A Hierarchical Model of Temporal Perception

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Ernst Pöppel
Ludwig-Maximilians-University of Munich

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A hierarchical model of temporal perception

Ernst Pöppel

Temporal perception comprises subjective phenomena such as simultaneity, successiveness, temporal order, subjective present, temporal continuity and subjective duration. These elementary temporal experiences are hierarchically related to each other. Functional system states with a duration of 30 ms are implemented by neuronal oscillations and they provide a mechanism to define successiveness. These system states are also responsible for the identification of basic events. For a sequential representation of several events time tags are allocated, resulting in an ordinal representation of such events. A mechanism of temporal integration binds successive events into perceptual units of 3 s duration. Such temporal integration, which is automatic and presemantic, is also operative in movement control and other cognitive activities. Because of the omnipresence of this integration mechanism it is used for a pragmatic definition of the subjective present. Temporal continuity is the result of a semantic connection between successive integration intervals. Subjective duration is known to depend on mental load and attentional demand, high load resulting in long time estimates. In the hierarchical model proposed, system states of 30 ms and integration intervals of 3 s, together with a memory store, provide an explanatory neuro-cognitive machinery for differential subjective duration.

E. Pöppel is at Forschungszentrum Jülich, D-52425 Jülich, Germany.

tel: +49 2461 613900
fax: +49 2461 612640
e-mail: A.Conrad@kfa-juelich.de

Temporal perception comprises phenomena, such as simultaneity, successiveness, temporal order, subjective present, anticipation, temporal continuity and duration. Are these phenomena temporal markers of events or actions related to each other or do they represent independent categories? I will argue that as elementary temporal experiences they are hierarchically connected with each other; the neuro-cognitive algorithms implementing each of them are, however, independent.

In a strict sense, 'time perception' should not occur because receptors for what we refer to as 'time' do not exist. I suggest that we obtain access to the notion of time from elementary temporal experiences, like Newton's dictum in his *Principia Mathematica*: 'absolute, true, and mathematical time, of itself and from its own nature, flows equably without relation to anything external'; that is, time is a mental construction.

The principal concepts that still guide research today were developed in the sixties of the last century[1]. In 1860 von Baer introduced the notion of a perceptual moment, suggesting that different durations of such moments result in a different flow of subjective time. In 1865 Mach looked for Weber's law in temporal perception, and he observed that 30 ms is the lower limit for subjective durations. Later, in 1868, Donders presented the reaction-time paradigm which, until today, remains the basis for chronometric analyses of mental processes. In the same year Vierordt investigated temporal integration using the paradigm of stimulus reproduction. These ideas were setting the stage for many decades but then, for reasons difficult to understand, interest declined. Only more recently has temporal perception become a central issue again[2], because cognitive processes cannot be understood without their temporal dynamics; furthermore, certain logistical problems the brain has to deal with require an understanding of temporal processing.

Temporal challenges in sensorimotor coordination

Stimulus transduction in the sensory modalities is characterized by qualitatively different mechanisms[3]. Because of

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the different time courses of transduction, central availability of sense data from different channels can vary significantly. If an object is defined by optic and acoustic information, intermodal integration has to overcome the problem of an earlier auditory than visual availability, because transduction in the auditory system is shorter than in the visual system. If the object moves away from the observer, the longer transduction time in the visual system is, however, compensated for by the time the sound takes to travel from its source. Under photopic adaptation conditions, a 'horizon of simultaneity'[4] is reached at ~12 m distance, when signals in the two sensory modalities become available simultaneously. Because objects move (and obviously do not carry time tags), for one object to be defined the neuro-cognitive machinery has to overcome temporal indeterminacy by appropriate organizational measures[5].

Another organizational problem is due to the mode of functional representation. Segregation of function, as demonstrated anatomically[6], and distributed spatial representation of function, as shown paradigmatically for pain perception by modern imaging technology[7], or as implied by theoretical considerations[8], require integrative mechanisms that supersede local activities and allow the neuro-cognitive system to overcome temporal indeterminacies[9,10].

