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REVIEWS

Biology and Phenomenology of Temporal Encoding: A Review of Studies and Models

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Abstract—Encoding of temporal information (also termed time or temporal encoding in the literature) is a key function of biological systems underlying perception, learning, decision-making, and behavior synchronization. Despite a large amount of empirical research data and many theoretical models, a unified concept of temporal encoding has not yet been formulated. This paper overviews research works devoted to time encoding in living organisms. It examines current views on the neural correlates of time encoding. The evolution of approaches and models is traced from classical scalar timing models to more complex network, population, and Bayesian concepts. The main trends and paradigm shifts in modeling time memorization and prediction are highlighted. The key properties of time encoding observed in most vertebrate species are indicated. The first fundamental phenomenological models—the *internal clock model* and the *Scalar Expectancy Theory* (SET)—are described in detail. Their significance for control theory, artificial intelligence, and robotics is substantiated.

Keywords: temporal encoding, memorization of time intervals, rhythmic activity, internal clock, timing models

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1. INTRODUCTION

The problem of temporal encoding is fundamental in neuroscience, psychology, and mathematical modeling of behavior. For control theoreticians, the problem of encoding time intervals is primarily related to robotics (in general) and biologically inspired technologies (in particular). Time is a universal parameter that determines processes such as motor planning, learning, synchronization, rhythm and speech perception, and event prediction. The precise neural mechanisms used by biological systems to represent, memorize, and reproduce time intervals are still the subject of intensive research. There exists no unified theory due to the multiplicity of time scales, differences between sensory and motor tasks, and limitations of experimental methods.

Numerous studies aim to understand the brain's operation of temporal information, the degree of (local or global) distribution of time perception and memorization mechanisms, and investigate the properties of neural network dynamics involved in these mechanisms. This review is mainly intended to systematize approaches to modeling the memorization and reproduction of time intervals. We trace the evolution of ideas regarding the perception and memorization of time by living organisms and, accordingly, the evolution of models for encoding time intervals. The existing approaches are classified, key conceptual directions are identified, and current trends in the development of theoretical models are revealed. Special attention is paid to the first internal clock models that emerged in the 1960s and became firmly established as fundamental concepts of timing, guiding further research for several decades. Since then, experimental scientists have obtained a huge amount of new data, leading to several hypotheses and more complex models. The internal clock model and the Scalar Expectancy Theory (SET) have been much criticized. However, they remain the most influential theories of memorization and reproduction of time intervals and deserve close attention, even despite the variety of new approaches and methods; see below.

The practical significance of internal clock models is due to their application in neurointerfaces, robotics, adaptive control systems, and neuropsychological diagnostic tools. Particularly in robotics, temporal encoding is necessary for organizing sequential actions, synchronizing with external events, processing rhythmic signals, and predicting operation durations. Biologically inspired models of time can lead to more flexible and adaptive behavior of artificial agents in dynamically changing environments.

Some research into temporal encoding up to 2020 was reviewed in [1]. The paper described the main internal clock models used by the authors to search for correlates in brain activity patterns. The local and global encoding of duration was considered (at the levels of individual cells and interaction between brain areas, respectively). The degree of matching between experimental data and the models was analyzed; according to the authors' conclusion, the matching is still insufficient. The above review will be repeatedly mentioned below. From a psychological perspective, cognitive theories of time perception were surveyed in [2]. Unfortunately, this is one of the few Russian-language papers devoted to temporal encoding. Note also that it contains no references to relevant studies by Russian scholars. A more thorough search has revealed one more Russian-language publication on a similar topic, devoted to the psychophysiological assessment of the sense of time in football referees [3]. This lacuna in research makes our review even more topical, as it will help the Russian scientific community to form an idea of this fairly extensive field of knowledge and models.

The remainder of this paper is organized as follows. Section 2 is devoted to a brief description of neurobiological research in the field of temporal encoding. We present a small part of experimental works related to the search for correlates of temporal encoding in the brain and in nervous systems in general [4–24] and show the complexity and degree of distribution of the system responsible for temporal encoding. Section 3 discusses in detail the two early phenomenological models, namely, the *internal clock model* by Treisman [25–28] and the *Scalar Expectancy Theory* by Gibbon and Church [29–37]; in addition, the methodological principles for constructing models of temporal encoding are outlined, and the relevance of scalar models at the present time is justified. In Section 4, we continue the historical review, providing the further periodization of research associated with the emergence of new technologies and new discoveries in the neurobiology of time. The transition from local mechanistic models to dynamic network models and distributed systems [38–46] is traced. For current trends, the main directions of development are identified and briefly described as follows: the discovery of time cells in the hippocampus [7–9], the transition to population models [47–49], Bayesian approaches to time perception [50–53], the models linking timing with decision processes [54, 55], and some studies of the influence of neurochemistry on the encoding and memorization of time intervals [56–61]. The presentation in Section 4 is rather abstract: this paper mainly aims to provide a broad, albeit inevitably less detailed, overview of modern research and timing models, as well as to show that the latest data confirm the key properties of time perception in animals and humans formulated in the first phenomenological models. In the Conclusions, we summarize the review's outcomes and discuss the advantages of phenomenological models as applied to control theory, including some ways to improve them.

2. SEARCH FOR THE NEUROBIOLOGICAL CORRELATES OF TIME

In neuroscience, as in other experimental disciplines, the validity and accuracy of models directly depend on the quality of empirical data and the correctness of their interpretation. In contrast to the exact sciences, biological systems are characterized by a high degree of variability and multifactorial causality of phenomena observed. Experimental data in neuroscience inevitably contain a significant noise component due to methodological constraints and the complexity and heterogeneity of biological objects. Moreover, the same effects can be obtained by activating different structures, and the study of distributed mechanisms is accompanied by the danger of data incompleteness. The multiplicity of possible interpretations and the probability of erroneous conclusions create fundamental difficulties for testing hypotheses, constructing theories, and building models.

This section outlines directions of neurobiological research, not so much to immerse the reader in this field deeply, but rather to "map" time processing in the brain schematically and illustrate the challenges faced by scholars when modeling timing and related processes.

The neurobiological correlates of temporal encoding are found in different parts of the vertebrate brain and the nervous system as a whole in simpler organisms. Temporal encoding is studied in different species of living organisms, from crickets [4] to humans [5]. Localizing and detecting brain areas involved in time processing in vertebrates is a complex task partially solved by many researchers, but a complete picture has not yet been obtained. The mechanisms of *sensorimotor control* in humans and non-human primates and their connection with time processing were examined in [6]. As emphasized therein, neural dynamics in sensorimotor areas are involved in timing based on rhythms generated. Encoding time and temporal sequences of events in the *hippocampus* was investigated in [7–11]. As claimed in [12, 13], neurons in the *entorhinal cortex* are responsible for accurate time perception. The neurons responsible for different stages of timing behavior in the *prefrontal* and *anterior cingulate cortex* were identified in [14]. The studies and modeling of temporal encoding by *cerebellar* neurons were presented in [5, 15–20]. Based on experimental functional magnetic resonance imaging (fMRI) data, a model of time processing in the human *visual cortex* was constructed in [21]. Even this list of references makes it evident how complex the processing of durations and sequences of time intervals by nervous systems is. As a result, research is shifting toward *distributed systems* [22, 23]. In opposition to the above studies, Robbe places the function of time perception in humans outside the brain [24].

However, one should keep in mind that not only vertebrates but also simpler species have the ability to estimate time. Referring to [42, 56], the authors of [1] suggested that ancient evolutionary mechanisms are responsible for timing. Most species, from insects to primates, process temporal information as if they were using a stopwatch; this indicates the existence of an internal clock function preserved throughout evolution.

Nevertheless, despite the cross-species similarity of time processing and evolutionary continuity, researchers currently have no doubt that temporal encoding in the mammalian brain is extremely complex. It is distributed across different brain areas that generate coordinated activity patterns. Different durations may be handled by different brain areas, and the areas responsible for perception, planning, and decision-making are closely interconnected.

3. THE PRECLINICAL PERIOD OF TIME PERCEPTION RESEARCH. PHENOMENOLOGICAL MODELS

The neural correlates of timing is a young research area associated with the emergence of technical capabilities for the precise detection of neural activity. However, the study and modeling of temporal encoding have been ongoing for over 60 years. The chronology of models and methods can be conditionally divided into several periods with a common theme. Of course, the boundaries of these periods are blurred and have many intersections, but certain milestones can be identified to mark new research directions. The main interest for our review is the earliest, so-called *preclinical period*, when the main properties of subjective time estimation in humans and animals were discovered. They continue to find new confirmations in the modern era.

The preclinical period began with Treisman's paper [25], published in 1963. His internal clock model was generalized to the *Scalar Expectancy Theory* by Gibbon and Church. The two models transferred the study of time perception from a descriptive field into an exact science with predictive power. They showed that even such a subjective phenomenon as the sense of time obeys strict mathematical laws and can be modeled quantitatively. With all their simplicity, the models reproduce the basic properties of perception and memorization of time intervals inherent in both animals and humans.

