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Is conscious perception a series of discrete temporal frames?

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Abstract

This paper reviews proposals that conscious perception consists, in whole or part, of successive discrete temporal frames on the sub-second time scale, each frame containing information registered as simultaneous or static. Although the idea of discrete frames in conscious perception cannot be regarded as falsified, there are many problems. Evidence does not consistently support any proposed duration or range of durations for frames. EEG waveforms provide evidence of periodicity in brain activity, but not necessarily in conscious perception. Temporal properties of perceptual processes are flexible in response to competing processing demands, which is hard to reconcile with the relative inflexibility of regular frames. There are also problems concerning the definition of frames, the need for informational connections between frames, the means by which boundaries between frames are established, and the apparent requirement for a storage buffer for information awaiting entry to the next frame.

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1: Introduction

Subjectively, conscious perception is smooth and continuous. Things move on from one moment to the next, and we perceive motion and all other forms of change (while they are going on) without any hint of discontinuity. Conscious percepts must have some level of temporal granularity, and that may be set by fundamental operating characteristics of neurons. That level of granularity could be far below the temporal resolution of perception, much as the level of granularity in a digital photograph, the pixel, is usually far below the resolution of the photograph that is detectable to the eye. The finest temporal resolution in perception is found in specialised processors such as echolocation mechanisms in bats and electric field fluctuation detectors in electric fish, which can detect temporal phenomena on the nanosecond time scale (Carr, 1993; Simmons, 1973, 1979). In humans, differences in arrival times of sound to the two ears can be resolved on a scale of microseconds (Grothe, 2003). There is no percept of temporal succession at that level, however. Instead, the percept is of spatial localisation of a single sound source, and this does not resolve into a percept of two successive sounds until the time difference is ~5 ms (Wallach, Newman, and Rosenzweig, 1949). This is an indication that the fundamental temporal resolution in conscious perception may be on the millisecond time scale but perhaps < 10 ms.

Some authors, however, have proposed a level of temporal resolution in conscious percepts that is much coarser than that. In general terms, the proposal is that perceptual experience is packaged into discrete temporal frames on the sub-second scale, and that the apparent flow and continuity of perceptual experience over time is a superficial phenomenon that is underlain by temporal discontinuity on a time scale of a substantial fraction of a second. The aim of the present paper is to review and assess such proposals. Table 1 sets out the structure of the review.

1.1: What is a frame of conscious perception?

Most proposals have had little to say about how a frame should be defined, but it is possible to point to some general features that will suffice for the time being. A common feature of the definition of frames is that they mark a boundary between events that are perceived as simultaneous versus nonsimultaneous (e.g. Crick & Koch, 2003; Pöppel, 1997, 2009; VanRullen & Koch, 2003). Thus, all information within a given frame has experienced contemporaneity, and events can only be perceived as occurring at different times if they occur in different frames. This implies a certain level of co-ordination in perceptual processing: given that different processes are separate, both functionally and neuroanatomically, especially if they occur in different modalities, there must be some kind of process that effectively assigns their products to bins in a co-ordinated way, as the foundation for experienced contemporaneity. It is sometimes stated in addition that the partitioning of percepts into temporal frames is endogenous and not affected by times of occurrence of external events (Harter, 1967; Stroud, 1956; Ulrich, 1987). However, Haber and Hershenson (1973) proposed that a series of frames could be initiated by the onset of a stimulus and ended at the frame containing the termination of the stimulus. It is also sometimes argued that a frame represents an updating interval: in effect, frames represent the maintenance of information in a static representation, and a new frame starts when some process of frame construction or updating is completed (Kozma & Freeman, 2017; VanRullen, Zoefel, & Ilhan, 2014).

The extreme form of the frame hypothesis is that there is just a single frame (at a time) that encompasses all of perception. This extreme form is hardly every encountered in the literature. It seems to be implied in Stroud's (1956) proposal of a psychological moment, and is explicit in Pöppel (1997, 2009), where research evidence from multiple areas, supposedly converging on a common duration for a frame of conscious perception, is taken as evidence for the generality of the proposed frame. Most other authors have endorsed frames that are local, sometimes to modalities (usually vision), sometimes to defined activities, processes, or mechanisms within modalities, such as visual attention, and sometimes of variable duration.

1.2: Discrete frames and the subjective continuity of perceptual experience

An analogy is sometimes taken with film projection, originally by Ansbacher (1944) and Stroud (1956), and by others since, including Craig (2009a), Freeman (2006), Hogendoorn (2016), Kozma and Freeman (2017), McComas and Cupido (1999), and Pockett, Brennan, Bold, and Holmes (2011). In this analogy, the frame of conscious perception is equivalent to a single frame of a film in the gate of the projector, and the subjective fluency of conscious perception is equivalent to the continuity of the film as projected on the screen. The analogy is imperfect because, in fact, the projection on the screen is also a series of stills, and the illusion of temporal continuity is a product of the operating characteristics of visual information processing, such as the flicker fusion frequency (Carmel, Saker, Rees, & Lavie, 2007; Curran & Wattis, 1998).[1] However, the analogy does serve to elucidate a significant problem for the frame hypothesis: if everything within a single frame is experienced as contemporaneous, and then it is replaced by a new frame, within which again everything is experienced as contemporaneous, why does the succession of static frames not give rise to subjective jerkiness in conscious perception, and how is the subjective continuity of conscious perception established?

An analogy can be taken with the patient suffering from akinetopsia studied by Zihl, von Cramon, and Mai (1983). Based on her self-report, her visual world consisted of a series of static images lacking any motion information, which left her able to make judgments about temporal succession but unable to judge simple practical matters such as when to stop pouring tea into a cup. The time scale of image succession is not clear but could have been around 1 s or more; clinical testing suggested that this depended on factors such as speed of stimulus motion. However, the point is that the discrete frame hypothesis implies that conscious perception should proceed in a series of static images with jerks marking the transition from one frame to the next, resulting in a faster version of akinetopsia. In fact, our perceptual experience does not resemble that of the patient with akinetopsia, even allowing for the slower frame-rate she may have experienced.

There are at least two possible solutions to that problem. One is that limited temporal resolution in specific areas of information processing may result in a kind of smearing of information across multiple frames, which effectively obscures frame boundaries. Taking up the analogy with film projection, when watching a film, continuous motion and change are perceived because the rate of frame presentation is faster than the flicker fusion rate (Carmel et al., 2007; Curran & Wattis, 1998). Perceptible flicker or jerkiness only occurs if the frame-rate of the film projection is reduced to a value below the flicker fusion rate. Thus, so long as frame duration is shorter than the temporal resolution of relevant processes, the progression of frames should not be experienced as jerky. The second solution is that the continuity of experience may be created by some kind of filling-in process, such as model-fitting, which would impose a model of continuity on discrete packets of information (VanRullen et al., 2014). VanRullen et al.

(2014) argued that this could be a temporal analogue of the visual mechanisms that fill in the blind spot in the visual field (Durgin, Tripathy, & Levi, 1995; Fiorani, de Oliveira, Volchan, Pessoa, Gattass, & Rocha-Miranda, 2003).

2: Early proposals

The idea that conscious percepts fall into discrete temporal frames has a long history: something like it appeared over 2,000 years ago in Buddhist thinking (Herzog, Kammer, & Scharnowski, 2016; Pockett et al., 2011). In more recent scientific work it may date back to von Baer (1862)[2], although the original presentation does not survive and there is uncertainty about its content (Elliott & Giersch, 2016). Elliott and Giersch (2016) stated that von Baer had proposed "a fundamental quantum of experienced time" (Elliott & Giersch, 2016, p. 1) with a duration of about 55 ms. This is consistent with research by Brecher (1932) showing a nonsimultaneity threshold of about 55 ms with both tactile and visual stimuli although, as we shall see, more recent research has shown a wide range of nonsimultaneity thresholds and Brecher's results can no longer be regarded as definitive in that respect. Clay (1882) proposed a "specious present", a kind of psychological moment that extends beyond the present, encompassing some of the past: an example he gave was that all of the notes in a short tune seem to be contained in the present.[3] James (1890) further developed that idea, and suggested a time scale of about 5 - 6 s. Proposals about frames on a time scale of greater than 1 s have been reviewed elsewhere (White, 2017a). Here the concern is specifically with frames on the sub-second scale: that is, short periods of time within which, hypothetically at least, events are experienced as contemporaneous. Proposals falling into that category date back to the 1940s: a brief survey of these is a useful way of introducing themes and issues that apply to the topic as a whole.

2.1: Frames in vision: Ansbacher (1944)

Ansbacher (1944) presented a rotating wheel on which an arc of 36° was presented. Participants judged the length of the arc they perceived, and Ansbacher found that the perceived arc was shorter than the actual arc, with the perceived shrinkage increasing as rotation rate increased. Other stimuli, such as sine waves and triangles, resulted in even greater perceived shrinkage. Ansbacher argued that the findings could be explained on the hypothesis that visual events were sampled at periodic intervals. With periodic sampling, one sample of the arc's location is liable to overlap with the next. Ansbacher argued that overlapping segments were suppressed due to some form of contrast masking, so that only non-overlapping portions were perceived. He was able to account for the results, not only the change in shrinkage with rotation rate, but also differences in degree of shrinkage between different kinds of stimuli, by assuming a sampling rate of about 12 Hz. He argued that this represented a general operating property of the visual system, that the system is active for short periods separated by short periods of inactivity. This is, therefore, a proposal of a general frame in vision with a duration of ~80 ms.

Subsequent research has led to the postulation of other explanations for the effect. Anstis, Stürzel, and Spillmann (1999) pointed out that perception involves summation or integration of visual information over time (McKee & Welch, 1985; Simpson, 1994; Snowden & Braddick, 1991), and that this would result in perceptual elongation of moving objects along the axis of motion. They argued for a perceptual foreshortening process that compensates for this to result in percepts that are approximately correct, and they argued that both their results and those reported by Ansbacher (1944) and others could be explained as an effect of this compensation mechanism. However, it is not clear why compensation would result in perceptual shrinkage rather than accurate length perception. Geremek, Stürzel, da Pos, and Spillmann (2002) found evidence for the involvement of backward masking and argued that perceptual shrinkage effects could result from that. At present, there is still uncertainty about the correct explanation for the perceptual shrinkage phenomenon, and it should additionally be noted that most studies have found less shrinkage that was reported by Ansbacher (Anstis et al., 1999). However, it is likely that the explanation lies with one or more low level visual mechanisms, and that it is a specific effect of the operation of those mechanisms. That is, there is no need to postulate a general frame of vision, much less a general frame of conscious perception, because the phenomenon is process-specific. In this case, there is not even a need to propose a local or process-specific frame, because the phenomenon can be explained without recourse to that idea. This is a theme that will recur in this review: that frame-like phenomena can be explained by reference to operating characteristics of local processing, without a need to propose even local frames of perception.

2.2: Cortical scanning and the psychological moment hypothesis

The cortical scanning hypothesis originated with Pitts & McCulloch (1947), who proposed an initial layer of neurons from which impulses descend to a second level where they are averaged or otherwise integrated over a fixed time period which is the duration of the scanning cycle. Scanning is a cyclical activity in which layers of the cortex go through phases of increased or decreased receptivity to incoming information: thus, a frame would be the summed information content of a single receptive cycle. Pitts and McCullogh associated this with the alpha rhythm, about which more will be said later (sections 2.3 and 3.3). This was developed into the psychological moment hypothesis by Stroud (1949, 1956). Stroud's idea was that a scanning cycle eliminated information about temporality, through the summing or combining or averaging process; thus, perceived movement or change was the result of an inference based on differences between successive psychological moments. Stroud (1956, 1967) argued that the impression of motion when watching a movie occurs because "at the level of data processing of which we are aware, our visual system processes visual inputs in similar logical blocks" (1967, p. 624), which are the psychological moments. He argued that events within a given psychological moment are experienced as cotemporal, and that the impression of motion occurs when there is at least one frame of a movie per psychological moment. He proposed a duration for the psychological moment of about 100 ms, with a range from about 50 ms or less to about 200 ms. This range was based on a survey of research on several different topics including brightness matching, auditory stimulus thresholds, reaction times, and the effects of short bursts of white noise on speech intelligibility (Stroud, 1956). One line of research discussed by Stroud (1956) was that by von Békésy (1936), showing that threshold intensity for tones of low frequency exhibits a step function when plotted against frequency. Stroud predicted (or, strictly speaking, postdicted) the locations of the steps by assuming an integration interval of 106 ms. Subsequent research has shown a range of stimulus discrimination thresholds and temporal integration intervals far greater and more variable than that in the research discussed by Stroud (1956): both that research and its relevance to the psychological moment hypothesis will be discussed in section 4.2.

Evidence relevant to Stroud's hypothesis was reviewed by Shallice (1964). Of particular interest is Shallice's analysis of research on perceptual causality by Michotte (1963). Michotte presented visual stimuli in which a moving object (A) contacted an initially stationary object (B), whereupon B moved off in the same direction and at the same speed. This usually gives rise to a perceptual impression that A made B move (Hubbard, 2013a, 2013b; Michotte, 1963; White, 2017b). In one experiment there was a delay between A contacting B and B starting to move. Michotte found that the causal impression reliably occurred with delays up to 56 ms. With delays between 56 and 140 ms an intermediate impression occurred, such that the causal impression was there but B was perceived as delayed or as sticking to A temporarily. With delays over 140 ms the motion of B was almost never perceived as caused by A. Shallice argued that the causal impression depends on the operation of a change detector that integrates information from successive perceptual "moments". If the contact time of A and B covers two (or more) consecutive "moments", then no change is detected and no causal impression will occur. If the contact time covers part of a single "moment" then change is detected and the causal impression occurs. If the contact time covers the whole of a "moment" then also change is detected and the causal impression occurs, but because A and B are perceived as in contact for the duration of a "moment", then the "sticking" impression will occur. From Michotte's data it is possible to estimate the duration of a "moment" on the basis of that reasoning, and Shallice judged it to be close to 100 ms, similar to the value proposed by Stroud (1956).

There are two problems with that argument. One is that Stroud argued that events within a psychological moment are experienced as cotemporal. In that case, a psychological moment has no subjective duration. Therefore, being in contact for the duration of a psychological moment cannot explain the "sticking" impression, which is obviously characterised by temporal extension, because there is zero experienced duration. The second problem is that different effects of delay have been found in subsequent studies, with causal impressions being reported under substantially longer delays than found by Michotte, with variations in presentation conditions (Guski & Troje, 2003; Powesland, 1959; Schlottmann, Ray, Mitchell, & Demetriou, 2006; Young, Rogers, & Beckmann, 2005). There is some uncertainty about these findings: reports and ratings may be influenced by post-perceptual processing and may therefore not reflect the actual perceptual impression. However, the findings cast doubt on the idea that the delay effect is a guide to the existence and duration of a psychological moment. It should also be pointed out that there are other ways of explaining the delay effect (Hubbard, 2013a, 2013b; White, 1988, 2017b), so at present the delay effect does not unambiguously support the psychological moment hypothesis.

2.3: Cortical excitability

The hypothesis of a cortical excitability cycle appears to have originated in work by Bishop (1932), who demonstrated variations in the responsiveness of neurons to stimuli with regular repeating cycles of about 200 ms duration. That was in rabbits, but it has been argued that that cycle corresponds to the alpha rhythm in humans, with a cycle duration of about 100 ms (Harter, 1967; Lindsley, 1952). Supportive evidence for a similar variation in responsiveness in humans, on the time scale of human alpha, was reported by Bechtereva and Zontov (1962) and Callaway and Laine (1964). The strategy of the research was to present successive flashes of light, and it was shown that the greatest response to the second light occurred when it was presented about 100 ms and about 200 ms after the first, and the least response when it was presented about 150 ms and about 250 ms after the first. Thus, the alpha rhythm, in this case stimulus-driven, was interpreted as a periodic variation in excitability of the relevant area of the cortex.