At least two independent processing systems are characterized by discrete time sampling[11,12]. Both are fundamental for the instantiation of perceptual acts, cognitive processing or volitional movement control. Firstly, I will discuss a high-frequency processing system that generates discrete time quanta of 30 ms duration; this system provides a basis to overcome the two organizational problems mentioned above. I will then consider a low-frequency processing system that sets up functional states of 3 s and is believed to be the operative basis for what we refer to as 'subjective present'[4,12]. These two processing systems also provide the essential elements for duration estimation. The numerical values of 30 ms or 3 s indicate operating ranges and should not be misunderstood as physical time constants.

Obviously, there are a number of perceptual phenomena which are characterized by other time constants than these two operating levels, for instance, as is seen in experiments on masking or on adaptation at the receptor level. The two operating levels being advocated here (30 ms and 3 s) are, however, characterized by their generality. In each case, completely different experimental paradigms disclose operating characteristics in the same time domain. Each single experiment may be too weak to draw a general conclusion on temporal processing, but taking all the experimental evidence together it is difficult to avoid the hypothesis that the neuro-cognitive machinery is controlled by two temporal processing systems in different time domains.

Temporal system states as implemented by oscillations

Evidence for a high-frequency processing system comes, in part, from studies on temporal order thresholds[13,14]. If the temporal order of two stimuli has to be indicated, independent of sensory modality, a threshold of 30 ms is observed. Data picked up within 30 ms are treated as co-temporal, that is, a relationship between separate stimuli with respect to the before-after dimension cannot be established. This does not mean that the central nervous system cannot process information for shorter intervals than 30 ms (the localization of objects in auditory space requires a higher temporal resolution)[15], however, distinct events require a minimum of 30 ms to be perceived as successive.

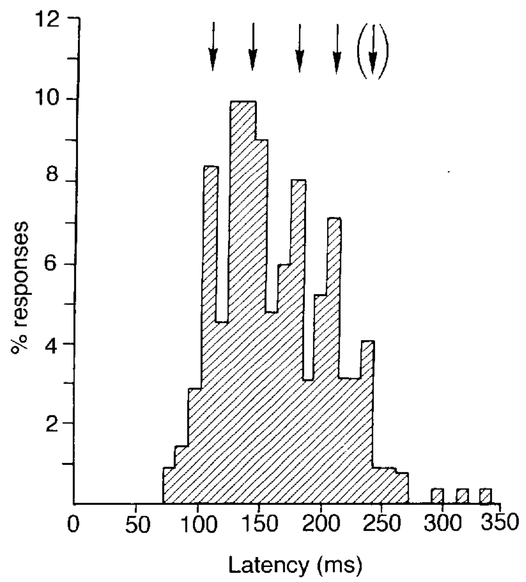

Fig. 1 Histogram on the basis of 463 latencies of pursuit eye movements in three subjects. Temporal resolution for latency measurements was 3 ms; data are summarized in 10 ms bins. Arrows indicate the temporal position of modes that are separated by 30 to 40 ms. Note that even the raw data of the three different subjects being summarized here result in a multimodal response distribution indicating an interindividual stability of an underlying temporal mechanism of information processing. Data from Ref. 18.

Thus, temporal order thresholds in the different sensory modalities also indicate a lower limit for event identification. In stating such a temporal limit, it is not implied that each system state of 30 ms needs to carry an event to become consciously available; the temporal continuity of stimulus availability resulting in constant neuronal activity (neuronal 'hysteresis effect') may lead to a linkage of successive system states implementing longer intervals for event identification.

Support for distinct system states comes from a variety of studies using different paradigms[1,4,12]. Under stationary conditions response distributions of reaction time[16,17], or pursuit eye movements[18] show multimodal characteristics with a 30 ms separation of distinct response modes (Fig. 1). These multimodalities can be explained on the basis of neuronal oscillations[16]. After the transduction of a stimulus, an oscillation with a period of 30 ms is initiated that is phase-locked to the stimulus. Such an oscillatory mechanism, being under environmental stimulus control, allows integration of information from different sensory modalities, that is, data from various sources can be collected within one period, which defines a basic system state[5]. The separate response modes possibly represent similar successive and discrete decision-making stages, as are assumed in the high-speed scanning of short-term memory[19].

