Influence of temporal information gaps on decision making: describing the dynamics of working memory

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Abstract

During decision making, choices are made based on assessing potential options and their expected outcomes. Traditional laboratory investigations of decision making often employ tasks involving the discrimination of perceptual evidence, where sensory information is constant and presented continuously. However, during natural behavior, this is unlikely the case. Usually, perceptual information is dynamic and presented intermittently, which requires maintaining information in memory. Thus, understanding decision making requires considering the dynamics of working memory. Here, we used a perceptual decision-making task where fifteen tokens jump from a central circle to one of two peripheral ones and disappear shortly after. Participants were required to report which target they believed would have received most tokens by the trial's end. Half of the trials included a temporal gap, during which no information was displayed. In those cases, we found that participants made choices with less available information, but their accuracy remained unchanged. Computational modeling revealed that this behavior was best explained by a model in which stored perceptual information leaks away due to the arrival of new information, rather than by the passage of time. Our results provide evidence of a decision-making process that evolves even in the absence of perceptual information, challenging the idea of a frozen state resilient to temporal gaps and shedding light on the dynamics of working memory. This study highlights the importance of considering working memory dynamics in understanding decision-making processes, particularly in environments with intermittent perceptual information.

Significance statement

Our research challenges the notion of a decision-making process that freezes in the absence of perceptual information. Through a novel task with temporal gaps, we demonstrate that decision making continues to evolve even when perceptual cues are absent. Additionally, we highlight the importance of working memory dynamics in such process. We show that choices are the result of a combination of mnemonic evidence with urgency, a signal that reflects the need to respond. Computational modeling supports a working memory model where stored perceptual information leaks away due to the arrival of new events but remains stable between events. These findings offer insights into the decision-making process, emphasizing the importance of considering working memory dynamics in understanding human behavior.

Introduction

Perceptual decision making is thought to be the result of a deliberative process that takes into account sensory evidence over time (Smith and Ratcliff, 2004; Gold and Shadlen, 2007). In the majority of real-world scenarios, such perceptual evidence tends to fluctuate or be intermittently available. In those cases, a working memory mechanism becomes essential to maintain a record of information that is no longer present and to drive action (Marcos et al., 2019; Ferrucci et al., 2021). Nevertheless, despite the crucial role of working memory in keeping track of the world and guiding decisions accordingly, the study of its dynamics during decision making has been very limited. Indeed, in most decision-making models, memory emerges from the dynamics of decision making and is not considered as a distinct cognitive process. An example of this is the so-called drift-diffusion model (Stone, 1960; Van Zandt et al., 2000; Churchland et al., 2011; Cassey et al., 2014) that proposes that decisions are the result of a process that gathers

and accumulates perceptual evidence, thereby retaining previous information within this accumulation. However, while these models can elucidate behavior in situations with constant flow of information, they fail to do so when confronted with sensory evidence that varies over time (Cisek et al., 2009; Thura and Cisek, 2014; Winkel et al., 2014; Holmes et al., 2016; Ferrucci et al., 2021; Trueblood et al., 2021). This emphasizes the need for studies that specially target dynamic sensory information and investigate working-memory dynamics as a distinct process that influences decision making. Here, we employ a behavioral task along with computational models to elucidate the dynamics of working memory, with a specific focus on understanding the impact of memory degradation (Ferrucci et al., 2021).

