Are we close to deciphering the timer's enigma?

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Abstract

Among the theoretical models, Gibbon and Church's temporal infor-
mation processing model is by far the most popular explanatory device
in the domain of animal timing, and timing recorded using the peak
procedure is considered to reflect pure cognitive time. Neuropharma-
cological breakthroughs suggest that different neurotransmitter systems
subserve different functions or stages, as specified by the temporal
information processing model. Cerebral activations correlated to timing
performance have been described in humans. However, several ques-
tions remain unanswered, particularly those regarding the specificity of
the neural and biochemical correlates of timing performance. At the be-
havioral level, the dynamic aspects of timing, as well as timing patterns
which cannot be explained within the framework of existing models,
deserve a renewal of interest.

Key words: Time performance, neural substrates, models.

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In some of his paintings, Salvador Dali drew what he labelled "soft watches" – plausibly illustrating the inconsistency of psychological time. Had he known about experimental psychology (but as a surrealist he showed more inclination, of course, towards psychoanalysis), he might have proposed his semi-liquid clocks as appropriate representations of the state of scientific knowledge concerning psychological time in those days. Experts were few, and considered as somewhat marginal; they were paid little attention by their colleagues working on more recognized topics; they were offered little space, if any, in scientific meetings and publications. Until the late seventies, a young researcher engaging in the study of time was really taking risks for his/her career.

Things have changed in the last twenty five years or so. The psychology of time has developed enormously, with an increasing number of involved specialists, a proliferation of meetings and publications, an impressive production of empirical data collected from both humans and animals, and a blossoming of theoretical models. It has become a very promising field, one to be recommended to any young investigator. The lack of solid substance typical of Dali's models has given way to hard flow-chart models and to precise techniques aimed at capturing psychological time proper, uncontaminated with all accessory factors altering its behavioral manifestations. Among the theoretical models (see for instance in Block, 1990; Helfrich, 1996; Lejeune & Macar, 1993; or Macar, Pouthas, & Friedman, 1992), Church's so-called temporal information processing model and its variants is by far the most popular "explanatory device" in the domain of animal timing, and it is no wonder that most studies reviewed by Macar in her concise updated survey of the *Neural Bases of Internal Timers* refer more or less directly to it. According to this model, time estimation depends on the integrated functioning of a "clock level" that provides the metric units devoted to measuring the duration of an ongoing event, a "memory level", where measured durations can be stored, and a "decision level", which controls behavioral output on the basis of a similarity rule that operates when a most recent duration has to match some criterion duration previously stored in reference memory (Church, 1984; Gibbon & Church, 1984; Gibbon, Church, & Meck, 1984). In short, it is a clock/comparison model that functions according to the rules of scalar timing, which generalizes Weber's law to response timing (Gibbon, 1977). In other respects, human prospective timing, where the subject is asked to estimate, produce, or reproduce a target duration, seems to be well ex-

plained within the framework of the attentional model and its variants, which posit that remembered durations will be a function of attentional resources allocated to an internal timer (Thomas & Weaver, 1975; Block & Zakay, 1996), whereas the estimation of the duration of past events, retrospective timing, is well accounted for by the contextual change hypothesis (Block, 1990; Block & Zakay, 1996), according to which duration has to be constructed on the basis of retrieved contextual changes stored in memory. We shall not dwell on cognitive models applied to human data, but rather focus on the Gibbon and Church's temporal information treatment model (see Figure 1).

Equally significant is the prominent use of one experimental technique – the so-called Peak Interval Procedure (to be explained below) – out of a large array of available laboratory procedures, which yields behavior, offering an ideal match to the architecture of the internal clock proposed by the temporal information processing model. We shall comment briefly on the almost exclusive use of that model and that technique in current research.

