

1.1 | Discrete perception

Classically, ideas about discrete perception have in common that no temporal information is thought to be available during a discrete epoch (Crick & Koch, 2003; Pöppel, 1997; VanRullen & Koch, 2003). For instance, White (2018) states: “A common feature of the definition of frames is that they mark a boundary between events that are perceived as simultaneous versus non-simultaneous.” However, what does this mean exactly? In the cinema metaphor, for example, each discrete percept corresponds to a static slide, and motion is perceived when the slides are changing (with an appropriate sampling rate). Akinetopsia, a neuropsychological disorder characterized by an impairment in motion perception while the perception of static objects is preserved (Zeki, 1991), could, in this context, be regarded as a failure of computing motion across frames, resulting from too low sampling rates. Other metaphors suggest that perception is like a (surveillance) camera sampling information from the environment only at certain moments in time, such as every second. Finally, it is sometimes argued that motion is added, “painted” on snapshots (Crick & Koch, 2003; Gruber & Block, 2013) and, just like color or orientation features, held constant within one snapshot. In general, all of the above suggestions share the idea that a conscious percept *itself*, as well as its conscious *content*, have no temporal extension. This implies that changes in between static stills, such as motion, cannot be perceived.

Another aspect frequently discussed concerns the discretization of perception. Discrete perception can come in two flavors: periodic and non-periodic. The idea of periodic perception gained popularity in the 1950s when perception was thought to be similar to digital computers, operating on a fixed processing rate (Stroud, 1956, 1967). This proposal was taken up by neurophysiologists and periodic processes were equated with brain waves of certain frequencies. However, there have been, and still are, controversial debates about the

proper frequency that parses consciousness into discrete chunks (Allport, 1968; Efron & Lee, 1971; Geissler, 1987; Von Békésy, 1936). Experimentally, it was shown that reaction times are quantized, indicating that responses occur more frequently during specific time intervals rather than being emitted randomly (Dehaene, 1993; Pöppel, 1970). Perception was further found to be modulated periodically with changes in the alpha range (~8–13 Hz), as, for example, in the continuous wagon wheel illusion (VanRullen et al., 2005, 2006; but see Kline et al., 2004, 2006). When participants were asked to report the perceived direction of a rotating wheel, the motion was sometimes perceived in the opposite direction, which is known to occur due to temporal aliasing when a period pattern in continuous motion is sampled by a discrete process. By subsequently analyzing the EEG power spectrum, it was shown that the power at 13 Hz could predict either the onset of illusory motion or the transition to real motion. These results have been interpreted as direct evidence that the visual system samples information periodically, producing slightly more than 10 frames per second. Similar effects have been found in the flickering wheel illusion (Sokolik & VanRullen, 2013), long-lasting perceptual echoes (VanRullen & Macdonald, 2012), or perceptual reverberation (Gulbinaite et al., 2017). Most of the findings have been controversially discussed both in terms of their experimental validity as well as their conceptual implications (for a review, see White, 2018). Here, we focus only on the conceptual implications (for a recent review on analysis methods, see Lundqvist & Wust, 2021). Besides, there are further aspects of discrete perception that are often not spelled out explicitly and can, consequently, lead to confusion. We first propose a list of critical aspects of discreteness that need to be clearly addressed when one attempts to relate brain wave findings to discrete perception. Second, we apply this guideline to exemplary theories proposing that brain waves play a direct role in discrete perception.

2 | A GUIDELINE FOR LINKING BRAIN WAVES TO SPECIFIC ASPECTS OF DISCRETE PERCEPTION

Links between perception and brain wave findings are often rather vague. In fact, it is not even well established whether brain waves can be used as evidence of discrete percepts or whether they represent a means of increasing our understanding of perceptual processes. Moreover, it is often unclear what aspects of discrete perception are experimentally addressed (see Figure 1).

