Research report

High-speed memory scanning: a behavioral argument for a serial oscillatory model

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Abstract

In order to account for the memory span [G.A. Miller, The magical number seven, plus minus two: some limits on our capacity for processing information, Psychol. Rev. 63 (1956) 81–97.], the magical number seven, plus minus two, and high-speed scanning in human memory [S. Sternberg, High speed scanning in human memory, Science 153 (1966) 652–654.], Lisman and collaborators [O. Jensen, J.E. Lisman, An oscillatory short-term memory buffer model can account for data on the Sternberg task, J. Neurosci. 18 (1998) 10688–10699; J.E. Lisman, M.A.P. Idiart, Storage of 7 ± 2 short-term memories in oscillatory subcycles, Science 267 (1995), 1512–1515.] proposed an oscillatory short-term memory buffer model. In this neurophysiological model: ''a single brain network can separately maintain up to seven memories by a multiplexing mechanism that uses theta and gamma brain oscillations for clocking. A memory is represented by groups of neurons that fire in the same gamma cycle'' [O. Jensen, J.E. Lisman, An oscillatory short-term memory buffer model can account for data on the Sternberg task, J. Neurosci. 18 (1998) 10688–10699, p. 10688]. To test this model, we tried to modify the memory scanning time by shifting the gamma oscillation frequency. To this aim, we replicated the visual short-term memory scanning task [S. Sternberg, High speed scanning in human memory, Science 153 (1966) 652–654.], and we simultaneously used the protocol that Treisman [M. Treisman, A. Faulkner, P.L.N. Naish, D. Brogan, The internal clock: evidence for a temporal oscillator underlying time perception with some estimates of its characteristics frequency, Perception 19 (1990) 705–743.] designed to drive, slowing down or speeding up, a temporal oscillator acting in the gamma range [J.G.R. Jefferys, R.D. Traub, M.A. Whittington, Neuronal networks for induced ''40 Hz'' rhythms, Trends Neurosci. 19 (1996) 202–208; W. MacKay, Synchronized neuronal oscillations and their role in motor processes, Trends Cog. Sci. 1 (1997) 176–183; M. Treisman, N. Cook, P.L.N. Naish, J.K. MacCrone, The internal clock: electroencephalographic evidence for oscillatory processes underlying time perception, Q. J. Exp. Psychol. 47A (1994) 241–289.]. In this protocol, an auditory periodic stimulus (click train) was delivered at various frequencies during the task. The reaction time (RT), the slope, and the intercept of the linear function associating RT to memorized list length showed systematic modulations according to the stimulation frequency. The predicted driving effects due to the click trains were obtained, consisting of localised modulations of performance on the stimulation frequency band. We argue that memory scanning is indeed paced by a temporal oscillator, thus providing behavioral arguments for the serial oscillatory model of Lisman. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Memory scanning; Internal clock; Cortical oscillation; Reaction time; Human

1. Introduction

In human memory studies, Sternberg's contributions [28,29] shed light on the temporal constraints for memory retrieval. The task used was as follows: the subject first memorized a list of items, for example digits. The list length was varied across experimental conditions. Then, a digit was presented to the subject, who had to indicate as fast as possible if the stimulus did or did not belong to the memorized list. The typical result was that the reaction time (RT) was a linear function of list length, with a slope value around 40 ms per item. This linearity was interpreted as follows: once the stimulus is presented, the subject has to identify it; the identification time is supposed to be the same whatever the number of items in the memorized list. The memorized list is then scanned, and the stimulus is compared serially to each of the memorized items. Let us call ''scanning time'' the time necessary to compare the stimulus to one of the memorized items; the total comparison time is $N \times$ scanning time, N being the number of

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items in the list. After this comparison is done, the subject has to give his response. The time necessary for the motoric processes is independent of the list length, [1] as the identification time. The linear increase of the RT is thus only due to the linear relationship between the comparison time and the number of items. In this case, the slope of the linear regression between RT and list length gives the value of the scanning time, i.e. about 40 ms. Furthermore, the slope for the positive trials — where the stimulus belonged to the list — and for the negative trials — where the stimulus did not belonged to the list — were shown to be the same. This equality is non-trivial as it suggests that even for the positive trials, the serial search is exhaustive. On the contrary, if the search is auto-terminated, when the list is composed of, let us say, four items, and that the stimulus belongs to the list, the match should occur equiprobably after the first, the second, the third, or the fourth comparison. The average comparison time should thus be $(N/2) \times$ scanning time. The slope when the stimulus belongs to the memorized list should be half the one when the stimulus does not. However, the slopes are usually equal. Although counter-intuitive, this similarity suggests that the scanning process is exhaustive even for the positive trials.

Given this result, Sternberg [29] argued that the information stored is serially and exhaustively scanned before the subject gives a response. Since this pioneering work, numerous studies have replicated and extended this finding.

The serial interpretation was nevertheless questioned by the demonstration by Townsend [33,34] that serial and parallel models can mimic each other (nevertheless, see Roberts and Sternberg [25], for further developments). Following this theoretical work, many authors tried to show that processing was parallel rather than serial [19,23]. Some arguments were based on experimental and theoretical data indicating the potential limits of the serial exhaustive model [2,6]. Another popular argument used against serial processing was the parallel nature of cortical organization. Nevertheless, as pointed out by Miller [21], the parallel structure of the brain is highly compatible with a broad class of serial models.

1.1. Lisman and collaborators' model of short-term memory

In the memory scanning context, recent work by Lisman and collaborators has shed some light on this debate. They proposed [15,17] that a neural network using theta (5–12 Hz) and gamma (20–60 Hz) oscillations can main-

tain, without confusion, about seven items in memory, i.e. the memory span [20]. This model is of real importance. Firstly, it is a ''physiologically realistic'' serial model of memory retrieval. Secondly, it can account very well for the RT distributions (means, variances, and skewness) obtained in the classical Sternberg task [14]. Thirdly, it describes the scanning mechanism in a physiological and original way.