But prior to this, let us say a few words about the core of Macar's contribution, that is, the neural bases of the internal timer, although we shall not venture into a detailed assay of the findings she reports, because we lack the required expertise. It must suffice to point to the drastic change observed in this aspect of the study of psychological time since the pioneering epoch referred to above. The "sense of time", as it has sometimes been called, not having any specific receptor, and therefore no conducting tracks, was not amenable to physiological study as were sensory modalities, for which sense organs and related pathways could be clearly identified and analyzed, eventually leading to central areas. Its status was, in that respect, closer to the status of memory than to the status of perceptual processes. Time in the nervous system has long been as elusive as the engram.

However, the search for neural substrates is now in progress – following very much the same trajectory as the search for the neural correlates of memory processes – as clearly illustrated by some of the contributions reviewed by Macar. One major advance should be emphasized: formal models are now being supplemented by plausible real candidates – oscillators of various kinds, neurotransmitter paths, etc. Ingenious experimental designs have been developed to track the plausible neural substrates of the various components of the temporal information processing model. This will be illustrated with two examples using the

Peak Interval Procedure (PIP) in rats. This procedure is a modified version of a simpler procedure called the Fixed Interval schedule, in which a subject is reinforced for a response produced after a fixed amount of time has elapsed, with the interval recycling automatically after each reinforced response. The PIP differs from that schedule in two aspects: first, it is a discrete trial procedure, rather than a continuous one; that is to say, each interval is signalled by an external stimulus; secondly, not all trials are reinforced: in a certain proportion of them, after the time has elapsed, the stimulus is maintained for an amount of time (usually equal to or longer than twice the duration of the interval) and responses
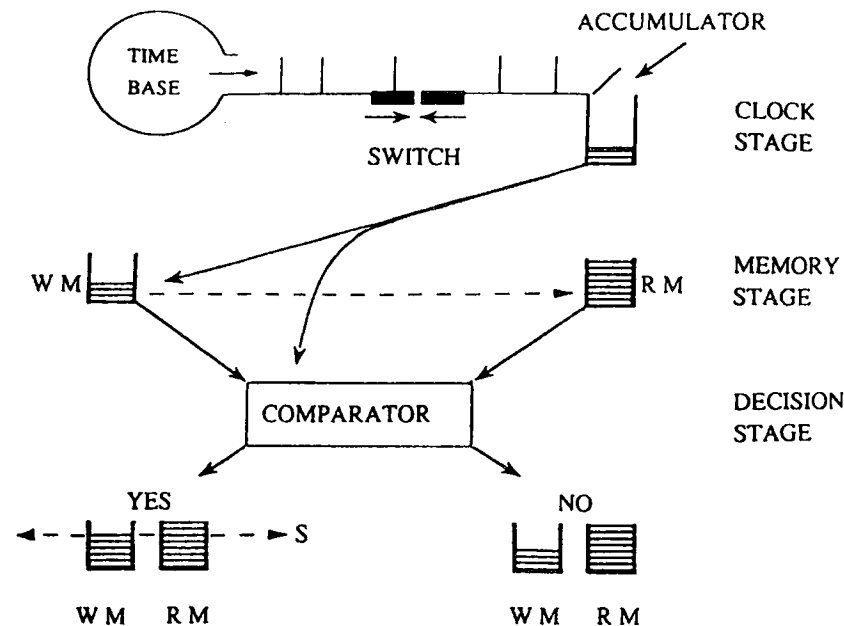

Figure 1. Schematic representation of Church and Gibbon's Temporal Information Processing model. When a duration has to be measured, the time base produces impulses which are gated to the accumulator via a switch. At the memory stage, a working memory (WM) stores pulse counts accumulated at the clock stage. The reference memory (RM) stores the temporal parameters of behaviors reinforced during previous trials. At the decision stage, the comparator compares online the value stored in the accumulator (or the WM) with a value sampled from reference memory. Decision to respond (YES) follows if the difference between both values is less than or equal to a similarity rule (S)

