



Review article

Time marking in perception

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ABSTRACT

Several authors have proposed that perceptual information carries labels that identify temporal features, including time of occurrence, ordinal temporal relations, and brief durations. These labels serve to locate and organise perceptual objects, features, and events in time. In some proposals time marking has local, specific functions such as synchronisation of different features in perceptual processing. In other proposals time marking has general significance and is responsible for rendering perceptual experience temporally coherent, just as various forms of spatial information render the visual environment spatially coherent. These proposals, which all concern time marking on the millisecond time scale, are reviewed. It is concluded that time marking is vital to the construction of a multisensory perceptual world in which things are orderly with respect to both space and time, but that much more research is needed to ascertain its functions in perception and its neurophysiological foundations.

1. Time marking in perception

Suppose a stimulus of an object in a complex large space is presented and visually perceived. The perception of the object will include information about its features, and also various kinds of spatial information, such as its distance from the observer, whether it is within reach or not, and its spatial relations with other objects. "Information" is the key word in that. The representation of space in the brain is not actual space. It is neural activity that encodes spatial features. The content of perception is information about spatial features, not actual space.

What holds for space holds for time as well. Suppose a brief visual stimulus is presented. The percept of the stimulus will include various kinds of temporal information, such as its location in time, temporal relations with other stimuli, and duration. Again, "information" is the key word. The representation of time in the brain is not actual time. It is neural activity that encodes temporal features. The content of perception is information about temporal features, not actual time.

There has been abundant research on the informational representation of space. Multiple kinds of spatial information have been identified and, in some cases, located in the brain (Brozzoli et al., 2011; Hafting et al., 2005; McNaughton et al., 2006; O'Keefe, 1976; Taube et al., 1990; Serino, 2019; Sugar and Moser, 2019). By contrast, there has been little acknowledgement of the informational representation of time in psychology and neuroscience. There has been much research on non-simultaneity and temporal order judgement at short time scales (e.g. Brown and Sainsbury, 2002; Fostick and Babkoff, 2013; Nicholls, 1994;

Westheimer and McKee, 1977) and also on how duration is perceived and judged (e.g., Eagleman and Pariyadath, 2009; Grondin, 2010; Ivry and Spencer, 2004; Lewis and Miall, 2003; van Wassenhove et al., 2008), but the informational nature of temporal perception has received little attention in that body of research.

This paper reviews a number of proposals that have in common a hypothesis about the nature of temporal information in perception. That hypothesis is that this information takes the form of time markers. Time markers can be characterised as semantic labels, not visible but part of the perceptual interpretation of the stimulus. To understand what this means, take the example of a simple visual stimulus. Visual processing registers elements of surface visual features such as local edges and colours and luminance and binds these together in a representation of the object. Not only is the assembled perceptual object a collection of surface visual features, it also includes semantic features such as identity (e.g. a cricket ball) and nonvisible properties such as mass (Runeson and Frykholm, 1981). Although not visible, these semantic features are still part of the perceptual interpretation of the stimulus. There is also spatial and temporal information, semantic information that locates the ball in various meaningful ways in terms of the brain's representation of space and time. A spatial example would concern peripersonal space, identifying whether the ball is in a position to act on or be acted on by the perceiver (Colby, 1998; Serino, 2019). Time marking information, as will be shown in this paper, may include how long ago an event occurred (on the sub-second time scale), its ordinal temporal relation to some other event, or its duration (again on the sub-second scale). This applies

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not just to visual information but also to information in other modalities.

It will be shown that time markers may have numerous functions in perception. These include binding of features into perceptual objects, locating events in time, indicating durations of events within frames of conscious perception, and supporting perception of things happening. Time marking is useful, and indeed possibly fundamental, in perceptual processing, in ways that are only just starting to be appreciated. The review is confined to research in psychology and neuroscience. There has been some acknowledgement of the issue in philosophy; for that, readers are referred to other publications (Bergson, 1910; Dainton, 2008; Smart, 1980; Zimmermann, 2011).

It is important to distinguish perception and post-perceptual judgement. When a participant reports a duration judgement in an experiment, that report is the outcome of a judgement process. A judgement of duration might be considered a form of time marking, but it is optional, occurring only when the duration judgement process is engaged. This review is concerned with time marking before post-perceptual processing, that is as part of perceptual processing. It will be shown below that time marking can occur early in perceptual processing, before or during assembly of local information into coherent perceptual objects.

It is also important to distinguish between the natural temporal order in which external stimuli enter the system and the representation of temporal order generated in perceptual processing. When hearing a musical scale from A to G, B flat does indeed enter the system after A and that is the natural or objective temporal order. But perceiving B flat as occurring after A requires information about temporality to be processed. Perception of B flat as occurring after A is a matter of time marking information being generated and attached to the perceptual information about each note. We do not experience natural temporal order, only the temporal order information that is constructed in perceptual processing, just as the pitches of the notes are.

The hypotheses discussed in this review fall into two categories. One, which may be called specific, concerns proposals of time marking for a particular function in perceptual processing, with no implication that it applies generally. The other, which may be called global, concerns proposals of time marking as essentially ubiquitous in perceptual processing. It will be seen that the specific proposals have the advantage that they are testable, and there is research evidence that bears on them, whereas the global proposals have not, so far, been tested, and it is not yet clear what sort of test could be run. The two kinds will be addressed in turn.

2. Specific time marking proposals

2.1. Libet's subjective backward referral proposal

The first proposal of a time marking hypothesis in psychology can be found in Libet et al. (1979). The background to that proposal is research by Libet et al. (1964) and Libet et al. (1967). They found that threshold level electrical stimulation to the exposed surface of the somatosensory cortex gave rise to a reportable percept only after 500 ms of stimulation (in fact 500–1000 ms depending on the individual participant). That is, stimulation had to be maintained for 500 ms for a reportable percept to occur: 400 ms was not enough. They also reported evidence that brief threshold level stimulation to the skin could give rise to a reportable percept, also with a latency of about 500 ms. The stimulus duration could be as short as ~100 ms (thresholds were determined for individual participants) but the percept still had a latency of 500 ms.

In Libet et al. (1979) continuous direct electrical stimulation was again applied to the cortex. A brief stimulus was then applied to the skin, starting 200 ms after the onset of the cortical stimulation. If, as Libet et al. (1964, 1967) found, latency to reportable percept was 500 ms for both kinds of stimuli, the skin stimulus should be reported as occurring after the cortical stimulus. In fact, participants reported that the skin stimulus occurred before the cortical stimulation. Libet et al. (1979) argued that the percept of the skin stimulus occurred with a latency of

500 ms, based on their earlier research, but that it was then referred back in time to approximately the time of the skin stimulation. This is the backward referral hypothesis.

Libet et al. (1979) stated that backward referral was accomplished with the aid of a time marker, and that there is a neurophysiologically plausible way in which that could happen. Libet et al. (1979) expressed the time marker hypothesis as follows: "(1) Some neuronal process associated with the early or *primary evoked response*, of SI (somatosensory) cortex to a skin stimulus, is postulated to serve as a 'time-marker'. (2) There is an automatic *subjective referral of the conscious experience backwards in time* to this time-marker, after the delayed neuronal adequacy at cerebral levels has been achieved. The sensory experience would be 'antedated' from the actual delayed time at which the neuronal state becomes adequate to elicit it; and the experience would appear subjectively to occur with no significant delay from the arrival of the fast projection volley" (pp. 201–202). The time marker alluded to by Libet et al. (1979) supposedly occurs in the cortex just 10–20 ms after the peripheral stimulation.

The hypothesis is illustrated in Fig. 1, based on the stimuli used by Libet et al. (1979). In effect, the hypothesis states that the time of an early cortical response to the skin stimulus is registered with a time of occurrence marker; then, when the stimulus is perceived, 500 ms after stimulus onset, it is perceived as having occurred at the registered time of the early cortical response. Note that the arrow in Fig. 1 goes from the time marker to the conscious percept, not the other way round. The term "backward referral" is misleading: the time marker just persists in the system until the conscious percept emerges, and is then attached to it. The stimulus is never perceived as occurring in the present, but is perceived as having occurred at a time in the past. That time, initially about 500 ms in the past, will obviously move further into the past as time continues to go by. But the key point is that, because the time marker states that the stimulus occurred at a time 10–20 ms after the peripheral stimulation, it will be perceived as having occurred before the cortical stimulation. Thus, the perceived time of occurrence of a stimulus is set, not by the time of emergence of a percept of it, but by the operation of a time marker process that uses some cue to the time of occurrence of the stimulus to attach a time marker to the percept. That is the hypothesised role of time marking in the backward referral process.