Several authors argued that alpha waves could serve as a temporal coding mechanism (Harter, 1967). For example, Ellingson (1956) proposed that "when the excitability cycles of a group of neurons are synchronized, then the flow of impulses through that group will be timed by the frequency and phase of the cycle" (p. 9). Timing in this case means something more like gating, because the supposed advantage of it is to prevent the smearing or distortion that a continuous input of stimuli would generate (Lindsley, 1952). The example that Lindsley used to illustrate the idea was eye movements in reading, where the written text appears sharp and clear despite the blurring that ought to be caused by the movement of the eyes. This immediately seems rather odd: a continuous input of stimuli is broken up into discrete packages to prevent smearing, but the discrete packages would still have to be temporally integrated to prevent a rapid version of akinetopsia in which the visual world consisted of a mere succession of static images (Zihl et al., 1983). It is possible that an excitability cycle represents a temporal bin in which information is accumulated to the point where the stimulus can be detected. However, such a function would not be usefully subserved by a neuronal system that ran at a constant frequency. Consider, as an example, visible persistence, the maintenance of an image of a stimulus beyond the termination of the stimulus. As Farrell (1984) pointed out, there is a need to find a compromise between minimising the smear generated by moving stimuli and maximising the time available for analysis of the stimuli. The visual system makes the compromise in a flexible way, so that the duration of visible persistence varies depending on the duration of a static stimulus and on stimulus motion (Di Lollo, 1977, 1980; Dixon & Di Lollo, 1994). This flexibility cannot be accommodated within an excitability cycle of fixed frequency. The cortical excitability hypothesis in relation to alpha is still alive and well, however, and I shall offer a more up-to-date perspective on it in the sub-section on EEG research.

2.4: Central and perceptual intermittency

The idea of central intermittency was first proposed by Craik (1947). Craik set the task of pointing at a moving target, and he found that adjustments were made at discrete intervals, not continuously. Craik interpreted this as indicating that the mechanism of behavioural choice went through a fixed process and completed it before starting anew. This would generate intermittency in adjustments to ongoing behaviour. The idea was further developed by Welford (1952), and research on it was reviewed by Bertelson (1966). Two observations suffice for present purposes. One is that the observed frequency of adjustment was about 2 Hz, which is far to low to form a plausible general frame of conscious perception. The other is that intermittent adjustment was observed with novices, but with increasing expertise the adjustment was more continuous. This indicates that it is a local phenomenon, possibly confined to motor learning.

In principle, intermittency could be a feature of any mechanism that runs in a fixed way and cannot handle any further input until processing of the current input has been completed. There could, therefore, be perceptual intermittency as well as motor intermittency (Allport, 1968; Harter, 1967; Kristofferson, 1967a). Kristofferson (1967a) proposed that perceptual intermittency is governed by a clock that generates time points at intervals of about 50 ms. These time points determine when attention switching can occur, and when information can be transmitted from one stage of a process to the next. This is consistent with the single channel theory of information processing, according to which only one signal or channel is attended at a time and attention switches between signals or channels at intervals. To the extent that this is a discrete frame hypothesis, it is specific to attentive processing, as Kristofferson acknowledged. Kristofferson argued that two kinds of evidence were relevant to the intermittency hypothesis, concerning successiveness discrimination and reaction times. Successiveness discrimination refers to the ability to detect whether two stimuli were presented at the same time or not: the discrimination threshold can be treated as evidence for the frequency of time points or frames.

Reaction times in this case referred specifically to the case where the participant must respond to a stimulus that could occur in either of two channels. Kristofferson (1967a) presented evidence that supported the proposed time point interval of 50 ms (see also Schmidt & Kristofferson, 1963).

There have been many other studies of both temporal discrimination and reaction time phenomena, and I shall review both bodies of evidence later in the paper (sections 4.2 and 3.4, respectively). For now, it suffices to say that there is much evidence that does not accord with the 50 ms hypothesis, and that shows temporal discrimination thresholds at least an order of magnitude shorter than that. In a later revision, Kristofferson (1984) postulated instead a time quantum with a value that can vary from 12 ms to 200 ms depending on stimulus presentation conditions, and also postulated multiple clocks instead of a single clock, an idea that has developed greatly since then (Buonomano, Bramen, & Khodadadifar, 2009; Gamache & Grondin, 2010; Goel & Buonomano, 2014; Gorea, 2011; Hogendoorn, Verstraten, & Johnston, 2010; Mauk & Buonomano, 2004).

Harter (1967) argued that there must be a cortical mechanism for dividing and grouping incoming sensory information into discrete temporal units, in the interests of efficient operation. The implication is that information cannot be processed faster than the frequency of the temporal units. Harter reviewed two hypotheses about the mechanism of central intermittency: these were the cortical scanning and cortical excitability cycle hypotheses, which have already been discussed. Harter reviewed several kinds of evidence that support the discrete processing hypothesis. I will not go into details because that research (like that cited by Stroud, 1956) has been largely superseded by subsequent studies that will be reviewed shortly. Harter argued that, collectively, the research supported the hypothesis of a time period of about 100 ms, with a range from 50 - 200 ms. This was not strictly correct even in the evidence Harter surveyed: reported time periods ranged from 20 ms (Hirsh & Sherrick, 1961) to 500 ms (Craik, 1947).

2.5: Overview of early proposals

In the early proposals, in most cases, frames or discontinuous processing were proposed as features of specific processes or activities such as pointing at moving targets, or temporal discrimination with visual stimuli, not as general features of conscious percepts. Stroud (1949, 1956, 1967) proposed the psychological moment as a general feature of visual processing but did not extend the proposal to other modalities. Some themes have emerged that are of continued relevance to more recent work. Discrete frames may be a feature of local processes, which means that evidence must be obtained from many different processes in different modalities before a case can be made for frames as a general feature of conscious perception, even within a single modality. Periodic switching of attention between stimuli or channels may be a means of coping with complex informational input, and discrete processing epochs may be a consequence of attention switching. EEG regularities such as alpha may be indicators of periodic phenomena in information processing such as receptivity to new input. Individual frames do not give rise to any experience or perception of a temporally extended property, of any kind of change (e.g. motion), or of duration, because everything within a single frame is experienced as contemporaneous: for perception of change, some form of integration of information across more than one frame is necessary. This last point, as I shall show in the following review, is not correct.

3: Recent proposals about discrete frames

Specific proposals will be briefly summarised and evaluated against either the kinds of evidence on which the authors of the proposals called or on evidence relevant to the proposed frame durations. Issues that apply to all the proposals will be addressed in section 4.

3.1: Attention-based periodic sampling

The most sustained research investigation of discrete frames in conscious perception is that by VanRullen and colleagues (Busch, Dubois, & VanRullen, 2009; Busch & VanRullen, 2010; Chakravarthi & VanRullen, 2012; Dubois & VanRullen, 2011; Ilhan & VanRullen, 2012; Macdonald, Cavanagh, & VanRullen, 2014; Miconi & VanRullen, 2010; VanRullen, 2016; VanRullen, Busch, Drewes, & Dubois, 2011; VanRullen, Carlson, & Cavanagh, 2007; VanRullen & Dubois, 2011; VanRullen & Koch, 2003; VanRullen & Macdonald, 2012; VanRullen, Reddy, & Koch, 2005, 2006; VanRullen et al., 2014). The earliest paper in the series, VanRullen and Koch (2003), posited that "[c]onscious perception might well be constant within a snapshot of variable duration... 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" (p. 207). Thus, a frame of conscious perception would be defined in terms of subjective contemporaneity of events within it, and would be explained as a product of the modus operandi of perceptual processing. Although the quotation does not specify a modality, in fact all of the research that has been called on as support for the frame hypothesis in this body of work concerns vision, as will be shown in this section. VanRullen (2016) favoured the hypothesis of "multiple perceptual cycles, in distinct brain networks, with different periodicities" (p. 725). If that is a valid reflection of the evidence, then it effectively disconfirms the hypothesis of a general frame for all of conscious perception, instead supporting a hypothesis that frames are local processing phenomena.

Within vision, the frame hypothesis most generally advocated in this body of research is specific to attentive visual processing. VanRullen and Dubois (2011) and VanRullen et al. (2014) argued that attentive processing is periodic, essentially analysing successive discrete samples of information as units, and that this enables attention to take samples of information from a single perceptual target or object, and also to scan multiple targets sequentially, which is a contemporary version of the single channel theory of information processing. VanRullen et al. (2014) stated, "Attention is often considered as the gateway to consciousness..., and it follows that if the gate opens periodically, the contents of consciousness will also update periodically" (p. 5). Based on the research evidence, the periodicity of attentive sampling is about 7 - 13 Hz, corresponding to frame durations of about 80 - 140 ms. VanRullen (2016) reviewed a large body of research on effects of pre-stimulus oscillatory phase on perception, concluding that the research showed two peaks at 7 Hz and 11 Hz. He argued that the latter reflected sensory/perceptual processing and the former reflected periodic attentive sampling. This would imply that attentive sampling may account for some periodicity, but that peridiocity is also a feature of other forms of processing. VanRullen (2016) concluded: "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" (p. 732). Thus, while there has been an emphasis on frames with a duration in the range 80 - 140 ms, it is acknowledged that there may be other, process-specific frame rates, so that there may be little or no co-ordination of frames across modalities. I shall now survey the range of evidence that has been called on in this body of literature.

3.1.1: The continuous wagon wheel illusion

It has long been known that images of rotating wagon wheels on cinema screens can appear to depict rotation in the wrong direction, because of the temporal relationship between the rotation rate of the wheel and the frame rate of film projection technology (Levichkina, Fedorov, & van Leeuwen, 2014). However, many studies have shown that a similar illusion of motion reversal can occur with real rotating objects, such as discs with a sunburst pattern on them, under continuous illumination (Arnold, Pearce, & Marinovic, 2014; Purves, Paydarfar, & Andrews, 1996; VanRullen et al., 2005). The aim here is not to review the literature on this, known as the continuous wagon wheel illusion (cWWI), but specifically to assess whether the findings support the hypothesis of conscious (visual) perception as a discrete frame updated at periodic intervals.

Using a sunburst pattern of alternating black and white spokes on a rotating disc, the frequency with which colours alternate at any given spatial location can be varied by manipulating either the width of the spokes or the rotation rate. By varying these, VanRullen et al. (2005) found that, under a variety of different conditions, the peak rate of reporting the cWWI occurred at an alternation rate of about 10 Hz. They argued that this can be explained as a result of "discrete attentional "snapshots" taken every 50-100 ms" (p. 5296). Two further observations are relevant here. They found the same 10 Hz peak with both first-order and second-order motion, indicating that the illusion cannot be completely explained by reference to low-level visual mechanisms (Burr & Thompson, 2011). They also found that the peak at 10 Hz did not occur if a distractor task was used, indicating that the involvement of attention may be necessary for the illusion to occur. The evidence is, therefore, consistent with the hypothesis that perceptual frames are a product of periodic attentive sampling. Several other studies of the cWWI have reported evidence supporting discrete snapshots at a rate of approximately 13 Hz (see Arnold et al., 2014; Macdonald et al., 2014; Simpson et al., 2005; VanRullen et al., 2006).

There are several problems with that evidence and argument in relation to the discrete frame hypothesis. The cWWI does not occur on most trials: even at the rate of peak occurrence, in the study by VanRullen et al. (2005) the illusion was reported on no more than 30% of trials. If discrete frames are being constructed all the time, it is hard to explain why the illusion does not occur more often. Moreover, the illusion does not occur on first exposure to the stimulus, and in fact at least 14 s of adaptation is necessary for the illusion to occur (Kline, Holcombe, & Eagleman, 2004, 2006). It is not clear why adaptation should be necessary if the illusion is a product of discrete frame construction that is going on all the time. Thus, if the evidence concerning the cWWI does support a frame hypothesis, it could only be a frame hypothesis that was not only modality-specific and process-specific, but also temporally specific, occurring at some times and not at others. This is very far from supporting a claim that all attentive visual processing proceeds in discrete frames.

In addition, although the peak rate of reporting the illusion in the study by VanRullen et al. (2005) occurred at 10 Hz, rates of reporting the illusion did not vary much at longer periods, and even at 40 Hz the rate was greater than 10%. Beyond 30 Hz the frequency of reporting any motion declined sharply because the stimulus was increasingly perceived just as a blur with no clear motion direction. However, while correct direction perception declined in lockstep with the overall decrease in reporting motion, illusory reversal did not decline. Because of this, considering only those trials on which a direction of motion was reported, the percentage of trials that were illusory motion actually <u>increased</u> as the alternation rate increased, and approached 50% at 40 Hz (VanRullen et al., 2005, Figures 1a and 1b). There is, at least, a wide spread of frequencies over which the cWWI occurs, and only a small proportion of occurrences are at 10 Hz. A spread of responses in the opposite direction was reported by Arnold et al. (2014): illusory motion reversals occurred quite often (compared to the peak frequency) at just 2 Hz (500 ms). Simpson, Shahani, and Manahilov (2005), on the other hand, found results consistent with a peak sampling rate of 16 Hz. These varied results indicate that there must be factors, possibly specific to the methods of individual studies, that influence the rate at which the cWWI occurs. In order to reconcile these findings with even a local discrete frame hypothesis, it would be necessary to accept that frames do not have a fixed periodicity, but instead vary over a range from 2 Hz to 40 Hz, at least. In that case, at low frame rates the problem of jerkiness arises and is less easy to deal with.

Arnold et al. (2014) found evidence for different peak frequencies of reporting the illusion depending on whether the sunburst pattern was created by luminance variations with constant colour (grey) or by colour variations (red-green) with constant luminance. They found peaks at 10 Hz for luminance-defined patterns (replicating VanRullen et al., 2005 and several other studies) and at 5 Hz for colour-defined patterns. It is not likely that the rate of discrete frames of conscious perception would vary by a factor of two depending just on whether a sunburst was grey with luminance differences or coloured without luminance differences. Finally, Kline et al. (2004) presented two stimuli simultaneously and found times where the illusion occurred with one stimulus and not the other. This is a strong indication that the illusion is a local phenomenon, in which case it could not be an indicator of something general to conscious visual perception.

Arnold et al. (2014) proposed a different kind of explanation for the cWWI. A full account of this lies outside the scope of the present paper. However, it is based on the idea that attentive tracking of object features operates with a relatively low temporal resolution, so that features cannot be tracked if the rate of change in them exceeds ~10 Hz. This can result in mismatching features such that, with a rotating sunburst pattern, one spoke may be incorrectly matched to an adjacent spoke. In effect, because of its poor temporal resolution, attentive processing loses track of which spoke is which, with consequent erroneous or illusory perception. This explanation has yet to be confirmed in further research, but it does exemplify the possibility that the cWWI can be explained by local processing characteristics, without recourse to the discrete frame hypothesis.

In conclusion, the findings of studies on the cWWI do not support the discrete frame hypothesis. Whatever the explanation for the cWWI, it is a phenomenon that is occasional in occurrence, variable in rate of occurrence from 2 Hz to 40 Hz, localised in the visual field, specific to the visual system, and possible explicable as a phenomenon of fatigue or adaptation, or problems caused by low temporal resolution in visual processing. An additional problem is that the peak frequency of the cWWI is in the region of 10 - 13 Hz, which is outside the value of 7 Hz proposed for periodic attentive sampling by VanRullen (2016) on the basis of EEG evidence.