In most laboratory studies investigating decision making, experimental paradigms entail a continuous and consistent flow of sensory information, with animals or humans being required to report their decisions at the end of such presentations (Ratcliff, 1978; Shadlen and Newsome, 2001; Roitman and Shadlen, 2002; Mazurek et al., 2003; Kiani et al., 2008; Kiani et al., 2013). In such cases of continuous information and sequential perception-action paradigms, perceptual decisions are unaffected by temporal gaps of information. This led to the proposition that, during temporal delays, a neural mechanism freezes the decision-making process (Kiani et al., 2013; Waskom and Kiani, 2018; Tohidi-Moghaddam et al., 2019; Azizi and Ebrahimpour, 2023). Such stability in the process is usually described as a sustained neuronal activity that is robust to external forces (Marcos et al., 2019). However, the results could be confounded by different factors. On the one hand, the fact that the information is continuous and consistent before and after the temporal gaps allows solving the task by gathering and evaluating the last presented information, without the need of tracking previous evidence. In such scenario, there is no need for retaining information in working memory. On the other hand, the use of a single measurement (accuracy) restricts the evaluation of behavior (Kiani et al., 2013). Indeed, recent research has highlighted the necessity of incorporating additional variables, like fluctuations in overall sensory evidence, decision times and the temporal placement of information release to fully understand the decision-making process (Kiani et al., 2008; Cisek et al., 2009; Thura et al., 2012; Brunton et al., 2013; Hanks et al., 2015; Carland et al., 2016; Piet et al., 2018; Ferrucci et al., 2021; Trueblood et al., 2021). In this work we addressed a dual challenge. First, our study investigated whether decisions are influenced by temporal gaps of information when perceptual evidence fluctuates. Second, it aimed to elucidate the dynamics of working memory, encompassing retention, updating and projection into the decision-making process throughout the acquisition of perceptual evidence. In our experimental set-up, participants were required to track perceptual information, which continuously changed over time, and to make their decision at any point of the trial, allowing for the measurement of decision times.

The experimental task was based on the tokens task (Cisek et al., 2009; Ferrucci et al., 2021). In brief, fifteen tokens appeared within a central circle on the screen and sequentially jumped to one of two peripheral circles (targets), disappearing before the next token jumped. In half of the cases, a temporal gap of information of 300 ms was introduced within the sequence of jumps (Materials and Methods). Participants were instructed to guess which of the two targets would have more tokens by the end of the trial and report their choice by placing the mouse cursor within the chosen target. Different profiles of jumps were introduced to specifically investigate the impact of the temporal gap on some of those sequences (Fig 1).

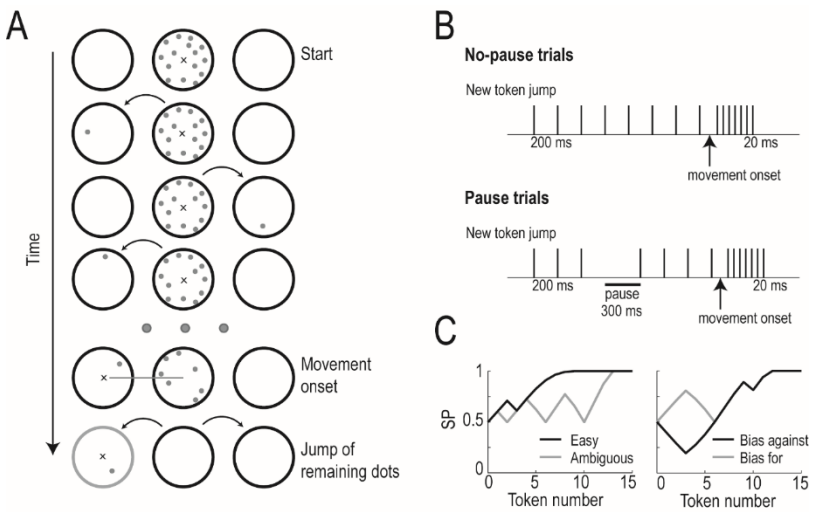

Figure 1. Experimental design. (A) *Temporal sequence of task events. At the beginning of each trial, fifteen tokens are presented on a central circle on the screen. When the participant moves the mouse cursor within the central circle, the tokens start to sequentially jump (every 200 ms) to one of the two peripheral circles (targets), disappearing shortly after. Participants are asked to select the peripheral target that they think will accumulate the majority of the tokens by the end of the trial. To make their choice, they have to move the cursor within the selected target.* ***(B)*** *Sequential order of tokens' jumps for no-pause (Top panel) and pause trials (Bottom panel).* ***(C)*** *Success probability (SP) for specific trial's profiles: easy and ambiguous trials (Left panel), bias-for and bias-against trials (Right panel).*