The backward referral hypothesis has since been discredited (Churchland, 1981; Gomes, 1998; Klein, 2002; Pockett, 2002; Pollen, 2004). Libet seems to have adopted the hypothesis that the 500 ms latency to reportable percept holds for any level of stimulation to the cortex (Libet, 1993), whereas the evidence supports the view that it holds only for threshold level stimulation. Possible explanations for this long latency for threshold level stimuli in terms of facilitation or temporal summation can be found in Pockett (2002) and van de Grind

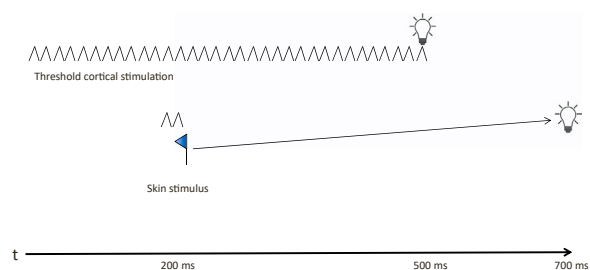


Fig. 1. Libet's backward referral hypothesis. Continuous direct stimulation is applied to the cortex for 500 ms, and a brief stimulus is applied to the skin 200 ms after the start of the cortical stimulation. Light bulbs show the times at which conscious percepts of the respective stimuli emerge, in Libet's interpretation. The initial (non-conscious) response to the skin stimulus generates a time marker (the flag). When the conscious percept of the skin stimulus emerges, 500 ms later, the time marker is attached to it. Thus, it appears to have occurred before the cortical stimulation. Note that there is no time marker for the cortical stimulation.

(2002). It is likely that Libet's claim that a reportable percept of supra-threshold skin stimulation occurs with a latency of 500 ms is also incorrect. More recent research has found differentiation in neural activity between perceived and unperceived somatosensory stimuli less than 100 ms after stimulus onset (Palva et al., 2005), and in event-related potential (ERP) data with a latency of about 100 ms (Schubert et al., 2006). Thus, the skin stimulus was reported as occurring before the cortical stimulus because the latency to perception was ~100 ms, which would mean that it appeared about 200 ms before the cortical stimulation was perceived. Backward referral is not needed to explain that result.

Nevertheless, Libet's time marker hypothesis was an innovative idea that suggested an important point about timing information in perception: the time at which we perceive an event occurring is not the time at which it actually occurs, nor the time at which it emerges from perceptual processing, but the time at which it is labelled as occurring. Thus, we seem to be perceiving the present not because we are (which cannot be the case because perceptual processing takes time) but because most if not all of the products of perceptual processing are time marked as in the present (White, 2020). Our perception of the "present-ness" of the world around us is just a consequence of the fact that all of that information is labelled with a "present" time marker. That is perhaps the fundamental point about time marking. Our perceptual experience of the time at which something happens is just the time marker that is attached to the perceptual information about that event, and is not a feature of reality directly apprehended.

2.2. Dennett and Kinsbourne's time marker hypothesis

In their discussion of the backward referral hypothesis, Dennett and Kinsbourne (1992) raised the possibility that the conscious percept of the stimulus might carry "something like a postmark" (p. 196). That was an allusion to their own time marker hypothesis. They pointed out that neural transmission and processing latencies can result in inaccurate information about temporal relations between events. For example, transmission time to the brain for somatosensory stimuli presented to the foot is longer than that for stimuli presented to the shoulder. That could result in incorrect perception of the temporal order of the stimuli. To solve that problem, Dennett and Kinsbourne took an analogy with a postal system that labels postal items with the date on which they were sent, so the recipient does not interpret the order in which they arrive as indicating the order in which they were sent. Thus, stimuli presented simultaneously to the foot and the shoulder can be perceived as simultaneous, despite the difference in neural transmission times, if they are labelled at the outset with their time of occurrence. That label is received at the brain along with the rest of the stimulus information.

Thus, they argued, perception of temporal order in events is not a matter of one event being perceived and then the other. It is a matter of one event having a time label that places it earlier in time than the time label on the other event. Information that A occurred before B is not in the form of a percept of A followed by a percept of B (although that might well occur); it is in the form of pieces of information saying that A occurred before B. That is a time marker hypothesis. It is not a duration marker but a different kind of time marking information, an ordinal time marker, labelling events by the relationship between them in time.

Instead of date stamps, Dennett and Kinsbourne (1992) proposed a system that they called "context-sensitive settling" (p. 189) for synchronising perceived events. They took an analogy with a film studio where sound recordings are synchronised with the visual part of the film by finding temporal correspondences or correlations between the content of each. That is problematic because establishing temporal correlations requires information retained over an extended period of time. Instead of a mechanism that compensates for neural transmission time differences between the shoulder and the foot, it would have to be supposed that there is an extended series of items of perceptual information that can act as a standard or baseline for allocating temporal

labels to other information. The analogy suggests that this is done cross-modally, perhaps with vision supplying the reference frame. This temporally extended process would still depend on time marking for synchronisation. Individual events in the series would be labelled with their ordinal temporal relations.

It should be noted that "synchronisation" can mean two things (if not more). In one meaning, perceptual synchrony or simultaneity is two items of perceptual information having the same time marker. In the other meaning, perceptual synchrony is the product of a judgement made in post-perceptual processing. In the argument made by Dennett and Kinsbourne (1992), such a judgement could be informed by time marker information. Without time markers, the perceptual world would be temporally indeterminate or chaotic. Time markers attached to perceptual information are what constitutes experiences of things as simultaneous or temporally successive, as the case may be. Time marker information could then be fed into some sort of comparison process in order to make an explicit judgement of simultaneity or nonsimultaneity. Time markers would be necessary but not sufficient for accuracy in such judgements, because error could be introduced through memory storage and processing subsequent to perception.

It is not certain whether the particular synchronisation mechanism proposed by Dennett and Kinsbourne operates in the brain. Macefield et al. (1989) reported a neural conduction velocity for afferent fibres associated with skin pressure sensors of about 55 m/s. Vroomen and Keetels (2010) calculated that this would result in a difference in arrival times at the cortex for stimuli presented simultaneously to toe and nose of about 30 ms. The difference in arrival times for stimuli presented simultaneously to hand and foot is about 20 ms (Halliday and Mingay, 1964). The difference between foot and shoulder might be greater. Temporal order discrimination thresholds for stimuli presented to different hands can be much longer, even greater than 100 ms under some circumstances (Miyazaki et al., 2016; Wada et al., 2004; Yamamoto and Kitazawa, 2001), so it would be surprising if there were a mechanism to compensate for differences as small as 20 ms. Indeed, Halliday and Mingay (1964) found no evidence for any compensation for differences in neural transmission times, so the mechanism postulated by Dennett and Kinsbourne (1964) may not exist. That still leaves open the possibility of temporal adjustment mechanisms operating under other circumstances. Even within modalities, cortical processing latencies differ for different kinds of information. That causes problems for synchronisation that a time marking process might be able to solve. That is the topic of the next section.

2.3. Time marking in feature binding in early perceptual processing

In early visual processing, different features are processed in parallel by different systems. As processing continues, features are assembled into perceptual object representations (Feldman, 2007; Heinen et al., 2005; Vecera and O'Reilly, 1998). However, the assembled perceptual object is not always an accurate representation of the stimulus. Moutoussis and Zeki (1997a) presented stimuli in which colour and motion information alternated rapidly between two values (e.g. up versus down for motion and red versus green for colour). Participants were unable to judge which value of one feature was temporally associated with which value of the other feature (Moutoussis and Zeki, 1997a). The results showed inaccurate binding of features: "for example, subjects pair the direction of motion that was present on a screen at time t , with the colour that was present 80 ms earlier" (Zeki, 2015, p. 3). Moutoussis and Zeki (1997a, 1997b) argued that the inaccurate binding or perceptual asynchrony can be explained in terms of differing processing latencies between features. They interpreted their results as showing that processing of motion information takes about 40 ms longer than processing of orientation information, and processing of orientation information takes about 40 ms longer than processing of colour information. If the different processing latencies are not compensated in the feature binding process, that would account for the results (Moutoussis and Zeki, 1997a,

1997b; Zeki, 2015).