(unreinforced) are recorded. In these so-called "peak trials", response rates typically follow a fairly normal curve with a peak value around the value of the interval (hence the name Peak Interval Procedure). In a first example, where rats must simultaneously time two durations (two peak interval procedures with different criterion durations, long and short, were scheduled to occur, the short one starting after and ending before the long one), and thus divide attentional resources between the tasks, lesions of the frontal cortex or the nucleus basalis magnocellularis severely impaired the ability to simultaneously time both durations. After the second duration was introduced, while the first was still in progress, lesioned rats stopped timing the first stimulus and successfully timed the second. When the second stimulus went off, they recalled the value of the first duration and continued to time it. As a consequence, control rats had peak times located precisely at their respective criterion duration, whereas lesioned rats had the peak time of the long duration increased by the duration of the second shorter PIP task. These data tend to show that the frontal cortex plays an important role in attention allocation to different cognitive tasks (and here we come close to the attentional models of human timing). Hippocampal lesions, on the other hand, do not impair the ability to simultaneously time two durations. Another dissociation between frontal and hippocampal functions was shown in rats performing in a single peak procedure with a gap (the stimulus which signals the ongoing trial is switched off for a few seconds). Hippocampal lesions typically produced an amnesia for the signal duration preceding the gap, whereas frontal lesions did not. This suggested that the hippocampus, but not the frontal cortex, is involved in working memory functions (see Meck, 1996; or Gibbon, Malapani, Dale, & Gallistel, 1997, for reviews).

Modern techniques of cerebral imagery have been put to work with humans and have already produced encouraging results. First, evidence has been provided that activation linked with time estimation does occur (Jueptner et al., 1995; Maquet et al., 1996). Second, the areas concerned involve the frontal cortex, the thalamus, the striatum, and the cerebellum. In particular, striato-thalamo-cortical loops are thought to be critical for the transmission of temporal information generated in the basal ganglia (Hinton, Meck, & MacFall, 1996). Third, there is some indication that the networks involved are the same, irrespective of the psychological procedure used: that is so say, the same network is activated whatever the particular task required from the subject. For in-

stance, conjunction analysis of PET activations has shown that the right prefrontal cortex, the right inferior parietal lobe, the anterior cingulate cortex, the left putamen, and the left cerebellar hemisphere are activated to the same extent in human adults performing duration discrimination (temporal generalization, i.e., a sensory timing task) or production tasks (synchronization, i.e., a motor timing task). Furthermore, these similar activations occurred for target durations ranging from 0.5 (generalization) to 2.7 seconds (synchronization), i.e., durations crossing the 1-second limit, which is usually thought to mark a division between different timing systems. Such data begin to challenge the claim that cerebellar activation is specific to durations under one second, whereas basal ganglia would be involved in the second-to-minute range (Ivry & Keele, 1989; Gibbon et al., 1997; Lejeune et al., 1997). Most importantly, the question of the *specificity* of activation related to timing comes under close scrutiny. Demonstration that the activation of a particular area or network occurs *only* during timing performance (and not during a cognitive control task that matches the timing task in all respects but the temporal dimension) has not yet been provided. However, convergent data seem to indicate that the striatum (in particular the putamen) is a plausible candidate (Hinton et al., 1996; Lejeune et al., 1997; Rao et al., 1997).

Although those who work in that area will agree that they are still in the exploration stage, it is clear that new avenues of research have been opened up, which give real hope of tracking psychological time in the brain; powerful methodological synergies are being developed, which combine "global" activation (PET, for instance) with the measure of the temporal dynamics of the ongoing brain processes (ERPs). Whether or not they will eventually lead to a confirmation of theoretical models offered by psychologists is an unanswered question. Besides activation and ERP recordings, the neuropharmacology of temporal functions has also undergone considerable development over the last decade or so. Elegant experiments conducted mostly in Meck and his associates' laboratory (Meck, 1996, for a review) have singled out neurotransmitter systems subserving different functions or stages, as specified by the temporal information processing model. Animal data tend to indicate that the clock stage of the timer is linked to the dopaminergic functions of the basal ganglia, whereas reference memory for time as well as attention could be subserved by acetylcholine functions in the frontal cortex. However, a number of problems remain unsolved. Classical

studies using a wide variety of psychotropic drugs on a large array of temporal regulations of behavior have not suggested such clearcut effects. But we shall not elaborate further on this point here. Neural correlates, be they captured through brain imagery or through pharmacological approach, should of course be taken into account, not only as mere confirmation of a given stage of the model (in which case one might claim that the model is definitive and should not be exposed to further revision), but as a possible source of falsifying the model, either partially or totally.