3.1.2: EEG oscillations

Numerous periodic oscillations have been shown to occur in the brain. Other authors have also suggested that EEG oscillations might be indicators of discrete frames in perception or consciousness (e.g. Freeman, 2004, 2006), but in this section I focus on studies that have been taken as evidence supporting the attention sampling hypothesis of VanRullen and colleagues. Specifically, there is evidence of an association between pre-stimulus oscillatory phase and perception, such as ability to detect a near-threshold stimulus (Busch et al., 2009; Busch & VanRullen, 2010; Drewes & VanRullen, 2011; VanRullen, 2016; VanRullen et al., 2011). VanRullen (2016), compiling the results of several studies conducted by him and his colleagues, reported that the clearest evidence of a relationship between pre-stimulus phase and perception occurred with oscillations around 7 Hz and 10 Hz. As discussed earlier, VanRullen argued that the former was a marker of the rate of attentive sampling, and the latter was associated with perceptual processing. The question is whether this evidence, particularly the evidence about the 7 Hz oscillation, really supports the hypothesis of discrete frames in conscious, attentive visual perception. Five main concerns can be raised.

One concern, noted by VanRullen (2016), is that, across the whole range of studies in his review, the oscillatory frequencies that were associated with perceptual effects ranged from 1 Hz to 30 Hz "but without any apparent logic relating frequency to perceptual or cognitive function" (VanRullen, 2016, p. 727). Clearly conscious perception cannot proceed in discrete frames of 1,000 ms in duration, which would be implied if they were set by an oscillatory frequency of 1 Hz. This would result in very obvious and disabling disruption to visual perception, resembling that experienced by the patient with akinetopsia (Zihl et al., 1983). Presumably only some of the reported influential frequencies act to set discrete frames of conscious perception, but which ones and why? That is, if some do and some do not, what marks the difference between them? It could be argued that the 7 Hz oscillation is special in that regard, because it is found most commonly and it is linked to attentive sampling. However, it does not occur all the time, and in particular is suppressed when the eyes are opened (Bazanova & Vernon, 2014; Harter, 1967; Klimesch, Sauseng, & Hanslmayr, 2007; McComas & Cupido, 1999). It is perhaps not impossible that visual perception could consist of discrete frames some of the time but not all of the time, but it seems likely that there would be some associated difference that would be evident in perception. I shall return to this issue at the end of this sub-section.

A second concern, also noted by VanRullen (2016), is that the variability in perception that is accounted for by oscillatory phase is small. For the collective set of studies reviewed by VanRullen (2016), it was 10 - 20%: as an example, in Busch et al. (2009) it was 16%. VanRullen et al. (2007), who first reported the 7 Hz result, interpreted it as showing that attention periodically sampled information at a rate of approximately seven elements per second. Busch and VanRullen (2010) stated, even more strongly, that the spotlight of attention "blinks on and off every 100 - 150 ms" (p. 16051). The results do not support such an extreme claim: there is just a small difference in the probability of detecting a near-threshold stimulus depending on oscillatory phase. Measurement issues could mean that the difference between opposite phases is greater than it appears: VanRullen (2016) commented, "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" (p. 732). As they stand, however, the results do not support the hypothesis of attention switching on and off: at most, there is a significant but small decrement in attention depending on the phase of the oscillation.

The clearest problem for a discrete frame with a frequency of 7 Hz, and indeed for any hypothesized frame of that order of magnitude, concerns the definition of a discrete frame adopted by VanRullen and colleagues (and by other authors - e.g. Wittmann, 2009, 2011), that events within a single frame are experienced as contemporaneous. Suppose a frame has a duration of ~140 ms, as implied by a rate of 7 Hz. If two events are separated by 10 ms, there is a 93% probability that they will fall into the same frame, and a 7% probability that they will occur in different frames. If events within one frame are experienced as contemporaneous and events in different frames are experienced as successive, then a temporal discrimination judgment will be correct 7% of the time and will be at chance level the other 93% of the time. Several studies, however, have shown various kinds of visual temporal discrimination, such as experienced nonsimultaneity, for stimuli separated by less than 10 ms (Georgeson & Georgeson, 1985; Sweet, 1953; Tadin, Lappin, Blake, & Glasser, 2010; Wehrhahn & Rapf, 1992; Westheimer & McKee, 1977). The only way to maintain the hypothesis of a discrete frame with a duration of 140 ms in the face of that evidence is to abandon the definition in terms of perceived contemporaneity. A possible alternative would refer to frequency of updating. A frame can be conceived as a brief store of perceptual information derived by perceptual processing. Thus, a perceptual discrimination process could generate information that one stimulus occurred 5 ms after another; that information could be entered into a frame; and it would remain there until the frame was next updated. In that way long frame duration could be rendered compatible with short temporal discriminations.

VanRullen et al. (2011) argued that, if discrete frames are defined in terms of experienced contemporaneity, then it should be possible to predict whether two events are experienced as contemporaneous or sequential from their relationship to the phase of oscillations. Some recent studies have now found evidence for this, in vision and in the somatosensory modality (Baumgarten, Schnitzler, and Lange, 2015, discussed in section 3.1.4).[4] Milton and Pleydell-Pearce (2016) asked participants to judge whether onset of two visual stimuli was synchronous or asynchronous and found an association between alpha phase and tendency to correct judgment of stimuli as asynchronous. Samaha and Postle (2015) used a temporal discrimination task where participants had to judge whether one flash or two were presented. The authors argued that, if alpha marks the frame rate of conscious perception, then the smaller the frame duration, the greater the temporal resolution of vision should be. They found this in an individual differences analysis: participants with a faster alpha rhythm showed superior temporal discrimination to those with a slower alpha rhythm. Cecere, Rees, and Romei (2015) investigated the double flash illusion. In this illusion, a single flash is presented in temporal association with two auditory tones and, sometimes, two flashes are perceived. Cecere et al. used transcranial magnetic stimulation (TMS) to alter the oscillatory frequency of alpha, and found that the temporal window for occurrence of the double flash illusion increased when the frequency of alpha was reduced and decreased when the frequency of alpha was increased. The authors suggested that "alpha oscillations might represent the temporal unit of visual processing that cyclically gates perception" (p. 231).

Those results are consistent with the hypothesis of a discrete frame in vision with a frequency corresponding to, and indeed possibly set by, alpha. Other findings, however, cast doubt on that interpretation. Ronconi, Oosterhof, Bonmassar, and Melcher (2017) presented a brief visual flash followed after a short inter-stimulus interval (ISI) by a second flash either at the same location or at another nearby location. The ISI was timed so that perception of one or two flashes, in the former case, and perception of apparent motion or two independent flashes, in the latter case, was about equally likely. Perception of one versus two flashes could be predicted from the phase of alpha oscillation (8 - 10 Hz), but perception of apparent motion could be predicted from the phase of theta oscillation (6 - 7 Hz); note that these are not endogenous oscillations, but oscillations triggered by the stimulus. If the results have any implications for discrete frames, it would be that frame duration varies depending on the oscillatory frequency generated by the stimulus, and different kinds of stimuli generate different oscillatory frequencies. But it is more likely that the findings show only that the temporal window of integration differs between different perceptual processes, and that they have no implications for the discrete frame hypothesis. As Ronconi et al. pointed out (and see section 4.3), temporal integration occurs on multiple time scales ranging from a few milliseconds to 2 s or more. If all of those time scales were frames of conscious perception, there would be frames with multiple durations occurring contemporaneously. It is more likely that effects of oscillatory frequency on perceptual phenomena show only evidence for local variations in temporal integration windows for specific perceptual processes. In other words, temporal windows of integration occur in processing prior to the point at which frames might occur, and the issue is whether the products of all those different processes are than marshalled into periodically updated global representations. Effects of oscillatory frequency on temporal integration do not speak to that issue.

A fifth problem for the 7 Hz oscillation hypothesis is that attention and perception are not the same. It is possible that attentive processing involves periodic switching on a time scale of 7 Hz, but that conscious perception does not. Conscious percepts could be actively maintained continuously while being updated periodically. Under the attention switching hypothesis, periodicity may lie behind conscious perception, but not within it. Thus, for example, the results of the study by Samaha and Postle (2015) might show that alpha rhythm ia s marker of the frequency of attentive sampling of input, but this is still compatible with conscious percepts being effectively continuous, or continuously updated. The temporal resolution of a perceptual process affects the content of information that gets into conscious perception, but without necessarily imposing a frame-like structure on conscious perception.

3.1.3: "Perceptual echoes"

VanRullen and Macdonald (2012) presented stimuli comprising a random series of luminance values at 160 frames per second. EEG responses to each luminance change (except those in the early and late stages of the sequence) were recorded and compiled to yield a cross-correlation summary. The results showed a waveform triggered by the stimulus with a period of about 10 Hz that continued for approximately 10 cycles (1,000 ms). They also found evidence that reported visual flicker intensity was correlated with 10 Hz oscillations triggered by stimuli displayed about 500 - 1,000 ms previously.

As the authors noted, numerous studies have previously found that alpha phase can be reset or entrained by visual stimuli. The difference, they argued, is that, in their study, the oscillations were triggered by nonperiodic stimuli. Not all previous studies were different in that respect, however. Barlow (1960) observed a periodic response with a frequency of 10.6 Hz, closely matching that found by VanRullen and Macdonald (2012), to regularly repeated visual stimuli (brief flashes). This frequency did not match the repetition frequency of the flash, which was 1.2 Hz. To exclude the possibility that the periodic response "might represent a higher harmonic of the flash frequency" (p. 318), Barlow presented stimuli with variable intervals (0.8 to 2.0 s) and found the same 10 Hz response. Figure 2 in Barlow (1960) shows the periodic response damping out over a period of about 1 s, also similar to that reported by VanRullen and Macdonald (2012). The phenomenon was picturesquely described as "ringing" by Harter (1967). This appears similar to the finding reported by VanRullen and Macdonald (2012).

VanRullen and Macdonald (2012) suggested that the functional significance of these oscillations could relate to iconic memory, which in vision has been shown to retain information on a time scale up to about 1 s (Coltheart, 1980; Haber, 1983; Sperling, 1960), hence their use of the term "perceptual echoes", to capture the idea of a periodically reverberant but decaying memory store.

There are some problems with that interpretation. Ilhan and VanRullen (2012) sought evidence for equivalent "perceptual echoes" in audition but did not find them. This adds to the case that, if there are discrete frames, they do not encompass the whole of perception. In this case, however, the interpretation proposed by the authors implies local discrete frames of short-term visual storage, not of conscious perception, so it may not even be relevant to the frame hypothesis. And research evidence about iconic memory indicates not a periodically fluctuating informational representation but a continuously maintained representation that decays over time with an exponential function (Coltheart, 1980; Haber, 1983; Sperling, 1960). Furthermore, the evidence that the alpha oscillations were correlated with reported visual flicker suggests an effect on perceptual processing, not memorial processing.

The question that should be asked is, what activity might be triggered by the occurrence of a novel visual stimulus? Mere storage is certainly one possibility, but there are others. Another possibility is that the stimulus triggers some kind of attentive monitoring, for example for detecting further stimuli at the same location or changes in the existing stimulus. This would be consistent with the proposal of periodic attentive sampling, except that the frequency is about 10 Hz instead of the 7 Hz found in the attentive sampling research (VanRullen et al., 2007, 2011, 2014). Other possibilities concern functions proposed for alpha in general, which will be briefly reviewed in section 3.3. The existing evidence does not allow any informed choice between different hypotheses about the functional significance of the oscillations, so the term "perceptual echoes" should not be used until and unless that particular functional hypothesis is confirmed by further research.

The oscillations appear to have been triggered by each luminance change. Since luminance changes were presented at a rate of 160 Hz, this seems to imply that 160 separate oscillations would be triggered per second, which means that, if each one persists for 1,000 ms, there would be about 160 of them going on at any one time until the stimulus sequence terminates. If each oscillation is an informational representation of a luminance change, then the iconic storage hypothesis is not correct, because the capacity of iconic store has been estimated at ~40 bits of information (Sperling, 1960; see also Sligte, Vandenbroucke, Scholte, & Lamme, 2010): 160 representations of events is well beyond that capacity limit. However, the possibility of 160 contemporaneous oscillations is also incompatible with any hypothesis involving attention, because attention does not have the capacity to be divided between 160 stimuli. It should also be noted that a presentation rate of 160 Hz implies a duration for each luminance event of about 6 ms, which is far below the flicker fusion frequency (Carmel et al., 2007; Curran & Wattis, 1998), so it is likely that individual events would not register in conscious perception at all. The functional significance of the oscillations reported by VanRullen and Macdonald (2012) therefore remains mysterious at present.

3.1.4: Other modalities

VanRullen et al. (2014) sought evidence equivalent to that reported for vision (and summarised in the foregoing three sub-sections) in the auditory modality. They reported that there was no evidence for an auditory equivalent to the cWWI, no evidence for effects of pre-stimulus oscillatory phase on detection of near-threshold auditory stimuli (see also Zoefel & Heil, 2013), and no evidence for a stimulus-triggered 10 Hz oscillation in response to auditory events presented at 160 Hz (Ilhan & VanRullen, 2012). They suggested that perceptual cycles (or discrete frames) could occur in audition, but be manifested in different ways and at different frequencies. In fact, there is plenty of evidence for that.

Much auditory processing involves sampling over time. For example, perception of loudness can involve summation of information over about 200 ms (Räsänen & Laine, 2013; Rimmele, Sussman, & Poeppel, 2015; Zwislocki, 1969; see also Näätänen & Winkler, 1999).

This raises the possibility that periodic oscillations have a functional role in temporal integration of auditory information. Taking speech perception as an example, it has been shown that speech sounds have a hierarchical set of temporal structures ranging from low level features such as formant transitions on a time scale of 20 - 40 ms, equivalent to an oscillatory frequency in the range of 25 - 50 Hz (Poeppel, 2003; Rosen, 1992), to syllables and whole words on a time scale of hundreds of milliseconds (Chait, Greenberg, Arai, Simon, & Poeppel, 2015; Poeppel, 2003), and even beyond to narrative units on a scale of many seconds (Hasson, Chen, & Honey, 2015). Chait et al. (2015) made a case that speech signals are analysed on multiple time scales and that information generated by these analyses is integrated to form speech percepts. It would seem plausible, then, that periodic oscillations might have functional significance in analyses of speech components such as syllables that have consistent durations.

Several studies have found evidence for stimulus-triggered oscillations in response to speech input. Mai, Minett, and Wang (2016) reviewed evidence for the involvement of oscillations at 4 - 8 Hz (theta), 13 - 30 Hz (beta), and 30 - 50 Hz (gamma). In their own study they found associations between phonological processing and delta and theta (for both words and non-words), beta associated possibly with memory processing and auditory-motor interactions, and gamma possibly associated with lexical memory retrieval (to do with distinguishing words from non-words). These results at least hint at functional roles for oscillations in speech processing, including adding meaning to speech representations as well as analysing the temporal structure of speech. Ortiz-Mantilla, Hämäläinen, Realpe-Bonilla, and Benasich (2016) showed changes in EEG responses to native and non-native phonemes between 6 and 12 months of age. They suggested that theta oscillations support syllable processing, which is consistent with the fact that theta oscillation frequencies approximately match typical syllable durations (Giraud & Poeppel, 2012), and that gamma oscillations "underlie phonemic perceptual narrowing, progressively favouring mapping of native over non-native language across the first year of life" (Ortiz-Mantilla et al., 2016, p. 12095). It is noteworthy that none of the research has implicated alpha.