3.1. Treisman's Internal Clock Model

The term "internal clock" was introduced, and the model itself was proposed, by Treisman in the two-part paper [25]. The first part described seven series of experiments with humans on memorizing intervals of various durations. The experimental design varied from series to series. The second part was devoted to the description of the model, developed in an attempt to explain and connect the psychophysical data.

The experiments revealed fundamental and stable patterns of human time memorization errors. First, humans demonstrate a predictable bias in duration estimation: short intervals are systematically overestimated, and long intervals are underestimated (the so-called Vierordt's law, see the discussion below). Second, the variance of estimates increases with increasing duration (Weber's law). Third, as the series of trials continues, all time estimates and reproductions have a bias to longer durations (the lengthening effect), and this bias becomes more pronounced for shorter original intervals. These errors manifest regardless of the method (reproduction, production, comparison, or verbal estimation), indicating deeply ingrained mechanisms of internal timing. Additional experimental conditions (changes in stimulus intensity, motor response format) can enhance or modify these patterns, but do not eliminate them.

The author's goal was to construct a minimal model, i.e., to find a minimum set of components and links between them necessary for the perception, memorization, and estimation of time intervals. The resulting mechanism must be capable of partial error correction: a deviation or limitation at one point in the system must be compensated by adaptation in others, ensuring overall stability. In addition, it must reproduce the systematic errors characteristic of human perception. Considering the fundamental limitations and features underlying typical human errors in time memorization and estimation allows constructing practical models both for explaining experiments and for engineering applications.

The internal clock model includes the following main components and operating principles:

- a *pacemaker*, a generator that produces a series of equal-duration pulses propagating along a certain path;
- a *counter*, an accumulator that sums the number of pulses in a given time interval and transfers this value to the store;
- a *store*, a memory block to write or retrieve the counting results for further comparison;
- a *comparator*, a decision mechanism that retrieves data from the store and compares them with the current counter results to determine the counting stop moment or to select an appropriate response;
- a *verbal selective mechanism*, a block that facilitates the retrieval of information from the store by referring to symbolic labels (e.g., "1 second," "2 minutes");
- a *specific arousal center*, a regulator that acts on the pacemaker to change its frequency, thereby regulating pulse generation.

In subsequent reviews, this model is often reduced to a four-component one (*pacemaker—counter—store—comparator*) and sometimes even to a three-component one (*pacemaker—counter—store*); for example, see [1]. The last two blocks are usually eliminated; in the three-

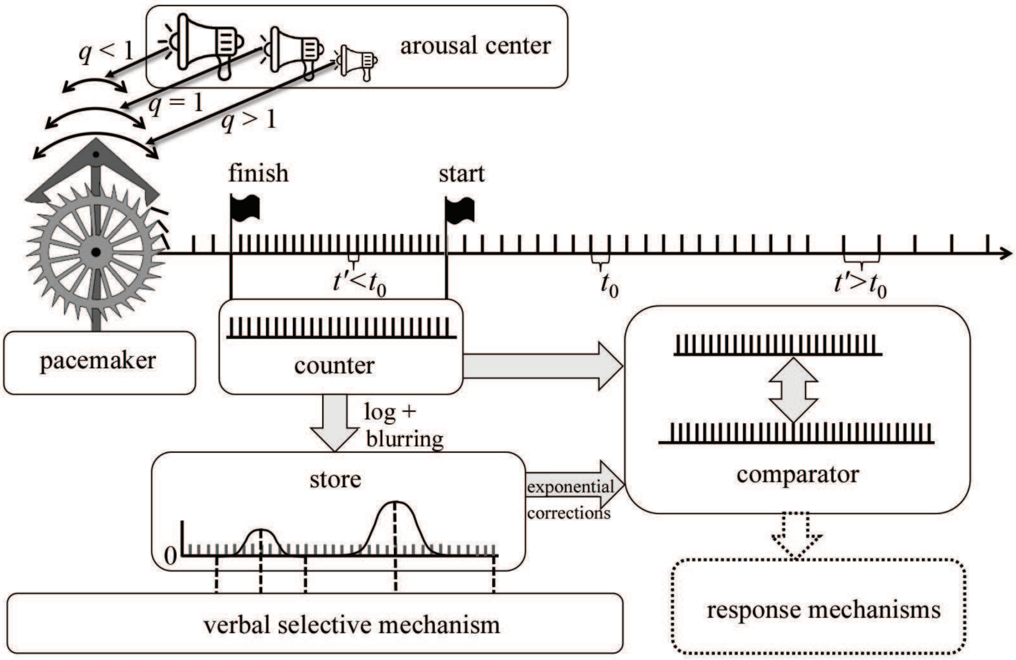

Fig. 1. Treisman's internal clock model. The figure reflects the model scheme and its textual description in [25].

component model, the comparison mechanism is transferred from the structural part to the functional one. The removal of the verbal mechanism from subsequent schemes is natural: the internal clock model turned out to be applicable not only to humans but also to many animal species. The frequency modulator is apparently considered secondary to the basic blocks of the model. However, in this section, the model is described in its original form; see the structure in Fig. 1.

The model's operation is described by eight postulates.

1. The *pacemaker* generates sequential pulses moving along a certain path (Fig. 1) at a constant speed. The basic interval between sequential pulses is t_0 with variance σ_t^2. Treisman wrote that his predecessors drew a parallel between such a mechanism and the action of a pacemaker neuron propagating an action potential along an axon. The same principle is used in this model, albeit without direct analogies with neural mechanisms.

2. The pacemaker's activity is regulated by a *specific arousal center*, which influences the rate of pulse generation. A definite level of specific arousal sets an average interval t' between pulses, which is calculated as $t' = qt_0$ with $q > 1$ and $q < 1$ for low and high arousal levels, respectively. The specific arousal level may depend on features of the experimental procedure, significant aspects of the situation, or other factors; under stable conditions (e.g., during presentation of a time interval), it usually remains constant or changes very slowly. Therefore, within a single trial, variations in t' are minimal, but its value may change from trial to trial.

3. The counter can operate in two modes: for writing to the store or for comparing the store with the current count. The interval durations in these modes are calculated by different formulas. This dual approach is necessary to minimize transformation errors (see below).

4. The measured interval is recorded in the *store* and retrieved from it by the comparator. The memory is a one-dimensional array of cells or addresses starting at a *zero point.* The model uses a logarithmic scale, so the best analogy for the memory block is a slide rule. Each cell corresponds to a certain number of pulses. If the counter detects n pulses, this measure will be read into a

cell at a distance of $\log n$ from the zero point. Activation spreads to neighboring cells, forming a distribution with a peak at $\log n$.

5. The *verbal selective mechanism* is an analog of long-term memory. It is intended to store symbolic time labels associated with certain points in the store ("two seconds," "one minute"). If the connection between the label and real experience is misaligned, the association will be corrected.

6. Retrieving a value (measure) from the store, the comparator transforms it back to a linear scale, thereby leveling possible errors. If the comparator has a systematic bias to the zero point, $\log n$ will be transformed to $\log n + \log m$, where $\log m$ is the bias value. After exponential transformation, a possible error constant r is added. The complete transformation is as follows:

$$RM = \exp(\log n + \log m) + r = nm + r,$$

where RM is the retrieved measure.

This measure is compared by the comparator with the current counter value to make a decision (e.g., when to stop or which response to choose). Different modifications of the formula for RM are given for different experiments.

7. The model provides feedback for the dynamic adjustment of memory parameters (logarithmic bias) based on the frequency of a particular response or on the total degree of store activation, thereby ensuring automatic error compensation and adaptation to experimental conditions.

8. Activation of any area in the store shifts $\log m$ toward the optimal value for the corresponding interval; thus, the value of $\log m$ at any moment will partially depend on the average effect of all areas active at this moment.

The value of Treisman's model lies not in the particular formulas but in the fundamental blocks, their structure and interrelation, as well as in the introduction of principles and parameters correcting errors and, conversely, adding systematic biases. These principles include the logarithmic storage of an interval with the correction term $\log m$, the arousal and inhibition effect of the pacemaker (the term q), and the additive correction r. The values of these corrections can be varied considerably without significantly affecting many predictions derived from the model's basic assumptions.

Treisman's model explains and generalizes a number of known psychophysiological phenomena, such as Weber's law for time intervals, the indifference interval, Vierordt's law, the crawling lengthening effect (the tendency for reproduced intervals to increase gradually during an experimental session), and other experimental effects observed in the studies of subjective time perception.

Let us dwell on several phenomena that have proven universal for many animal species, not only humans.

Timing obeys Weber's law. According to this empirical psychophysiological law [62], the minimum increase in a stimulus that will produce a detectable increase in sensation is proportional to the existing stimulus.