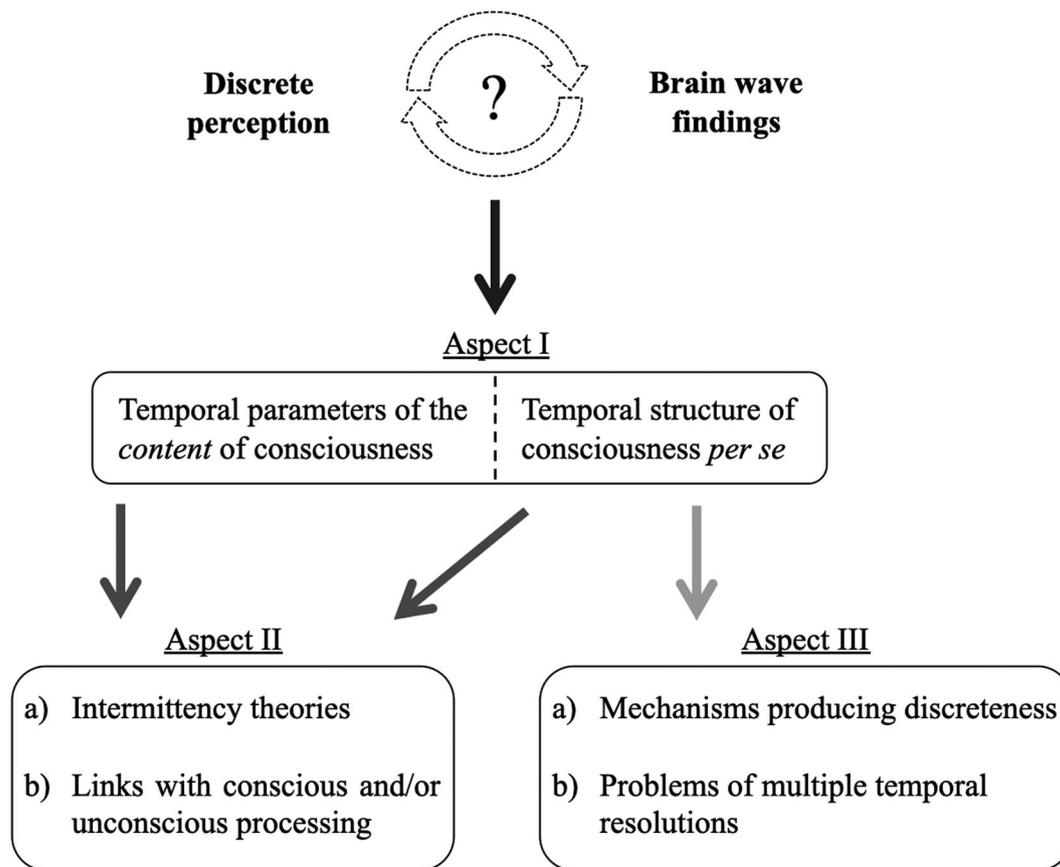


FIGURE 1 Linking brain wave findings to discrete perception: What aspects of discrete perception are addressed? The first aspect requires clarifying whether findings are about the content of consciousness or the temporal structure of consciousness *per se*, since the two are independent. The second aspect requires specifying the choice of intermittency theory and its consequences on conscious and unconscious processing. The third and last aspect, when findings are assumed to provide direct information about consciousness *per se*, requires showing whether sampling in discrete perception is necessarily thought to be periodical and/or causally linked to specific brain rhythms at particular frequencies. In addition, a convincing account for the issue of multiple temporal resolutions should be put forward

2.1 | Aspect I. Addressing temporal consciousness

One needs to distinguish between the *content* of consciousness, such as the perceived duration of a stimulus or simultaneity of two stimuli, and the temporal structure of consciousness *per se* (e.g., how long a conscious percept *itself* lasts). Although these two aspects always come together (i.e., there is no pure content-free consciousness), they are logically independent (Herzog et al., 2016, 2020; van Wassenhove, 2017). In particular, the temporal resolution, investigated through the *content* of consciousness, cannot be used to determine the temporal structure of consciousness *per se*. For instance, quantized reaction times may or may not result from a simple (unconscious) thresholding process, which is later fed into consciousness, rather than from switches of consciousness *itself*. As a clinical example, schizophrenia patients often report that their vision is strongly distorted in time. However, the

distortions do not seem to be related to changes in the duration of percepts, but rather to distortions of the context. For example, schizophrenia patients require longer delays between two asynchronous stimuli to perceive them as asynchronous (Giersch et al., 2009), reflecting diminished asynchrony detectors rather than prolonged discrete epochs. These examples illustrate the need for clarifying whether findings on brain waves relate to the temporal aspects of the *content* of consciousness, the time course of consciousness *per se*, or both. Alternatively, authors may refute a distinction between the *content* of consciousness and consciousness *per se*. In any case, these links should be made explicit.