The main problem with the proposed association between temporal levels of speech organisation and oscillatory frequencies is that the duration of elements in speech is not fixed. Syllables, for example, vary in duration by 150 ms or more (Hickok & Poeppel, 2007), and these variations occur continuously through ongoing speech. Giraud and Poeppel (2012) have proposed that salient points in speech input, such as boundaries between syllables or words, reset the phase of the relevant oscillation. This would presumably mean that the phase is reset at each boundary except when two or more consecutive syllables have the same duration. In that case, the oscillations would not exhibit regular periodicity. It would make functional sense for oscillations to be reset at unit boundaries, assuming that a single oscillation marks some kind of processing unit. A study by Kösem, Basirat, Azizi, and van Wassenhove (2016) found that high frequency oscillations (including gamma) showed phase shifts as a function of the spoken word, supporting the hypothesis of Giraud and Poeppel (2012) that gamma oscillations are associated with encoding of phonemes. However, the low frequency oscillations they observed (delta and theta) did not seem to match the temporal features of the acoustic structures they were supposed to be tracking. They suggested that the low-frequency oscillations represented attentional modulation of acoustic processing, not chunking of semantic units.

This is a large and complex literature (see, e.g., Zoefel & VanRullen, 2015), but the research does have some import for the discrete frame issue. First, the differences in salient oscillatory frequencies between vision and audition add further weight to the case against general discrete frames of conscious perception. The speech perception findings are specific to speech processing, in particular in the fact that they are entrained or reset by relevant features of speech input. And, while they may mark fluctuations in attentive sampling, they do not seem to mark boundaries between temporally unitary and meaningful percepts, which is what would be expected of discrete frames of perception. This undermines the case that periodicity in attentive sampling or attention switching indicates discrete frames in conscious perception.

One more study is relevant in this context. Baumgarten et al. (2015) investigated the relationship between oscillations and temporal discrimination in the sensorimotor modality. They found that correct detection of two (versus one) somatosensory stimuli depended on the phase of beta oscillations, in the range 8 - 20 Hz, though with the greatest effect between 14 and 18 Hz. Detection rate rose from 40% at one phase to more than 70% at the opposite phase. The authors argued that the results supported a hypothesis of discrete sampling, such that if two stimuli are presented within a single sampling period they are experienced as one, but if they are presented either side of a frame boundary they are experienced as two. This result again shows effects of modality-specific periodicity, because the critical oscillatory frequency differs from that most often found in vision. However, discrete sampling is not the same as discrete frames of conscious perception. It is likely that the beta oscillation does mark periodic variations in something relevant to temporal discrimination: that something might be receptivity to input, as proposed by VanRullen (2016; VanRullen et al., 2014) or the cortical excitability hypothesis (Harter, 1967; Lindsley, 1952). If reduced attention means a reduction in processing resources applied to input information, then temporal differences are less likely to be detected during the reducted receptivity phase of the cycle. That has no necessary implication for whether or not conscious percepts are organised in discrete successive frames. They are just two different things.

3.1.5: "Visual trails"

The term "visual trails" was used by Dubois and VanRullen (2011) to refer to a specific effect that sometimes occurs after taking certain drugs, such as LSD and nefazodone. The effect is not a trail in the sense of a continuous image or a streak, but a series of discrete images that persist behind a percept of a moving object and gradually fade, usually in no more than a few seconds but persisting for as much as one minute in at least one case (Ihde-Scholl & Jefferson, 2001). Dubois and VanRullen suggested that the periodic nature of the images in the trails could relate to periodic activity in motion perception. Thus, if visual perceptual processing generates a series of discrete frames, then the effect of the drug could be to perpetuate information from previous frames so that they are retained in conscious perception, or to disrupt the normal process of suppression of previous frames. In that case, the evidence of visual trails could support the hypothesis of discrete frames in conscious visual perception.

Dubois and VanRullen (2011) acknowledged other possible interpretations of visual trails. They discussed the possibility of visual streak suppression, discussed earlier (Anstis et al., 1999). If the visual streak suppression mechanism failed then one might expect perceptual elongation of objects along the axis of motion. As the term "streak" suggests, however, this would not yield a trail of distinct images of objects, but just a perceptual distortion of the moving object, or possibly a smear behind its trailing edge.

Visual trails are just one entry in a catalogue of visual disturbances involving multiplication or extension of moving objects (Bender, Feldman, & Sobin, 1968; Gersztenkorn & Lee, 2015; Yun, Lavin, Schatz, & Lesser, 2015). The general category is palinopsia, defined by Bender et al. (1968) as "the persistence or recurrence of visual images after the exciting stimulus object has been removed" (p. 321). This definition implies that the condition is not confined to the perception of moving objects, and indeed one of the patients described by Bender et al. found that an image of an object looked at, such as a clock, would persist no matter where she looked, even if she closed her eyes. The cases discussed by Bender et al. show that palinopsia is often associated with other disorders of vision such as illusory distortion of objects, and they commented: "Palinopsia never occurred as an isolated sign" (p. 330). Gersztenkorn and Lee (2015) described eight categories of palinopsia, of which visual trailing is one, and they also described several other types of visual disturbance often associated with palinopsia; akinetopsia was one of these.

Palinopsia has many causes, including brain lesions, epilepsy, metabolic disease, inflammatory demyelination in multiple sclerosis, migraine, some illicit drugs, and some prescription drugs. Of course those are global causes that do not specify changes in visual information processing. However, as Gersztenkorn and Lee (2015) pointed out, there are mechanisms in visual perception that operate to maintain sharp and distinct visual images during eye movements and perception of moving objects; these include visual streak suppression (Anstis et al., 1999) and visible persistence (Di Lollo, 1977; Farrell, 1984). Gersztenkorn and Lee suggested that the initiating causes of palinopsia may act by creating what they called "persistent, diffuse, neuronal hyperexcitability" (p. 6), and that this could produce failures of visual masking and visual streak suppression. A simulation by Kilpatrick and Ermentrout (2012) supported this line of reasoning. This explanation does not seem to account for the occurrence of discrete images of the object, but would be more likely to produce extensive smearing or streaking. However, the hypothesis of general perseverance of previous discrete frames does not account for the effect either. This is because most of the visual field moves on as normal, but the visual trail is superimposed on it, and clearly represents just a portion of the preceding visual percept. In fact the trails are sometimes very specific: Yun et al. (2015) discussed a patient who reported visual trails with her own arm movements but not with her leg movements nor with anything else. It would be hard for a discrete frame interpretation to account for this very local effect.

At present, then, palinopsia in general, and visual trails in particular, constitute an intriguing set of malfunctions in visual processing that has no satisfactory explanation. Their relevance to the discrete frame hypothesis is unclear at present but further investigation of them, particularly at the neurophysiological level, could potentially reveal more about framing, sampling, or updating in visual processing.

3.1.6: Overview of the attentive sampling hypothesis

There is strong evidence for effects of pre-stimulus oscillations at a frequency of about 7 Hz on detection of near-threshold visual stimuli (VanRullen, 2016). This is consistent with the hypothesis that attention samples stimulus information periodically, or more probably a less extreme hypothesis in which the degree of attentive engagement with stimulus information fluctuates periodically. There is also evidence for effects of oscillations at various other frequencies, particularly in modalities other than vision. That evidence is not consistent with the hypothesis of a general discrete frame for the whole of conscious perception on the time scale of the 7 Hz oscillation. One possibility that is consistent with the research evidence is that there are local discrete frames in perception, where "local" may mean modality-specific or process-specific. However, the oscillations account for only a small proportion of the variance in perceptual detection: the spotlight of attention may wax and wane a little, but does not switch on and off, so it is not clear that attentional fluctuations mark definite boundaries between frames. Finally, if attentive processing does proceed in oscillations, this does not entail that conscious perception does the same. Percepts may be maintained continuously but modified periodically (and locally), and it is not clear that modifications of different perceptual features are temporally co-ordinated.

3.2: The cinematic theory of cognition

The cinematic theory of cognition was developed in several papers by Freeman and colleagues (principally Freeman, 2004, 2006; Kozma & Freeman, 2017). Here I shall focus mainly on the most recent version, by Kozma and Freeman (2017). The basis for the theory is the observation of large-scale co-ordination in cortical activity, manifested as cyclical periods of high amplitude (about 100 - 200 ms in duration) separated by brief episodes (~20 ms) of low analytic power, called null spikes. Null spikes does not mean that nothing is going on, only that neural activity is not co-ordinated. Kozma and Freeman argued that the high amplitude phases are metastable patterns carrying cognitive (or perceptual) content in the form of frames, while the low analytic power episodes mark breaks or "shutters" between successive frames. The shutters mark periods of receptivity to new input in which neurons process input individually: thus, frames of perception reflecting a synchronised, metastable representation are established, maintained for a brief period, and then replaced by new frames constructed by ordering the output of individual neurons. This is, of course, a greatly oversimplified rendition of the model. I am concerned mainly to get across the central contention of the model that perception proceeds in global frames separated by "shutters" in which perception is temporarily shut off and a new frame is in the process of construction.

Conscious percepts consist of frames separated by phase transitions between disordered and ordered activity.

The predictions of the model for the content of percepts are not entirely clear. The frame hypothesis seems to imply that each frame is a static representation, since it does not itself change until it is shut down and replaced. However, that need not be the case, because there could be a static representation of information about ongoing change. In that case, evidence for temporal discrimination on a time scale shorter than that of a frame need not be disconfirmatory for it because the temporal discrimination could be made in perceptual processing and then inserted as a piece of information into the frame currently under construction.

The authors did not discuss perception beyond claiming that the amplitude patterns are frames of cognition, and offered no evidence for the central claim about the frame-like nature of perception. For that reason it is difficult to know what sort of evidence would falsify the model. It would appear to be compatible with other interpretations, for example the attentive sampling interpretation under which attention waxes and wanes (in this case possibly to zero during the "shutter" periods) but percepts are maintained continuously. There are at least four problems that the model would have to address.

First, the frames identified by Kozma and Freeman have long durations, up to 200 ms. It is not clear, therefore, how the model can accommodate the evidence of temporal discrimination thresholds on the order of 5 ms, which will be discussed in more detail in section 4.2.

Second, the long duration of frames reawakens the problem of jerkiness discussed in the introduction. As far as vision is concerned, the frame duration is far beyond the flicker fusion frequency, which would seem to imply some form of jerkiness representing the transitions between frames. It is possible that the jerkiness could be obviated by some form of model-fitting that would interpolate links between one frame and the next: presumably those links would involve postdictive filling-in of the absence of information during the phase transition, so that the current frame always looks back and sees continuity with the previous frame (metaphorically speaking). At least, the account requires some sort of explanation for the absence of subjective jerkiness.

Third, the long frame duration of 100 - 200 ms is not confirmed by the results of a study by Pockett et al. (2011). Pockett et al. found periodic fluctuations in the brains of people who were awake but had no specific task to do, that did not occur in the brains of anaesthetized patients. Pockett et al. interpreted these in a way that is consonant with the cinematic theory of cognition, with short periods of minimal activity (null spikes) separating longer periods apparently representing large-scale co-ordination in activity. However, the periodicity was 50 - 100 ms. This difference in frame durations between what otherwise appear to be similar accounts and similar kinds of evidence needs to be explained.

Fourth, if the whole of perception proceeds in discrete frames, as the account seems to imply, then those frames would have to be maintained continuously during the waking state. There is no evidence for that: on the contrary, there is evidence that oscillations on the time scale proposed by the authors as marking frames do not occur continuously. A simple illustration is the study by Smith, Gosselin, and Schyns (2006) that will be discussed in the next section, showing that one version of a visual stimulus generated oscillations in the theta range and another generated oscillations in the beta range. I should also point to the evidence reviewed above that oscillation frequencies vary between modalities.

There is no reason to doubt that the oscillatory patterns described by Freeman and colleagues are pervasive and probably functionally important in information processing, but there is as yet no clear evidence that the oscillatory patterns indicate cinematic frames of conscious perception, and there are several problems for that hypothesis to address.

3.3: A broader look at EEG evidence

The two recent proposals discussed so far have both drawn on EEG evidence as support. Some authors additional to those discussed above have also proposed variants of the frame hypothesis based on regular oscillations (Joliot, Ribary, & Llinás, 1994; Lehmann, Faber, Gianotti, Kochi, & Pascual-Marqui, 2006; Lehmann, Ozaki, & Pal, 1987; Pockett et al., 2011). A thorough survey of EEG research is far beyond the scope of this paper: my aim is just to make a few observations that are of relevance to the discrete frame hypothesis. Is it possible that any kind of repeating pattern in EEG data could mark the occurrence of discrete frames of conscious perception?

One problem with assessing the status of EEG evidence with regard to the discrete frame hypothesis is that there are numerous other hypotheses about the functional significance of EEG waveforms. For example, many studies have shown that oscillations are associated with attentive processing, related to co-ordination of activity across different areas of the brain and temporal segmentation of the processing of stimulus information (e.g. Bazanova & Vernon, 2014; Doesburg, Roggeveen, Kitajo, & Ward, 2008; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jensen, Gips, Bergmann, & Bonnefond, 2014; Klimesch, 2012; Lisman & Jensen, 2013; Mathewson, Lleras, Beck, Fabiani, Ro, & Gratton, 2011; Myers, Stokes, Walther, & Nobre, 2014; Roberts, Hsieh, & Ranganath, 2013; Tallon-Baudry, 2012; Walz, Goldman, Carapezza, Muraskin, Brown, & Sajda, 2015; Weisz, Hartmann, Muller, Lorenz, & Obleser, 2011). I shall briefly discuss two hypotheses, both concerning alpha.

One hypothesis is the cortical excitability hypothesis mentioned in the section on early proposals. The functional interpretation of periodic fluctuations in cortical excitability is not fully understood, but I shall briefly mention one proposal for illustrative purposes. Lange, Keil, Schnitzler, van Dijk, and Weisz (2014) argued that cortical excitability affects stability of perceptions. Stability is high when alpha power is high and low when alpha power is low. In support of this they discussed a study by Strüber and Herrmann (2002) who used an alternating dot pattern that could give rise to a percept of either horizontal or vertical motion, and reversals in the direction of perceived motion occurred apparently spontaneously. Strüber and Herrmann found that perceptual reversal was more likely to occur when alpha power was low than when it was high. This suggests that stability is high when alpha power is high, and receptivity to new processing is higher when alpha power is low. This was specifically for endogenous (spontaneous) alpha, not for alpha triggered by the stimulus. Lange et al. argued that the results of several other studies in both vision and audition supported the perceptual stability hypothesis, including VanRullen et al. (2006). In effect, there is a trade-off between stability and precision in perception, and at states of high excitability (low alpha power) precision analysis dominates, resulting in increased likelihood of change in the percept, whether that change be improved accuracy or a perceptual reversal in an illusory bistable figure.

Another hypothesis is that alpha represents a periodic shift between attentive processing of relevant stimuli and active suppression of irrelevant stimuli, or prioritising stimuli for attentive processing (Gleiss & Kayser, 2014; Jensen, Bonnefond, & VanRullen, 2012; Jensen et al., 2014; Payne & Sekuler, 2014). The amount of information in sensory input per unit time is far greater than the brain's capacity to process it, so information is selected according to processing priorities. This selection process involves suppression of low priority information. The authors cited here have argued, in different ways, that selecting, prioritising, and suppressing information depending on relevance or importance is a function of alpha, and that the oscillation represents cycling between selecting relevant information and suppressing irrelevant information.