Treisman used the *Weber function*, i.e., a linear generalization of the original Weber's law [62] that better approximates the *difference threshold for time intervals*:

$$\Delta T = k(T + a),$$

where k and a are multiplicative and additive parameters, respectively. They take different values for different experiments. Due to this formula, the longer the time interval is, the greater variance its estimate will have. But the coefficient of variation remains approximately constant.

Timing obeys Vierordt's law. Vierordt's law [63] is a psychological phenomenon in the field of time perception, stating that humans systematically overestimate short time intervals and underestimate long ones. The law was established by German physiologist Vierordt in the mid-19th

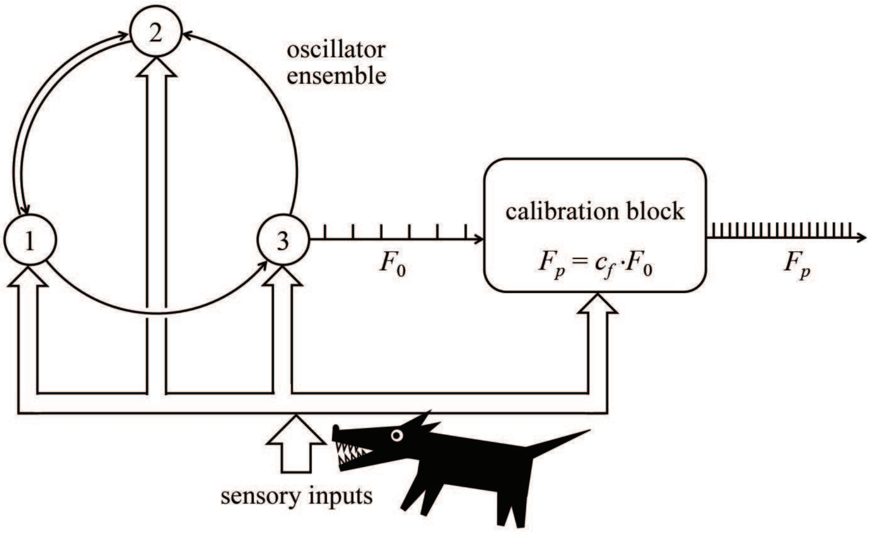

Fig. 2. The temporal pacemaker model consisting of two components: an oscillator and a calibration block. The scheme corresponds to the model from [27]; the sensory input, indicating “danger” and accelerating the rhythm, was added by the author.

century through experiments with stimuli of different durations. It explains one of the persistent errors observed in subjective time estimation and is often observed in a wide variety of experiments on time psychology.

If short intervals are overestimated and long ones underestimated, there must exist a boundary value that can be estimated accurately by a human. This value was called the *indifference interval.* During his experiments, Treisman tried to find it. The indifference interval varied across series; moreover, it grew due to the lengthening effect of reproduced intervals as fatigue accumulated during long experiments.

Nevertheless, three modes of time perception and reproduction can be distinguished:

- the subsecond interval, characterized by high sensitivity, low variance, and overestimation;
- the indifference interval (0.5–2 s), where the value of $\frac{\Delta T}{T}$ is minimal: $\frac{\Delta T}{T} \approx 0.07$;
- the supersecond interval, characterized by increasing errors and underestimation during reproduction.

The Weber function is usually considered for intervals exceeding the indifference interval.

Despite its simplicity, the model became very popular, and Treisman’s pioneering paper [25] is still actively read today.

Note that Treisman is an expert in cognitive psychology, and his model has great practical and theoretical value for him and his followers. His subsequent studies, such as [26, 27] and others, presented evidence confirming the theory based on new experimental data. In [27], the pacemaker model was made more complex by adding a new block, the so-called “temporal pacemaker.” It consists of two components, namely, an oscillator and a calibration block. In turn, the oscillator consists of three elements with excitatory and inhibitory links that generate a rhythm of a given frequency F_0. The output of the oscillator leads to the calibration block. The activity of the calibration block depends on a sensory input. Upon receiving a signal from the sensors, it forms a calibration factor c_f and outputs the new frequency $F_p = c_f F_0$ (Fig. 2).

This modification of the model makes a step toward biological plausibility. The elements of the oscillator block were called “conceptual neurons” by the authors. Indeed, the above scheme corresponds to a simple neural ensemble generating activity with a given frequency that is modulated by external inputs.

Summarizing this subsection, Treisman's scheme was the first to link a number of empirical phenomena via a single simple mechanism, unified Weber's and Vierordt's principles, substantiated the scalar nature of errors, and laid the foundation for subsequent quantitative theories such as SET. The model proved surprisingly robust to experimental tests and, despite its simplicity, remains one of the most influential in the psychology of time.

3.2. Scalar Expectancy Theory

Treisman's internal clock model was generalized to the *Scalar Expectancy Theory* by Gibbon and Church. This theory is a minimal information-processing model of the internal timer in animals and humans that explains the scalar property of errors in temporal tasks. It was proposed almost one and a half decades after the internal clock model in the paper [34].

According to the *scalar property*, which gave the theory its name, the error (spread) in the estimate of a time interval is proportional to the duration of the interval itself, so that the relative accuracy (coefficient of variation) of duration perception is preserved for different time ranges. Based on these estimates, animals form intervals of reward expectation; the difference between real and expected time is estimated as the ratio of these two values. The results confirmed Weber's law in the perception of time by animals.

A large amount of experimental data on the perception and memorization of time by animals was analyzed in [34]. Experiments with rats and pigeons were described: the animals' response to time intervals under various reinforcement learning procedures was studied. As shown, the animals estimate reinforcement time using a so-called "scalar synchronization process" that scales estimates for different time interval durations.

Gibbon analyzed experiments on behavior under fixed reinforcement intervals, with the tasks to estimate and reproduce duration. In fixed-interval experiments, animals learn to expect reinforcement after a strictly defined time period, and their response changes in a specific way when approaching the time of reinforcement. A large number of published experimental data on the behavior of rats and pigeons were analyzed. According to the analysis results, the spread of time estimation errors is proportional to the time interval itself. This makes the coefficient of variation constant for different intervals, analogously to Weber's law in sensory systems.

The model developed by Gibbon is similar to Treisman's internal clock model. However, there are several important differences to note. First, the Scalar Expectancy Theory was proposed for estimating time intervals in animals, not humans. This leaves an imprint on the model: there is no verbal mechanism. Second, the scalar law is realized using a much simpler procedure. SET has no logarithmic scale, as it analyzes the *ratio* of the remembered interval to the current one. Activation occurs if this ratio exceeds a given threshold. Changes also affected the memory block, split into *working* and *reference* memory. Another distinctive feature of SET is that, unlike Treisman, Gibbon strived for biological plausibility only in the reproduced phenomena, not in the structure. For instance, the pacemaker in his model is just a generator of ticks or pulses, produced at some average rate without binding to real time. In other words, they are some internal units of the model. Thus, SET models temporal encoding in a more general way; moreover, further research has shown that it is valid for both animals and humans.

Here are the key components of the first SET model:

- a *pacemaker*, generating a sequence of pulses (time units) at some average rate;
- an *accumulator*, collecting pulses from the pacemaker while the animal counts a given interval;
- *memory*, storing the accumulated pulses as a reference interval (reference memory) and retaining the current count (working memory);
- a *comparator/decision mechanism*, comparing the current accumulator (ongoing) with a sample from reference memory and determines the response moment or decision moment.

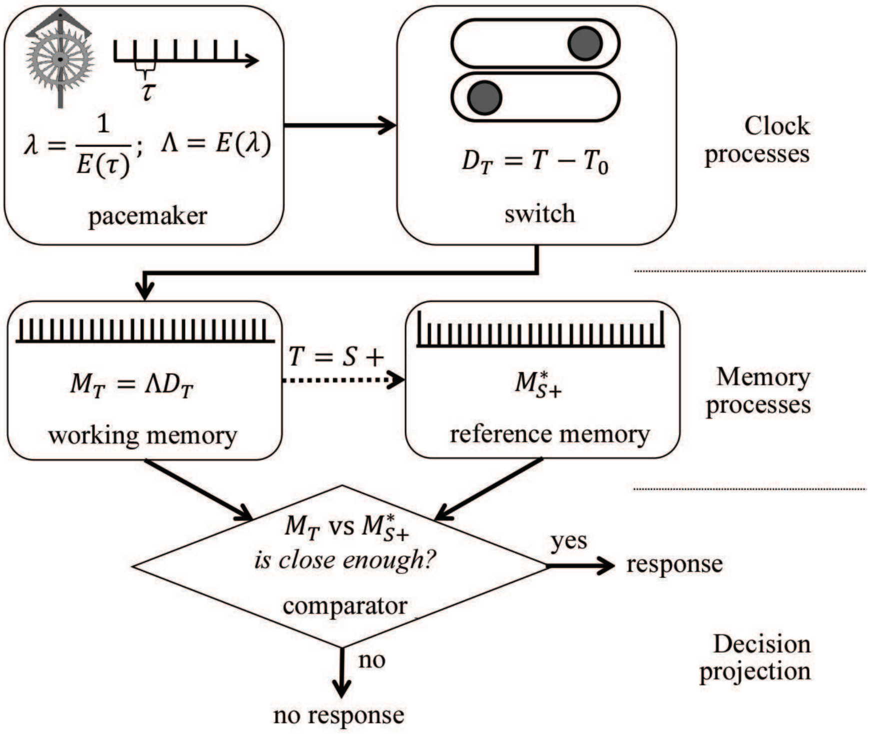

Fig. 3. The model of temporal information processing.