Additional evidence favours the processing latency hypothesis. [Bartels and Zeki \(2006\)](#) studied features being paired with themselves (e.g. colour with colour) for stimuli that are presented to different hemispheres. They found that the critical alternation period for binding was shorter for motion-motion pairings than for colour-colour pairings. That is the opposite of what is found for pairings of different features. That result was explained as showing faster interhemispheric signal conduction velocities of the fibres for colour than for motion ([Bartels and Zeki, 2006; Zeki, 2015](#)), and it therefore fits with the processing latency hypothesis.

[Nishida and Johnston \(2002\)](#) proposed an alternative explanation based on time markers. They distinguished two kinds of temporal changes, first-order and second-order. In the case of motion, transition or spatial displacement is a first-order change, but turning point (change of direction) is a second-order change, a "second-order derivative of spatial position with respect to time" (p. 363). A transition in motion requires measurements at two points in time, to determine whether the feature is in the same state or not. But a turning point or second-order change requires measurements at three points in time. Two points are needed to determine the transition and a third to determine whether the change continues in the same direction or not. They argued that transitions and turning points can be labelled with time markers to aid synchronisation. At rapid alternation rates, of the sort used by [Moutoussis and Zeki \(1997a\)](#), the requirement of three measurements makes detecting turning points difficult so the visual system matches transitions instead. Time markers for colour change identify the first-order change from one colour to another. Time markers for motion identify first-order position change, not the second-order turning point. Because of this, the time marker is located, on average, in the middle of the position change, not at the time of the turning point. The time marker therefore lies between two turning points. This means that the time markers for the turning points cannot be matched to the time markers for the colour changes. This is illustrated in [Fig. 2](#). In brief, time markers are needed for synchronisation, but they are not all there is to synchronisation. Synchronisation results from matching of time markers for different features. Incorrect feature matching occurs when time markers for different features cannot be matched correctly.

[Nishida and Johnston \(2002\)](#) found that the perceptual asynchrony did not occur at slower alternation rates. That fits with their account because, at slower alternation rates, the visual system is able to time mark the second-order motion property, the turning point, and hence to match it appropriately with the time markers for the colour change. The

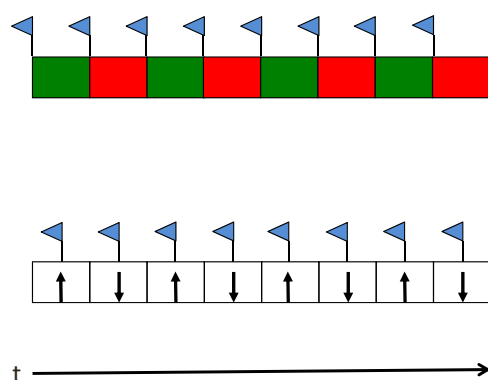


Fig. 2. [Nishida and Johnston's \(2002\)](#) time marking hypothesis. A sequence of alternating colours and motion directions is presented. Transitions of colour are time marked. For motion, the turning point cannot be time marked because the alternations are too rapid, so the transition (i.e. displacement) is time marked instead. The average location of the transition time marker for each direction is in the middle of each period of motion, so the time markers cannot be matched to the corresponding time markers for colour change. Based on [Fig. 1C](#) in [Nishida and Johnston \(2002\)](#).

processing latency difference account does not explain this result because processing latency differences are constant across alternation rates, so the same perceptual asynchrony should occur at any alternation rate. [Arrighi et al. \(2005\)](#) found further evidence that perceptual asynchrony depends on whether the change in the feature is first-order or second-order, and also found evidence for an equivalent effect in audition, and in audiovisual cross-modal stimuli. They concluded that "physically simultaneous first- and second-order oscillations are almost always perceived as asynchronous" (p. 453). Those results are consistent with the time marker hypothesis. On the other hand the time marker hypothesis cannot account for perceptual asynchrony with colour and orientation information ([Moutoussis and Zeki, 1997b](#)), because colour change and orientation change are both first-order changes.

It could be argued that, while [Nishida and Johnston \(2002\)](#) used the language of time marking, their use of the term might not be the same as that of others who have put forward time marking proposals. However, [Nishida and Johnston \(2002\)](#) distinguished between brain time (i.e. differing processing latencies) and mechanisms that encode signals to register temporal information. For the latter, they took a parallel with [Marr's \(1982\)](#) use of the term "token" to represent elements of spatial patterns that are then input to grouping processes on the road to perceptual object construction. They argued that temporal information such as processing latencies is similarly registered in the form of tokens, "temporally localized representations of salient temporal features" (p. 360). Perceptual asynchrony would then result from groupings of these temporal tokens. In other words, the perceptual system is utilising markers of temporal information, not the actual time course of processing, and what is perceived results from that.

[Nishida and Johnston \(2002\)](#) proposed that time markers are amodal tokens that denote the time at which a specific event occurs in the world; perceptual synchrony or asynchrony results from matching of the time referents on these tokens across different stimulus features. In fact they agreed with [Libet et al. \(1979\)](#) that an event-time signal is triggered by the stimulus; that is, the time marker indicates the time of occurrence of the stimulus, not the time of emergence of the percept from perceptual processing. In the model they proposed, a temporal comparator assesses temporal relations by extracting and comparing features labelled with time markers from different sensory channels. So theirs is a genuine time marker hypothesis and has points of resemblance with the earlier proposals by [Libet et al. \(1979\)](#) and [Dennett and Kinsbourne \(1992\)](#).

Further studies have complicated the picture somewhat. A full review of that literature lies outside the remit of this paper (see [Nishida, 2011](#)), which is concerned specifically with time marking hypotheses, but some brief pertinent observations can be made.

[Linares and López-Moliner \(2006\)](#) presented a series of colour changes with just a single change in motion direction and found evidence of perceptual asynchrony. This is not predicted by the time marking account because a single change is equivalent to a slow alternation rate, so it would be predicted that the visual system would be able to time mark the second-order motion property accurately. If the direction change was 90° instead of 180°, the perceptual asynchrony was significantly reduced. [Linares and López-Moliner](#) suggested that, for colour changes, a form of backward masking was involved, where the presentation of a new colour masked the previous colour over a short time period. That would alter the temporal relationship between the perceived colour change and the motion change. This seems not to explain the absence of perceptual asynchrony with slow alternation rates in the study by [Nishida and Johnston \(2002\)](#), but it is a reminder that many factors may be involved in a full understanding of perceptual asynchrony, and support for one does not necessarily disconfirm others.

An alternative possible explanation has been proposed by [Clifford et al. \(2003\)](#). They presented stimuli in which orientation and colour switched abruptly between two values, and they varied the time difference between these switches. In one condition participants made a forced choice of which colour was paired with which orientation. Results were consistent with colour lagging orientation by about 50 ms,

consistent with the results reported by [Moutoussis and Zeki \(1997b\)](#). In another condition participants judged whether colour and orientation change were simultaneous or not. In this condition the results suggested that orientation lagged colour, but only by less than 10 ms. This does not seem to be consistent with the processing latency explanation.

Clifford et al. suggested that the two judgements are based on different features of the stimuli. The simultaneity judgement is based on processing latencies, which would then be similar for both (contrary to [Moutoussis and Zeki, 1997b](#)). The pairing judgement is based on correlations between colour and orientation. That is, the pairing judgement requires an estimate of the amount of time for which values of each attribute are presented together, whereas simultaneity judgement can be based on momentary change information. Thus, evidence of inaccurate feature binding can be interpreted as outcomes of estimated temporal overlap of temporally extended stimuli. They suggested that the temporal correlation judgement could be based on "conventional rate-modulated neural representations" (p. 2249), referring to a review by [Shadlen and Movshon \(1999\)](#) showing that performance on psychophysical tasks varies with changes in neural firing rate.

[Moutoussis and Zeki \(1997a, 1997b\)](#) and [Zeki \(2015\)](#) claimed that colour information has a processing latency about 80 ms less than that for motion information. That was the basis for their processing latency explanation for perceptual asynchrony. [Wang, He, Fan, Liu, and Chen \(2006\)](#) found evidence from both reaction time and EEG data that the opposite is the case, with motion processing being faster than colour processing by about 40 ms. They pointed out that this is consistent with many results from primate research. If this is correct then the empirical basis for the processing latency explanation is overturned.