The first version of the model [17] addressed two important issues: (1) how to maintain a given piece of information in memory for several seconds (or minutes), and (2) how to maintain several pieces of information without confusion. We will briefly describe these two points. First, an item is stored in a population of neurons firing synchronously [26]. This population of neurons receives a non-specific subthreshold oscillatory input in the theta range which makes the membrane potential oscillate [1], and a suprathreshold input carrying specific information which makes the population of neurons fire. This firing induces an after depolarization [7,30]. This afterdepolarization makes the firing probability of the population of neurons change with time, with a maximum at about 150 ms. The combination of the membrane oscillations and the after depolarization makes the population of neurons always fire at the same phase of each theta cycle [15,17]. Second, when several items are stored, a feedback inhibition in the gamma range maintains a phase difference between the various populations of neurons coding for different items. Once the items are stored, during information retrieval, each item becomes serially active in each gamma cycle, within the theta cycle.

Furthermore, in order to account more precisely for the data obtained by Sternberg [28,29], Jensen and Lisman [14] proposed two models for high-speed memory scanning, which differed only slightly: the first model, ''adapting theta'', assumes that the period of the theta rhythm depends on the memorized list length (the longer the list, the slower the rhythm); whereas in the second model, the period does not vary, but a reset of the theta rhythm occurs after the scan of the last item. In both cases, however, the time between successive activations of a given item depends on the number of items stored. This common characteristic is sufficient for the present study, and we will not describe the models further.

Let us focus on the functional properties and on the chronometric parameters of the model accounting for data obtained in the Sternberg task. One important assumption in the model is that the scanning process can start only at the trough of a theta cycle where no items are stored. Thus, after the list has been memorized, when the stimulus is presented, several operations of specific duration take place. The subject has to identify the stimulus (it takes time $t_{identify}$), to wait for the next theta cycle (t_{wait}), then to scan all the memorized items, i.e. to go through the whole theta cycle (t_{scan}), and finally to prepare and produce the response (t_{motor}). After the first scanning cycle, if the

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[1] This assumption was verified experimentally in some studies [29].

decision threshold is not reached, then a new scan begins; this was termed ''skipping'' (t_{skip}). Consequently, the RT is the sum:

$$RT = t_{\text{identify}} + t_{\text{wait}} + t_{\text{scan}} + t_{\text{skip}} + t_{\text{motor}}$$

Among these variables, two are independent of the memorized list length: t_{identify} and t_{motor}, i.e. the so-called peripheral factors. On the contrary, the distributions of t_{wait}, t_{scan} and t_{skip} are sensitive to the list length. Note that, in this model, t_{scan} is equal to $N \times$ scanning time, with ''scanning time'' being equal to the period of the gamma oscillation. With this model, Jensen and Lisman [14] nicely fitted the data obtained by Sternberg [27] and others [2].

A significant aspect of this model is that it establishes a link between the memory scanning time, estimated by the slope of the regression, and the period of the cortical oscillations in the gamma range. These oscillations revealed in various species including humans, display a high degree of spatial organization and thereby would provide a mechanism for various cognitive experiences. Gamma-band activity had been observed in many behavioral situations, including, focalization of attention [3], visual search tasks [31], and during the delay of a visual short-term memory task [32]. It has been proposed that such oscillations could act as internal clocks in the brain [12,18,36].

1.2. M. Treisman's experimental protocol

To study such internal clocks, Treisman et al. [36–38] have developed an experimental protocol to drive the pacemaker of the clock. Treisman hypothesized that even if the pacemaker of such clocks must be protected from outside stimulations to keep its frequency stable, strong enough periodic sensory stimulation might drive it when the pacemaker frequency, or one of its simple harmonic, and the stimulation frequency are close. This protocol led to changes in the clock frequency, which can be detected on the subject's performance, under certain conditions. If the stimulation frequency is just lower than that of the pacemaker, then a slowing down of the clock will occur. On the other hand, if the stimulation frequency is just higher than that of the pacemaker, then the internal clock will speed up.