These hypotheses illustrate the general point that alpha is involved in maintenance and adjustment of percepts, such that changes are more likely to occur at some times than at others. Change is probabilistic: there is perhaps no time at which a percept cannot be changed, and no time at which change must always occur. This is consistent with the finding that the amount of variability in perception that is accounted for by oscillatory phase or power is small (VanRullen, 2016). The functional significance of oscillations can be elucidated without reference to discrete temporal frames of perception. That in itself is not sufficient to disprove the EEG version of the frame hypothesis, but the problems listed earlier render it unlikely to be correct. There are two more problems worthy of mention here, both concerned with the requirement that discrete frames of conscious experience should go on all the time in the waking state.

One problem is that, even within vision, alpha is not triggered by all kinds of stimuli. For example, Smith et al. (2006) made use of a painting with an ambiguous figure that gave rise to bistable perceptions. They created sparse versions of the painting by focussing on specific spatial frequency bandwidths and participants reported which, if either, perception occurred with each stimulus. Smith et al. found that theta waves (4 - 8 Hz) were associated with one perception of the figure and beta waves (12 - 25 Hz) were associated with the other. As was discussed in section 3.1.2, Ronconi et al. (2017) found that perception of one kind of visual stimulus could be predicted from the phase of alpha oscillation (8 - 10 Hz), but perception of another kind could be predicted from the phase of theta oscillation (6 - 7 Hz).

Those studies serve to make some important points. In the Smith et al. study, neither of the observed frequencies was in the alpha band, thus showing that alpha does not occur in response to all visual stimuli. The results also show that there is no fixed periodic response to visual stimuli: the periodicity that occurred differed substantially depending on stimulus features, even when (in the Smith et al. study) the experimental stimuli were derived from the same painting. The theta waves observed in one condition do match the 7 Hz frequency that was interpreted by VanRullen and colleagues as indicating the rate of attentive sampling (VanRullen et al., 2007, 2014). However, if attentive sampling was occurring in response to both versions of the stimulus, as seems plausible, it is not clear why the 7 Hz oscillation was not found for the other version. The two studies show that different stimuli trigger oscillations with different frequencies, and that different oscillatory frequencies are functional for different perceptual phenomena. The exact functional significance of the oscillations is a topic that lies outside the remit of the present paper. For present purposes, the specificity of association of different oscillatory frequencies with different perceptual processing tasks is hard to reconcile with the frame hypothesis.

The other problem is that McComas and Cupido (1999) reported a finding that "approximately 10% of otherwise normal individuals appear to lack α-rhythms under any circumstances" (p. 1988). The empirical basis for this report is not clear and it should perhaps be regarded as in need of confirmation[5], but, if valid, it would obviously rule out any hypothesis that alpha could be the basis of discrete temporal frames of perception. It would be valuable to discover whether there is any detectable difference in attentive processing of perceptual information between people who do and do not have alpha. In any case, as was noted earlier, alpha is suppressed when the eyes are opened (Bazanova & Vernon, 2014), yet there is no evident effect of that on conscious perception.

Periodic fluctuations in neural activity revealed by EEG waveforms are widespread and occur on multiple time scales, and it is likely that they subserve multiple functions in information processing. However, there is no clear evidence that those functions include constructing discrete frames of conscious perception. Indeed, it is not clear what sort of evidence would support such a hypothesis. Fluctuations in attention go on at a level below that of conscious perception and are compatible with continuity of maintenance and change in conscious perception. And there is no proof that any oscillation, whether endogenous or stimulus-triggered, goes on everywhere and all the time in the waking state. The oscillations observed by Pockett et al. (2011) and by Freeman and colleagues (Kozma & Freeman, 2017) may go on all the time and may be specific to the waking state, but it has not been established that they are connected with conscious perception, and they could relate to some function outside of conscious perception. There could be local, transient discrete frames associated with particular processes or functions, although again there is no clear evidence for such a thing. If that were the case, then one could imagine conscious perception as a concatenated set of local frames starting and stopping and with different and variable periodicities. Even then, the evidence favours the hypothesis that fluctuations are a matter of degree, and are not like on/off switches. Attention does not switch on and off seven times a second; instead, its level of activation varies in a continuous and periodic way (e.g. Landau & Fries, 2012). New information is more likely to be registered at some times than at others; change to a percept is more likely to occur at some times than at others. That is, perhaps, as close to discrete frames as EEG oscillations get.

There are clearly many hypotheses about the functional significance of EEG oscillations that do not require reference to discrete frames. However, as I observed when reviewing research on the attentive sampling hypothesis, the processes that operate cyclically go on behind perceptual experience rather than in it. For example, a particular percept of an ambiguous bistable figure, such as the alternating dot pattern used by Strüber and Herrmann (2002), is maintained continuously over a period of a few seconds, while beneath it alpha of gradually decreasing power is occurring. The likelihood of a switch in perception increases as alpha power decreases, but the effect of periodicity is to alter the probability of a switch in a specific percept at any given time, not to make perception progress in a series of discrete frames.

At present, then, the hypothesis of local discrete frames of perception marked by periodicities in EEG is not disconfirmed, but the evidence does not strongly favour it, there are several problems for it, and there are many alternative hypotheses about the functional significance of EEG periodicities that do not call on the notion of discrete frames. Terms like "blinking spotlight" (VanRullen et al., 2007), "perceptual echoes" (VanRullen & Macdonald, 2012), and "ringing" (Harter, 1967) are rhetorical devices that attract the reader's mind to a clear and definite image of what is going on, and it is then hard to let go of that image and perceive the rather murkier reality that lies in the results.

3.4: Pre-semantically defined temporal windows

Pöppel (1997, 2009; Pöppel, Schill, & von Steinbüchel, 1990) argued that system states with a duration of ~30 ms are units of temporal experience: events occurring within a 30 ms period are experienced as contemporaneous, and successions of such states give rise to the experience of successiveness. A stimulus gives rise to a neuronal oscillation with a frequency of 30 ms (30 Hz), which subserves inter-modal integration. Events within the same oscillatory cycle as the stimulus are experienced as contemporaneous with it, and events outside that cycle are experienced as successive. Pöppel drew on several lines of research to show that the 30 ms period is a general feature of brain activity, and that is the evidence that will be evaluated here.

A key feature of the argument is that the critical duration of 30 ms should be detectable across sensory modalities. Pöppel (1997, 2009) cited research on temporal order judgment by Hirsh and Sherrick (1961) as supporting similar temporal thresholds for visual, auditory, and tactile stimuli. Hirsh and Sherrick did find similar relations between temporal difference and accuracy of temporal order judgment for all three modalities, but they reported that the difference at which judgments were 75% correct (their chosen criterion) was 20 ms, not 30 ms. Also, the line relating time difference to accuracy of judgment was straight to a good approximation across the range of differences studied, which means that the critical duration depends on the criterion level of accuracy set by the researchers. If the criterion was set at 90%, for example, the critical duration would be 40 ms. Pöppel (2009) cited Kanabus, Szeląg, Rojek, and Pöppel (2002) as supporting similar temporal thresholds for visual and auditory temporal order judgment. By the criterion they set, which was 75% correct responding, both visual and auditory time differences had to be >40 ms before accurate responding was achieved. However, performance on auditory stimuli was superior to that on visual stimuli at all durations from 5 ms to 40 ms, and was consistently better than chance (between 60 % and 75% correct). Furthermore, performance in both modalities continued to improve up to asymptote at approximately 150 ms. There are certainly similarities in the level of accuracy of temporal order judgment across the three modalities of vision, audition, and touch, but the studies do not indicate that there is anything special about 30 ms. As will be shown in section 4.2, there is evidence for a great range of temporal discrimination thresholds, and no evidence for a peak around 30 ms.

Madler and Pöppel (1987) presented auditory clicks to patients while the patients were awake and while under general anaesthesia. They found a periodicity of 25 ms in auditory evoked potentials for awake patients, but no periodicity for anaesthetised patients. This does suggest a temporal unit of experience because it does not occur under anaesthesia. However, other studies have found different periodicities under similar circumstances, either comparing awake with unconscious patients (50 - 100 ms; Pockett et al., 2011) or studying participants who were awake but relaxing with eyes closed (50 ms; Lehmann, 1971). Neither result is consistent with what Madler and Pöppel (1987) found. It is likely that their result reflects something specific to auditory processing, but without further research this cannot be certain.

Pöppel (1997, 2009) reported research supporting the 30 ms unit on choice reaction times. Pöppel (1970) studied choice reaction times for both visual and auditory stimuli and found multimodal distributions of response times with a period of 30 ms. The method of that study and others has been criticised (Vorberg & Schwartz, 1987; Vroon, 1970, 1974). Vorberg and Schwartz (1987) demonstrated that an appearance of regular oscillations can occur in data distributions by chance and there is no clear evidence that the distributions obtained by Pöppel (1970) were not chance phenomena. They argued that the analysis requires a data sample size at least 50 times greater than that obtained by Pöppel (1970). Vroon (1974) generated 1,200 values for time estimates constrained to have a normal distribution but with noise fluctuations. Vroon showed that, if the estimates were assigned to bins with durations of 30 ms, strong peaks emerged around 45 ms and 90 ms, despite the fact that the data were essentially random. This suggests that apparent periodicities obtained from data sets that are not much larger than that cannot be trusted to reveal psychologically meaningful periodicities. Following this, Jokeit (1990) ran a more systematic analysis of reaction time data and found a basic period of 10 ms. There was also evidence for a minor peak between about 20 ms and 40 ms, but it was much smaller.

Other studies have found different periodicities in reaction time data. Harter and White (1968) found periods of 25 ms and 65 ms for both visual and auditory stimuli. Latour (1967) studied eye movement reaction times to visual stimuli and found periodicity of 14.5 ms in right to left movement and 9.7 ms in left to right movement. Venables (1960) studied reaction times to visual stimuli and found periodicity of 10 ms for the people with schizophrenia and 20 ms for those without. Ilmberger (1986) studied choice reaction times to acoustic stimuli and reported a series of modes separated by intervals of 40 ms. Dehaene (1993) found various periodicities ranging from 10.2 ms to 36.6 ms, depending in part on task complexity. So, if there are meaningful periodicities in reaction times, they vary considerably, probably as a function of the particular task set and of its complexity.

Finally, Pöppel (1997, 2009) called on a study by Pöppel and Logothetis (1986) of response latency in smooth pursuit eye movements. The results showed peaks in the histogram of response latency that were approximately 30 - 40 ms apart. However, there are some problems with the study. The authors varied target velocity between 1 and 10 deg s^{-1} but only reported results for 6 deg s^{-1}, so it is not clear whether the same periodicity was found at the other target velocities. There were only four or possibly five peaks in the data, and it is hard to assess the probability of that small number occurring by chance (Vorberg & Schwartz, 1987). At 6 deg s^{-1} there were 462 data points that were collected in bins of 10 ms, but the temporal resolution of the measure of response latency was 3 ms, so it is not clear why a bin size of 10 ms was chosen. Vroon (1970) showed that peaks occur at different places depending on bin size, even for the same set of data, and the simulation run by Vroon (1974) shows that 462 data points is far too few for meaningful results to be obtained. In short, there are too many degrees of freedom in the data analysis, and there is a need for replication with more systematic analysis and a much larger set of data.

In summary, some of the evidence is of questionable validity and the rest does not fit with the prediction of a significant concentration of findings around 30 ms, so it can be concluded that the hypothesized 30 ms unit of temporal experience lacks support.

3.5: The time quantum model

The time quantum model is a proposal that brain activity is temporally organised in the form of oscillatory or cyclic carrier processes (Geissler & Kompass, 2001; Geissler, Schebera, & Kompass, 1999) According to Geissler et al. (1999), "quantal timing represents a tool for the brain to ensure fast, temporally extremely precise communication among neural units that, depending on their function and phylogenetic origin, may differ widely in their temporal characteristics" (p. 708). They argued that there is an overall coherence of activity in the brain due to phase-locking between cycles that have different periods. The function of frames, therefore, is to promote coherence in brain activity. There is a fundamental oscillatory frequency of 4.5 - 4.6 ms (in fact precisely 4.57 ms according to Geissler et al., 1999), which they called a time quantum, and other activities operate on time scales that are multiples of the time quantum, thereby facilitating phase-locking. For example, they argued that there was evidence for two critical periodicities of 55 ms and 111 ms, which are 12 and 24 times, respectively, the length of the base unit. Different periods (as multiples of the base period of the time quantum) emerge depending on task and stimulus conditions.

The time quantum model itself cannot be fully reviewed here (see Geissler & Kompass, 2001, and Geissler et al., 1999, for more detailed exposition). However, the prediction of a fundamental frame duration of 4.57 ms and of the temporal organisation of brain activity in multiples of the time quantum can be tested, and evidence relevant to that is assessed here.

The findings cited by Geissler and Kompass (2001) as support for this proposal were from some studies of stimulus discrimination thresholds (Brecher, 1932; von Békésy, 1936), and a series of studies on successiveness discrimination thresholds by Kristofferson (Kristofferson, 1967a, 1967b, 1980, 1984). Examination of those studies shows that the range of variation in thresholds is too great to support any specific conclusion about time quanta. For example, Kristofferson (1967a) reported a mean successiveness discrimination threshold of 48 ms, but means for individual participants varied from 40 to 60 ms. In Kristofferson (1967b), the reported mean was 54 ms with a range across individuals from 33 to 77 ms. Neither 48 nor 54 is an exact multiple of 4.57. The data from individuals show too much variability to support the hypothesis of a time quantum of 4.57 ms. Moreover, in later research Kristofferson (1984) reported much greater variation and favoured a model in which the critical durations were a function of doubling from a base quantum of 12.5 ms (though this was put forward just as a model of duration or successiveness discrimination and not as a discrete frame hypothesis): 12.5 is not a multiple of 4.6. Matthews and Grondin (2012) failed to replicate some of the time quantum values that Kristofferson (1980) reported. Many of the studies discussed in section 3.4 found evidence for periods that are not exact multiples of 4.57. To give just one example, the 10.2 ms period found by Dehaene (1993) is 2.2 x 4.57, and that is only one of several periods found in that study.

The study by Geissler et al. (1999) was concerned with apparent motion, specifically what is called long-range beta motion. Beta motion is the apparent motion that is perceived between two spatially separated and temporally successive flashes of light, and long-range beta motion occurs with angular separations > 2°. The design manipulated exposure duration and angular separation. The procedure was that the ISI was gradually reduced for a given stimulus until the participant reported that apparent motion had ceased. A histogram showed statistically significant peaks in the response distribution for ISI values of 9, 22, 27, 43, 55, and 107 ms. Dividing each of these by the hypothesized time quantum value of 4.57 ms should yield a close approximation to a whole number. In fact the results of division by 4.57 are, respectively, 1.97, 4.81, 5.91, 9.41, 12.04, and 23.41. There are, therefore, close matches for three of the six durations. There are in addition seventeen other multiples of 4.57 between 0 and 107 ms, for which peaks were not found, including 4.57 ms itself: there is no peak at either 4 or 5 ms. Overall, this cannot be regarded as strong support for the time quantum model.

The brief but penetrating methodological critiques by Vorberg and Schwartz (1987) and Vroon (1970, 1974) should be borne in mind in relation to much of the literature discussed in this subsection: very large data samples and analytic procedures that are fixed before data collection are the minimum requirement, as indeed is investigation of the roles of task content and complexity.