In the current state of the literature, then, the time marking hypothesis to explain perceptual asynchrony is still viable but not a complete explanation for the effect.

3. Global time marking hypotheses

3.1. Time marking in hypothesised frames of conscious perception

Many authors have proposed that conscious perception proceeds in a series of discontinuous frames ([White, 2018](#)). In those proposals, each frame would comprise a static set of information, and would then be replaced by the next frame after a regular interval. In a series of papers, Herzog and colleagues have argued that there are frames of conscious perception with a time span up to 370–450 ms ([Herzog et al., 2016](#); [Drissi-Daoudi et al., 2019](#); [Herzog et al., 2020](#)). This is perhaps the longest proposed frame duration in the literature ([White, 2018](#)). A hypothesised frame with such a long time span appears problematic. Subjectively, time and events do not appear to jump along in a series of static and independent frames. The temporal order of events can be accurately perceived when the events in question are separated by only a few ms ([Babkoff, 1975](#); [Craig and Baihua, 1990](#); [Westheimer and McKee, 1977](#)). That seems not to be compatible with a static frame of conscious perception that is held for up to 450 ms. [Herzog et al. \(2016\)](#) proposed time marking as a solution to that problem.

[Herzog et al. \(2016\)](#) argued for an initial stage of non-conscious visual scene analysis over about 400 ms: features are "quasi-continuously and unconsciously analyzed" ([Herzog et al., 2016](#), p. 1). Among the features analysed in that period are temporal features such as duration and simultaneity. But the duration that gets into the eventual frame of conscious perception is not an actual duration. It is a semantic marker indicating what duration the stimulus in question had. [Herzog et al. \(2016\)](#) argued that this is no different than labels for colour or orientation. Although the features are of different kinds, the labels are of the same kind: an informational indicator of the value taken by the feature. Thus, a stimulus with a duration of 50 ms is not perceived during the time of its presentation, because processing that follows its presentation is non-conscious. When the stimulus becomes conscious, meaning when the frame that contains it is in conscious perception, the conscious

perception of the stimulus as having a duration of 50 ms consists of an informational representation of the stimulus with a label attached to it saying what its duration was. All information content of a conscious frame is labelled with duration markers. This is illustrated in [Fig. 3](#). The postulated frames of conscious perception are temporally discrete, analogous to the way in which a movie consists of discrete and successively projected images (though on a much shorter time scale than that of the proposed frames of conscious perception), but they are generated by non-conscious processing that is continuous.

This is a different kind of proposal from those considered previously because it implies that time markers for duration are ubiquitous in perceptual processing. Our entire conscious perceptual experience of duration is in the form of duration markers. These are constructed, along with other perceptual features, during the initial non-conscious stage of processing, and are then released to conscious perception as contents of a frame covering about 400 ms. The subjective continuity of time and events is a construction of time markers that tell us how long things lasted for, and they are held in a static representation until they are replaced by whatever is in the next frame.

Supporting evidence for the frame hypothesis comes from a study by [Scharnowski et al. \(2009\)](#). They presented stimuli comprising verniers, two vertical bars presented one above the other but with a small horizontal offset. Two such verniers were presented in rapid succession (30 ms each with zero inter-stimulus interval) at the same retinal location with spatial offsets in opposite directions, as shown in [Fig. 4](#). What is perceived is a single vernier with a spatial offset that is a weighted average of the offsets in the two stimuli: the individual verniers are not perceived as such. [Scharnowski et al. \(2009\)](#) applied brief transcranial magnetic stimulation (TMS) at intervals from onset of the first stimulus to 420 ms after. For TMS onset latencies from 45 ms to 120 ms the second vernier dominated the fused percept; for latencies from 145 ms to 370 ms the first vernier dominated the fused percept. [Scharnowski et al.](#) argued that information about each of the verniers must be retained in the visual system for at least 370 ms because that is the only way the weighting of the two stimuli in the fused percept could vary on that time scale. [Herzog et al. \(2016\)](#) argued that that research supported their frame proposal. The individual verniers were never consciously perceived, despite the evidence that information about each was retained for at least 370 ms. Only the fused vernier was perceived. Thus, there is a phase of nonconscious information retention and processing lasting about 370 ms and then the conscious percept is generated.

More evidence for temporal integration of vernier stimuli over 290–450 ms was reported by [Drissi-Daoudi et al. \(2019\)](#). These authors presented a long series of vernier stimuli over about 750 ms. [Drissi-Daoudi et al. \(2019\)](#) found that vernier stimuli presented more than 450 ms after the first one were not integrated with those presented during the first 450 ms, even though they formed part of a continuous sequence. They concluded that a window of integration is initiated by the onset of the first stimulus and has a maximum time span of 450 ms. A second window is initiated when the first one closes.

The present review is concerned not with the frame proposal but with the time marker proposal. As [Herzog et al. \(2020\)](#) pointed out, construction of duration information requires some kind of timing mechanism. They argued that temporal discrimination of not more than 3 ms would be required. That is supported by evidence of temporal discrimination thresholds of 2–3 ms ([Babkoff, 1975](#); [Elhilali et al., 2009](#); [Wehrhahn and Rapp, 1992](#); [Westheimer and McKee, 1977](#)), and there is evidence for millisecond precision in timing in the cerebellum ([Bareš et al. \(2019\)](#)). Many neurophysiologically plausible timing mechanisms have been proposed ([Buonomano and Merzenich, 1995](#); [Gorea, 2011](#); [Grondin, 2010](#); [Mauk and Buonomano, 2004](#); [Merchant et al., 2013](#); [Paton and Buonomano, 2018](#)), but there is still uncertainty over which of them might support millisecond scale temporal discrimination in the human brain. Two points can be made about timing mechanisms here. One is that they are not alternatives to time markers: they are possible explanations for how time markers, specifically in this case duration or

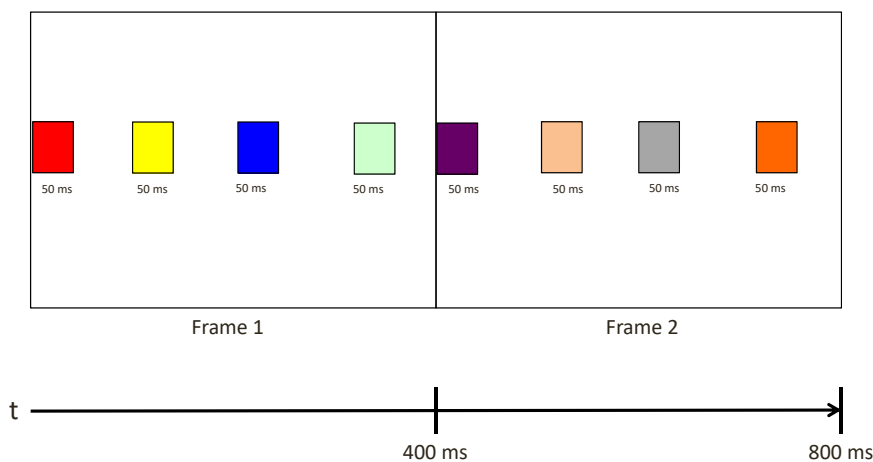


Fig. 3. Frame hypothesis of Herzog et al. (2016). A series of coloured rectangles is presented, each for 50 ms with brief gaps between. Common sense would suggest that each rectangle is perceived one after the other. Instead, Herzog et al. proposed that conscious perception proceeds in frames of ~ 400 ms time scale. Thus, the first four rectangles are nonconsciously processed and are then consciously perceived all at once after ~ 400 ms, each accompanied by time markers indicating their duration. That frame persists for ~ 400 ms and is then replaced by frame 2, which contains the next four rectangles, also with duration markers. Each frame is initiated by the first stimulus; in the case of the second frame, that would be the first stimulus presented after the time limit on the first frame is reached. Note that the proposal does not mention temporal ordering of the rectangles, but that information must be there.