The operation of this model can be schematically described as follows. At the start of an interval, the pacemaker is triggered, and pulses begin to be counted by the accumulator. At the moment of reinforcement, the result enters memory and becomes a reference. In subsequent trials, the animal counts time, comparing the current number of pulses with the value from reference memory. When the current count is close to the reference (their ratio exceeds a threshold), the animal begins or stops responding.

Comparison of ratios explains the scalar property: the error and variance of time estimates increase proportionally to the interval length, and the shapes of psychometric functions for different intervals superimpose when converted to a relative time scale.

The scalar expectancy theory received its final form in [36]. The model of temporal information processing presented therein is shown in Fig. 3. It consists of three rows. The first row represents the clock process, including a pacemaker and a switch that allows pulses into an accumulator of working memory. The pacemaker generates pulses at an average frequency Λ, which is assumed to be sufficiently high relative to the time values used in experiments (from seconds to minutes). After appropriate training, the switch opens and allows pulses to pass for an average time of D_T into the accumulator of working memory (the second row) during a synchronization signal. The accumulator detects and stores the number of pulses (the mean value M_T). When, at the end of some trial, the subject exhibits the desired response and receives reinforcement ($T = S+$), the time value recorded in working memory during this trial is stored in longer-term reference memory for reinforced values (the mean value M^*_{S+}). The third row shows the decision process. A response occurs when the comparator judges that the current value in working memory on this trial is sufficiently close to the value in reference memory for the reinforced duration to warrant a response.

In [36], as in many subsequent publications by these authors (for example, see another program paper [37]), an experimental verification of the scalar property in time interval estimation by animals was associated with the so-called “peak procedure.”

The *peak procedure* is a technique used to study the memorization and reproduction of time intervals in animals: food (or other reinforcement) becomes available after performing some action, usually pressing a pedal or lever (operant tasks), or is provided after a fixed period of time in training trials (Pavlovian tasks). After training, in test trials, reinforcement is omitted, and the animals' responses are tracked. In operant tasks, the pedal pressing rate typically increases toward the expected time of reinforcement, reaches a maximum (peak), and then declines. This procedure allows assessing how an animal subjectively perceives the time interval, as well as how accurately it can predict the time of reward. Both types of experiments confirm the main tenets of scalar expectancy theory and Weber's law.

The peak procedure is often used in modern behaviorist research related to timing. Its application to study interval time estimation in a large number of bird, fish, and mammal species, including domestic chickens, pigeons, wood pigeons, black-capped chickadees, goldfish, mice, rats, fox possums, and humans, was described in [64]. The resulting data were analyzed in two ways. The first is an analysis of data averaged across multiple trials [65]. A common characteristic of interval timing is that animals, including humans, measure short intervals more accurately than long ones. Remarkably, when plotting the response-to-peak time ratio, the response curves overlap and are almost identical regardless of the interval measured. This feature, confirming the scalar property of time processing across different species, was documented in birds, fish, and mammals.

The second way is the analysis of individual trial data, in which three indicators are typically extracted from response patterns in individual trials: the start time (the transition from low to high level, i.e., to more intense pedal or lever pressing), the stop time (the transition from high to low level), and the run time (the duration of the intense phase). In [66], these data were used to compare scalar and connectionist models of time estimation; the results unequivocally illustrated the advantage of scalar models.

3.3. Methodological Principles for Constructing Temporal Encoding Models

When developing models for memorizing and reproducing time intervals for robotic systems and engineering applications, a key requirement is finding a compromise between biological plausibility and technical simplicity. On the one hand, a model must reproduce the fundamental principles of temporal encoding characteristic of living systems: the dependence of estimation accuracy on duration, the shifting of estimates toward the mean, and adaptation to changing conditions. This is necessary for robotic or artificial intelligence (AI) systems to act in real time as flexibly and efficiently as biological organisms, e.g., to respond to signals in a timely manner or to learn complex sequences of actions. However, a direct copy of highly complex neurophysiological mechanisms is not the best solution: hardware and software require resource-intensive computations, and excessive architectural complexity does not always improve the quality of results.

In this context, the most rational way is to construct phenomenologically grounded models that do not represent exact copies of biological processes but accurately embody their main properties. Treisman's internal clock model and Gibbon and Church's Scalar Expectancy Theory are examples of such a compromise: despite their extremely simple and straightforward mechanisms (compared to real brain networks), these models are consistently confirmed by empirical studies, in experiments with animals and with humans as well. The effects they predict—the scalar ratio of errors, variability, and shifts in interval estimates—are found in all types of time estimation tasks. Hence, these models are a convenient theoretical basis for constructing effective timing algorithms suitable for a wide range of practical problems in engineering, robotics, and cognitive science.

As an additional argument, we present a brief polemic between two groups of scholars. The authors of [67] criticized the classical internal clock concept as overly mechanistic and limited in understanding causality in biological systems, proposing to look at timing more integratively and abandon rigid mechanistic models. A response to that paper was published the same year [68], where internal clock models were defended by arguing that they retain important explanatory power and serve as an effective foundation for understanding temporal processes; also, the incorrect or incomplete interpretation of the models by critics was underlined therein. The same opinion was stated by the authors of the review [1], mentioned at the beginning of this paper. Based on the above arguments, here we give close attention to internal clock models and the Scalar Expectancy Theory stemming from the former. The subsequent periods of research into the perception and memorization of time intervals will be described in less detail below. However, a thorough description of the properties and operating principles of the network models mentioned in subsection 4.3, together with a detailed discussion of state-of-the-art results, deserves a separate large paper.

4. FURTHER CHRONOLOGY OF TEMPORAL ENCODING STUDIES

The models and theoretical results obtained in the preclinical period turned out to be so universal that they continue to receive new confirmations. Behaviorist studies of timing mechanisms permeate all stages up to the present. Nevertheless, with the advent of new equipment and new data, research on temporal encoding required new methods.

4.1. The Neurophysiological Turn (1980–1990)

The transition from behavioral to neurophysiological studies of timing in the 1980s was associated with the emergence of new experimental methods and paradigms for investigating the neural mechanisms of temporal processing. Starting from the 1980s, the focus was gradually shifting from the models of human and animal behavior and the search for formal psychophysical regularities (such as Weber's law) to the analysis of the functioning of neural circuits, brain structures, and neurotransmitter systems involved in temporal processing. Here, we highlight the research works of Ivry, Meck, and their colleagues.

Are common neural mechanisms used in time perception and the motor reproduction of time intervals? The studies for answering this question were carried out in [69]. According to the experiments, there are significant individual differences in the accuracy of motor timing (rhythmic finger and foot tapping) and perceptual estimation of short intervals, supporting the idea of a common "clock mechanism" involved in both perception and motor production of time, with additional contributions from specific motor processes. These results laid the groundwork for subsequent theories of distributed timing.

A series of experiments with patients with cerebellar lesions was described in [16–19]. Note that these experiments were conducted over many years, and the cited works belong to different periods; for a more holistic picture, they will be described together. The influence of various types of neurological disorders on time measurement functions was studied in [16]. As shown therein, the cerebellum plays a key role in the accurate perception and reproduction of time intervals in both motor and perceptual tasks. Patients with cerebellar damage have significant impairments in these functions, whereas other neurological groups do not suffer from such problems. This indicates a specific role of the cerebellum as a central timing mechanism operating independently of the task type. Thus, the cerebellum is considered an important component of the distributed timing system in the brain.

According to [17], patients with cerebellar lesions have difficulty estimating the duration of a short auditory stimulus and the speed of a moving visual stimulus. The cerebellum was described not as a single oscillator but as a network of many timers activated for different tasks, i.e., from motor to sensory learning. The authors also discussed that cerebellar activation in cognitive experiments may reflect the preparation of temporal response patterns rather than the analysis of abstract data. The studies of patients with cerebellar lesions in tasks requiring timing coordination of events and actions were continued in [18]. Previous research into temporal encoding was summarized in the paper [19]. It considered motor and perceptual tasks in which critical events occur at different time intervals (hundreds of milliseconds and several seconds). One key question is whether the representation of temporal information depends on a specialized system, is distributed, or is computed locally, depending on the task. The authors again emphasize the crucial role of the cerebellum, as it is associated with tasks requiring precise time measurement. In addition, they paid attention to the basal ganglia as a specialized system for time measurement, especially for longer intervals. By the authors' hypothesis, this structure is associated with decision processes. The authors were already less categorical in the later publication [70], formulating two alternative models for the perception of time flow, namely, specialized and universal (intrinsic). The former model emphasizes that the stimulus duration is estimated by specialized neural mechanisms intended to represent temporal relationships between events. The latter model is based on the assumption that duration representation may be universal, arising from the intrinsic dynamics of non-specialized neural mechanisms. The authors analyzed both models, albeit without final conclusions, merely outlining directions for further research related to the integration of these two paradigms.