Thus, in an RT task, if we vary the click trains step by step around the hypothetical internal clock frequency, and if we plot the mean RT as a function of click train frequency, then we should obtain a characteristic ''driving pattern'' (Fig. 1b) of the performance according to the stimulation frequency: (1) no effect of the periodic stimulation on RT, for some frequencies, (2) for a given frequency, a relative lengthening of the RT, due to the slowing down of the clock, (3) for the just higher stimulation frequency, a shortening of the RT, due to the speeding up of the clock. We called this precise succession on the frequency band between RT lengthening and RT shortening ''driving pattern''. The fundamental frequency of the internal clock, or one of its simple harmonics, is supposed to be between the slowing down and the speeding up frequencies [37,38]. Treisman and colleagues used a wide range of frequencies in their studies, from 5 to 50 Hz. Three points are worth noticing: first they obtained some ''driving patterns'' at several frequencies. These frequencies are supposed to be harmonics of the clock frequency. From the distribution of these harmonics, they estimated
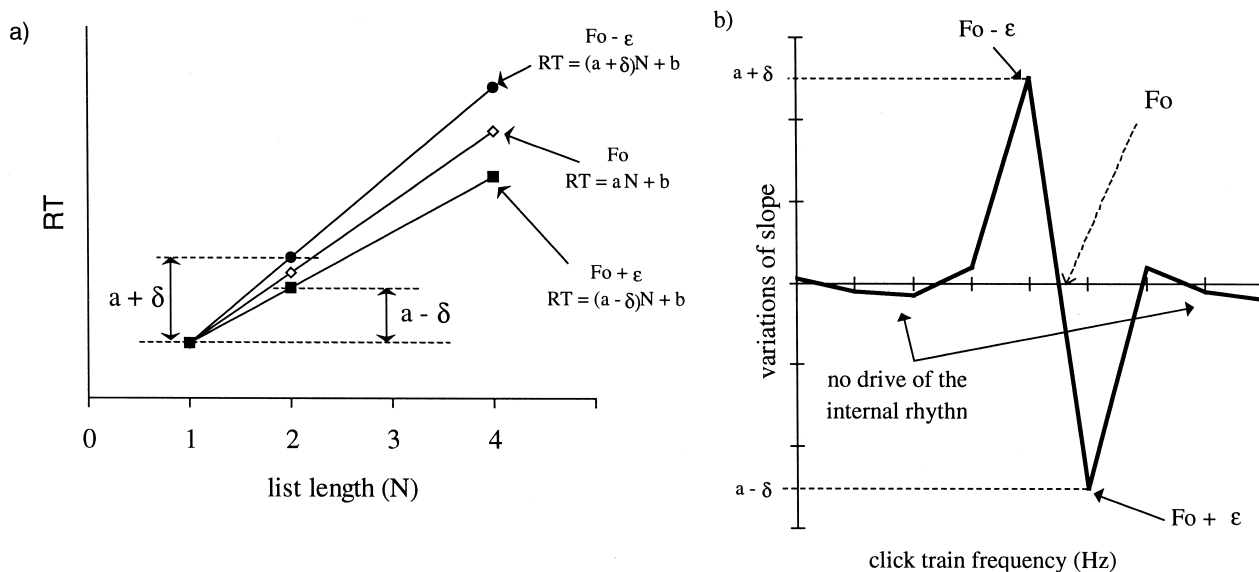

Fig. 1. (a) Schema of the driving effects of the repetitive stimulation (click train). A slowing down of the pacemaker of the internal clock ($F_o - \varepsilon$) leads to an increase in the scanning time, and hence of the slope ($a + \delta$), and inversely. (b) The expected variations of the slope according to click train frequency make up the ''driving pattern''. For click train frequencies far from the frequency of the internal rhythm (F_o), no driving effect is observed. When the click train frequency is close to the frequency of the internal rhythm, driving effects occur, i.e. a slowing down directly followed by a speeding up.

the closest fundamental frequency which could account for such a distribution on the frequency band. Their various estimates of this frequency were in the gamma range (almost between 35 and 50 Hz). Second, although they estimated the frequency to be within the gamma range, the driving patterns where most pronounced at lowest frequencies (around 20 Hz) than at the simple frequencies (around 40 Hz). The authors argued that this is probably due to the temporal limits of the sensory discrimination [10,11]. Third, these effects do not depend on the modality of the stimulation, since comparable results were obtained with visual flashes [35].

It has been shown, with this protocol, that such a pacemaker paces some components of the RT [4,37], and particularly, the transmission of information between processing stages [5]. In two previous experiments, we obtained a driving pattern centred between 20.5 and 21 Hz [4,5].

In the present study, we used the experimental click train situation designed by Treisman to test the serial oscillatory model of Jensen and Lisman, which physiologically accounts for the short-term memory scanning data on the Sternberg task. The periodic stimulation in Treisman's protocol is assumed to drive oscillations in the gamma range. In Jensen and Lisman's model, the scanning time is directly related to the frequency of these oscillations. Thus, a variation of the oscillation frequency will change the scanning time, and, hence, the slope of the regression. [2] This value of the slope relating RT to list length is schematized in Fig. 1a. Thus, if the items stored in short-term memory are serially active during successive gamma cycles, using Treisman's protocol, with successive increments of the periodical stimulation frequency, then we should obtain an increase followed by a decrease in the scanning time. Now, if we plot the scanning time as a function of the click train frequency, we should obtain the predicted driving pattern.

2. Method

2.1. Subjects

Six subjects, three males and three females, from 24 to 31 years of age (mean age: 27.5 years), participated in the experiment. They signed informed consent forms and were paid for participating.

2.2. Apparatus

The subjects were comfortably seated, 60 cm away from a digit presentation device (model LTS-3401LP,

LITE ON) composed of seven-segment (1 cm long) Light-Emitting Diodes, arranged in a rectangular form (2×1) with the seventh placed in the center of the rectangle (Fig. 2b). The response signals (one of the 10 digits) were presented on the seven-segment device for greater temporal precision (less than 1 ms). For familiarization, before the experiment, the 10 digits were presented in ascending order. The whole list to be learned, called the positive set, was composed of 1, 2, or 4 digits, and was presented immediately at the beginning of each block on a computer screen just above the digit presentation device. The responses were given by a light key pressing, either with the right or the left thumb, depending on the response signal. When a response signal appeared, the subjects had to respond if the digit belonged to the positive set or not as fast as possible. Half of the subjects responded with the right hand when it did, the other half with the left hand. A key press stopped the click train and turned off the digit. The RT was measured with 1-ms precision.

2.3. Procedure

The choice of the frequency range was based on several grounds: first, as the driving effect of the clicks is small relative to the intrinsic variance of RT, we need a lot of trials to make such a driving effect to appear. For this reason, it is not possible to used a very large frequency range. Second, as exposed in Section 1, although the simple frequency of the oscillations is thought to be in the gamma range, low amplitudes driving patterns were obtained in this range [37,38]. In contrast driving effect were often obtained around 20 Hz, i.e. half the supposed frequency of the gamma oscillation. Thus we decided to use frequencies around 20 Hz. This choice was reinforced by previous results [4,5,37]. On the basis of the data of Treisman and collaborators, in a previous experiment [4], we used 11 frequencies from 19.4 to 25.4 Hz in 0.6-Hz steps. All of the eight subjects presented a driving pattern, from 20.6 Hz (slowing down) to 21.2 Hz (speeding up), of RT performance. In a second experiment [5], we examined more precisely the vicinity of these two frequencies. Six frequencies were chosen, ranging from 19.5 to 22 Hz in 0.5-Hz steps. The slowing down or accelerating effects of the periodic stimulation, according to its frequency, allowed an estimate to be made of a simple harmonic of the frequency of the internal clock, between 20.5 and 21 Hz. So, in the present experiment, we persevered with the same frequency band.