Let us now focus on two aspects of the current theorizing, both on the cognitive side. One is the model itself. As noted in the preceding paragraph, it appears that the temporal information processing model has received some validation from lesion or neuropharmacological studies (human neuropharmacological data have also recently been described; for instance, Malapani et al., 1993). If this is largely true, such a close matching should be taken as evidence of the validity of the model, which therefore should not require further modification. Yet, the model has undergone a number of changes through time, aimed at more precisely fitting the complexity of the empirical data. However, the developments of the initial model have not fundamentally altered its basic architecture, since the clock, memory, and decision stages have been retained. One of the transformations, the connectionist version of the information processing model (Church & Broadbent, 1990) proposed replacing the pulse-generating pacemaker by an array of oscillators whose coordinated functioning allows it to account, at least in theory, for timing performance spanning wider time ranges than before (a similar path was followed by Miall, 1989, 1993, for instance). The initial reference memory with its finite storage capacity was replaced by a connection matrix which offers an elegant solution to that problem (see also Wearden & Doherty, 1995). Attention, which was not a "full-fledged" part of the initial model, without being ignored or disregarded (as early as 1984, Church mentioned that attention could modulate the functioning of the switch; experiments by Meck, 1984, lent support to this hypothesis) has recently been the center of renewed interest, both at the psychological and neuropharmacological levels (Meck, 1996). Indeed, the attentional-gate model by Zakay and Block (1996, see also Block & Zakay, 1996) introduced attention as a major component (they added an "attention" box to the clock level, between the pacemaker and the switch) and thus merged the temporal information processing model

(mostly referred to in animal psychology) with the attentional model of prospective timing familiar to those who work with human subjects.

The appeal to attentional processes as a necessary ingredient in accounting for time estimation, however, has not been exclusively a matter of theoretical inclination. Some recent behavioral and biochemical studies provide empirical data which argue for granting attention its due place. Bringing attention into focus will certainly have a positive impact on studies which explore the applicability of scalar timing to human performance. It has recently been shown, for instance, that variations in task difficulty produce changes in the timing sensitivity of human subjects, that is, timing sensitivity increases (as evidenced by temporal generalization) as the discriminability of stimuli to be compared decreases, i.e., as the discrimination between relevant stimuli becomes more difficult (Ferrara, Lejeune, & Wearden, 1997). This can plausibly be explained in terms of the allocation of attentional resources depending upon the situation (e.g., we may feel, and indeed be more attentive, in rush hour traffic than when driving on a quiet country road). Ferrara et al. resort to a modified version of the Church and Gibbon model (MCG), initially elaborated by Wearden, which essentially brings attention into the picture (Ferrara et al., 1997). Macar, Grondin, and Casini (1994) elegantly showed that, in the dual-task procedure, shifting attention, in accordance with the experimenter's instructions, from the duration to the other non-temporal task, makes a difference in time estimation accuracy. Perhaps attention should not be locked into a box and given its place in the model diagrams (Block & Zakay, 1996), but should instead be viewed as a parameter pervading the whole process, or any phase of it.