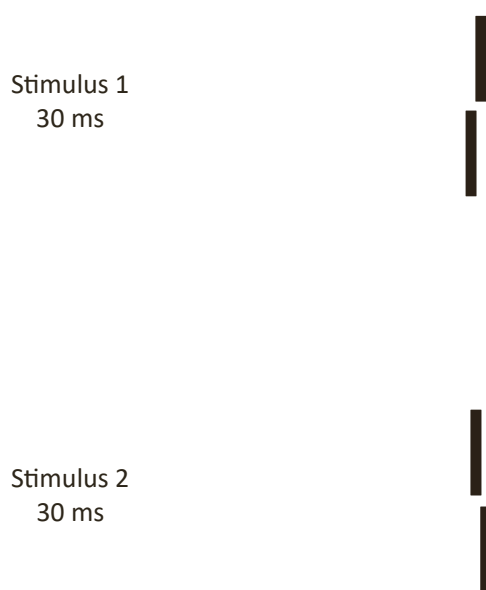


Fig. 4. Schematic representation of stimuli used by Scharnowski et al. (2009). The two stimuli are presented consecutively and without a break, to the same retinal and spatial location. Amount of offset in each vernier was manipulated.

interval markers, may be generated. The second point is that some if not all timing mechanisms may generate post-perceptual duration judgements, that is, duration judgements that can be reported in some way by participants in research studies. It is important to distinguish between timing information in perception and timing information derived from perceptual information at some later stage of processing. The time markers proposed by Herzog et al., (2016, 2020) are within perceptual processing, not after it, and it would be important to find a timing mechanism that is integrated with perceptual processing, not with post-perceptual processing.

There is currently no evidence relevant to the timer marker proposal put forward by Herzog et al., (2016, 2020). They argued that time markers are necessary for their hypothesis of long frames of conscious perception: time markers fill the explanatory gap between short temporal discrimination thresholds and the proposed long time span of the frame of conscious perception by explaining how short durations can be perceived despite the lengthy interval encompassed by a single frame of conscious perception. That argument might well be right, if the frame hypothesis itself is right, but the evidential foundation is not yet there.

3.2. Time marking for perceived happening

Consider watching a ball moving through the air after being thrown. How is that motion perceived? One possible answer is low-level velocity detectors (Adelson and Bergen, 1985; Burr and Thompson, 2011; Clifford and Ibbotson, 2003). A simple hypothetical motion detector, the Reichardt detector, involves a neuron that receives input from two other neurons that respond to local luminance changes. The neuron is activated by a specific temporal pattern in the firing of the luminance detectors, and that registers local velocity. Such mechanisms do not account for perception of the ball's motion, however. The velocity information is low-level and local; it is not attached to the object representation for the ball, so velocity information over multiple detectors would need to be integrated and attached to the perceptual representation of the ball. In addition, the velocity information is momentary: it indicates what the velocity is at a moment, which can be defined as the shortest temporal resolution in perception. Clearly, perception of a ball in flight is not like that. It incorporates recent history: we would know, for example, whether the ball was thrown or hit by a racquet about 200 ms ago or not, and that is part of the active perceptual history that constitutes perception of the ball as a coherent, temporally extended perceptual object, persisting and moving over time. The same applies to all features of perceptual objects and contexts. I do not perceive my desk as having no history beyond the immediate present. Part of what I perceive is the desk as having been where it is and as it is in the recent past, meaning in this case the millisecond time scale (though of course memory for its existence may go back much further in time than that).

To account for that, White (2021) proposed that perceived happening comprises products of perceptual processing entered into an organised information structure on the millisecond time scale. The main features are four kinds of information that bind percepts together over time, over the time scale of the representation. Two of these are information about perceptual objects and features: vector information, which indicates what and how much change is going on for a given feature or object at a given moment, and connectives, which link successive vector representations over time to generate a coherent overall representation of recent history.

Information about change in object features is not enough, however. To be able to link together change information over successive moments in history, that change information must be supported by temporal information. The information structure must be organised in temporal coordinates that function as a foundation for the temporal organisation of information about happening. Two kinds of temporal information were proposed for that purpose. Time distance information indicates how far in the past, relative to the perceived present, a given item of information is. Thus, the ball as perceived now is accompanied by an informational trail that is organised by time markers that indicate how far back from

the present any given piece of information is. It was also proposed that ordinal temporal information is required: an item of information is identified as immediately before or after another one. These two kinds of temporal information function as a substrate on which the informational history of the ball (and, by generalisation, everything else in current perception) is organised. Without these two kinds of time markers, recent perceptual history would be jumbled or incoherent: we would not know when anything happened or how one moment of happening connected to any other. The basic ingredients of the proposed information structure are schematically depicted in Fig. 5.

It is important to note that this information structure represents recent history but is not itself history. That is, it is all there at a single moment: that is the point of the word "now" at the bottom of Fig. 5b. The problem with actual history is that it does not exist. Perceiving history, even on a scale of milliseconds, requires the retention of historical information in the present. This implies that our entire perception of temporality is a matter of time markers. All retained information about the recent past is located in perceived history by time markers. The flight of the ball is perceived as connected over time because the surviving perceptual information about it is bound together by time markers. This applies even to the perceived present. Because of perceptual processing latencies, the most recent available perceptual information lags behind the objective present. Despite that, it is still perceived as the present, and that is not because it really is but because all the information in it is time marked as present. Then, connected to that, is a series of information about the recent past, also labelled with time markers. Without that, there would be no perceptual experience of time, or of things as happening in time.

Although the whole body of information about the recent past exists at a moment, it is not a frame of conscious perception. In the proposal (White, 2021), information is updated continuously, or as and when new products of perceptual processing become available, meaning on the time scale of temporal resolution of perceptual information. If it could be shown that the entire body of information was updated at once periodically, then it could be regarded as a frame of conscious perception, but there is no evidence for that.

The proposal suffers from the same problem as that by Herzog et al. (2016): there is no research evidence for the kinds of time marking postulated. The justification for the time markers is different. Herzog et al. (2016) proposed time markers to represent durations in frames of

conscious perception, to avoid the subjective impression of progression through time in a series of jumps. In the proposal by White (2021) time markers are proposed as necessary to organise the temporal history of recent events in perception. The time markers postulated for that function are different from duration markers: they specifically locate events in time and in relation to each other. It could be argued that the absence of such information from the proposal by Herzog et al. (2016) is a weakness: a given frame could contain information about multiple events with different durations, but those events would not be temporally organised or related. There would just be a disorganised collection of events with duration markers. Time distance and ordinal temporal information are needed to hold the world of recent perceptual history, and to differentiate and organise items of information in a kind of temporal map. Duration information could be there as well, but it does not play a fundamental role in the way that time distance and ordinal temporal information do.

4. General discussion

This paper has, for the first time, brought together a number of proposals that have in common the idea that perceptual objects, features, and events are located in time by means of time marker information. This is semantic information that may indicate various temporal features such as absolute time of occurrence, duration, and ordinal relation to other features and events. It is functionally equivalent to the many kinds of spatial information that are generated in perceptual processing, in that it renders perceptual information coherent and organised with respect to time. Without that, perceptual information would lack temporal reference. To give a simple example, if a rapid series of musical tones is presented, the tones would enter the system in order but that order information would not be constructed in perceptual processing, so the perceptual information about the notes would be a temporal jumble.

The proposals discussed here are not free of problems. Libet's backwards referral hypothesis has been discredited, the time marking hypothesis of Dennett and Kinsbourne (1992) lacks evidential support, and the proposal by Nishida and Johnston (2002) is not the only contender in its field. The problems, however, are not directly concerned with the time marking part of the proposals. Backwards referral has been disconfirmed, but Libet's idea of time marking as a way of indicating