2.2 | Aspect IIa. Specifying the type of intermittency theory

One needs to address what happens, and is perceived, during discrete epochs. Discrete perception can be seen

as a mapping from a continuous world to discrete percepts. For this reason, the cinema metaphor is not very helpful as it describes the inverse process: how to go from the discrete frames of a movie to continuous perception. The surveillance-camera metaphor, instead, suggests that information is sampled from the environment only at certain moments in time, often rather sparsely. In this case, sampling happens at the sensory level. These types of theories are called peripheral intermittency theories, as opposed to central intermittency theories where information is sampled from the brain's processing stream. As an example for peripheral intermittency theories, Schneider (2018) proposed that the Fröhlich and the flash-lag effect can be explained by discrete sensory sampling rates between 5 and 10 Hz. However, such peripheral intermittency theories, in which all information between snapshots is lost, can be ruled out since temporal resolution in humans can be as low as 3 ms in vision (Westheimer & McKee, 1977) and even shorter in audition. Consequently, one may argue that sampling must have a very high rate (<3 ms). This, however, could not explain why in other paradigms, such as simultaneity judgments, temporal resolution is much lower (>40 ms). As a potential solution, it has been proposed that different stimuli come with different types of discrete processing (for a review, see van Wassenhove, 2009). Yet, such an account is not viable because concurrently presented stimuli may then reach consciousness at different time points. For these reasons, central intermittency theories are generally privileged. In these theories, sampling occurs with respect to the ongoing brain processing and discrete percepts. Some models seem to propose that information within a moment is summed or averaged and that we perceive only this sum or average (for related studies on motion perception, see McKee & Welch, 1985; Snowden & Braddick, 1991; Simpson, 1994), in analogy to a camera where all incoming light is accumulated as long as the shutter is open. Other models explicitly allow unconscious processing of which the output is perceived consciously (VanRullen, 2016, 2018; VanRullen & Koch, 2003). Finally, recent models propose that entire event structures are computed during an epoch and are rendered conscious at discrete times (Herzog et al., 2016). These models are supported by empirical evidence using long-lasting postdictive effects, in which a stimulus can modify the perception of stimuli presented a few hundred milliseconds earlier (Herzog et al., 2020). Overall, it should therefore be made clear whether results on brain waves are interpreted within a discrete peripheral or central intermittency framework, and whether and how brain waves are related to this framework.

2.3 | Aspect IIb. Identifying links with conscious and/or unconscious processing

Related to the choice of intermittency theory (Aspect IIa), one needs to take sides and address whether brain wave findings relate to conscious or unconscious aspects of processing. As mentioned above, in central intermittency theories, a percept is preceded by some amount of unconscious processing, ranging from passive averaging to complex and sophisticated processing. As a consequence, a percept can only be perceived at the end of a moment. Often, it is proposed that motion, or change in general, can only be perceived across moments since, by definition, no change can be detected during a single moment. In this case, a percept of change can only occur at the end of the second moment. When correlating brain waves with percepts, it is important to specify at what time a percept is expected to occur. In addition, one needs to specify what is perceived.

2.4 | Aspect IIIa. Clarifying the mechanisms that produce discreteness

One needs to explain how discreteness occurs in perception. If periodicity is assumed, the mechanisms that underlie the periodicities have to be clearly identified. It needs to be made clear whether brain waves are thought to cause or support periodicity, are an (epiphenomenal) consequence of periodicity, or are unrelated to periodicity. If brain waves are causal for discrete perception, it needs to be explained how continuous functions, which brain waves are, give rise to a non-smooth step function, which discrete perception is by definition.