Besides attention, another dimension was neglected in the framework of scalar timing and in the temporal information processing model developed in close relationship with animal *steady-state* performance. Intuitively, a dynamic dimension was lacking. This dimension, however, was at the core of a competing but less popular approach represented by Staddon's group, which for a number of years studied the dynamics of time discrimination (Innis & Staddon, 1971; Staddon, 1967; Wynne & Staddon, 1988, 1992; Higa, Thaw, & Staddon, 1993; Wynne, Staddon, & Delius, 1996), and developed the one-back linear waiting model and its variants. This model is concerned with how waiting time in an interfood interval is influenced by the immediately preceding (or a few before that) interfood interval(s), when that interval is frequently changed or when a constant interfood interval is interrupted by shorter "impulse" intervals (Higa, 1996). This dynamic aspect has only begun to be explored with the PIP, and some data are in agreement with those from Staddon's group (Lejeune, Ferrara, Simons, & Wearden, 1997).

The second issue we would like to raise is the almost exclusive use of two procedures as a source of data in support of the scalar model, namely, the PIP and bisection. The Peak Interval Procedure is one of maybe two dozen procedures that have been designed to explore the organism's capacities to estimate time, be it with reference to external events or in their own behavior. The major advantage of the procedure, as claimed by its users, is that it provides for a clear separation between timing processes proper and variables such as deprivation, likely to affect the ongoing behavior in terms of rate of response, for example. The peak value of the response rate function is said to reflect (with no bias) the functioning of the internal timer. By manipulating independent variables, such as drugs, it should be possible to disentangle the effects on timing mechanisms that are relevant for our understanding of psychological time, and accessory effects that alter various irrelevant aspects of behavior. This is essentially what has been done by Church's group (Gibbon, Roberts, Meck, and others) in a long series of studies in which data collected using the PIP and bisection, and elaboration of the scalar model, have given each other reciprocal support. This undoubtedly impressive outcome raises some questions, however.

First, there are some replication problems. Data have been accumulated almost exclusively, until very recently, in the same laboratory or in the same group of researchers, with little replication by other groups.

Secondly, there is a more general and trivial issue with respect to the exclusive use of a few procedures. Having explored for many years the diversity of behavioral manifestations of timing in various species, at different ages, using different situations imposing different constraints on the subjects, we think that the decision to pick out one or two of them as giving access to *pure* cognitive time, and therefore offering *the* basis for the model of psychological timers, is questionable. This was done at the expense of observed diversity, and leaves unanswered questions raised many years ago. The paradox of spontaneous vs. required temporal regulation of behavior is a case in point – and we shall limit ourselves, before concluding, to that example – which will bring Macar back to her early studies on timing: it has long been observed that in the

same individual organism, accurate timing occurs for much longer periods of time when it is not a necessary condition for the subject to be reinforced (spontaneous temporal regulation) than when reinforcement depends upon accuracy (required temporal regulation). Maybe the problem can be solved by adding a box to the model. Maybe that box would have something to do with attention, or, who knows, with inhibition. Other problems may eventually lead us to add as many boxes as needed. The lesson to be learned from this is that the elegance of current models should not mask the complexity of what has to be accounted for: this complexity should not be reduced, with the risk of simplifying the abstract model built to explain it, and the neural mechanisms underlying psychological time.

For sure, our models of psychological time are not as soft as in Dali's imagination. However, they might not yet be as strong as is sometimes claimed. They still have something of the approximation and fragility of Klee's "vegetal clocks".

RÉSUMÉ

Les régulations temporelles obtenues chez l'animal avec la "peak procedure" ont, de manière prépondérante, été interprétées dans le cadre du modèle de traitement de l'information temporelle de Gibbon et Church et des systèmes de neurotransmetteurs différents sont supposés sous-tendre les diverses fonctions spécifiées par ce modèle. Par ailleurs, des activations cérébrales corrélatives de la mesure du temps ont été décrites chez l'homme. Cependant, plusieurs questions restent en suspens, parmi lesquelles celle de la spécificité des corrélats neurologiques et biochimiques de l'estimation du temps. Les aspects dynamiques des conduites temporelles et les performances qui ne peuvent être expliquées dans le cadre des modèles existants devraient susciter un regain d'intérêt.

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