The external periodic stimulation used to drive the clock consisted of 0.1-ms auditory clicks. The intensity of the click train, recorded at head level, was 75 dB (A). Six frequencies were used, ranging from 19.5 to 22 Hz in steps of 0.5 Hz. The order of the frequencies within each block was randomly distributed. Clicks were presented about 500

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[2] In Lisman's model, the value of the slope does not exactly correspond to the scanning time, as t_{wait} and t_{skip} also contribute to this value. This is an important difference from Sternberg's initial model.
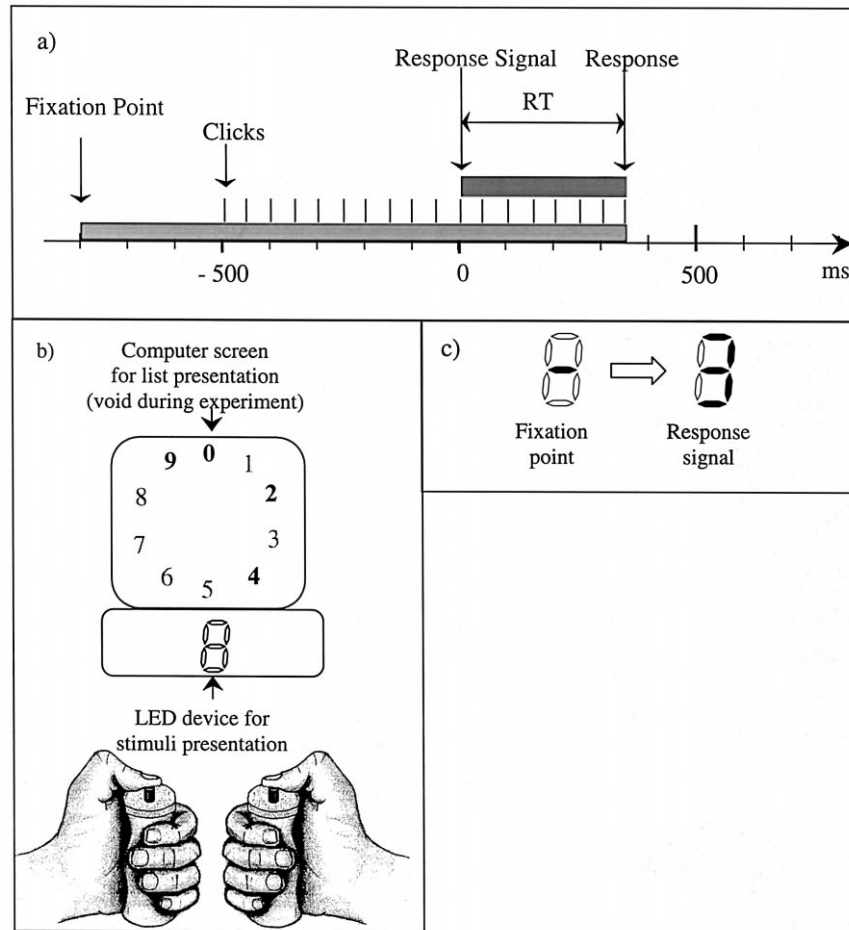
Fig. 2. (a) Time course of a trial: the central fixation segment switches on 800 ms before the response signal was lit; the clicks stopped with the subject's response. (b) Experimental apparatus and stimuli presentation device. The list to be learned was composed of 1, 2, or 4 digits and was presented at once at the beginning of each block on a computer screen with a clock-like configuration. (c) The response signal, one of the 10 digits, was presented on a seven-segment device. The response was to be given as fast as possible by pressing a push button with one of the two thumbs, depending on the belonging of the digit to the list.

ms before the response signal. To prevent response signal onset between the clicks from affecting the frequency of the sensorial stimulation, it was always synchronized with a click. The time between the beginning of the click train and the response signal was, thus, frequency-dependent. As a consequence, variations ranged from 488 to 524 ms. It was verified in previous studies [4,5] that these very small variations could not account for the variations obtained in RT.

For each trial, the central segment, which was used as a fixation point, came on 800 ms before the response signal (Fig. 2b).

Subjects performed two training sessions with the three list lengths. The first training session was performed without clicks, the second with clicks, in order to accustom the subjects to this noise. The maximum time allowed to respond was reduced from the first to the second training session, and set to the mean + 2 S.D. of the previous session.

The subjects then performed six experimental sessions. Each subject usually performed two sessions on the same day. The three list lengths were presented in each session. The order of list length presentation was counterbalanced for each subject between sessions, and for each session between subjects. Each block, either training or experimental, was preceded by the presentation of the positive set. It stayed on the screen until the subject began the block by pressing the right key. The experimental blocks were constituted by 180 trials, with 48 positive responses and 132 negative responses, whatever the list length. Then, both response and stimulus entropies were held constant as the positive list length varied, according to the Sternberg [28] procedure.