Some neurophysiological observations support the notion of discrete temporal processing on the basis of system states implemented by oscillations. The auditory evoked

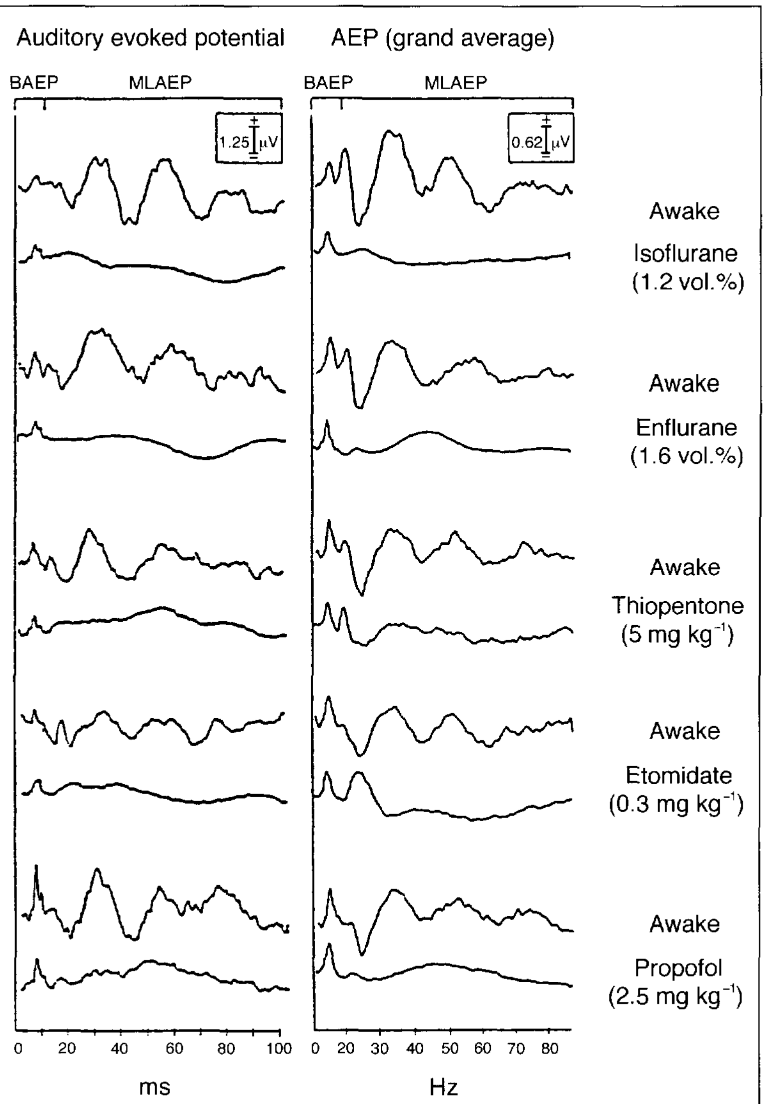

Fig. 2 Auditory evoked potentials. Left, original tracings of five individual subjects; right, interindividual grand averages of ten patients during wakefulness and under general anaesthesia with the nonspecific anaesthetics isoflurane, enflurane, thiopentone, etomidate and propofol. During wakefulness an oscillatory 30- to 40-Hz component is present in the midlatency range. Under general anaesthesia (bottom part of each trace) the brainstem-generated potentials are nearly unchanged, whereas the oscillatory components in the midlatency region are suppressed. Data from Ref. 22.

potential in the midlatency region shows an oscillatory component with a period of 30 ms (Ref. 20). This component is a sensitive marker for the anaesthetic state because it selectively disappears during general anaesthesia[21]. Oscillations with a period of 30 ms represent functional system states that are apparently necessary prerequisites for the establishment of events[22] (Fig. 2). If temporal coherence within a neuronal network, as expressed by oscillations, is removed (for example, with the administration of a general anaesthetic) I should like to propose that conscious representation would be interrupted. This hypothesis is partly based on the observation that, after such anaesthetic states, patients usually report that no time at all has elapsed (contrary to sleep); events as functional 'building blocks' of conscious activity appear not to be implemented. When oscillatory activity is still present, as in the case of receptor-specific anaesthetics (for example, fentanyl or ketamine), information processing is not completely interrupted: implicit memory is still functional[22].