Another line of studies is associated with neurotransmitter systems and neuromodulation in temporal encoding. Pharmacological research by Meck et al. demonstrated the different effects of dopaminergic and cholinergic drugs on time measurement [57–59]. The results of the experiments were interpreted within the scalar timing theory. As discovered in [58], an impact on the dopaminergic system mainly affects the perception phase of duration: with dopamine deficiency, time intervals are subjectively stretched. The impact of cholinergic drugs on time memory was investigated in [59]. The main experiment was to assess how increasing or blocking the level of acetylcholine in the brain with drugs affects memory for time intervals when performing a time discrimination task. It was suggested that the level of acetylcholine in the brain determines the "transfer rate" between the internal clock and memory. A cholinergic agonist increases the speed of duration memorization, causing underestimation of time; an antagonist slows it down, leading to overestimation.

In addition to transmitter modulation of time perception, Meck and colleagues also investigated neural correlates of temporal encoding. Their paper [71] is one of the most influential works on temporal encoding in the hippocampus. It showed a crucial role of the hippocampus in the retention and integration of temporal traces in working and long-term memory, not just in sensitivity to signal length. This work was one of the first to link temporal and spatial memory directly with hippocampal function in animals.

In [72], Meck and Church proposed a model where the brain's internal system can switch between counting events and measuring time intervals. This universal system uses the same mechanisms for both tasks, changing settings depending on the demands of the situation. According to animal experiments, both counting and timing obey similar laws and exhibit the scalar property of errors. Thus, the model explains how the brain flexibly manages time and quantity using a single adaptive system. In a continuation of that research, the authors experimentally proved the possibility of simultaneously measuring multiple intervals (clock multitasking) [73]. This result strengthened the position of models with several independent or context-tunable internal timers and expanded the universal timing model proposed in [72].

While investigating the neural mechanisms of working memory and action control, Niki and Watanabe tried to identify the neurophysiological correlates of temporal processing in various areas of the monkey cerebral cortex, primarily in the prefrontal and anterior cingulate cortex [14]. Neurons responsible for various stages of timing behavior–expectation, action preparation, and responding—were identified. The work was one of the first to associate neural activity in the prefrontal cortex with counting time intervals and mechanisms of temporal expectation. These results became the basis for subsequent studies of working memory, temporal encoding, and cognitive control.

Thus, during the period under consideration, it became possible to build behavioral models and, moreover, to link timing directly to definite brain structures (cerebellum, basal ganglia, prefrontal cortex, and hippocampus). The use of pharmacological interventions to “dissociate” different components of the scalar timing model was initiated. And the concept of a distributed timing system appeared: temporal processing began to be seen as a function of distributed neural networks rather than a single “biological chronometer.” The above advances prepared the transition to the next period.

4.2. Distributed Neural Networks and Network Modeling of Timing (1990–2000)

The 1990s in neuroscience were called the “decade of the brain” due to large-scale initiatives to study brain structure and function [74]. In the research of neural temporal encoding, this period marked a transition from the search for a single center of time to the concept of distributed neural timing systems involving the cerebellum, basal ganglia, supplementary motor area (SMA), and frontal and parietal cortex. Neuroimaging methods (fMRI, PET) began to be introduced into research to map brain networks involved in temporal processing.

During those years, ideas about temporal processing as a function of distributed, dynamically connected brain systems took shape. The first distributed neural network models of temporal encoding were presented [32, 38, 40–42]. As a rule, the main research method was observation of patients with various brain lesions and identification of dysfunctions associated with these lesions. In the previous section, such experiments were described in [16–19]. They localized brain regions responsible for some aspects of time perception. A new important task was to separate the internal clock components from other sources of temporal variability.

A key review on the neurobiology of time during that period was provided in [43]. The main models and neural mechanisms underlying the perception and reproduction of time intervals in humans and animals were considered therein. Hazeltine et al. summarized experimental data indicating that timing is realized by distributed neural systems. Different brain areas (cerebellum, basal ganglia, premotor cortex, and SMA) participate differently in various tasks, e.g., motor and perceptual. Thus, there is no single center of time; rather, temporal processing functions are distributed and context-dependent. As demonstrated, there exist common mechanisms for motor and perceptual timing: the variation of errors in time is similar in both motor and sensory tasks, indicating the operation of a single or closely related timing system. At the same time, the difference in processing short and long intervals may be explained by the involvement of different neural pathways and the interaction of memory and attention. The authors considered the hypothesis of multiple specialized timers (e.g., independent processes for different limbs or for different contexts) that can be integrated at a higher level when performing complex sequential or parallel actions. That paper played an important role in the transition from searching for a neural time center to understanding timing as the result of distributed, specialized, and interacting brain networks.

With the new instrumental base, research into the impact of neurotransmitters on time perception continued. The role of neurochemistry (dopamine and acetylcholine) was demonstrated, and it was confirmed that disturbances in the systems cause specific timing deficits. Also note a fundamental review devoted to the role of brain neurochemical systems in the mechanisms of perception, estimation, and storage of time [60]; data from laboratory experiments, pharmacology, and clinical research were integrated therein to reveal how different neurotransmitters influence the internal clock and memory processes. The new data confirmed that dopamine regulates the speed of the internal clock mechanism, while acetylcholine is responsible for storing temporal information in memory. Studies with pharmacological manipulations and clinical observations demonstrated that disturbances in these neurochemical systems lead to characteristic errors in time estimation: either accelerating or slowing down subjective time, or impairing memory of time intervals.

Based on experimental data, the theoretical preclinical models of time were tested in humans and animals. The scalar expectancy theory was confirmed by the results of several new experiments and gained a second wind [32, 33]. The new work by Church, Meck, and Gibbon [33] aimed to determine the characteristics of the internal clock, temporal memory, and decision processes involved in temporal integration, based on analysis of individual trials in rats. Three groups of 10 rats each were trained with reinforcement after 15, 30, or 60 seconds. Along with the reinforced intervals, long non-reinforced test trials were included in the consideration. On each test interval, the times of start, stop, and peak of the active response period (e.g., lever pressing) were measured to analyze the behavior structure not by averages but by individual sessions and responses. The following behavioral model was proposed and validated: in each individual trial, the animal is guided with a random sample of reinforcement time retrieved from memory, and the decisions to start and stop responding are determined by independent thresholds. According to the covariance analysis of different behavioral characteristics (the start and stop times, the peak and width of the active period), the scalar properties—the interval's spread proportional to its length—manifest at the level of individual trials as well, not only in averaged data.

One of the first connectionist models of temporal encoding was proposed by Church and Broadbent [32]. As pointed out in their work, the scalar timing theory explains well the ability of animals to estimate time intervals (on the one hand) but relies on some cognitive phenomena that are difficult to reproduce with known biological mechanisms (on the other hand). Therefore, a new connectionist model of the scalar expectancy theory was developed to explain how organisms can accurately measure time intervals at the level of neural networks. The model is based on the operation of a group of neural oscillators. Each oscillator has its own frequency; combinations of their states at the time of reinforcement (e.g., receiving a reward) are stored in memory. When it is necessary to reproduce this interval again, the current phase of each oscillator is compared with the stored pattern from memory. The decision to start/stop an action is made when the current set of phases matches that recorded during learning. The emphasis is on real or simulated neural network mechanisms instead of an abstract pulse generator and accumulator. The model describes the realization of temporal processing in biological neural networks without the need for a single center of time. The model successfully explains experimental data on operant timing tasks and confirms the distributed nature of temporal processing in the brain.

Theoretical models explaining how neural networks and individual neurons can encode, store, and reproduce time intervals were surveyed [40]. According to the author, although the central nervous system is obviously capable of accurately encoding time, the realization of the mechanisms for storing and processing temporal information is completely unclear. It is difficult to understand how neurons can accurately operate on different time scales from seconds to minutes; however, this occurs in the control of everyday behavior. The main difficulties of neural time encoding, as well as some ways of using neurons to encode temporal information, were described in the paper. Models based on the following different principles were reviewed: accumulation of pulses or signals; use of groups of neural oscillators (oscillator models); and dynamics of large neural networks for encoding long intervals. Two original models where not individual cells but a population of neurons jointly encodes a time interval were discussed in detail. Such approaches enable more robust and plastic time reproduction even under the variability and noise in neural systems. It was described how artificial neural network models learn to recognize and extract temporal patterns, and which of these properties could potentially be realized in the brain. As shown by computer simulations of various approaches (oscillator, population, and network models), such mechanisms can explain experimentally observed timing properties in animals and humans. The author wondered which of the model solutions are actually realized in real neural tissue and emphasized the need for further empirical research to find an answer.