2.4. Data processing

2.4.1. Search for driving pattern

Treisman et al. [38] proposed that the clicks (or flashes [35]) they used had an arousing effect on the pacemaker of
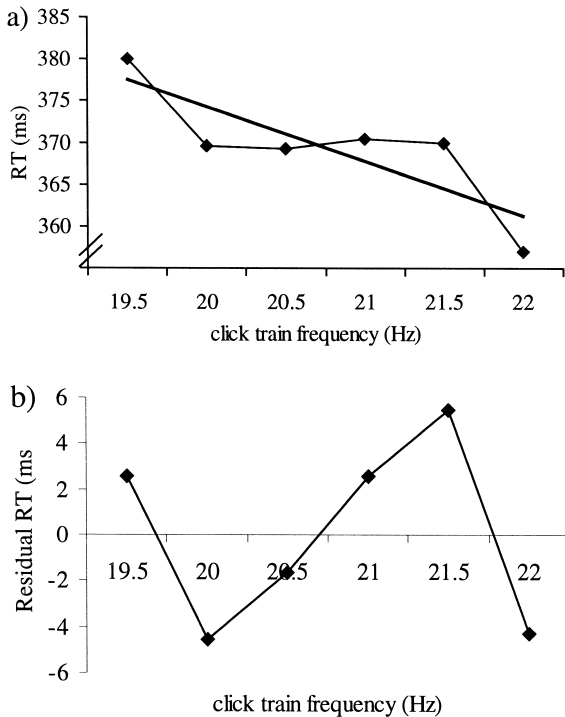
Fig. 3. Raw data for a typical subject to illustrate the method used to separate the driving effects from the non-specific arousing effect. (a) Raw mean RT averaged for the three list lengths as a function of click train frequency, and regression slope computed on these data. There is a trend toward a decrease of RT as the click train frequency increases. This trend add to the variance in a systematic way and makes a significant effect induced by the stimulation more likely to appear. (b) Mean residual RTs (expanded scale) obtained for the same subject by subtracting the linear component from the raw data.

the internal clock and hence, that they have a non-specific, approximately linear, activating effect on the performance. Recently [22], new evidence in favor of this hypothesis was provided. This trend increases the variance induced by the stimulations in a systematic way and makes a significant effect of frequency more likely to appear. As we are not interested in this subsidiary effect, we have to separate the linear activating effects from the non-linear driving effects. For this purpose, a linear regression $X = a + bf$ (with X being the chronometric variable to be analyzed and f being the frequencies) was computed for the RT, for the intercept and for the slope of the regression associating RT with list length (Fig. 3a). We computed residuals (experimental values − regression values) (Fig. 3b). It should be noted that if the deviations from the RT predicted by the regression analysis are randomly distributed across the six frequencies, then averaging the data should make the deviations disappear. On the contrary, if these deviations were due to a particular driving by the internal clock, then they would accumulate in systematic positions in the frequency distribution.

In order to differentiate the linear activating effect of the clicks [22] from the driving effect, statistical analysis was performed on residuals, and the degrees of freedom

were the same as for the regression analysis ($N − 2$). All of the reported analysis of variances have been performed following the design: response (positive or negative) × list length (1, 2 or 4).

3. Results

In all of the following analysis of variance, the error term was the mean square of the interaction between the effect of the subjects and the effect of the factor under analysis.

3.1. Error rate

Proportions cannot be submitted to analysis of variance as their means and variances are not independent. Thus, the analysis of variance has been done on the arcsine transform of the error rate [39]. The error rate in the whole experiment was 1.87%. This rate was far higher when the digit belonged to the set (5.8%) than when it did not (0.72%) ($F(1,5) = 37.1$; $p < 0.005$). Subjects made more errors as the list length increased ($F(2,10) = 7.47$; $p < 0.02$). These two factors interact significantly ($F(2,10) =$
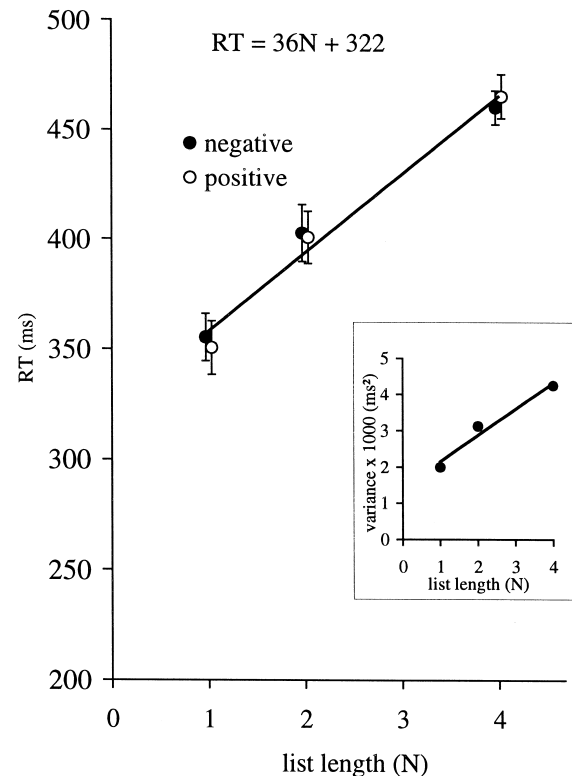

Fig. 4. Mean values and S.E. of raw RT for the six subjects as a function of list length when the digit did (positive: open circles) or did not (negative: filled circles) belong to the memorized list. As no difference occurred between positive and negative responses, regression parameters were estimated on the average values. Inset: mean variances as a function of list length.

4.57; $p < 0.05$). Conditioned comparisons demonstrated that there was no effect of list length when the digit did not belong to the set ($F(2,10) = 1.22$), but that the error rate did increase with list length when the digit belonged to the set ($F(2,10) = 6.02$; $p < 0.02$). This pattern of error suggests that there were more ''misses'' than ''false alarms'', and that ''misses'', but not ''false alarms'' increased with list length.