2.5 | Aspect IIIb. Solving the problem of multiple temporal resolutions

One needs to address whether there is one discrete epoch for all aspects of processing or whether there are individual epochs for each sensory modality or even each individual paradigm (Dennett & Kinsbourne, 1995; Recio et al., 2019; van Wassenhove et al., 2008). As a matter of fact, estimates of the duration of a discrete epoch vary vastly, ranging from 4.5–4.6 ms (Geissler & Kompass, 2001) to 100–200 ms (Kozma & Freeman, 2017). Likewise, EEG and MEG recordings reveal the presence of many brain dynamics with different frequencies (Buzsáki, 2006). If authors want to determine the period from the temporal resolution given by the cycle of one unique oscillatory frequency, they also need to clarify how findings on that particular frequency

relate to other findings focusing on different frequencies. Critically, it should be made clear whether and why some frequencies, such as alpha-band oscillations, are privileged. Alternatively, when several frequencies are identified, authors need to discuss how these frequencies are integrated to enable discrete sampling, unless they play no role in such sampling. Discrete theories relying on brain waves need to explain how oscillatory frequencies can support their models: a discrete model has to show either a stable epoch duration or a mechanism that explains how the discreteness occurs (Aspect IIIa).

3 | HOW ARE THESE ASPECTS ADDRESSED IN PROMINENT BRAIN WAVE THEORIES?

Numerous studies have tried to understand perception with respect to neural oscillations, notably in the alpha frequency band (8–13 Hz). For example, a series of experiments showed that the detection of near-threshold stimuli depends on the phase of the alpha cycle just before stimulus presentation (Busch et al., 2009; Dugué et al., 2011; Mathewson et al., 2009; VanRullen et al., 2011).¹ Further, while some authors proposed that low performance occurs when the stimulus is presented at the trough of an alpha cycle (Mathewson et al., 2009), others remained vague about the precise phase (e.g., peak versus trough) (see VanRullen, 2018).

In the theory of perceptual cycles, VanRullen (2016, 2018) interprets these findings as evidence that brain rhythms contribute to the generation of discreteness in conscious perception. Two main assumptions are made: first, perception is periodically modulated by specific oscillations (termed “rhythmic perception”). VanRullen (2018) associates this idea with the shutter of a camera that opens and closes periodically. For example, an increase or a decrease in the frequency of alpha oscillations between different individuals predicts similar modulations of their perceptual abilities, since it directly affects the resolution of perception. Second, the oscillatory phases at (or just before) the onset of brief stimuli modulate the perceptual outcome and the temporal relation between these stimuli (termed “temporal parsing”). Two stimuli falling into the same cycle are perceived as simultaneous, whereas they are separately and

independently perceived if they fall into distinct cycles. Moreover, it is proposed that for two strong inputs that both consistently reach the perceptual threshold, the specific phase at the moment of their arrival modifies the timing at which they reach that threshold (VanRullen, 2016), which eventually can also modulate the perceived temporal relations (i.e., simultaneity versus asynchrony) between these two inputs.

Rhythmic perception seems to be related to the *content* of consciousness (Aspect I). The idea that the oscillatory phase periodically modulates the probability and/or intensity of perception is in line with recent demonstrations showing that fluctuations in neuronal excitability bias the detection criterion rather than improving sensitivity (Iemi et al., 2017; Iemi & Busch, 2018; Limbach & Corballis, 2016). In this respect, VanRullen (2016) seems to endorse a central intermittency framework since several stimuli are integrated together as long as they are processed in the same cycle of a given brain wave (Aspect IIa). While there is no explicit quote, the claims of VanRullen would be compatible with a scenario in which brain waves modulate unconscious, rather than conscious processing (Aspect IIb). In particular, the incoming information could be weighted by the alpha rhythm during an epoch and the combined information would be perceived at the end of the cycle.

However, VanRullen (2016, 2018) also seems to link these findings to the structure of consciousness *per se* (Aspect I) since temporal parsing is proposed to support the discretization of conscious percepts. However, the mechanisms by which this would be achieved remain unclear (Aspect IIIa). Critically, it should be clarified how, for example, alpha oscillations are discretized (i.e., whether it is the peak, the trough, or any other part of the phase that is crucial in the creation of chunks), what precisely an epoch encompasses, and, consequently, what is actually perceived and at what point in time. As mentioned above, it should also be explained how continuous processes, which brain waves are, give rise to discreteness. An additional issue derives from the evident lack of a single sampling rhythm reported in the literature (varying from 1 to 30 Hz; see VanRullen, 2016; Ruzzoli et al., 2019; Morrow & Samaha, 2021).² This leaves open the question of how several rhythms, accounting for distinct sensory modalities and stimulus properties, can coexist and underlie perception (Aspect

¹A number of experiments have also manipulated alpha oscillations, usually using TMS or sensory entrainment methods, in order to assess their causal effects on perception (Cecere et al., 2015; Ronconi & Melcher, 2017; Ronconi et al., 2018, for a review, see Kastén & Herrmann, 2020). However, such studies provide rather indirect evidence for rhythmic processing, instead of evidence for discrete perception.