Neuropsychological observations on time tags and temporal retardation

The above considerations refer to minimal temporal requirements, as expressed by system states, and how they relate to event identification. If several events have to be brought into an explicit sequence a further neuro-cognitive mechanism has to be envisaged which labels successive events with time tags. Successiveness of two or more events is necessary, but not sufficient, to allow a cognitive representation of a string of events such that each one can be characterized by an ordinal number defining its position in a sequence. Observations on patients with certain brain diseases (for example, Korsakoff syndrome), suggest that time tags of events might be lost selectively[1], indicating a specific mechanism that sets up temporal ordinality.

The importance of the integrity of temporal system states for cognitive processing is stressed by other neuropsychological studies. Patients with acquired aphasia show prolonged temporal-order thresholds[14]: sometimes values of more than 100 ms are observed. This means that successive speech sounds enter one system state with the consequence that their sequence no longer can be decoded. Applying a specific training with such patients, temporal order threshold could be normalized again with a positive transfer to speech processing: such patients were significantly improved and could discriminate certain phonemes[23]. Recently, similar observations (a slowing down of temporal processing and an improvement after training) has also been demonstrated with dyslexic children[24,25]. Because speech is particularly sensitive to temporal disruptions, as demonstrated in word deafness[26] or dyslexia in adults[27], a 'temporal therapy' in these and other cases represents a new challenge[23].

Perceptual units as a consequence of temporal integration

Independently of this high-frequency mechanism implementing system states for event identification, a low-frequency mechanism binds successive events of up to 3 s into perceptual units. Support for such a binding operation comes from studies on the temporal reproduction of stimuli with different duration[1,28,29]. Whereas stimuli are reproduced almost veridically up to 3 s (although a slightly longer reproduction is probably due to the reaction time component), longer stimuli are reproduced significantly shorter (Fig. 3) and with much greater variability. Intervals of up to 3 s can be mentally preserved, or grasped as a unit, suggesting a specific integration mechanism; this led Fraisse[30] to suggest that time perception works for such short intervals but that 'time estimation' is used for longer intervals.

By studying brain injured patients, it has been found that frontal brain structures are involved in temporal integration[14]. Patients with lesions in the left frontal lobe show shorter temporal integration while those with right frontal lesions show longer temporal integration. On the basis of interhemispheric inhibitory connections, these observations suggest a push–pull mechanism between homologous frontal regions; a tendency towards temporal dilation is controlled by contralateral temporal compression and vice versa. This reciprocal control leads to a long-term stabilization of temporal integration implementing regular, successive intervals.

Spontaneous alteration rates of ambiguous figures support the notion of temporal integration. If stimuli can be perceived with two perspectives (for example, the Necker cube, Fig. 4), there is an automatic shift of perceptual content after 3 s (Refs 4,12,14). Such a perceptual shift also occurs when interpreting ambiguous auditory material, such as the phoneme sequence CU–BA–CU, where one hears either CUBA or BACU. The spontaneous alteration rate in the two modalities suggests that after an exhaust period of 3 s attentional mechanisms are elicited that open sensory channels for new information; if the physical stimulus remains the same, the alternative interpretation of the stimulus will gain control. Metaphorically, every 3 s, the brain asks: 'what is new?', and with unusual stimuli, such as ambiguous material, the temporal eigen-operations of the brain are unmasked.

A study in which the amplitude of the mismatch negativity as a function of interstimulus interval has been investigated[31] supports the above considerations. The mismatch negativity, a component of the auditory event-related potential, is elicited by a physically deviant stimulus (such as frequency, intensity or duration) in a homogeneous stimulus sequence[32] and it may reflect a neuronal mechanism specific to the auditory system. If during the experiment the interstimulus interval is systematically altered, the largest amplitude of the mismatch negativity is observed with interstimulus intervals of 3 s. As negativity indicates increased neuronal activity, the results suggest that the auditory channel is characterized by a higher activity in regular temporal intervals. This modulation of neuronal activity is endogenously determined, being a property of the neuro-cognitive machinery itself, and it implies that every 3 s the sensory channel is more sensitive than at other times for new information coming from the external or internal environment.