3.2. Mean RT

There was a significant main effect of list length on RT ($F(2,10) = 158.76$; $p < 0.001$) (Fig. 4). In contrast, there was no difference when the digit did or did not belong to the memorized set, neither as a main effect ($F(1,5) = 0.21$), nor as an interaction with list length ($F(1,5) = 0.995$). The linear component of the list length was highly significant ($F(1,5) = 187.1$; $p < 0.001$). However, the quadratic component was also significant ($F(1,5) = 20.5$; $p < 0.01$). The mean slope was 36 ms per item.

3.3. Variances

As did the mean RT, the variances increased linearly with list length ($F(1,5) = 12.40$; $p < 0.02$). In contrast to the means, the quadratic component was not significant ($F(1,5) = 3.24$; $p = 0.13$) (Fig. 4 inset).

3.4. Distributions analysis

An argument put forward against serial processing in high-speed memory scanning was that the relation between RT and list length is sometimes curved instead of linear. Note that it is the case in the present study since the quadratic component of the mean was significant. We thus tried more thoroughly to analyse this curved relationship. In visual search tasks, which are similar, subjects make ''timing guesses'' or ''belated guesses'' on some trials [9]. This means that after a sufficient duration, due to the time pressure, the subject is urged to give a response, and he (she) gives a response by chance (yes or no). We suppose that such belated guesses occur more frequently when the list length increased leading to longer RT. Belated guesses could explain the curved relationship we observed on average between RT and list length. But, regardless of the list length, this explanation should be especially true for the longer RT, but not for the shorter RT. In order to evaluate this possibility we performed a vincentization of the RT distributions [24]. This analysis is typically performed in four steps: (1) for each subjects, the RTs are listed in ascending order for the various experimental conditions; (2) these distributions are divided into proportional bins (here, 10 bins — each composed of 10% of the trials); (3) the mean of each bin is computed; (4) the mean values of each bin are averaged across subjects. We thus
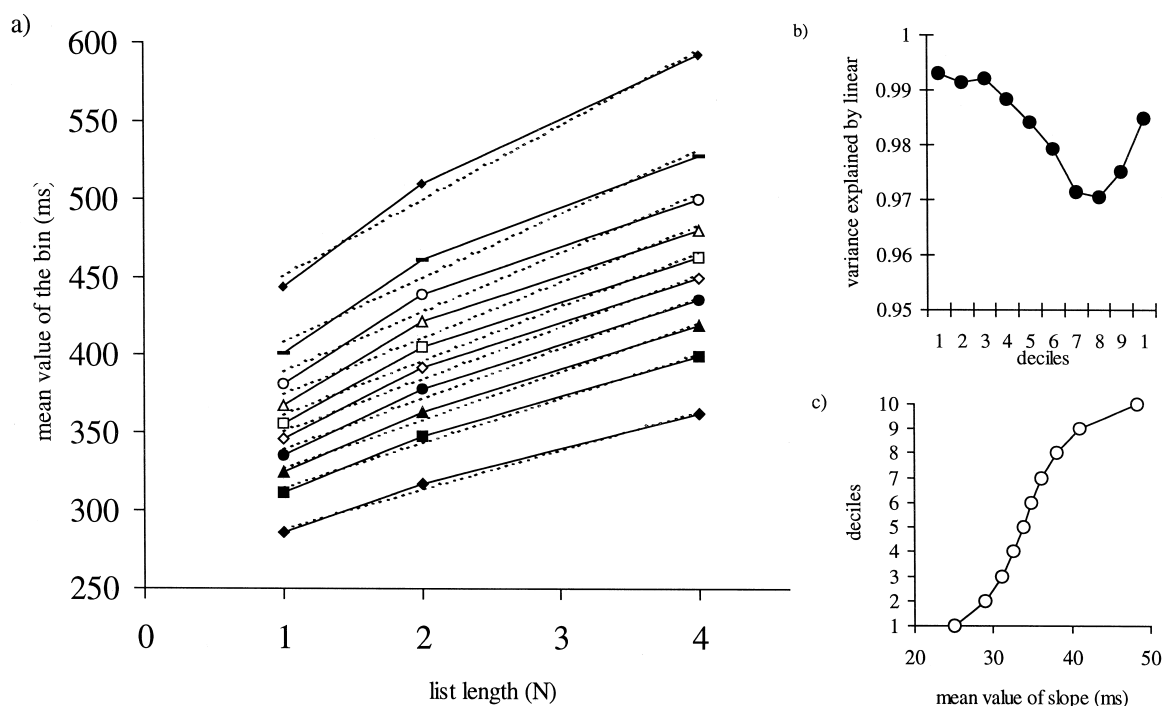

Fig. 5. Analysis of the RT distributions. The RTs were listed in ascending order for the various conditions. These distributions were then divided into 10 bins composed of 10% of the trials, and the mean values of each bin were averaged across subjects [24]: (a) mean decile values in ascending order as a function of list length (ex. filled square for the second decile). Dotted line are the best linear fits. (b) Percent of variance explained by linear fit as a function of deciles (> 99% for the 3 first deciles containing the faster RT). (c) Mean values of the slope (X-axis) for the consecutive deciles (Y-axis), ranging from 25 ms for the first decile (faster RT) to 48 ms.
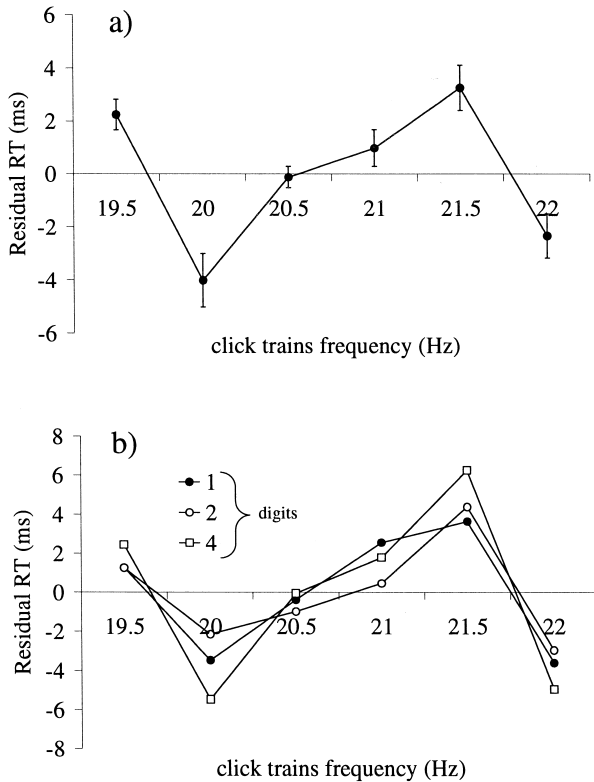
Fig. 6. (a) Mean residual RT and S.E. as a function of click train frequency. (b) Superposition for the three list lengths.