A three-layer neural network reproducing the results of classical experiments on duration discrimination in animals was proposed in [38]. The first layer consists of clusters of neurons with probabilistic internal feedback that maintain short-term (working) activity for a random period. The second layer is a spiking neuron that continues to be active as long as a sufficient number of clusters from the first layer remain active. The third layer responds to the end of activity in the second layer by generating a short burst of spikes. The model generates time intervals with a distribution depending on three parameters, namely, the number of clusters in the first layer, their activity time, and the threshold of the neuron in the second layer. Intervals can be trained at different layers of the network by changing the corresponding parameters to obtain different Weber fraction characteristics, from S-shaped to linear and saturating curves. The model shows how populations of interacting neuron clusters can measure time intervals with characteristics corresponding to the scalar regularities observed in animals and humans.

The concept of state-dependent timing was laid out in [41] and widely developed later. Buonomano and Merzenich investigated how biologically plausible neural networks can transform temporal information (structure in time, e.g., a sequence of signals or intervals) into a spatial code, i.e., a stable pattern of activity in neural populations. A neural network was created in which neurons are connected according to some real properties of the brain (with time delays and synaptic plasticity). The network is capable of memorizing a definite temporal sequence of input stimuli, so that a unique spatial pattern of neural activation corresponds to a specific temporal sequence. The model uses parameters analogous to real cortical networks, confirming the possibility of such a temporal-to-spatial transformation in living neural circuits. Such a mechanism may explain how the brain recognizes and distinguishes complex temporal patterns (words, rhythms, or sequences of stimuli) without requiring specialized clocks or universal timing. The above work was one of the first demonstrations that neural networks can represent temporal information spatially, which is extremely important for understanding sensory processing, learning, and memory. The flourishing of state-dependent network models came in the next decade. They will be discussed in detail in subsection 4.3.

The authors of [42] formulated one of the most interesting problems in the field of interval timing: how the brain measures events lasting minutes using neural processes based on milliseconds. The main attention was paid to models resting on the coincidence of activity in different neural circuits, i.e., the so-called coincidence-detection mechanisms. By assumption, time intervals can be encoded according to the principle of coincidence in the operation of many oscillating and interacting neural units. The authors emphasized the evolutionary aspect by considering the role of similar mechanisms in different animal species. The universality and fundamentality of this temporal encoding method for the brain were underlined. Interval encoding mechanisms were linked to the neurobiological foundations of learning, memory, and integration of sensory information. As in most works of this period, it was concluded that timing is realized in the brain by distributed networks, not a single chronometer. In addition, the coincidence mechanism may be a universal principle of time representation in vertebrates. As in other Meck's works, attention was also paid to the key neurotransmitters involved in temporal information processing.

Thus, the main trend of the period under consideration is the shift of research toward distributed mechanisms of temporal encoding and the search for the neural correlates of time interval processing in several brain areas. Attempts were made to build biologically plausible models that, on the one hand, would satisfy Weber's law, and on the other hand, would have some properties of biological neural ensembles.

4.3. Systems Neuroscience (2000–2010)

The period 2000–2010 can be characterized as an era of neuroimaging revolution and integration of cognitive neuroscience in the study of timing. While the 1990s were devoted to functional mapping and the conceptualization of distributed systems, the 2000s were marked by the widespread introduction of modern neuroimaging methods to investigate the neurobiological correlates of temporal encoding. During this period, functional MRI (fMRI) became a standard tool for studying temporal processing in humans, as it maps brain activity during timing tasks with high spatial resolution. The development of positron emission tomography and high-resolution electroencephalography became key to studying the temporal dynamics of neural processes.

There was a transition from the analysis of individual (albeit multiple) structures to the study of their network interactions and functional connectivity between brain areas. In the 2000s, the idea that the brain uses several specialized systems for time processing depending on the temporal scale and task type finally took shape. Among them are "automatic systems" for short intervals (milliseconds to seconds), associated with motor control, and "cognitively controlled systems" for long intervals (seconds to minutes), requiring attention and working memory.

The neurochemistry of timing received a deeper comprehension. Studies detailing the role of various neurotransmitter systems in temporal processing appeared, especially dopaminergic and cholinergic systems, with an emphasis on clinical studies of several diseases (Parkinson's disease, schizophrenia, etc.).

The active development of computational neuroscience led to the creation of biologically plausible timing models integrating neuroimaging data with theoretical constructs.

The main shift of the 2000s–2010s was the transition from simple structural mapping and experimental models to a comprehensive analysis of distributed brain networks in cognitive, computational, and clinical contexts.

A classical paper of this period, also coauthored by Meck, has the telling title *What Makes Us Tick?* [56]. This is a fundamental review devoted to the functional and neural mechanisms of interval timing, i.e., the brain's ability to estimate and control time intervals from seconds to minutes. The authors presented the brain as a complex time machine, where understanding the mechanisms of time tracking is key to understanding all brain functions. The paper considered interval timing as a central mechanism occupying an intermediate position between two other temporal systems: circadian rhythms (24-hour cycle) and millisecond timers (motor control, speech). Buhusi and Meck described how organisms have developed multiple timing systems active over more than 10 orders of magnitude of duration with varying degrees of precision. In mammals, the main intervals include (1) circadian clocks in the suprachiasmatic nucleus, (2) an automatic timer for millisecond motor control (cerebellum), and (3) a common flexible timer for seconds to hours (thalamo-cortico-striatal circuits).

The central conclusion was as follows. The brain represents time in a distributed manner, and timing occurs by detecting the coincident activation of different neural populations. Each brain structure contributes its resonance, and all these oscillations are tracked and integrated by basal ganglia circuits, acting like a conductor of an orchestra. As emphasized in the paper, the hallmark of interval timing is the proportionality of the estimation error to the interval length (duration), a property known as scalar timing, corresponding to Weber's law for most sensory modalities. Thus, the scalar expectancy theory, proposed thirty years earlier, was once again confirmed using advanced research methods.

The above paper continued neurochemical research as well. As shown therein, dopamine regulates the pace of subjective time, while acetylcholine is responsible for the storage of temporal information. Disturbances in these systems lead to specific errors in time perception and reproduction, as demonstrated in laboratory and clinical studies by the authors and their colleagues. The paper discussed changes in timing mechanisms for patients with Parkinson's disease depending on the level of dopamine in the brain. According to the studies, patients taking medication estimate time quite normally, but as the effect of the medication wears off, their clock slows down.

The neural mechanisms of cognitive time measurement in humans were investigated in [75]. Special attention was paid to the functions of the right hemisphere prefrontal cortex. The work presented an analysis of two previously published experiments using different cognitive tasks for time estimation (sub-second and supra-second intervals). Based on their comparison, commonalities and differences in brain activation during time measurement were identified. The authors hypothesized the existence of a specialized cognitive system in the right hemisphere prefrontal cortex that provides a universal mechanism for time estimation in different tasks (from simple duration comparison to complex temporal sequences). The right-hemisphere specifics are consistent with clinical observations: damage to the right prefrontal area leads to deficits in temporal estimation. Lewis and Miall supported the idea of separate automatic (motor, short intervals) and cognitive (long and complex) clock systems in the human brain, noting the unique role of the right dorsolateral prefrontal cortex in cognitive timing.

Many publications on the neural mechanisms of time perception in humans belong to Harrington and colleagues. Let us dwell on the two most cited studies of the decade under consideration. How are different areas of the human brain activated during tasks of perception and comparison of time intervals? This issue was investigated in the paper [76]. Using event-related functional magnetic resonance imaging, the authors traced the evolution of activation of various brain areas at different stages of temporal information processing. According to their conclusion, time processing is the result of dynamic interaction between cortical and subcortical structures, and different stages of the task involve different brain areas. In [54], using fMRI, Harrington et al. aimed to discriminate and study two key processes of temporal processing: encoding time intervals and decision-making regarding their duration. The main goal of that work was to separate the neural systems involved in forming representations of time from the systems and processes associated with decision-making regarding interval durations. This important discrimination provides a better understanding of how the brain processes temporal information at different stages. The results showed the independence of the systems ensuring interval encoding and decision processes. Based on this significant finding, temporal processing involves several separate, albeit interacting, neural components.