Geissler et al. (1999) argued that temporal discrimination thresholds, including nonsimultaneity and temporal order thresholds, are phenomena where critical periods ought to match multiples of the time quantum. I have recently carried out a systematic survey of studies of temporal discrimination thresholds (White, 2018), which involved the construction of a large table of research findings. I examined the table to see how many of the mean threshold values reported matched multiples of the time quantum. I allowed a match to count if the mean divided by the time quantum value of 4.57 was within ± 0.1 of a whole number. This gives a chance expectation of matches in 20% of values. The first point to note is that many threshold values reported were less than 4.57 ms, and therefore cannot be explained by the time quantum model (Elhilali, Ma, Micheyi, Oxenham, & Shamma, 2009; Heinrich, de la Rosa, & Schneider, 2014; Heinrich & Schneider, 2006; Lackner & Teuber, 1973; Leshowitz, 1971; Lotze, Wittmann, von Steinbüchel, Pöppel, & Roenneberg, 1999; Pichora-Fuller, Schneider, Benson, Hamstra, &

Storzer, 2006; Wiegrebe & Krumbholz, 1999; Zera & Green, 1993). In addition to those just cited, a large number of studies have replicated the same finding of an auditory gap detection threshold of about 2 ms (White, 2018). The second point to note is that many of the studies included in the table reported a range of discrimination thresholds dependent on the independent variables in the study in question, and those were excluded from the present calculation. For the remander, 15 out of 81 findings were a match. This is a match rate of 18.5%, which is close to, and certainly not more than, the chance expectation. It could be argued that individual responses, not means, should be the units of analysis. However, individual responses should certainly converge on means that match the critical periods, so the fact that there is no evidence for that in a survey of 81 studies carries some disconfirmatory weight.

In summary, the evidence reviewed here, which includes a very large survey of temporal discrimination thresholds encompassing vast quantities of data, gives no support to the proposed time quantum.

3.6: Time chunks

McComas and Cupido (1999) reported evidence that successive somatosensory (electrical) stimuli are only perceived as two stimuli if the ISI exceeds 50 ms. They referred to other evidence which, they claimed, supported the idea of time chunks on a time scale of ~50 ms (Andrews, White, Binder, & Purves, 1996; Hirsh & Sherrick, 1961; Marks, Girvin, O'Keefe, Ning, Quest, Antunes, & Dobelle, 1982; Purves et al., 1996).

To explain this, they proposed that information processing in the sensory cortex occurs in chunks of time. They pointed to research involving intracellular recordings of responses to somatosensory stimuli. These showed a consistent temporal pattern: an initial excitatory response followed by a prolonged inhibitory postsynaptic potential, which was in turn followed by a rebound excitation. Both the initial excitatory response and the later rebound response were capable of generating action potentials. They argued that a time chunk corresponded to one of these sequences. They also argued that a different kind of cell, pyramidal cells in layers 2 and 3 of the sensory cortex, has properties that make them suitable for the function of storing information for the duration of a time chunk. This would subserve integration across the duration of a time chunk to generate a unified percept, which involves a further layer of cells reading out the states of the pyramidal cells. This is a very schematic summary of their model; for more detail, see McComas and Cupido (1999).

The model proposed by McComas and Cupido (1999) addresses some critical problems for a discrete frame hypothesis, principally concerning how information can be stored and integrated over the duration of a frame, and how input is tranformed into a percept through a series of processing stages. However, although they used the term "time chunk" and argued that their model might capture processing in general across the sensory cortex, it is not clear that the model generates a discrete frame for the whole of conscious perception. The initial response is stimulus-driven: "the initial... stimulus starts a time chunk" (p. 1991). This suggests that time chunks are triggered by specific stimuli. In fact the key evidence that the proposed mechanism is supposed to explain is evidence on temporal discrimination thresholds: stimuli are perceived as two stimuli when they are sufficiently far apart in time to fall into separate time chunks, and they are integrated into a single percept when the interval between them is less than that of a time chunk. It is likely, therefore, that time chunks would be local phenomena, meaning in this case that they would not be co-ordinated across large areas of conscious perception.

Temporal discrimination thresholds vary greatly not only between but also within modalities (see section 4.2). Even in the few studies cited by McComas and Cupido (1999) there is a wide range of variation, from ~20 ms (Hirsh & Sherrick, 1961) to over 1,000 ms (Marks et al., 1982). Some of this variation may be due to operating characteristics of peripheral sensors (Marks et al., 1982), but it is likely that the model would have to be adaptable to a range of time scales in cortical processing if it is to work as a general account of temporal discrimination. Also, although the cells they discuss have properties that are suitable for the proposed functions, there is no compelling evidence that the cells actually do have those functions, so the account is somewhat speculative. On the other hand, it is an attempt to root a discrete frame proposal in a neurophysiologically plausible model, something that is found in few other proposals. However, there does not appear to have been any further development or testing of the model.

3.7: Snapshots (Crick & Koch, 2003)

Crick and Koch (2003) proposed an approach to the understanding of consciousness in terms of the neural correlates of consciousness, combining ten different issues in an attempt to construct a coherent overall view of the phenomenon. One of these ten issues was their snapshot hypothesis: "We propose that conscious awareness (for vision) is a series of static snapshots, with motion 'painted' on them... By this we mean that perception occurs in discrete epochs" (p. 122). The phrase "static snapshot" seems to imply the lack of experienced temporality that is sometimes considered a defining feature of discrete frames. This is, therefore, a discrete frame hypothesis specific to vision, but apparently applying to the whole of vision. This must be qualified, however, by their comment that "[t]he durations of successive snapshots are unlikely to be constant" (p. 122), and by their further comment that "the time of a snapshot for shape, say, may not exactly coincide with that for, say, color" (p. 122). In their account, when neural activity for a feature crosses some sort of threshold, it is held there for a certain time, and that time is the time of the snapshot.

It is not within the remit of this paper to evaluate their proposals about consciousness as a whole: the concern is purely with the "snapshot" model of conscious visual percepts. As it stands, the proposal is difficult to evaluate because the duration, or range of durations, of snapshots is not specified, except for a suggestion that they might relate to alpha or delta oscillations. No supporting evidence for the snapshot proposal is cited. Also, the suggestion that the duration of a snapshot may vary, without any proposal as to the extent of the variation or the factors that might affect it, makes the proposal hard to falsify. Exactly what it means for motion to be "painted" onto a snapshot is not clear. It is possible to imagine that there are motion detectors in perceptual processing and that information about motion generated by those detectors is held in static form in a snapshot, but there is a need for further specification of the mechanisms that accomplish that. As it stands, the "static snapshot" view of discrete frames falls victim to the rapid akinetopsia problem discussed earlier: to perceive any kind of change, there must be some sort of integration across the contents of consecutive frames, and there must be some sort of perceptual product of that. That integration and its product would be hard to reconcile with the frame hypothesis. This will be further discussed in the general considerations section.

3.8: The interoceptive specious moment (Craig, 2009a, 2009b)

Interoception concerns all central processing of information from the body's internal sensors. Craig (2009b) listed many different kinds of interoceptive stimuli, among which are such things as pain, articular kinaesthesis, thirst, distension of the bladder, some components of emotional feelings such as disgust, awareness of the heartbeat, and input from receptors on or near the surface of the skin, such as thermoception. In some cases the interoceptive input may be a contributor to an experience rather than the sole determinant of it; this is perhaps especially the case with emotions, which have a cognitive component as well as an interoceptive one. However, the full list in Craig (2009b) makes it clear that interoception is a major and perhaps neglected component of conscious perception. Craig (2009a, 2009b) argued that interoceptive input, processed mainly in the anterior insular cortex (AIC), is a major contributor to the sense of self. For present purposes, however, the concern is just with the proposal of a global "specious moment" (Craig, 2009a, p. 1933) comprising the whole set of cortically processed interoceptive sensations at a given time, including the sense of a self that has those sensations.

Craig (2009a, 2009b) proposed that the global interoceptive representation is temporally structured as a series of moments, and that a memorial representation across a series of such moments provides a basis for experienced emotional (or, more generally, interoceptively self-related) continuity over time. Continuity is generated by comparisons over time (including anticipated future states) utilising information about previous moments held in storage buffers. It is not clear how a moment is defined in this model, but it seems to represent a time scale of integration across all interoception. That time scale is about 125 ms. To support this, Craig (2009a, 2009b) referred to a few studies relating temporal discrimination to activity in the AIC.

One of those studies was by Kranczioch, Debener, Schwarzbach, Goebel, and Engel (2005), in which participants attempted to detect visual targets in a rapid series of stimuli. When the latency between targets was 100 or 200 ms, detection rate of the second target was low. This indicates an "attentional blink" phenomenon in which attention appears to be transiently reduced following detection of the first target. The study found evidence of activation in the AIC and other areas when the second target was detected at that latency but not when it was not. Craig

(2009a, 2009b) interpreted this as indicating the temporal resolution of the AIC, and therefore of the specious moment. It is doubtful whether the findings can be interpreted that way, however. There is a substantial literature on the attentional blink, and there is general agreement that it occurs for a stimulus that is presented in the period about 200 - 500 ms after an initial stimulus (Broadbent & Broadbent, 1987; Dux & Marois, 2009; Martens & Wyble, 2010; Raymond, Shapiro, & Arnell, 1992; Reeves & Sperling, 1986). The results obtained by Kranczioch et al. (2005) are exceptional in that respect. In addition, although many explanations have been proposed for the attentional blink, most focus on the period in which perceptual information is being consolidated into working memory (Dux & Marois, 2009). Dux and Marois (2009) concluded from their review that the attentional blink "reflects the competition between targets for attentional resources, not only for working memory encoding, episodic registration and response selection..., but also for the enhancement of target representations and the inhibition of distractors" (p. 1696). Therefore, not only does the time scale of the phenomenon not fit with Craig's proposal, it is not connected with conscious perception at all, but occurs at a subsequent stage of processing, that of memory consolidation.

Craig (2009b) stated: "Psychophysical data from rapid-visual-search studies suggest that the maximal rate of passage of individual moments is ~8 Hz" (p. 68). The only study cited in support of that claim was by Deary, Simonotto, Meyer, Marshall, A., Marshall, M., Goddard, and Wardlaw (2004), who ran a line length discrimination study in which stimulus presentation time was manipulated. Performance declined from nearly perfect at 150 ms presentation to close to chance at 6 ms presentation. The authors reported increased activation in several brain areas as difficulty increased, including the AIC. Deary et al. suggested a functional role for the insular areas associated with effort in relation to stimulus complexity, task difficulty, or degraded percepts. It is not clear, however, that the results have implications for the duration of a specious moment. On the contrary, the results suggest that the AIC is involved with effortful processing of stimuli presented on a much shorter time scale than the proposed 125 ms. Nor is it clear what the basis for the claim of an 8 Hz (125 ms) moment is: the psychophysical results show that performance was close to ceiling at 75 ms stimulus presentation time, and did not change significantly as presentation time increased beyond that.

Craig (2009a) reviewed research evidence indicating a role for the AIC in time perception, but that role has no necessary connection with a frame hypothesis. As things stand, therefore, the hypothesis of a temporal frame of 125 ms in interoception, or indeed in effortful or attentive processing in general, lacks supporting evidence.

4: General considerations

4.1: Evidence

It is evident that the hypothesized duration of a discrete frame varies greatly between proposals, as shown in Table 2. This alone should suffice to raise a warning flag. What makes one proposal better than the others? In fact, as this review has shown, none of the proposals is strongly supported by evidence. The authors of the proposals have called upon evidence that is consistent with the frame duration they have proposed, but have paid little or no attention to the evidence that supports the frame durations proposed by others. This is possibly symptomatic of a general contemporary problem. There is such a superabundance of research evidence in psychology and neuroscience now that a tendency to focus on supportive evidence and to ignore disconfirmatory or inconsistent evidence is all too easily accommodated. Nobody can have a thorough working knowledge of all the relevant evidence, and new evidence accumulates faster than anyone can realistically absorb it. In this section some additional problems that have relevance for all discrete frame hypotheses are discussed.

Most of the evidence reviewed here falls into one of three categories. First, there is evidence that is better interpreted as the product of local processing and that, therefore, does not speak to the discrete frame hypothesis. This includes perceived shrinkage of arcs and other figures (Ansbacher, 1944), the effect of delay on visual impressions of causality (Michotte, 1963; Shallice, 1964), periodic adjustments to pointing movements (Bertelson, 1966; Craik, 1947), the continuous wagon wheel illusion (VanRullen et al., 2005), visual trails (Dubois & VanRullen, 2011), temporal discrimination thresholds (Pöppel, 1997, 2009), and research on the attentional blink (Craig, 2009a, 2009b). Second, there is evidence that is of dubious validity. This includes studies of reaction times and supposed stepwise functions in perceptual judgment (e.g. Geissler et al., 1999; Pöppel, 1970; von Békésy, 1936) that were critically evaluated by Vorberg and Schwartz (1987) and Vroon (1970, 1974). The third and most problematic category is evidence that relates to periodicity in perceptual or attentive processing. This is best treated in the context of theoretical propoals about frame generation.

4.1.1: Mechanisms for generating frames, and the periodicity issue

There have been several proposals for mechanisms that would generate or exhibit regular or semi-regular peridocity, and could therefore be responsible for discrete frames: scanning cycles (Pitts & McCulloch, 1947); cortical excitability cycles (Harter, 1967; Lindsley, 1952); central and perceptual intermittency (Craik, 1947; Harter, 1967; Kristofferson, 1967a); attention-based periodic sampling (VanRullen, 2016; VanRullen & Koch, 2003; VanRullen et al., 2014); null spikes as shutters (Freeman, 2004, 2006; Kozma & Freeman, 2017; Pockett et al., 2011);

neuronal oscillations subserving inter-modal integration (Pöppel, 1997, 2009); phase-locking of oscillatory cycles (Geissler & Kompass, 2001); and the excitatory/inhibitory/rebound neural response cycle (McComas & Cupido, 1999). The evidence called upon to support these hypothesized mechanisms has included evidence concerning the functional significance of EEG waveforms, originating with Bishop (1932) and continuing to recent work on attention switching (VanRullen, 2016; VanRullen et al., 2014), the so-called "perceptual echoes" (VanRullen & Macdonald, 2012), and other research on the functional significance of alpha (e.g. Jensen et al., 2014; Lange et al., 2014). There is little doubt that EEG waveforms are indicators of large-scale co-ordination in neural activity, and that some of that is related to attentive processing, such as switching between maintenance and adjustment of perceptual information. I reviewed some problems for that evidence in relation to the discrete frame hypothesis earlier, but there are two points that need to be reiterated and developed here.

One issue relating to the proposed mechanisms concerns whether they generate frames in conscious perception, or whether they represent periodic activities in perceptual processing prior to the emergence of conscious percepts, that do not carry over to set the characteristics of conscious perception itself. To illustrate, one possible hypothesis about conscious percepts is that they are locally maintained as they are until change is detected (Galletti & Fattori, 2003; Nortmann, Rekauzke, Onat, König, & Jancke, 2015), and then they are locally updated. I emphasize the word "locally" because it is most likely that that is how an updating mechanism based on change detection would operate. Under such an account, it is also possible that some or even all of perceptual processing exhibits periodicity in accordance with one or another of the proposed mechanisms. In that case, change is more likely to be detected at some times (e.g. phases of a cycle of activity) than at others. However, because the mechanisms are functionally separate, there need be little or no overall co-ordination in the temporal features of their activities. Thus, even though updating to a conscious percept may be affected by the cyclic activity of the process that generates the update, this would not impose a frame-like character on conscious perception. Perceptual processing would result in local updating occurring as quickly as possible, given the operating constraints.