obtain 10 distribution values (corresponding to each decile) for the three list lengths. The relationship between list length and the mean values of the deciles are then evaluated. Fig. 5a shows the results of this analysis. The Fig. 5b shows that the percentage of variance explained by a linear fit ($> 99\%$ for the 3 higher deciles) decreases with increasing deciles, which is in agreement with the idea that curved relationships are, at least partly, due to belated

guesses by the subjects (even if there is a slight increase for the last two points). This proposal is further supported by the increased error rate for the longest list (see above). Fig. 5c shows the increase of the slope computed for the consecutive deciles, ranging from 25 ms for the faster RT to 48 ms.

3.5. Effect of click trains on RT

3.5.1. Non-specific activation effect

The mean linear effect of click train frequencies on the RT was computed for each subject. For all the subjects, the RT decreased as stimulation frequency increased. The mean slope of the decrease (-2.30 ms/Hz) is significantly different from zero ($t_5 = 2.44$; $p < 0.05$, one-tailed). Note that the mean value of the decrease is very close to the one that we obtained previously (-2.11 ms/Hz) [5].

3.5.2. Specific driving effect

Fig. 6a shows the mean variations of the residual RT according to the click frequencies. Two driving patterns were obtained, the first centered between 19.5 and 20 Hz, and the second centered between 21.5 and 22 Hz. These variations are unlikely to be accounted for by chance ($F(4,16) = 11.16$; $p < 0.001$). Each of the six subjects individually shows similar results. Furthermore, the position of the driving pattern is clearly independent of list length, suggesting a constant pacemaker frequency whatever the list length (Fig. 6b).

3.6. Effects of click trains on the slope of the regression

Usually, in order to evaluate the scanning time, a regression analysis between list length and RT is computed. Nevertheless, when the relation between the variables is not linear, which is the case in the present study,
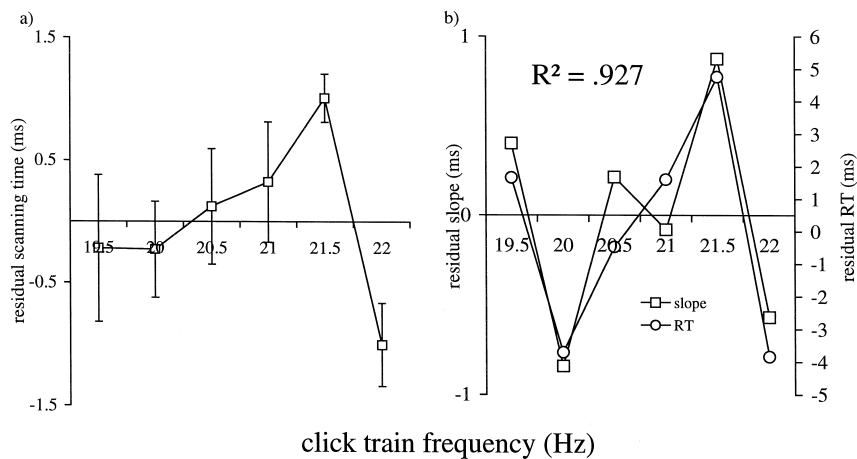

click train frequency (Hz)

Fig. 7. (a) Mean values and S.E. of the residual ''mean scanning time'' as a function of click train frequency for the six subjects. (b) Comparison between the mean residual slopes (left *Y*-axis) and the mean residual RTs (right *Y*-axis) as a function of the click train frequency (*X*-axis) for the only two subjects for whom the linear correlations for the six frequencies were above 0.98. The similarity between the direct recorded RT modulations and the computed slope modulations is expressed by a high coefficient of correlation between RT and slope variations.

the ''mean scanning time'' [16] has been shown to be an acceptable index to evaluate the scanning time. The mean scanning time is computed by subtracting the RT when there was only one digit in the list from the RT when there were 4 digits and then divided by 3 (three intervals). Note that when the relation between list length and RT is linear, the mean scanning time and the slope of the linear regression are equal. We computed the mean scanning time for the six frequencies. The mean values and S.E. of the residual mean scanning time are shown for the six subjects in Fig. 7b. Error bars show that only two points differ from zero: 21.5 and 22 Hz. An increase is followed by a decrease suggesting that a driving pattern is centered between these values, as in the RT data. The subject by subject analysis showed that all six subjects showed such a driving pattern centered between 21.5 and 22 Hz.

We further investigate the slope itself for the only two subjects for whom the linear correlations for the six frequencies were above 0.98. On both RT and slope, the two driving patterns previously described for the whole residual RT (3.5 above) were obtained (Fig. 7a). The striking similarity between the RT modulations (experimentally recorded) and the slope modulations (computed) is expressed by a high correlation between RT and slope variations ($R^2(4) = 0.927$; $p < 0.01$). This result supports the hypothesis that the memory scanning time was driven by the external periodical stimulations.