The work of neurobiologist Buonomano and his colleagues laid the foundations for research into state-dependent network (SDN) models. These models assume that temporal information is encoded in the state evolution of a neural network, i.e., in how activity parameters (excitation flows, spiking activity, etc.) change over time within the network itself, rather than in a separate timer or oscillator. An extensive review of time processing mechanisms in the brain at different time scales was presented in the paper [77]. The authors analyzed how neural networks encode time intervals—from milliseconds to seconds and minutes—and discussed which biological systems, structures, and processes may provide this ability in animals and humans. Two main groups of models were discussed in detail. The first one is oscillator or clock-based models, where time is determined by the accumulation of pulses or the coincidence of oscillator phases, most often for subsecond and second intervals. The second group is SDN models, where the duration of an interval is represented by the state evolution of a dynamic neural network in which the temporal sequence of exciting individual neurons reflects time processing. Experimental data on the role of the cerebellum, basal ganglia, prefrontal cortex, and local neural networks were analyzed. Particular attention was paid to how synaptic plasticity, neural network dynamics, and the properties of individual neurons realize temporal selectivity. The work emphasized the importance of learning and reorganization of synaptic connections for fine-tuning temporal processing in different tasks. The results of this paper agree with the conclusions of other researchers: temporal processing is the outcome of the cooperation of many structures and mechanisms specific to different task scales. Plasticity and learning ability make the timing system adaptive to external and internal changes: it is possible both to memorize new intervals and to adapt old ones to changed conditions.

This theme was developed in the paper [39]. As shown therein, time is encoded by the state evolution of multidimensional neural networks: each pattern of network activity carries information about the time elapsed since the last event. The SDN model explains why time estimation depends on context and previous stimulation, not just on the current stimulus. The work under consideration laid the foundations for the modern understanding of the internal network mechanisms of brain timing. The SDN model was further developed in [44, 45, 78, 79]. According to the arguments provided in [78], the brain's ability to perceive and discriminate time intervals (hundreds of milliseconds) can arise spontaneously from the dynamics of local neural networks, without special clock mechanisms. Temporal information is encoded by the time-varying patterns of activity in neural populations; this property was confirmed by data from both in vivo and in vitro experiments. Some experiments on cortical slices were described in [79]; as shown, if the same time interval is repeatedly supplied to a neural culture, the network will "learn" this interval, i.e., change its dynamic activity so as to predict the expected moment of the signal. Moreover, even isolated neural networks can store and reproduce time intervals only through internal changes in their dynamic properties, without external "time organizers."

A computer model of an internal clock based on a simple recurrent inhibitory neural network was presented in [80]. Temporal information in the model is encoded as the evolution of unique patterns of neural activity after an external signal. This model shows that the sequence of activation patterns can serve as an internal chronometer: time from the start signal is represented through changes in network state. In addition, the system is noise-resistant, reproducible, and can be restarted by a strong transient signal.

The role of neural oscillations in the operation of the brain's internal chronometer was examined in the paper [81]. The authors showed that not only individual frequencies (e.g., alpha or beta rhythms) but also the interaction of different brain rhythms are important for time estimation; the latter rhythms change depending on the task and time. Such a comprehensive approach better explains temporal information encoding by the brain through the dynamics of oscillatory processes.

Internal clock models (dedicated models) and SDN models (intrinsic models) were also compared by other researchers. Based on the analysis of the two models, Ivry, Spencer, and Karmarkar investigated how the brain encodes short time intervals (hundreds of milliseconds) [82]. Subjects were presented with sound signals of different structures (simple and with irrelevant tones) and asked to compare durations. Contextual variations helped test the sensitivity of temporal processing to interference. As it turned out, the presence of irrelevant sounds of variable duration, participants discriminated time worse (an argument in favor of intrinsic models that are sensitive to context). For longer intervals (300+ ms), the above effect disappeared, indicating a limitation of SDN models in terms of time range. However, the authors offered another explanation: factors related to attention may also influence performance on duration discrimination tasks. For instance, processing of short intervals strongly depends on the context; on the one hand, this may be an argument in favor of SDN models, and on the other hand, evidence of the influence of attention and task structure on time perception.

A biologically plausible model of time measurement based on neural integration (accumulation of signal to a threshold) was developed and analyzed in [83]. A neurobiological mechanism for measuring time intervals was presented; the neural integration of a signal to a threshold under noise explains the main behavioral regularities of interval timing (the scalar property and variations in errors) at the physiological level.

In a slightly later review of computational models of interval timing [84], the approaches existing at that time were divided into four main types: pacemaker–accumulator models (Treisman and Gibbon–Church models); multiple oscillator models; memory trace models based on SDN; and drift–diffusion models. Drift–diffusion models are a class of stochastic models that explain the brain's decisions on interval duration by gradual accumulation of a noisy signal until reaching a certain threshold. They clarify the distributions of time errors and responses. The longer the interval is, the greater the impact of noise (and hence, the scalar increase in the variability of decisions) will be. These models explain why, under the impact of attention, fatigue, or drugs, either the "drift rate" (the intensity of signal accumulation) or the width of the error band changes. For all four types, the authors proposed assessment criteria: the scalar property, the ability to reproduce retrospective/prospective timing effects, and the sensitivity to attention and neurochemical impacts.

Summarizing the intermediate results, the period 2000–2010 completed the transition from localist models to understanding timing as a function of complex, interacting neural networks. The widespread introduction of neuroimaging methods allowed shifting the focus of research from animals to humans and forming modern ideas of the multiplicity and flexibility of temporal processing systems in the brain.

The period under consideration laid the methodological and theoretical foundations for all subsequent research in the neuroscience of time, establishing standards for experimental design and creating a conceptual framework that researchers still use today.

4.4. The Era of Distributed and Integrative Approaches (2010–2020)

That period was characterized by several key shifts and trends. There was a sharp increase in the number of multidisciplinary publications, specialized journals appeared, and international forums and conferences were set up. The experimental arsenal was expanded by introducing high-density multi-electrode arrays, two-photon microscopy, genetic and optogenetic tools for direct investigation of neural network dynamics and causal interventions. Different models were synthesized and integrated. Hybrid models were built from parts of internal clock models, SDN, oscillator, and hybrid schemes. Such models are capable of explaining both retrospective and prospective time effects, rhythm, the scalar property, and the impact of attention and motivation. Active studies were devoted to interval timing and rhythm and, moreover, to temporal predictions, the order of events, and synchronization between agents. There was a growing interest in clinical aspects: models based on new clinical data were developed to explain timing changes in diseases (Parkinson's disease, depression, schizophrenia, ADHD, etc.), and neurorehabilitation protocols were created based on them.

One of the most important events of that period was the discovery of time cells in the hippocampus. The concept of time cells was introduced in the early 2010s by Eichenbaum's group of researchers. These neurons were described as cells that encode sequential moments of time within episodic memory, similar to how place cells encode position in space.

Neurons with properties of time cells were first described in 2008, see [7]. However, the term "time cells" appeared later, in 2011 ([8]). As is believed, the concept of time cells was substantiated in detail in the review [9], and the term became conventional.

Time cells are specialized neurons first discovered in the hippocampus of animals and then in humans. These cells fire actively at specific moments, marking the sequence of events in time within an episode or task. Using them, the brain forms the chronology and order of events, which is critical for episodic memory. As shown by studies, a novel result in the literature, the brain has temporal tags, similar to how place cells encode the animal's position in space. The discovery solved an old puzzle: how does the brain determine sequential events (e.g., word order, daily events)? Time cells sort moments within an episode to recall not only what and where happened, but also when it happened. After rodents, time cells were found in monkeys and humans, confirming the universality of this mechanism in mammals. A notable outcome was that the cells support the properties of scalar timing (the spread of errors in determining time is proportional to the interval length), which is consistent with leading theories of timing.

The same hippocampal neurons were demonstrated to act as place cells (encoding location) and as time cells, depending on context. Therefore, the hippocampus builds not only spatial but also temporal maps of experience.

The discovery of time cells proved crucial for understanding how the brain reconstructs the chronology and duration of events, why strong emotions compress the time scale, and why humans overestimate unusual moments. A new focus of researchers was placed on the learning and remapping of time cells: these cells can change their activity depending on the task, demands, and experience, showing plasticity of time representations. With the development of intracranial recordings and neuroimaging, time cells are being actively studied in cognitive and clinical tasks in humans.

Time cells became the basis for a new wave of research into episodic memory, memory flexibility, and time awareness. As a result, the emphasis shifted from abstract theories to direct studies of neural network mechanisms of time and chronology at the level of nerve cells. For example, experiments on rats with various motor activity tasks were described in [10]; time cells and "distance cells" were identified in the hippocampus.