A pragmatic definition of the subjective present

Temporal integration for intervals of up to 3 s has been seen with a number of other paradigms such as the temporal segmentation of spontaneous speech[33], the subjective structuring of a continuous string of auditory stimuli[34] and a classical experiment on short-term memory[35]; if rehearsal is not possible, the content in working memory is available for ~3 s only.

Temporal integration up to 3 s is also observed in sensorimotor behaviour. If a subject is requested to synchronize a regular sequence of auditory stimuli with finger taps, stimuli are anticipated by some tens of milliseconds[36,37]. Stimulus anticipation with high temporal precision is, however, possible only up to interstimulus intervals of 3 s (Fig. 5). If the next stimulus lies too far in the future (more than 3 s), it is not possible to programme an anticipatory movement that is precisely related to the stimulus. In such cases movements become temporally irregular.

Complementary observations on the duration of intentional movements in subjects from different cultures resulted in similar values[38]. One is led to conclude that a universal time constant of 3 s dominates those movements in humans that are under volitional control. Recently, it has been demonstrated that specific movement patterns in different mammalian species also last an average of 3 s (Ref. 39).

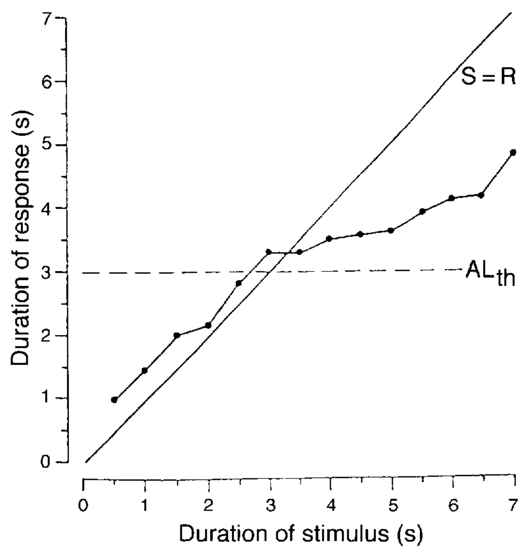

Fig. 3 Example for the reproduction of temporal stimuli between 0.5 and 7.0 s duration from one subject. Stimuli (14 different stimulus durations, each one being presented five times) were given in random order. A continuous light was used as stimulus. At S = R, stimulus duration equals reproduction. AL_{th} is the geometric mean of all stimulus durations. Note that for stimuli longer than 3.0 s temporal reproductions remain short. Data from Ref. 28.

This observation suggests a universal temporal mechanism transcending human behaviour. Movement patterns of higher mammals, including humans, are apparently controlled by homologous neuronal mechanisms that automatically bind successive activities within 3 s segments.

As the experiments referred to above employ qualitatively different paradigms covering perceptual processes, cognitive evaluations or movement control, I should like to propose that temporal integration up to 3 s is a general principle of the neuro-cognitive machinery. This integration is automatic and presemantic: the temporal limit is not determined by

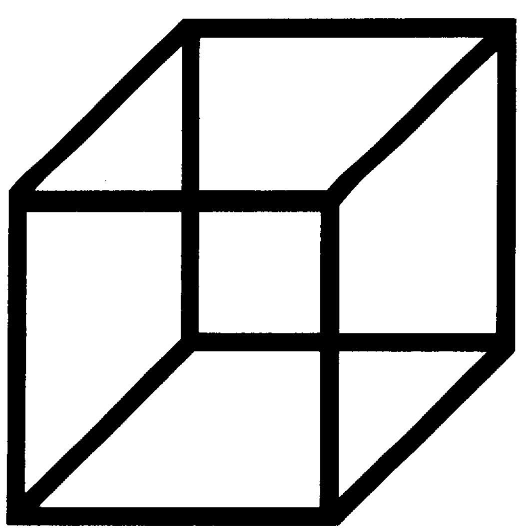

Fig. 4 The Necker cube. If subjects are able to perceive the two perspectives of the Necker cube, there is an automatic shift between the two perspectives in regular intervals of ~3 s duration. In patients with left or right prefrontal lesions, the reversal rate is slowed down significantly. Data from Ref. 14.