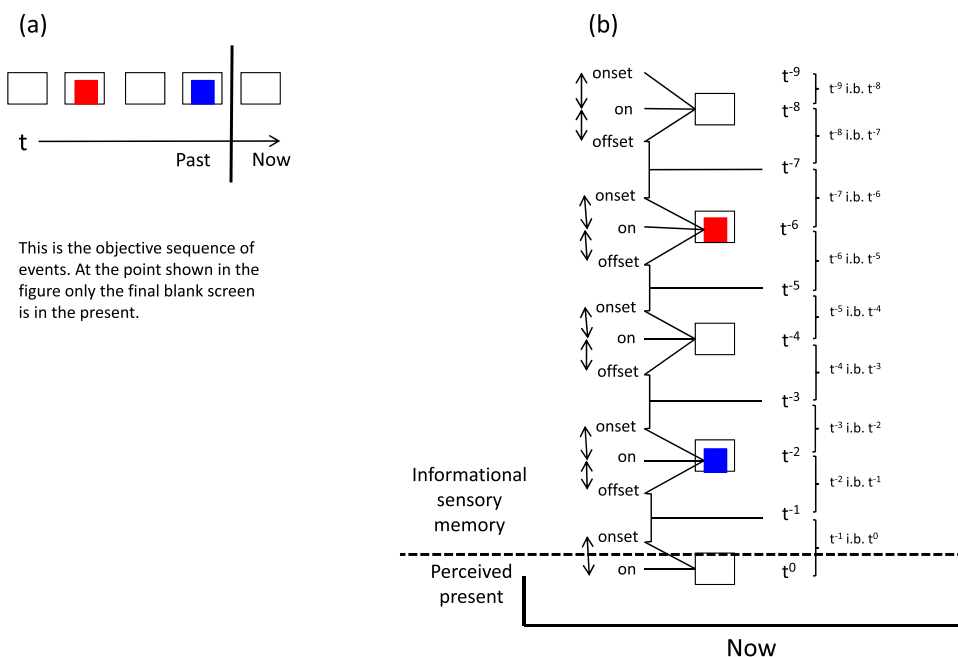


Fig. 5. Schematic depiction of the information structure for perceived happening proposed by White (2021). (a) shows a hypothetical stimulus presentation of a red square followed by a blue square with blank screen before, after, and between the two squares. At the moment labelled "now" only the final blank screen is in the present and the rest of the stimulus sequence is in the past and gone. (b) Schematic and simplified rendition of the proposed information structure as it is for the moment labelled "now" in (a). All of the information exists at a single moment in time. Labels from "t⁰" to "t⁹" are abstract markers of time distance. Labels from "t⁻¹ i.b. t⁰" to "t⁻⁹ i.b. t⁸" (where "i.b." = "immediately before") indicate ordinal temporal relations. The arrows and verbal labels to the left of the squares indicate vector and connective information.

time of occurrence has not been disconfirmed: it does not die just by virtue of its historical association with a disconfirmed hypothesis. The kind of time marking proposed by Nishida and Johnston (2002) could still occur, even if their proposal does not in fact account for the evidence on perceptual asynchrony. The proposals by Herzog et al. (2016) and White (2021) are short on supporting evidence, but mainly because they have not been tested. It is still uncertain whether time markers exist in the brain but, if they do, time marking could play a fundamental role in the organisation of perceptual information, so efforts to test them could be of some importance to a full understanding of perception. This would include not just psychological research on perception but also neuroscience research: an obvious target would be identifying timing mechanisms with millisecond scale resolution in the human brain, and showing how they are functionally connected with perceptual processing.

The hypothetical time markers reviewed here exist only in perceptual processing. It is not clear at what stage or latency of processing they are attached to perceptual information. In the proposal by Nishida and Johnston (2002) this would have to happen early in processing because the time marker information is attached to local information about features such as colour and motion. These are generated within the first 100–150 ms of perceptual processing (Fei-Fei et al., 2007; Feldman, 2007; Heinen et al., 2005). That is probably a reasonable guide for any time marking proposal. Time marker information may remain attached to perceptual information for a while, at least on the sub-second scale. However, any use made of time marker information takes us beyond time markers themselves and into the realm of late perceptual or post-perceptual processing. Time markers could be the informational source of duration judgements, for example. In the proposal by Herzog et al. (2016) durations of less than the time span of one frame of conscious perception (~400 ms) are represented by time markers within frames. It is possible that such information could be read off and reported in the same way that shape or colour could be reported, with minimal loss of accuracy. In other proposals even short durations would be derived more indirectly from time markers in perception, as in the time of occurrence markers in the proposal by Nishida and Johnston (2002). Thus, even if time markers represent temporal information accurately, they do not guarantee accuracy in subsequent storage and processing of temporal information.

There has been research on the encoding and representation of time, particularly involving the hippocampus (Bellmund et al., 2019; Buzsaki and Linas, 2017; Eichenbaum, 2017; Rolls and Mills, 2019; Sugar and Moser, 2019). However the time scale that has been studied is supra-second, in some cases covering large amounts of time. For example, Tsao et al. (2018) found evidence of time cells in the hippocampus that have receptive fields for durations up to 20 s. The passage of time is encoded in the firing rates of individual cells, which decline over time until they are reset by novel environmental events. The time marking research covered in this paper all involves events on the millisecond time scale, so the existing research on timing information does not address that issue.

Most of the research discussed here has been on vision, but time marking is likely to be of equal importance in multiple sensory modalities. The time marking hypothesis proposed by Dennett and Kinsbourne (1992) was applied to somatosensation, mainly because peripheral sensors for that modality lie at different distances, and therefore different neural conduction latencies, from central processing of somatosensory information. But time marking is not just for adjusting for differences in conduction and processing latencies; it is for organising perceptual information with respect to time, for constructing a multi-sensory perceptual world in which things are orderly with respect to both space and time.

4.1. Are time markers conscious?

Some of the proposals reviewed here have referred to conscious

experience or conscious perception in connection with time markers. There are many different possible meanings of the word "conscious". Some authors have argued that something is conscious when there is some kind of further thought, cognition, or information about that thing; this is a defining feature of what are called higher order theories of consciousness (Lau and Rosenthal, 2011; Naccache, 2018; Natsoulas, 1981; Rosenthal, 2005, 2008; Seth et al., 2008). As an example, we may become aware that some expected event is late. This would be a product of some form of post-perceptual processing. Time markers are products of perceptual processing, not post-perceptual processing, so they would not be conscious in this higher order sense, even though the judgement of lateness might be based on time marker information.

Other authors have argued that products of perceptual processing are or can be conscious, and indeed there is a considerable body of research supporting the hypothesis that conscious percepts can emerge around 200 ms after the onset of the stimulus in question (Dembski et al., 2021; Förster et al., 2020; Koivisto and Revonsuo, 2010). That research, incidentally, poses problems for the proposal by Herzog et al. (2016) that conscious percepts emerge after ~400 ms of nonconscious processing. The question of whether time marker information can be conscious in this sense is not easy to resolve. We can perceive an object as located in space, and we can perceive an object as located in time, without either of those things necessarily being at the forefront of our attention. They typically form part of the general background of perceptual information. If being attentively processed is the hallmark of conscious perception, then it is likely that time marker information is not usually conscious in that sense, though of course attention may be drawn to it under some circumstances. If perceptual information can be conscious without being attentively processed, then time markers are as much conscious as any other products of perceptual processing are. Given the ongoing conflict in the literature (see, e.g., Block, 2014; Bronfman et al., 2014; Kouider et al., 2010; Mack et al., 2015), these conditional statements are as much as can be said at present. It seems to me that, when I hear a sequence of auditory tones, temporal order information is as much a part of my conscious perception of the tones as, say, their timbre, and indeed it is essential to my experience of the tones as a piece of music. I cannot experience my own actions as anything other than extended in time. But anecdotal evidence is not sufficient to establish that time markers are part of conscious perception, so more research is needed on this.

4.2. The perceived present

It was stated earlier that we seem to be perceiving the present not because we are but because products of perceptual processing have a time marker identifying them as in the present. This time marker is transitory and changes rapidly as the information is represented as increasingly far into the past. It is not, however, infinitesimally brief. The fundamental limiting factor on the temporal extent of the perceived present is temporal discrimination thresholds; that is, the ability of the perceptual system to represent nonsimultaneous things as nonsimultaneous. There is not one single threshold for judgement of non-simultaneity or temporal order. As was stated earlier, there is evidence for discrimination on the order of 2–4 ms under some conditions. That might be the minimum time span of the perceived present. But there is also evidence for much longer thresholds, even more than 100 ms in some cases (Fink et al., 2006; Matthews and Welch, 2015; Szymaszek et al., 2009). To some extent such long thresholds may be effects of the short term memory storage and post-perceptual processing required for the making of an explicit judgement in an experiment: by the time such a judgement is made, the perceptual information is well into the remembered past. But it is possible that the time span of what is perceived as present may vary locally across a range of values, and that range could extend to ~100 ms.

5. Conclusion

It is likely that there are kinds of time markers that serve specific functions in perceptual processing. For example, time marking information could help to reduce, if not eliminate, discrepancies introduced by differences in neural transmission and processing latencies. But the argument advanced here is that time marking is fundamental to perception. Just as spatial aspects of perception are a matter of various kinds of spatial information being generated in perceptual processing, so it is for temporal aspects of perception. Our perception of things as happening in time is not disorganised. It is just as organised as our perception of things in space is: the whole perceptual world is bound and integrated with temporal as well as spatial information. That information is time marking information, and it serves important functions in differentiating and connecting things and events in time.