²Geissler (1987) proposed a unique multimodal perceptual periodicity around 220 Hz (i.e., discrete epochs of 4.5 ms). VanRullen (2018) recently called for abandoning the search for a single rhythm that underlies all sensory perceptions and, instead, for defining which perceptual functions are rhythmic, at which frequencies and/or phases, and how these perceptual rhythms can operate in parallel.

IIIb). VanRullen (2016) observes a special role of alpha-band oscillations in multimodal perceptual processing, but the reasons why the alpha rhythm is essential (e.g., causal power or bias in the literature), as well as the extent to which integration or neural multiplexing of the various other frequencies are performed, need to be addressed. To sum, while there are findings that speak for the involvement of alpha rhythms in modulating the *content* of consciousness, it remains unclear how the alpha rhythm parses consciousness *per se* into chunks.

In parallel, other theories consider the temporal and dynamic structure of the EEG field more broadly. In the operational architectonics (OA) framework (Fingelkurts & Fingelkurts, 2001, 2006), consciousness is interpreted as an emergent phenomenon that occurs through dynamic binding of brain operations. According to this model, discrete conscious percepts are produced by transient synchronized local neural assemblies within a complex hierarchical architecture (Fingelkurts & Fingelkurts, 2015). In patients in vegetative or minimally conscious states, for example, such neural assemblies are less prominent or even nonexistent. Interestingly, these changes in neural assemblies are exclusively observed in alpha and beta frequency oscillations, leading to the hypothesis that these rhythms are functionally involved in the emergence of consciousness (Fingelkurts et al., 2012). Alternatively, the cinematic theory of cognition (Freeman, 2006, 2007; Kozma & Freeman, 2017) also describes intermittent transitions between synchronized brain states, which are thought to underlie the cognitive or perceptual content, and desynchronized brain states, which are seen as brief moments (~20 ms) of receptivity to new inputs and associated with no conscious percept. Based on the analysis of high-frequency oscillations in evoked and spontaneous neural activity, this model suggests that transitions between periods of large-scale synchronization and periods of desynchronization occur at alpha-theta rates (Freeman et al., 2003; Kozma & Freeman, 2016).

By associating metastable or synchronized oscillatory patterns with frames of conscious perception, these two theories seem to rather focus on decomposing the continuity of experience into discrete neural assemblies, which we consider to be solely related to the temporal structure of consciousness *per se* (Aspect I). Critically, they do not explicitly study how stimuli are processed and how percepts are evoked by these stimuli with respect to the choice of intermittency theory (Aspect IIa), nor how brain waves are involved specifically in conscious or unconscious processing (Aspect IIb). There is also some discrepancy between the two

models.³ Furthermore, the OA framework does not seem to predict periodicity in discrete percepts (Aspect IIIa), since they are not directly based on individual oscillatory cycles but on transient synchronized functional neuronal assemblies (Fingelkurts & Fingelkurts, 2006). However, the causal role in the discretization of perception by the phase or the frequency of given oscillations (in this case, especially alpha and beta rhythms) remains vague (Aspect IIIb). In the cinematic theory of cognition, periodicity in discrete sampling is not presented as essential either. Yet, this model predicts more consistent durations of discrete epochs, ranging from 100 to 200 ms (Kozma & Freeman, 2017). This necessitates clarifying whether this cyclic period of sampling is specifically associated with, or modulated by, brain waves (Aspect IIIa). Moreover, when an estimate of the duration of discrete epochs is claimed, strong evidence should be provided to demonstrate that it is common to all types of processing (Aspect IIIb).