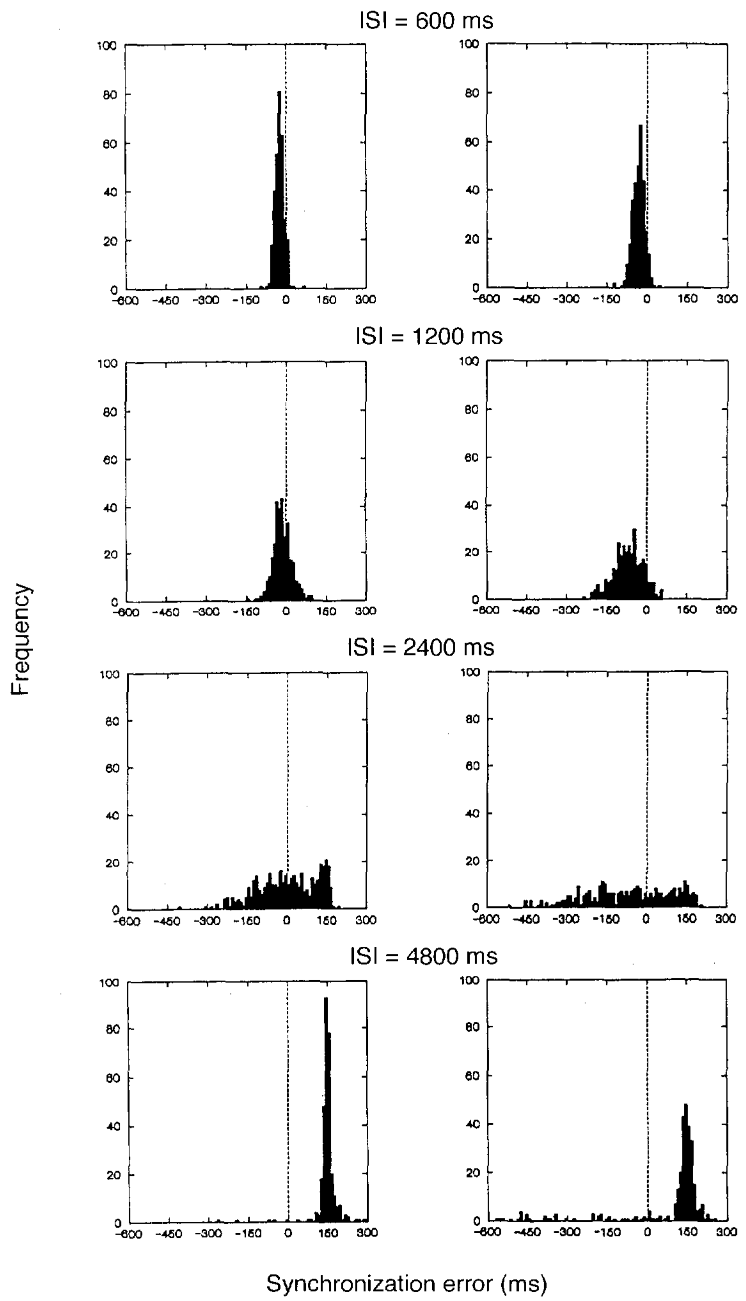

Fig. 5 Examples of synchronization error distributions in two different subjects for four interstimulus intervals (ISIs). Note the behavioural anticipation of stimuli in this task of sensorimotor synchronization for 600 and 1200 ms ISIs, the response to the stimuli for an ISI of 4800 ms and a transition zone for ISI of 2400 ms. Data from Ref. 36.

what is processed, but by intrinsic time constants. Because of the omnipresence of temporal integration, it can be used for a pragmatic definition of the subjective present, which is characterized phenomenally by a feeling of 'nowness', or one can relate temporal integration to singular 'states of being conscious'[4,12].