The foregoing review has established, if nothing else, that little is known about time markers: their functions in information processing, their neurophysiological foundations, and the timing mechanisms that support them, are under-researched and almost entirely mysterious. Yet they must be of fundamental importance in perception. The world as perceived is organised, coherent, differentiated, and orderly. These are informational features and they depend on both spatial and temporal markers. Identifying where perceptual features, objects, and contexts are in space and when they are in time is the foundation of coherence and order in perceptual information. Time marking processes almost literally hold the experienced world together for us.

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References

- Adelson, E.H., Bergen, J.R., 1985. Spatiotemporal energy models for the perception of motion. *J. Opt. Soc. Am.* 2, 284–299.
- Arrighi, R., Alais, D., Burr, D., 2005. Perceived timing of first- and second-order changes in vision and hearing. *Exp. Brain Res.* 166, 445–454.
- Babkoff, H., 1975. Dichotic temporal interactions: fusion and temporal order. *Percept. Psychophys.* 18, 267–272.
- Bareš, M., Apps, R., Avanzino, L., Breska, A., D'Angelo, E., Filip, P., Gerwig, M., Ivry, R. B., Lawrenson, C.L., Louis, E.D., Lusk, N.A., Manto, M., Meck, W.H., Mitoma, H., Petter, E.A., 2019. Consensus paper: decoding the contributions of the cerebellum as a time machine. From neurons to clinical applications. *Cerebellum* 18, 266–286.
- Bartels, A., Zeki, S., 2006. The temporal order of binding visual attributes. *Vis. Res.* 46, 2280–2286.
- Bellmund, J.L.S., Deuker, L., Doeller, C.F., 2019. Mapping sequence structure in the human lateral entorhinal cortex. *eLife* 8, e45333.
- Bergson, H., 1910. *Time and Free Will: An Essay on the Immediate Data of Consciousness*. George Allen & Unwin.
- Block, N., 2014. Rich conscious perception outside focal attention. *Trends Cogn. Sci.* 18, 445–447.
- Bronfman, Z.Z., Brezis, N., Jacobson, H., Usher, M., 2014. We see more than we can report: "cost free" color phenomenality outside focal attention. *Psychol. Sci.* 25, 1394–1403.
- Brown, L.N., Sainsbury, R.S., 2002. Age- and sex-related differences in temporal judgments to visual stimuli: support for hemispheric equivalence. *Percept. Psychophys.* 64, 693–702.
- Brozzoli, C., Gentile, G., Petkova, V.I., Ehrsson, H.H., 2011. fMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *J. Neurosci.* 31, 9023–9031.
- Buonomano, D.V., Merzenich, M.M., 1995. Temporal information transformed into a spatial code by a neural network with realistic properties. *Science* 267, 1028–1030.
- Burr, D.C., Thompson, P., 2011. Motion psychophysics: 1985–2010. *Vis. Res.* 51, 1431–1456.
- Buzsáki, G., Llinas, R., 2017. Space and time in the brain. *Science* 358, 482–485.
- Churchland, P.S., 1981. On the alleged backwards referral of experiences and its relevance to the mind-body problem. *Philos. Sci.* 48, 165–181.
- Clifford, C.W.G., Ibbotson, M.R., 2003. Fundamental mechanisms of visual motion detection: models, cells and functions. *Prog. Neurobiol.* 68, 409–437.
- Clifford, C.W.G., Arnold, D.H., Pearson, J., 2003. A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation. *Vis. Res.* 43, 2245–2253.
- Colby, C.L., 1998. Action-oriented spatial reference frames in cortex. *Neuron* 20, 15–24.
- Craig, J.C., Baihua, X., 1990. Temporal order and tactile patterns. *Percept. Psychophys.* 47, 22–34.
- Dainton, B., 2008. The experience of time and change. *Philos. Compass* 3/4, 619–638.
- van de Grind, W., 2002. Physical, neural, and mental timing. *Conscious. Cogn.* 11, 241–264.
- Dembski, Koch, Pitts, 2021. Perceptual awareness negativity: a physiological correlate of sensory consciousness. *Trends Cogn. Sci.* 25, 660–670.
- Dennett, D.C., Kinsbourne, M., 1992. Time and the observer: the where and when of consciousness in the brain. *Behav. Brain Sci.* 15, 183.
- Drissi-Daoudi, L., Doerig, A., Herzog, M.H., 2019. Feature integration within discrete time windows. *Nat. Commun.* 10, 1–8.
- Eagleman, D.M., Pariyadath, V., 2009. Is subjective duration a signature of coding efficiency? *Philos. Trans. R. Soc., B: Biol. Sci.* 364, 1841–1851.
- Eichenbaum, H., 2017. On the integration of space, time, and memory. *Neuron* 95, 1007–1018.
- Elhilali, M., Ma, L., Micheyi, C., Oxenham, A.J., Shamma, S.A., 2009. Temporal coherence in the perceptual organization and cortical representation of auditory scenes. *Neuron* 61, 317–329.
- Fei-Fei, L., Iyer, A., Koch, C., Perona, P., 2007. What do we perceive in a glance of a real-world scene? *J. Vis.* 7 (10), 1–29.
- Feldman, J., 2007. Formation of visual "objects" in the early computation of spatial relations. *Percept. Psychophys.* 69, 816–827.
- Fink, M., Ulbrich, P., Churan, J., Wittmann, M., 2006. Stimulus-dependent processing of temporal order. *Behav. Process.* 71, 344–352.
- Förster, J., Koivisto, M., Revonsuo, A., 2020. ERP and MEG correlates of consciousness: the second decade. *Conscious. Cogn.* 80 (102917), 1–24.
- Fostick, L., Babkoff, H., 2013. Different response patterns between auditory spectral and spatial temporal order judgment (TOJ). *Exp. Psychol.* 60, 432–443.
- Gomes, G., 1998. The timing of conscious experience: a critical review and reinterpretation of Libet's research. *Conscious. Cogn.* 7, 559–595.
- Gorea, A., 2011. Ticks per thought or thoughts per tick? A selective review of time perception with hints on future research. *J. Physiol. - Paris* 105, 153–163.
- Grondin, S., 2010. Timing and time perception: a review of recent behavioral and neuroscience findings and theoretical directions. *Atten., Percept., Psychophys.* 72, 561–582.
- Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., Moser, E.I., 2005. Microstructure of a spatial map in the entorhinal cortex. *Nature* 436, 801–806.
- Halliday, A.M., Mingay, R., 1964. On the resolution of small time intervals and the effect of conduction delays on the judgement of simultaneity. *Q. J. Exp. Psychol.* 16, 35–46.
- Heinen, K., Jolij, J., Lamme, V.A.F., 2005. Figure-ground segregation requires two distinct periods of activity in V1: a transcranial magnetic stimulation study. *Neuroreport* 16, 1483–1487.
- Herzog, M.H., Kammer, T., Scharnowski, F., 2016. Time slices: what is the duration of a percept? *Plos Biol.* 14, e1002433.
- Herzog, M.H., Drissi-Daoudi, L., Doerig, A., 2020. All in good time: long-lasting postdictive effects reveal discrete perception. *Trends Cogn. Sci.* 24, 826–837.
- Ivry, R.B., Spencer, R.M.C., 2004. The neural representation of time. *Curr. Opin. Neurobiol.* 14, 225–232.
- Klein, S., 2002. Libet's timing of mental events: commentary on the commentaries. *Conscious. Cogn.* 11, 326–333.
- Koivisto, M., Revonsuo, A., 2010. Event-related brain potential correlates of visual awareness. *Neurosci. Biobehav. Rev.* 34, 922–934.
- Kouider, S., de Gardelle, V., Sackur, J., Dupoux, E., 2010. How rich is consciousness? The partial awareness hypothesis. *Trends Cogn. Sci.* 14, 301–307.
- Lau, H., Rosenthal, D., 2011. Empirical support for higher order theories of conscious awareness. *Trends Cogn. Sci.* 15, 365–373.
- Lewis, P.A., Miall, R.C., 2003. Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Curr. Opin. Neurobiol.* 13, 250–255.
- Libet, B., 1993. *Neurophysiology of Consciousness: Selected Papers and New Essays by Benjamin Libet*. Birkhauser, Boston.
- Libet, B., Alberts, W.W., Wright, E.W., Delattre, L.D., Levin, G., Feinstein, B., 1964. Production of threshold levels of conscious sensation by electrical stimulation of human somatosensory cortex. *J. Neurophysiol.* 27, 546–578.
- Libet, B., Alberts, W.W., Wright, E.W., Feinstein, B., 1967. Responses of human somatosensory cortex to stimuli below threshold for conscious stimulation. *Science* 158, 1597–1600.
- Libet, B., Wright, E.W., Feinstein, B., Pearl, D.K., 1979. Subjective referral of the timing for a conscious sensory experience: a functional role for the somatosensory specific projection system in man. *Brain* 102, 193–224.
- Linares, D., López-Moliner, J., 2006. Perceptual asynchrony between color and motion with a single direction change. *J. Vis.* 6, 974–981.
- Macefield, G., Gandevia, S.C., Burke, D., 1989. Conduction velocities of muscle and cutaneous afferents in the upper and lower limbs of human subjects. *Brain* 112, 1519–1532.
- Mack, A., Erol, M., Clarke, J., 2015. Iconic memory is not a case of attention-free awareness. *Conscious. Cogn.* 33, 291–299.
- Marr, D., 1982. *Vision*. San Francisco: Freeman.
- Matthews, N., Welch, L., 2015. Left visual field attentional advantage in judging simultaneity and temporal order. *J. Vis.* 15 (2), 7 (No.).
- Mauk, M.D., Buonomano, D.V., 2004. The neural basis of temporal processing. *Annu. Rev. Neurosci.* 27, 307–340.

- McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., Moser, M.-B., 2006. Path integration and the neural basis of the 'cognitive map'. *Nat. Rev. Neurosci.* 7, 663–678.
- Merchant, H., Harrington, D.L., Meck, W.H., 2013. Neural basis of the perception and estimation of time. *Annu. Rev. Neurosci.* 36, 313–336.
- Miyazaki, M., Kadota, H., Matsuzaki, K.S., Takeuchi, S., Sekiguchi, H., Aoyama, T., Kochiyama, T., 2016. Dissociating the neural correlates of tactile temporal order and simultaneity judgements. *Sci. Rep.* 6 (23323).
- Moutoussis, K., Zeki, S., 1997a. A direct demonstration of perceptual asynchrony in vision. *Proc. R. Soc. Lond. B: Biol. Sci.* 264, 393–399.
- Moutoussis, K., Zeki, S., 1997b. Functional segregation and temporal hierarchy of the visual perceptive systems. *Proc. R. Soc. Lond. B: Biol. Sci.* 64, 1407–1414.
- Naccache, L., 2018. Why and how access consciousness can account for phenomenal consciousness. *Philos. Trans. R. Soc. B* 373, 20170357.
- Natsoulas, T., 1981. Basic problems of consciousness. *Journal of Personality and Social Psychology* 41, 132–178.
- Nicholls, M.E.R., 1994. Hemispheric asymmetries for temporal resolution: a signal detection analysis of threshold and bias. *Q. J. Exp. Psychol.* 47A, 291–310.
- Nishida, S., 2011. Advancement of motion psychophysics: review 2001–2010. *J. Vis.* 11 (11), 1–53 (No.).
- Nishida, S., Johnston, A., 2002. Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Curr. Biol.* 12, 359–368.
- O'Keefe, J.O., 1976. Place units in the hippocampus of the freely moving rat. *Exp. Neurol.* 51, 78–109.
- Palva, S., Linkenkaer-Hansen, K., Näätänen, R., Palva, J.M., 2005. Early neural correlates of conscious somatosensory perception. *J. Neurosci.* 25, 5248–5258.
- Paton, J.J., Buonomano, D.V., 2018. The neural basis of timing: distributed mechanisms for diverse functions. *Neuron* 98, 687–705.
- Pockett, S., 2002. On subjective back-referral and how long it takes to become conscious of a stimulus: a reinterpretation of Libet's data. *Conscious. Cogn.* 11, 144–161.
- Pollen, D.M., 2004. Brain stimulation and conscious experience. *Conscious. Cogn.* 13, 626–645.
- Rolls, E.T., Mills, P., 2019. The generation of time in the hippocampal memory system. *Cell Rep.* 28, 1649–1658.
- Rosenthal, D.M., 2005. *Consciousness and Mind*. Clarendon Press, Oxford.
- Rosenthal, D.M., 2008. Consciousness and its function. *Neuropsychologia* 46, 829–840.
- Runeson, S., Frykholm, G., 1981. Visual perception of lifted weight. *J. Exp. Psychol.: Hum. Percept. Perform.* 7, 733–740.
- Scharnowski, F., Rüter, J., Jolij, J., Hermens, F., Kammer, T., Herzog, M.H., 2009. Long-lasting modulation of feature integration by transcranial magnetic stimulation. *J. Vis.* 9 (1), 1–10.
- Schubert, R., Blankenburg, F., Lemm, S., Villringer, A., Curio, G., 2006. Now you feel it - now you don't: ERP correlates of somatosensory awareness. *Psychophysiology* 43, 31–40.
- Serino, A., 2019. Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the sense of self. *Neurosci. Biobehav. Rev.* 99, 138–159.
- Seth, A.K., Dienes, Z., Cleeremans, A., Overgaard, M., Pessoa, L., 2008. Measuring consciousness: relating behavioural and neurophysiological approaches. *Trends in Cognitive Sciences* 12, 314–321.
- Shadlen, M.N., Movshon, J.A., 1999. Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron* 24, 67–77.
- Smart, J.J.C., 1980. Time and becoming. In: van Inwagen, P. (Ed.), *Time and Cause*. Reidel, Dordrecht, pp. 3–15.
- Sugar, J., Moser, M.-B., 2019. Episodic memory: neuronal codes for what, where, and when. *Hippocampus* 29, 1190–1205.
- Szymaszek, A., Sereda, M., Pöppel, E., Szelag, E., 2009. Individual differences in the perception of temporal order: the effect of age and cognition. *Cogn. Neuropsychol.* 26, 135–147.
- Taube, J.S., Muller, R.U., Rankin Jr., J.B., 1990. Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience* 10, 420–435.
- Tsao, A., Sugar, J., Wang, C., Knierim, J.J., Moser, M.-B., Moser, E., 2018. Integrating time from experience in the lateral entorhinal cortex. *Nature* 561, 57–75.
- Vecera, S.P., O'Reilly, R.C., 1998. Figure-ground organization and object recognition processes: an interactive account. *J. Exp. Psychol.: Hum. Percept. Perform.* 24, 441–462.
- Vroomen, J., Keetels, M., 2010. Perception of intersensory synchrony: a tutorial review. *Atten., Percept., Psychophys.* 72, 871–884.
- Wada, M., Yamamoto, S., Kitazawa, S., 2004. Effects of handedness on tactile temporal order judgment. *Neuropsychologia* 42, 1887–1895.
- Wang, P., He, S., Fan, S.L., Liu, Z.X., Chen, L., 2006. Perceptual asynchrony: motion leads colour. *Neuroreport* 17, 1159–1163.
- van Wassenhove, V., Buonomano, D.V., Shimojo, S., Shams, L., 2008. Distortions of subjective time perception within and across senses. *Plos One* 1, e1437.
- Wehrhahn, C., Rapf, D., 1992. ON- and OFF-pathways form neural substrates for motion perception: psychophysical evidence. *J. Neurosci.* 12, 2247–2250.
- Westheimer, G., McKee, S.P., 1977. Perception of temporal order in adjacent visual stimuli. *Vis. Res.* 17, 887–892.
- White, P.A., 2018. Is conscious perception a series of discrete temporal frames? *Conscious. Cogn.* 60, 98–126.
- White, P.A., 2020. The perceived present: what is it and what is it there for? *Psychon. Bull. Rev.* 27, 583–601.
- White, P.A., 2021. Perception of happening: how the brain deals with the no-history problem. *Cogn. Sci.* 45, e13068.
- Yamamoto, S., Kitazawa, S., 2001. Reversal of subjective temporal order due to arm crossing. *Nat. Neurosci.* 4, 759–765.
- Zeki, S., 2015. A massively asynchronous, parallel brain. *Philos. Trans. R. Soc.: B* 370, 20140174.
- Zimmermann, D., 2011. Presentism and the space-time manifold. In: Callender, C. (Ed.), *Oxford Handbook of Philosophy of Time*. Oxford University Press, Oxford, pp. 163–244.