3.7. Effects of click trains on the intercept of the regression

The second component of the regression, namely the zero intercept, should theoretically represent the non-mnemonic components of the RT. We thus performed the same analysis as above on the value of the intercept. Fig. 8 shows the mean variations of the residual intercepts as a function of the click train frequencies for the six subjects. The two driving patterns previously described, centered between 19.5 and 20 Hz, and between 21.5 and 22 Hz, were obtained. The variations are significantly different from random ($F(4,16) = 4.33$; $p < 0.02$).
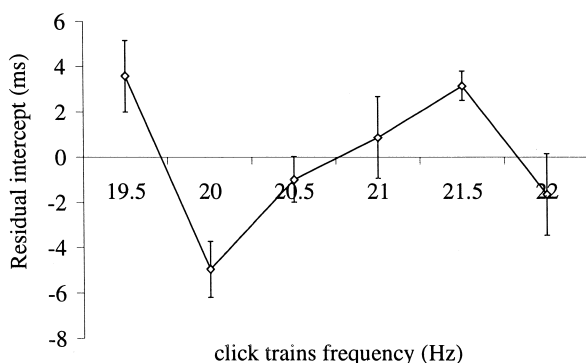

Fig. 8. Mean values and S.E. of the residual intercept for the six subjects as a function of click train frequency.

4. Discussion

The main results of this experiment may be summarized as follows: (1) systematic variations in performance were observed according to the click train frequencies, after statistical adjustment because of a non-specific activating effect of the stimulation; (2) the time course of the variations along the frequency band, a slowing down immediately followed by a speeding up, was fully predicted from Treisman's protocol and results [37,38], and from our previous data [4,5]; (3) driving patterns were obtained not only on basic recorded values (RT) but also on computed values: the slope and the intercept of the regression associating RT with list length. This last result confirms the reliability of the protocol of Treisman because the calculation of the slope contains a subtraction between conditions. Let us suppose an experimental bias in the RT modulations by the click train frequencies; it would probably disappear in the subtraction between the different values obtained according to the list length; (4) the modulations of the intercept suggest that an internal pacemaker paces into the non-mnemonic components of the RT as well; (5) the variations of the ''mean scanning time'' and the variations of the slope of the regression for the subjects presenting good linearity, strongly argue that the memory scanning is periodic.

According to Lisman's model of short-term memory, and following the proposals that cortical oscillations act as an internal clock in the brain [5,12,36], our results could mean that the external stimulation drove the gamma feedback inhibition sent to the networks coding for the memorized items, thus inducing variations in the scanning time. Such an interpretation of the data strongly support a serial oscillatory model of memory retrieval.

The present experiment addressed the nature of memory retrieval, in light of recent proposals [9,14]: Chun and Wolfe [9], in a visual search context, provided arguments in favor of ''timing guesses''. The present data suggest that timing guesses could explain, at least in part, the curved relationship between RT and list length. A linear relationship was obtained for fast RTs, less sensitive to timing guesses. It decreased as RT increased, i.e. when timing guesses increased.

In Lisman's model [14], contrary to the original proposals by Sternberg [29], the slope of the regression does not correspond exclusively to the scanning time; some other parameters contribute to this value, namely t_{wait} and the possibility of a second scanning of the memorized items if the first is insufficient for a decision to be taken. This process allows the value of the slope to vary, even if we suppose that scanning time is constant. Distributions analysis has shown that the slope increased with deciles (Fig. 5c). If we suppose the scanning time to be constant, then variations are due to t_{wait} and the possible repetition of scan (t_{skip}). Considering that for the first decile, the various components of the RT are at about their minimum

values, we assume that the participants performed only one scanning cycle for the first decile, and that t_{wait} is close to zero. In this case, the scanning time only contributes to the slope of the linear regression. The value that we obtained is about 25 ms, which corresponds to 40 Hz, the typical value given for gamma oscillations. This value supports the notion that gamma oscillations contribute to memory scanning, in agreement with the oscillatory model of Jensen and Lisman. Furthermore, the supposed scanning frequency value (40 Hz), is also consistent with the driving effect of the click trains. The increase followed by the decrease of the mean scanning time, obtained for all subjects, was located from 21.5 to 22 Hz. Thus, the estimated pacemaker frequency has a harmonic centered between these values.

A last point should be outlined. This study confirms previous findings on the existence of a pacemaker in the information processing system. However, it poses the question of the frequency of such a pacemaker and the question of the constancy of the frequency according to the task to be performed. In two previous experiments, using different protocols, we obtained a driving pattern centered between 20.5 and 21 Hz [4,5]. In the present study, the driving patterns are regularly centered elsewhere, but not far, in the frequency range. What is the meaning of this shift? It could be related to another aspect of Jensen and Lisman model [13] accounting for the Cavanagh effect [8]. Cavanagh reviewed the literature on memory scanning and on memory load. He showed that, for a given memorized material, there exists a correlation between memory load and scanning time. In the Jensen and Lisman model, this means that the frequency of the gamma rhythm is adjusted to the material to be stored, but once this value is set, it stays approximately constant whatever the number of item stored. Shifting of the driving patterns on the frequency range between the previous studies [4,5] and the present one is well explained by such frequency changes. On the other hand, Fig. 6b shows that the internal rhythm did not change for the three list lengths. The stability of the position of the driving pattern whatever the list length suggests a constant pacemaker frequency. In summary, it seems that the cognitive system is able to chose its optimized working frequency depending on the task, in the present study a memory retrieval of digits. Once the pacemaker frequency is set, it remains stable across the variation in the main parameter of the task, the number of items to memorize.

Acknowledgements

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