4 | DISCUSSION

Our main objective in this contribution is not to criticize specific theories about brain waves but rather to highlight that it is important to clarify what aspects of discrete perception are addressed within what framework of perception. We have recently argued that focusing on the temporal parameters of the *content* of consciousness does not allow one to derive conclusions about the temporal structure of consciousness *per se* (Herzog et al., 2016, 2020). For instance, the perceived duration of a stimulus (i.e., the subjective duration of the *content* of consciousness) cannot be used to determine whether the temporal structure of consciousness is continuous or discrete, since it only reflects the mere temporal resolution of the “detector” involved in the processing. In this respect, we think that VanRullen’s theory of perceptual cycles does not provide clear evidence for discreteness in consciousness *per se* but is rather related to the *content* of consciousness. Conversely, Fingelkurts and Fingelkurts’s OA framework and Kozma and Freeman’s cinematic theory of cognition seem to be about consciousness

³In the OA theory, the synchronized brief periods between neural assemblies are regarded as the places where percepts are experienced, whereas the neural assemblies, whose durations are highly variable (i.e., from 100 ms to 30 s), are the periods of processing (Fingelkurts & Fingelkurts, 2006). Curiously, the opposite is proposed in the cinematic theory of cognition: discrete static conscious percepts are associated with the longer epochs of synchronized activity (i.e., 100–200 ms), whereas the shutter periods in between are described as unconscious episodes during which new sensory stimuli can be rapidly processed (Kozma & Freeman, 2017).

per se, but their findings do not accurately define the timing and duration of conscious percepts.

Recently, using the sequential metacontrast paradigm (SQM), we were able to provide temporal estimates for the occurrence of discrete percepts (Drissi-Daoudi et al., 2019). In the SQM, a percept of two motion streams is elicited by the presentation of a sequence of lines that are diverging from the center. In this paradigm, if one of the lines has a horizontal vernier offset, this offset is attributed to the subsequent, straight lines in the same stream. Further, if several lines are offset in the same, or opposite, directions within a specific window of time, the offsets integrate mandatorily and cannot be perceived individually. This temporal window of integration has been estimated to last up to 450 ms, depending on the individual participant. Thus, the results suggest that a long-lasting period of integration is necessary, and that a discrete conscious percept emerges only at the end of such unconscious processing. These findings do not accurately determine the duration of a percept *itself* but provide upper and lower temporal bounds for the structure of consciousness (see Herzog et al., 2020).

Finally, an important issue that remains unanswered is whether consciousness is an epiphenomenon or whether it serves a real purpose (i.e., having computational power). As mentioned, it has often been proposed that we perceive motion and change only across stills (i.e., by comparing the stills) as they represent the outcomes of epochs without any temporal information. This implies that consciousness *itself* is capable of comparing the stills, meaning that it has its own computational power (van de Grind, 2002). Otherwise, there is a need for an unconscious mechanism that can compute motion across epochs. Both options are conceivable but come with several challenges. On the one hand, it is unclear what computational power of consciousness *per se* means since any mechanism (that can be written down as an equation) could work unconsciously too (Doerig et al., 2021). On the other hand, an unconscious comparison of stills may indeed give rise to a motion percept, similar to apparent motion, but (a) there needs to be a mechanism that compares the stills, which may lead to an infinite regress, and (b) motion resolution would be much lower than it is empirically (~3 ms). Hence, similarly to the question of the links between brain waves and aspects of conscious and/or unconscious processing (Aspect IIb), it needs to be made clear whether brain waves reflect the computational power of a conscious or an unconscious mechanism integrating information across a period. Up to now, no theory of discrete perception addresses this issue.

5 | CONCLUSION

Discrete theories, which assume that conscious perception consists of a series of distinct moments, still lack concrete neural mechanisms on which discreteness is based. In an effort to provide such explanations, brain waves have been extensively investigated during the last decade. A great difficulty is that we do not have a clear definition of consciousness *per se*. However, the problem discussed in this paper is less concerned with the nature of consciousness but rather with how discrete percepts emerge from continuous brain processing. We here propose that it is important to clarify how findings on brain waves are linked to specific aspects of discrete perception, and we suggest a set of critical aspects that may guide this process. We believe that specifically addressing these different aspects will help to build more robust arguments to demonstrate whether perception is discrete and to what extent it is related to brain waves. These aspects are not written in stone, some may be dropped, and others may be added.

Ultimately, unraveling the mechanisms of discrete perception could provide further explanations about consciousness, including how percepts are integrated into the seamless stream of perception.

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M.Q.M., L.V., and M.H.H. all contributed to the conception, writing, and revision of the manuscript.

CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

ETHICS STATEMENT

This work is an opinion paper that discusses theoretical models. No experiments have been conducted.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analysed.

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