I emphasize the illustrative nature of this: the change detection hypothesis is one among many possible hypotheses about how conscious percepts are constructed. The point is just to show that periodicity in mechanisms that generate conscious percepts does not necessarily generate periodicity in conscious percepts themselves. No hypothesized mechanism has yet been clearly established as a generator of discrete frames in conscious perception, as opposed to generating periodicity in the operation of (local) perceptual processing.

The other point is that periodicity does not imply discrete frames. We have seen, for example, that periodicity in attentive sampling is a matter of degree: attention does not switch on and off every 100 - 140 ms, but waxes and wanes on that time scale (VanRullen, 2016). The functional significance of periodic waxing and waning of attentive processing is still a matter of contention, but the case for supposing that attentive sampling is actually discrete, as opposed to just being stronger at some times than at others, is far from compelling. Second, it is not clear that a waxing and waning attentive process would generate experienced contemporaneity. On the contrary, it would seem more suited to generating information about change, which involves temporal succession, by periodically updating perceptual information. An obvious example here is a comparator process, which compares input information to an existing representation and detects discrepancies (e.g. Blakemore, 2003; Blakemore, Wolpert, & Frith, 2002; Fourneret & Jeannerod, 1998). This clearly does not involve experienced contemporaneity; instead, it involves ascertaining that something has changed, which requires information about differences between one point in time and another. Thus, just postulating an information processing function for periodic oscillations in neural activity is not enough to support a discrete frame hypothesis: it has to be shown that discrete frames are produced by such oscillations.

In summary, the evidence of periodicity does not show discrete frames marked by clear, all-or-nothing boundaries. Instead, there are fluctuations that are matters of degree, that operate on different time scales, that are stimulus-driven rather than endogenous, and that do not occur all the time. Thus, some of what gets into conscious perception is the product of processing that shows periodic variability, but that is not the same as saying that conscious perception consists of discrete frames.

4.1.2: Disconfirmatory evidence

There are findings that disconfirm predictions of discrete frame hypotheses. In addition to problems posed by research on temporal discrimination and temporal integration, which will be discussed in the next two sections, the most important findings both concern visible persistence. Several studies have shown that the duration of visible persistence varies inversely with stimulus duration, being maximal with stroboscopically presented stimuli and completely absent with stimulus durations longer than 100 - 130 ms (Di Lollo, 1977; Efron, 1970a, 1970b). Efron and Lee (1971) presented a radial line on a rotating disc that was intermittently stroboscopically illuminated. Suppose that visible persistence has a duration of 100 ms and that illumination occurs every 50 ms. In that case, two lines should be visible because the percept under the first flash has visible persistence that overlaps with the time of the second flash, but not with that of the third flash. It can be seen that the number of lines that are perceived as simultaneously present depends on the interval between flashes, other things being equal. Efron and Lee (1971) confirmed this and showed that the function relating interval between flashes and number of lines reported as simultaneous was a straight line, indicating a continuously variable function. They also found that the duration of persistence varied with level of illumination. Under the discrete frame hypothesis, the number of lines visible at any time depends just on the number of flashes that occur in a single frame. If a frame has a fixed duration, then that number will show a stepwise function, not a continuous one. So, as Efron and Lee argued, to mantain the frame hypothesis, the duration of a frame "would have to vary as a complex function of stimulus luminance, wavelength, state of adaptation, and so on" (p. 374). In other words, it makes more sense to interpret the results as showing that percepts are updated continuously, to the limits of measurement, and not in discrete frames.

A study by Di Lollo and Wilson (1978) added further disconfirmatory evidence. They presented a 5 x 5 grid and briefly flashed 24 dots. Participants had to indicate which grid location did not have a dot in it. The stimuli were presented in three brief flashes, A, B, and C. In all stimuli flash C occurred after flashes A and B, with gaps of 10 ms from the termination of flash A and 20 ms from the termination of flash B. The duration of flash A was manipulated by altering its onset time relative to the other stimuli. Under discrete frame hypotheses, the probability of integrating the information in all three flashes and correctly identifying the missing dot depends on the probability that all flashes occur in the same discrete frame. This is determined just by the intervals between the termination of flashes A and B and the onset of flash C: that is, it is constant for all stimuli. The discrete frame hypothesis therefore predicts that there should be no effect of manipulating the onset time of flash A. Contrary to that, Di Lollo and Wilson found that the probability of incorrectly identifying as missing one of the dots in flash A increased as the duration of flash A increased. The explanation for this is the aforementioned finding that visible persistence descreases to zero as the duration of a stimulus increases up to 100 ms. Thus, at long durations of flash A, there is no visible persistence and the dots in flash A cannot be integrated with those in flash C.

It is hard to see how the findings of the studies by Efron and Lee (1971) and Di Lollo and Wilson (1978) can be reconciled with the discrete frame hypothesis, but clearly there is a need for further research.

4.2: Temporal discrimination

As I stated in the introduction, frames of conscious perception are commonly defined, at least in part, in terms of experienced contemporaneity: all events in a single frame are experienced as contemporaneous, or there is zero subjective duration, so that no happening, change, or motion is registered on the time scale of a single frame. If that is the case, then the maximum time span of a frame is set by the threshold of experienced nonsimultaneity. If two events separated by *n* ms are (reportably) experienced as occurring at different times, then they must fall into different frames. If any change is detected on a time scale of *n* ms, then that time scale must encompass more than one frame.

By that criterion, the maximum possible time span of a frame is very short. Several studies have found experienced nonsimultaneity for events separated by less than 6 ms, in vision (Sweet, 1953; Wehrhahn & Rapf, 1992; Westheimer & McKee, 1977), audition (Babkoff & Sutton, 1963; Elhilali et al., 2009; Fostick & Babkoff, 2013; Miller & Taylor, 1948; Wiegrebe & Krumbholz, 1999), and somatosensation (Miyazaki, Kadota, Matsuzaki, Takeuchi, Sekiguchi, Aoyama, & Kochiyama, 2016). In some studies, very fine temporal discriminations have been found but it is not clear that a subjective impression of nonsimultaneity, or even of two distinct stimuli, has occurred; instead, the discrimination may be based on detectable qualititative differences in percepts (e.g. Henning & Gaskell, 1981). In the other studies cited here, however, the evidence for a genuine percept of temporal difference is strong.

The only way to save the frame hypothesis in the face of this evidence is to abandon the definition in terms of experienced simultaneity. An alternative possibility would be to define a frame in terms of updating frequency. A frame would contain an unchanging representation of informational states, and those states could include information about nonsimultaneity. For example, a process could generate the information that two stimuli, A and B, occurred at different times, such as 5 ms apart. That information could be entered as part of the content of a single frame, where it would remain for the duration of that frame. Thus, the information content of a single frame would be static, but it would include information about nonsimultaneity. One advantage of a static frame would be increased accessibility to further processing. If information that two stimuli occurred successively on a time scale of 5 ms were retained for a frame duration of, say, 100 ms, then it is more likely that it could be passed on to subsequent processing, such as attentive temporal judgment and verbal reporting processes. I would suggest, then, that the frame hypothesis requires a definition in terms of updating frequency, and that information within a single frame may be unchanging over the duration of that frame but does include specifications of change, nonsimultaneity, temporal order, and duration.

In addition, temporal discrimination thresholds vary over a very wide temporal range, and are affected by many factors. A comprehensive survey of that research is outside the scope of this paper (White, 2018), but a few brief observations will suffice for present purposes. Although nonsimultaneity judgment threshold can be less than 2 ms (Elhilali et al., 2009; Miyazaki et al., 2016; Zera & Green, 1993), thresholds in the region of 40 - 60 ms have been reported in other studies (Axelrod, Thompson, & Cohen, 1968; Elliott, Shi, & Sürer, 2007; Geffen, Rosa, &

Luciano, 2000; Kristofferson, 1967a). Thresholds for temporal order judgments, which differ from nonsimultaneity judgment in that participants must report the correct order of the stimuli, can be less than 5 ms (Babkoff & Sutton, 1963; Westheimer & McKee, 1977), but can also be more than 100 ms (Fink, Ulbrich, Churan, & Wittmann, 2006; Fostick, Ben-Artzi, & Babkoff, 2011; Nishikawa, Shimo, Wada, Hattori, & Kitazawa, 2015; Marks et al., 1982). Many factors have been shown to affect temporal discrimination thresholds, including duration and intensity of the stimulus (Babkoff & Fostick, 2013; Fostick & Babkoff, 2013; Schneider & Hamstra, 1999), stimulus rise time (Heinrich, de la Rosa, & Schneider, 2014), ISI (Fostick & Babkoff, 2013), stimulus type, such as clicks versus tones (Fink et al., 2006), synchronous or asynchronous presentation of a sub-threshold stimulus (Elliott et al., 2007), whether the arms are crossed or not (tactile stimuli, Heed & Azañón, 2014; Yamamoto & Kitazawa, 2001), age of participants (Lister & Roberts, 2005; Nishikawa et al., 2015), and mental health of participants (Nishikawa et al., 2015). To take just one example, Fink et al. (2006) found that the threshold for detecting the temporal order of two different stimuli varied depending on stimulus properties, being 31 ms for tones differing in frequency, 58 ms for clicks differing in location, one being presented to each ear, 47 ms for identical visual stimuli at different locations, and 107 ms for stimuli at the same location with different colours. Finally, there is no obvious peak in reported temporal discrimination thresholds at any time span: thresholds are just spread over a wide range (White, 2018).

It is clear, then, that temporal discrimination thresholds do not imply anything about discrete frames and their durations. Information about temporal discriminations, nonsimultaneity judgments, duration estimates, and so on, may be entered into a frame and held there for the duration of that frame (if not longer). But frame duration is not determined by temporal discrimination thresholds, and frames cannot be defined in terms of experienced simultaneity. It is more likely that discrimination thresholds reflect local processing characteristics that have nothing to do with frames. For example, Fink et al. (2006) argued that frequency (for tones) and location are processed by low level neurons selective for direction of frequency modulation and for apparent motion, respectively, and differences in temporal discrimination thresholds reflect the specific operating characteristics of the different processes. I shall return to the hypothesis of local mechanisms after considering temporal integration.

4.3: Temporal integration

In the most general sense, temporal integration covers any process that samples information across a period of time and generates some sort of unitary product. This can range from perceived brightness of a brief flash of light (Allan, Kristofferson, & Wiens, 1971; Stevens & Hall, 1966) to semantic interpretation of auditory speech input as a word (Hasson, Honey, & Chen, 2015; Hickok & Poeppel, 2007; Poeppel, 2003). Here too only a brief summary of research relevant to the discrete frame hypothesis will be given.

The main point is that durations of temporal integration vary across a wide range depending on many factors. There is no fixed time scale of temporal integration. Judged brightness of a flash of light depends, in part, on its duration, showing that perceived brightness emerges from summation of input information over time. Almost all of the summation occurs during the first 150 ms (Allan et al., 1971; Osaka, 1977; Stevens & Hall, 1966), but temporal integration for stimuli of low intrinsic brightness can cover about 300 ms (Aiba & Stevens, 1964), and possibly may continue for as much as 1,000 ms (Raab, 1962). Thus, one could have a percept of a stimulus of given brightness persisting for 50 ms or for 150 ms, but that does not happen: instead, the percept is of a stimulus that is brighter when its objective duration is 150 ms than when it is 50 ms. Something similar appears to be the case for perceived loudness of auditory stimuli, on a time scale of more than 200 ms under some conditions (Räsänen & Laine, 2013; Rimmele et al., 2015; Zwislocki, 1969). Visual motion percepts involve summation or integration on a time scale of about 80 - 130 ms (McKee & Welch, 1985; Simpson, 1994; Snowden & Braddick, 1991), but under some conditions temporal integration for both biological and non-biological motion perception can occur on a time scale up to about 3,000 ms (Burr & Santoro, 2001; Neri, Morrone, & Burr, 1998).

I have already discussed the example of visual persistence, showing that the duration of visible persistence is not fixed but varies depending on both stimulus duration and motion properties (Di Lollo, 1980; Farrell, 1984), which represents a compromise between the processing objectives of feature analysis and minimisation of visual smear (Farrell, 1984). Thus, although integration into a unitary percept with experienced contemporaneity does occur, it does not occur on a fixed time scale. The time scale is flexible, in accordance with conflicting processing priorities. There is no functional advantage, and indeed some functional disadvantage, in having frames, even local frames, with fixed durations. There is evidence that the duration of integration for a unitary percept on any given occasion is set not by a fixed time but by information density (Lerner, Honey, Katkov, & Hasson, 2014). Given that both information density and the objective duration of meaningful units of information input vary (for speech, in the case of the study by Lerner et al., 2014), it would make better functional sense for processing to have a time scale that was both flexible and responsive to the temporal characteristics of the input.

Variability in summation or temporal integration times is due in part to noise in the stimulus (Burr & Santoro, 2001). This indicates that at least some temporal integration processes can be understood as involving signal detection or decision criterion thresholds: integration time is flexible and the process stops, not after a fixed temporal interval, but when a signal has been detected or a decision criterion has been reached. Indeed, Räsänen and Laine (2013) argued that all products of perceptual processing involve temporal integration, even temporal discrimination, and that fine temporal discriminations just involve temporal integration over correspondingly brief intervals. Whether that is the case or not, it is clear from the research evidence that, not only is there no support for the occurrence of discrete frames, even local ones, of fixed duration, but such frames would be functionally inadequate, lacking the flexibility to deal with variations in stimulus conditions such as signal-to-noise ratio.

Research has shown, therefore, that temporal integration occurs on multiple time scales, and that variations in percepts are consistent with continuous processing and not with the stepwise functions that would be expected if updating were periodic. If discrete frames occur, they must have durations that vary as a function of many factors including signal detection, decision criteria, information density (Lerner et al., 2014), flexibility in the face of processing priorities (Farrell, 1984), stimulus luminance (Efron & Lee, 1971), and others.

This discussion has so far been concerned just with temporal integration within modalities. Perceptual information is integrated across modalities, and there is therefore a need to synchronise products of perceptual processes that have different latencies. Several studies have shown that the maximum window of cross-modal synchronisation is about 200 - 250 ms, meaning that events separated by that amount can be integrated into a synchronous percept (Conrey & Pisoni, 2006; Diederich & Colonius, 2015; Dixon & Spitz, 1980; Mégevand, Molholm, Nayak, & Foxe, 2013; van Wassenhove, Grant, & Poeppel, 2007; Wallace & Stevenson, 2014), but what, if anything, does that imply for the frame hypothesis? The temporal window of integration is not itself a frame of conscious perception. It concerns the integration of perceptual products that emerge with different latencies, registering them as simultaneous (or not). Updating of the synchronised information could take place on any time scale and is not related to the question of how far apart in time two perceptual products could be and still be integrated into a synchronous percept.

However, if there are discrete frames of perception, the evidence reviewed above indicates that the durations of those frames are likely to differ between modalities. In that case, the problem for the frame hypothesis is to explain how cross-modal synchronisation can occur when frames in different modalities have different durations. Suppose that there are frames with a consistent duration of 100 ms in vision, and frames with a consistent duration of 70 ms in audition. This means that temporal boundaries of frames in the two modalities would only rarely coincide, and it is not clear how cross-modal synchronisation would be accomplished. Is the content of a frame in audition, for example, synchronised to the frame in vision that was going on when the frame in audition started, or to the frame in vision that starts in the middle of the frame in audition? There is no research evidence that would suggest that cross-modal synchronisation occurs at the level of frames (Wallace & Stevenson, 2014). Synchronisation could be accomplished before frames are constructed, but that would seem to require that frames and their durations also be synchronised across modalities. In short, the frame hypothesis generates problems for explanatory accounts of cross-modal synchronisation that do not arise in the absence of frames.