The research work of Merchant, a leading researcher in the neurobiology of time, covered key aspects of understanding how the brain processes temporal information [85–89]. Experimental studies in primates demonstrated the existence of multiple neural chronometers in different brain areas that are activated differently in synchronization and rhythm continuation tasks [85]. In [86, 87], the reader will find an introduction to the neurobiology of interval timing, systematizing the main concepts, methods, and discoveries in the study of time measurement mechanisms from milliseconds to seconds, as well as a fundamental review of the neural foundations of time perception and estimation, summarizing knowledge on how different brain structures (cerebellum, basal ganglia, and cortex) participate in temporal processing at different scales. In the medial premotor areas of primates, the realization of multiple levels of neural clocks for estimating and reproducing time intervals in the hundreds of milliseconds was investigated in the paper [88]. The authors found that individual neuronal populations encode elapsed and remaining time, as well as the duration and order of intervals, forming a hierarchical multilayer system in which temporal information is represented by the dynamic activity of cell populations. According to these results, temporal processing is realized as a distributed network function, where each layer contributes to precise control of rhythmic movements and their coordination in time. A comparative cross-species study of the ability to find rhythm in humans and primates was provided in the paper [89], indicating the evolutionary and neural foundations of rhythmic behavior and synchronization with external temporal patterns. As shown by the studies, the brain uses distributed specialized timing systems depending on the task and temporal scale. Special emphasis was placed on rhythmic behavior as a fundamental ability linking time perception, motor control, and evolutionary aspects of temporal processing in primates and humans. According to another study [23] as well, time is encoded by different neural networks depending on the task.

How is temporal information encoded and used during nervous system development? This issue was the subject of the biological review [90]. The authors considered how neural stem cells read and decode temporal signals arising from complex interactions between molecules, cells, and tissues to correctly determine cell fate during brain development.

Note another review [91], describing studies of how the cerebral cortex realizes the temporal processing necessary for cognitive functions. The authors showed that temporal encoding is an intrinsic function of cortical neural networks, arising due to the temporal features of their activity and ability to plasticity. The role of neural circuit dynamics in maintaining "cognitive time" was highlighted: from moment-to-moment tracking of events to forming expectations and decision-making. As emphasized therein, understanding how the cortex encodes and uses time on short scales is crucial for building general models of cognitive brain activity, including perception, planning, prediction, and learning.

On the contrary, a highly specialized study was presented in [92]. It was demonstrated that professional percussionists reproduce time intervals with high accuracy and minimal errors compared to other people. This is due to their high sensory precision: they rely less on interval averaging and use more "optimal" temporal encoding.

Weber and Fairhall examined the role of neural adaptation in encoding and the dependence of the efficiency of processing changing environmental properties on the dynamic adjustment of neural sensitivity at different time scales [93].

Bayesian models of time interval memorization [50–53] radically changed the understanding of time perception, showing that systematic "errors" in duration estimation are not flaws but an optimal strategy of the brain to reduce uncertainty under internal noise. They are closely related to the concept of predictive processing in the brain; the main idea is that the brain constantly forms and updates hierarchical predictions about the external world based on an internal model, comparing them with real sensory data and minimizing prediction errors. These models treat the memorization and estimation of time intervals as a process of probabilistic inference, where prior experience is integrated with current sensory signals to obtain the most probable estimate. The brain combines current sensory data about time with prior experience, which shifts regression type toward the mean; however, exactly this feature makes the system more reliable in the long run. Neurochemical disturbances, such as dopamine deficiency in Parkinson's disease, change the balance between precise counting and the use of prior experience in favor of the latter, explaining specific patterns of temporal distortions in different clinical groups. Essentially, Bayesian models show that the human brain is not a precise chronometer, but an intelligent prediction system that sacrifices absolute accuracy for overall efficiency in an unpredictable world.

4.5. Modern Period

A review of recent research should be much more detailed. Many breakthrough works have been published, and new discoveries have been made. We hope to devote a separate paper to the results of recent years, with modern neurobiological studies and a focus on network models of encoding time intervals. This section only outlines the key milestones.

Modern studies have significantly expanded the class of computational and biological models by including recurrent neural networks, spiking systems, and hybrid architectures closely approximating real biological networks. A significant breakthrough has been the experimental confirmation of the role of neural oscillators and dynamic ensembles in the generation of time intervals, as well as evidence of the existence of a flexible and multimodal time encoding system in the brain. Works from this period have been integrating plasticity, adaptation, and error prediction mechanisms, as these concepts link temporal processing with memory and decision-making. According to several fresh studies, the distributed representation of time and its neural correlates are much more variable and complex than previously assumed, which calls into question rigid mechanistic models and stimulates a transition to ensemble and hierarchical models of temporal processing.

A new understanding of the computational mechanisms of time perception is being formed using neural network models, which are becoming a tool for explaining temporal computations in the brain [94]. A recurrent neural network model with plasticity capable of considering variability in temporal estimates has been presented in [95]. The scope of application of SDN models is expanding; they are now used to describe neuromodulation, particularly modulation of locomotion [96]. A model for learning temporal sequences based on spiking neural networks has been developed, with application to the study of musical memory [97]. It has been shown that time intervals in ensembles of neural networks can be encoded on a logarithmic principle [98], which refers back to Treisman's first internal clock model. An integrative model combining neural oscillators with computational memory mechanisms has been proposed, going beyond the traditional scalar timing theory [99]. In a review of current data on the neural bases of duration estimation [100], Tsao et al. have distinguished between prospective (current, clock-like) and retrospective (recollective, reconstructive) time perception; as demonstrated, both types of processes rely on the dynamics of neural population states, but are implemented by different computational and neurobiological mechanisms. According to [101], memory and time perception use partially common neural mechanisms; without considering time representation, it is impossible to fully understand how memory works. Each cognitive action is treated as unfolding in time, and memory as a mechanism organizing this temporal flow. The impact of time constraints on cognitive performance, including mathematical productivity, has been studied in [102]. The control principles of neural dynamics revealed through the study of timing are being analyzed [103]. Neural mechanisms that simultaneously track several independent and asynchronous time intervals and rapidly switch between them in response to changes in the environment are being investigated [104]. Brain's synchronization of movements with external (music) and internal (mental rhythm reproduction) signals is being studied [105]. As discovered, the brain is capable of compensating for functional impairments under different methods of rhythm cueing. Collectively, these works significantly deepen the understanding of the mechanisms of time perception and processing in the brain at different levels and from different perspectives.

Let us particularly emphasize one review and two historical publications. The main neurocomputational models of interval timing have been reviewed in [106]. Models have been classified according to several principles: the presence or absence of threshold and adaptive clocks, and whether timing is a function of building a dedicated clock or emergent temporal encoding at the population level. The classification highlights both the common statistical properties of models (e.g., the scalar property and the shift of temporal estimates) and the diversity of computational solutions by which the real brain can realize timing in behavioral and neurophysiological tasks. The authors have considered key models from the classical internal clock to modern neural trajectory models, underlining the need to see the overall picture of the field's development (see the woods for the trees).

Meck's scientific legacy and contribution to the study of time perception and interval timing have been described in the paper [107], including recollections of his colleagues and students about his personality and role in shaping the scientific community in the field.

Treisman's classical work [25] on the internal chronometer and its role in time perception, published in 1963, has been analyzed in detail in [108]. Highlighting the internal clock model proposed by Treisman, the author has examined the main experiments, demonstrated how this model explains key effects (e.g., Weber's law), and discussed the relationship between Treisman's theory and later models such as the Scalar Expectancy Theory. In addition, the significance of this work for the modern understanding of timing psychology has been noted.

5. CONCLUSIONS

According to this review, the two interrelated lines of research—Treisman's internal clock model and the Scalar Expectancy Theory (SET)—remain methodologically and empirically fruitful after decades. Their key assumptions are surprisingly robust: with increasing measurement precision and complication of biologically plausible models, the basic properties reproduced by these models are again confirmed. This robustness indicates the fundamental nature of the principles laid down in the models, making them a convenient support both for new data interpretations and for engineering applications.

The practical value of the models lies in their structural clarity and computational simplicity. In robotics and AI tasks, this is critical: biological plausibility here is reasonably understood as the reproducibility of observed phenomena (the scalar property, the bias of estimates toward the mean, and the superposition of curves in time) rather than as a literal reconstruction of physiology. The modular architecture (pacemaker, switch, working and reference memory, comparator, and decision mechanism) provides transparent error tracing, easy calibration, and portability across platforms and environments.

At the same time, a significant limitation of classical models is their low tolerance to noise and variability of natural signals. A promising direction is the transition to population encoding and network implementations, where temporal information is distributed across the states of dynamic systems. Network approaches, including state-dependent networks and recurrent architectures, can inherit the phenomenological advantages of internal clocks and SET, while increasing noise robustness, representational flexibility, and online adaptability. In this regard, we intend to systematically review the latest investigations of timing, with an emphasis on network models and mechanisms of the scalar property in distributed state representations.

We have started developing a model for memorizing and reproducing intervals that combines phenomenological verifiability with the robustness of population encoding. The first theoretical results have already been presented in [109]. We plan to create a simulation model, conduct experiments, and analyze the experimental data.

In general, the continuity from simple clocks to network time appears not as a rejection of classics, but as their natural development: the proven phenomena and criteria are preserved, but the carrier and encoding method change. This junction opens up opportunities for integrating cognitive theories of time with AI and robotics practices, taking into account real constraints of noise, resources, and adaptability.

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