Temporal continuity and the paradox of subjective duration

If each subjective present marks an isolated temporal segment, the question of how can we experience temporal continuity and duration arises. Integration intervals of 3 s reflect formal aspects of the neuro-cognitive machinery. They represent a logistical background for content representation[8]. As mental content is independent of temporal integration, and cognitive requirements with respect to what may be of subjective importance usually outlast temporal segments of a few seconds, continuity is assumed to be the consequence of a semantic connection of what is represented within each subjective present. Thus, temporal continuity is based on mental content and its ongoing representation within the neuro-cognitive machinery masking the discontinuity of the 3 s segments. Temporal discontinuity, however, results from changes in mental content when attention is focused on new perceptual material, either because of the stimulus situation or because of endogenous demands.

Temporal continuity is one aspect of subjective duration. An established fact on temporal perception is that subjective duration is dependent on mental load and on the amount of attention allocated to the passage of time[40]. However, this mechanism applies only to intervals that last up to several minutes. Estimation of longer time spans, such as hours, is related to temporal control by the circadian oscillator[41], and is possibly independent of cognitive factors. For short-term estimation of time, the two integration mechanisms discussed above provide a useful basis. Depending upon attentional or environmental demands, an interval of 3 s will be differentially filled by events: sometimes many system states will be allocated for event identification, at other times sparse representation may be the case. If one assumes a memory store, successive integration intervals of 3 s may be differentially loaded. In retrospective evaluation, a memory store with a high mental load will result in a longer duration than a store with a lower mental load. This mechanism for differential duration estimation does not require conventional time units (such as seconds) because the neuro-cognitive machinery with its two processing levels and a memory store is sufficient for dealing with subjective duration.

However, this mechanism works only for a retrospective estimation of time duration: paradoxically, the experience of time passing shows the opposite characteristics. When only small amounts of information are processed (that is, when only a few events are defined within an integration interval), time appears to pass slowly whereas, if a lot happens, time appears to pass quickly. The paradox of subjective duration is the consequence of different cognitive processes in the retrospective appreciation of an experience and in the experience itself. A low mental load draws attention directly to the flow of time, resulting in the impression of its reduced pace. During times of high mental load, attentional demands are different and time, as an experiential variable, does not exist. In such a situation time passes unnoticed, resulting in the paradoxical impression that time is flying.

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Outstanding questions

- Is the transition from the perception of simultaneity to nonsimultaneity of stimuli determined by the time constants of transduction in the different sensory systems?
- Is there a relationship between system states with a duration of ~30 ms which are implemented by stimulus-triggered oscillations and binding operations that are presumably mediated by stimulus-induced neuronal oscillations?
- How stable are system states of 30 ms duration and integration intervals of 3 s? Are these temporal mechanisms dependent on age, gender, fatigue or attentional demands?
- Is it conceivable that temporal processing within the brain's neurocognitive machinery is affected by cognitive content: is there a referential loop from semantics to syntax?
- Are neuronal oscillations that are implementing system states and temporal integration which results in isolated segments of ~3 s perceptual units necessary mechanisms for consciousness?
- What is the relationship between physical time, as discussed in classical physics or quantum mechanics, and subjective time, as discussed in the cognitive and neuro-sciences?

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CORRIGENDUM

In the **Opinion** article by Jacques Vauclair in the April issue of *TICS* (Vol. 1, pp. 35–39) the legend to Fig. 1 was incorrect. The correct version is printed below. We apologise to the author and to the readers for this error.

Fig. 1. A possible example of 'second-order' intentionality in baboons. A young baboon (A) looks at a female (T) while she eats rhizomes that A is looking for. Suddenly, A screams loudly, thus attracting his mother's attention: the mother (Tool) chases T away and the young baboon has free access to the food. The interpretation of the young baboon's behaviour (who had previously enacted this sequence with other individuals) would be that *he made his mother believe* that the female, T, had been aggressive to him, thus leading his mother to intervene and enable him to reach for the desired food. (Drawn by B.L. Deputte; adapted from Ref. 45.)