4.4: The need for informational connection between frames

If the information in a frame is unchanging over the duration of a frame, that would seem to be contrary to our experience of the world as continuous and smoothly flowing over time. The contradiction is not absolute, because the static frame may include information about temporal features such as motion and temporal order. The problem lies just in the fact (if it is one) that frames happen one at a time. There would be one frame with unchanging content for (say) 100 ms, which was then replaced by the next, and so on. This can be illustrated by the film analogy: as a new frame enters the shutter, so the previous frame exits and whatever was in it is no longer there. It is impossible to infer, from the contents of the current frame, what the contents of the previous frame were. They might be similar or they might be completely different (because of a cut in the editing). The outcome would be that percepts are isolated in a perpetual present. This is, in effect, the rapid akinetopsia problem.

To circumvent that problem, experienced continuity in the perceptual world requires some form of connection between one frame and the next. Once a frame has gone, it is really in the past and really gone. Experienced continuity, connection of information between frames, requires preservation of some of the information that had been in the previous frame. There could, for example, be some specification of how the information in the current frame differs from that in the previous one. Without that, conscious percepts would have the character of brief but static moments. Of course, some information is preserved: it moves on through an informational bottleneck to iconic time scale processing (Sligte et al., 2010; Sperling, 1960), and through another information bottleneck to working memory (Jacob, Breitmeyer, & Treviño, 2013; Öğmen, Ekiz, Huynh, Bedell, & Tripathy, 2013). But more than mere preservation is required. There must be connection, to yield percepts of things going on. Early in the paper I mentioned Clay's (1882) observation that the current note of a tune is perceived in a context of its history, which involves informational connection on a time scale of seconds. That is a simple illustration of the way in which preserved information about the recent past informs and is integrated with current percepts. So, at the very least, information in a frame must incorporate and integrate information about the content of previous frames. If the information content of successive frames is integrated, then it is questionable to what extent frames can be described as discrete.

4.5: How is updating done?

Eriksen and Collins (1967) asked, "Does an arriving stimulation enter an ongoing psychological moment or is it stored and then represented in the succeeding moment?" (p. 484). Fifty years later, that question has not been answered, and it is hard to find any frame proposal that even addresses it.

I have argued that frames cannot be defined in terms of experienced simultaneity. Instead, it is likely that they would be defined in terms of the processes that update and maintain the information content of frames. Under that definition, for a frame to be discrete, updating must occur in a temporally co-ordinated way across the entire frame, rather than on a local, piecemeal basis: the whole information content of a frame is updated at one time, and that time marks the boundary between one frame and the next. To be clear, this does not necessarily mean that all of the information is rewritten from scratch: instead, it is quite possible that information remains as it is unless new information requires revision of it (Galletti & Fattori, 2003; Nortmann et al., 2015). But updating only occurs at temporal boundaries between frames. Within a frame, information is unchanging.

VanRullen (2016) wrote: "Discretization does not necessarily entail that events coming 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" (p. 724). But if they are deferred, where are they held? The products of processes that emerge during the time span of the current frame must be stored in what may be characterised as a temporary storage buffer before being injected en masse into the next frame. Suppose that a frame lasts for ~100 ms. A product of a perceptual process may emerge after the frame has been in place for 1 ms, or after it has been in place for 99 ms. Different products emerge at different times. If the current frame is static, they cannot be put into it, so they must be held in a buffer until the next updating occurs.

No doubt a plausible mechanism for holding information prior to construction of the next frame could be developed, but the need for one is problematic. What does it mean to say that a product of a perceptual process has been generated when it is not yet in a frame? Is it conscious or not? It seems that it should not be, otherwise the concept of a discrete frame is fatally undermined. But what is the difference between information being held in a buffer prior to entering a frame, and information being in a frame? The information content is the same, so that cannot be used to distinguish the two things. And what is the difference, such that information is not conscious in the buffer but conscious in the frame? The discrete frame hypothesis requires that these questions be addressed.

4.6: What would frames do for us?

If there are discrete frames of conscious perception, they must have some functional significance. One possibility is that, by preserving information on the time scale of a frame, accessibility to subsequent processes might be enhanced. If information that two stimuli separated by 5 ms were nonsimultaneous lasts only for as long as the stimuli themselves, it is likely to be lost before it can be transferred to subsequent stores where it is available for further processing. If it can be held for, say, 100 ms, then there is a better chance that it will be transferred to subsequent stores. That would certainly be an advantage. Information is likely to be lost before it exits from perceptual processing, partly because of the need for attentive maintenance (Rensink, 2000) and partly because of the increasingly limited capacity of post-perceptual stores (Jacob et al., 2013; Öğmen et al., 2013; Sligte et al., 2010; Sperling, 1960). Maintenance of information in conscious perception for the duration of a frame might not only increase the likelihood of its survival into subsequent stores, but also facilitate selection of information in accordance with processing priorities. There are at least two problems, however.

One problem is that there are obvious practical needs for perception to be as up-to-date as possible. If a product of a perceptual process emerges 1 ms after the current frame has been set up, it must wait in the storage buffer for almost the entire duration of the frame before it can enter the next frame and thereby become potentially available to subsequent processing. This would appear to be disadvantageous.

The other problem is that discrete frames of fixed duration are too inflexible. We have already seen that temporal integration and decision making processes operate on time scales that are dictated by considerations such as noise in the input, information density, and the operation of criteria for decision making. In the example of visible persistence, there is a flexible compromise between holding information for further analysis and minimising the smear that results from holding it (Farrell, 1984). The temporal inflexibility of discrete frames renders them less than optimal for processing purposes.

A case can be made that frame duration is not completely inflexible. As discussed earlier, Cecere et al. (2015) found that the temporal window for occurrence of the double flash illusion varied in accordance with effects of TMS on the oscillatory frequency of alpha. The authors suggested that "alpha oscillations might represent the temporal unit of visual processing that cyclically gates perception" (p. 231). If that interpretation is correct, then discrete frame duration is not completely inflexible. However, there is as yet no evidence for the degree of flexibility shown by results of studies on visible persistence (Farrell, 1984): Cecere et al. (2015) adjusted alpha frequency by ±2 Hz, which is comparatively small. Also, it is possible to interpret the results of the study without recourse to the discrete frame hypothesis. I have already argued that the functional characteristics of temporal integration pose serious problems for the frame hypothesis (section 4.3), and will not repeat those arguments here. An argument specific to the study by Cecere et al. (2015) is that the two tones (and the illusory two flashes, when they occur) are perceived as temporally successive, whereas events falling within a single frame are supposed to be perceived as contemporaneous. Thus, alpha frequency might indicate a window of temporal integration, but the products of the integration process include information about temporal succession of events within a single window. This might point to the aforementioned need for frames to be defined in terms of updating frequency and not experienced simultaneity, but it might also point to an interpretation that does not call on frames at all. That interpretation could be any of the possible functions of alpha discussed earlier (section 3.3).

There is a growing body of evidence that EEG oscillation frequencies can be affected by experimental manipulations such as TMS and presentation of stimuli with fixed periodicity, and that the effects on oscillation frequency are associated with perceptual effects suggestive of an alteration to the time window of temporal integration (Cecere et al., 2015; Ronconi & Melcher, 2017). But that evidence does not speak to the frame hypothesis, primarily because many kinds of temporal integration occur, each with their own (and flexible) temporal windows, on several different time scales (Ronconi et al., 2017). They generate specific perceptual products that are affected by the duration of the window of integration, but (i) those products are not temporal frames but specific perceptual features, such as one or two flashes, and (ii) they are local phenomena and do not entail an overall temporal co-ordination in conscious perception. Therefore, whether there are discrete frames or not, flexibility in temporal windows of integration in association with variations in oscillatory frequencies does not constitute evidence about flexibility in duration of discrete frames. They are just different things.

A second possible function for discrete frames would be synchronisation of the output of perceptual processes. In the case of vision, there is abundant evidence that different features of objects have different processing latencies (Arnold, Clifford, & Wenderoth, 2001; Kang & Shevell, 2012; Moutoussis, 2012; Moutoussis & Zeki, 1997a, 1997b; Zeki, 2015). For example, the processing latency for colour has been found to be about 80 ms less than that for motion information (Moutoussis, 2012; Moutsoussis & Zeki, 1997a; Zeki, 2015). Products of individual feature analysers need to be integrated into a coherent percept of an individuated object, so it could be proposed that a discrete frame supports the synchronised representation of asynchronous products of feature analysers.

There are at least three problems for this as a function of discrete temporal frames. One is that, although there is evidence that gamma oscillations are functionally involved in visual feature binding, the functional characteristics of that activity do not involve constructing temporally discrete snapshots of the whole body of visual information. On the contrary, they involve segregating meaningful components of the body of information, such as figure and ground (Elliott & Du Bois, 2017). As Elliott and Du Bois (2017) put it, "features coding an object may be coded by virtue of oscillatory firing at one particular phase, while all features defining 'ground' or the context of an object may be responded to by firing at other phases" (p. 2). There must still be integration of figure and ground information, presumably at a subsequent processing stage, but the evidence does not favour temporal frames as the vehicle of that integration. The second is that there are other hypotheses about the functional significance of gamma (see, for example, Poch, Campo, & Barnes, 2014; Tallon-Baudry, 2012), and there is no more reason to associate gamma with discrete frames than there is for alpha. The third problem is that features of visual objects are not well synchronised.

The research, using stimulus presentations with rapidly alternating features, has consistently shown misbinding of object features. For example, as Kang and Shevell (2012) put it, "observers perceived at each moment a combination of color and orientation that never was presented to the eye" (p. A128). Discrete frames on a time scale of more than 80 ms provide an opportunity for objectively accurate synchronisation of perceived object features, but the evidence shows that the visual system has not taken that opportunity.

Frame-like properties in attentive processing subserve useful functions, such as oscillating between the competing requirements of maintenance and updating of perceptual information. However, as we have seen, those functions do not require conscious perception itself to be composed of discrete temporal frames. There is, therefore, a need for the functional significance of discrete frames in conscious perception to be elucidated, that has yet to be satisfied.

5: Conclusion

The hypothesis of discrete frames in conscious perception has not been falsified. It is very unlikely, in the current state of evidence, that there could be discrete frames encompassing the whole of conscious perception, or that there could be discrete frames encompassing an entire modality. Hypotheses concerning frames on a more local scale, such as specific kinds of perceptual processes, would be harder to falsify. However, the prospects are not encouraging. There is some disconfirmatory evidence, at least in the visual modality (Di Lollo & Wilson, 1978; Efron & Lee, 1971); there is no unambiguously supportive evidence, and indeed there seems to be conflict between bodies of evidence for periodicity on different time scales; there is as yet no plausible or adequately specified mechanism that would generate discrete frames in conscious perception, as opposed to periodic fluctuations in processes within perceptual processing prior to the emergence of conscious percepts; there is evidence that time scales of processes such as temporal integration and retention of visual information are flexible in response to processing priorities and decision criteria in signal detection processes, whereas discrete frames have a relative inflexibility that would render them ill-suited to the dynamically changing requirements of processing; and there are serious problems concerning the definition of frames, the need for informational connections between frames, the means by which boundaries between frames are established, and the apparent requirement for a storage buffer for information awaiting entry to the next frame, that have not been satisfactorily addressed.

As a final problem, it is not even clear what sort of evidence would demonstrate the occurrence of discrete frames. At longer time scales, in White (2017a) I discussed a study by Fairhall, Albi, and Melcher (2014). They scrambled film clips on time scales from 800 to 12800 ms, and found a sharp increase in reported difficulty of comprehending the clips when the scrambling duration exceeded 2000 - 3200 ms. I argued that this was the right kind of evidence to be seeking for a frame in the region of 3 s, and I suspect that something similar might be the case for a hypothetical frame on the millisecond time scale. If a frame means anything, it surely must relate to integration and co-ordination of information. Thus, if a temporal stream of input information is scrambled on time scales ranging from, say, 30 ms to 200 ms, there should be a sharp increase in problems in perception when the time scale of scrambling exceeds that of a single frame.

Although no such research appears to have been carried out, there is at least one study that might have some relevance. Chait et al. (2015), studying speech perception, found evidence for two temporal windows of integration, on time scales of 20 - 50 ms and 150 - 300 ms. These probably have functional significance in relation to the time scales of organisation of linguistically meaningful information in speech. However, that functional significance alone would suggest that those time scales are specific to speech processing and might not occur in other areas of perceptual processing. Nor is it clear that they give rise to discrete frames of conscious perception. On the contrary, they appear to be two time scales of activity that contribute to the synthesis of longer semantic units such as phonemes and words, which are then experienced as temporally unitary. As Chait et al. (2015) expressed it, "[s]ignals are concurrently analyzed on at least two separate time scales, the intermediate representations of these analyses are integrated, and the resulting bound percept has significant consequences for speech intelligibility" (p. 1).

In short, there are probably multiple time scales of integration of perceptual information, the time scales vary depending on the kind of stimulus input that is being handled, and probably depending on other factors such as competing processing priorities. Even then, the perceptual products of those processes do not proceed in discrete frames with any particular periodicity. Moreover, compiling information into frames that are updated on a scale of an appreciable fraction of a second would seem to entail cost in relation to (i) sensitivity to fine temporal structure, (ii) keeping information as up-to-date as possible, given the unavoidable latencies in perceptual processing, and (iii) flexibility to processing considerations such as information density. Making a convincing case for any kind of discrete temporal frame in conscious perception would appear to be quite a challenge.

Footnotes

1. Some authors have also taken an analogy with successive snapshots taken by a camera (Blais, Arguin, & Gosselin, 2013; VanRullen & Koch, 2003). This seems less appropriate because there is nothing to connect successive snapshots to generate an illusion of continuity in perceptual experience.

2. Brief accounts of what von Baer might have said can be found in Pöppel (2009) and Elliott and Giersch (2016).

3. Not having access to the original, I am indebted to Durgin and Sternberg (2002) for this information; see also Lloyd (2012).

4. VanRullen et al. (2011) reported one study apparently showing such an effect in connection with alpha rhythm (7 - 13 Hz) by Varela, Toro, John, and Schwartz (1981), but they also reported that attempts to replicate that result by themselves and others had failed. Here I focus on the recent successful studies.

5. It is not mentioned in the extensive review by Bazanova and Vernon (2014).

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Table 1

Contents

Table 2

Hypothesized durations of discrete frames

Duration (ms)	Authors
4.5 - 4.6[1]	Geissler & Kompass (2001)
12 - 15	Joliot et al. (1994)
~30	Pöppel (1997, 2009)
50	Kristofferson (1967)
50 - 100	Pockett et al. (2011)
50 - 100	VanRullen et al. (2005)
50 - 200	Stroud (1949, 1956, 1967)
50 - 200	Harter (1967)
~80	Ansbacher (1944)
~80	Macdonald et al. (2014)
80 - 120	Lehmann et al. (1998)
80 - 140	VanRullen et al. (2014)
100	VanRullen & Macdonald (2012)
100 - 200	Kozma & Freeman (2017)
~125	Craig (2009a, 2009b)
~140	VanRullen (2016)

Note 1. Periodicities in multiples of 4.5/4.6 ms were also proposed, and an exact frame duration of 4.57 was proposed by Geissler et al. (1999).