Results

Overall, participants performed the task with an accuracy above chance (mean accuracy: 78 ± 1 %). Moreover, the DTs, number of tokens at the target at DT and SPs were significantly different between correct and incorrect trials (Fig 2A; paired-samples *t*-test, $p < 0.01$, $t = 3.32$, $t = 3.41$, $t = -24.18$, respectively). Despite subjects exhibited longer DTs on incorrect trials, suggesting increased time for information processing, these trials also had lower SPs at DT. This counterintuitive result, however, is consistent with the observation that SPs increased rapidly with the first tokens but subsequently decreased toward the last tokens in slow decisions (Fig 2B; (Cisek et al., 2009)). Indeed, incorrect trials usually are those related with difficult perceptual information that have low SPs until the very end of the trial (Fig 1C-left). As shown in Fig 3, accuracy was modulated by the profile of the trial (Fig 1C-left), with the highest and lowest value for easy and ambiguous trials, respectively (Fig 3A; One-way ANOVA, $p < 10^{-33}$). In addition, choices were made with significantly lower number of tokens at DT for easy trials compared with the other profiles (One-way ANOVA, $p < 10^{-9}$), and the SP, aligning with accuracy, was dependent on the trials' profile (Fig. 3B; One-way ANOVA, $p < 10^{-35}$). Consistent with previous studies, these results indicate that decisions are influenced by the temporal structure of the information flow, leading to a modulation of behavior (Cisek et al., 2009; Ferrucci et al., 2021). Next, we asked whether such modulation could also be influenced by the presence or absence of the temporal gap.

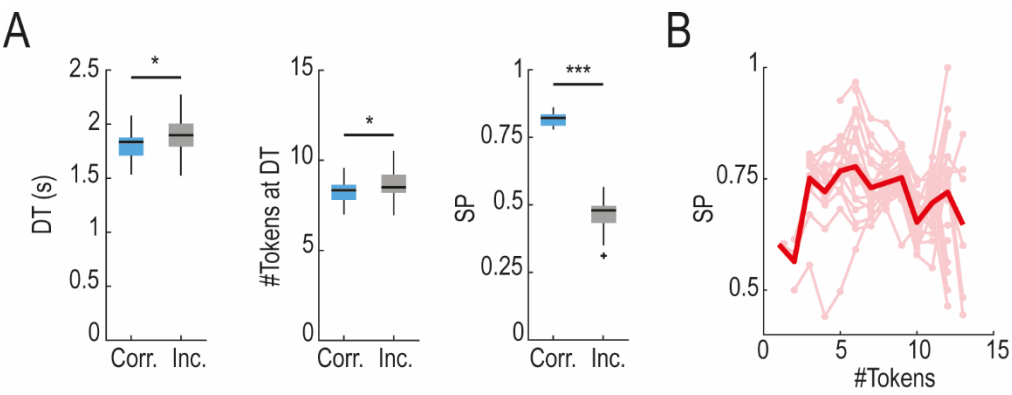

Figure 2. Behavior of subjects for correct and incorrect trials. (A) *Boxplot for DTs, number of tokens at DT and SP for all correct and incorrect trials (paired t-test, * = p < 0.01 and *** = p<0.0001).* ***(B)*** *SP for decisions made across different number of tokens at DT. Light red dots indicate the SP calculated for each subject and number of tokens at DT. Dark red line is the mean of those calculated SP values.*

Influence of time gap in decisions

Participants' responses were modulated by the presence of the temporal gap. They exhibited differences in their DTs between no-pause and pause trials, showing shorter DTs in the absence of a pause compared to trials with a pause (Fig 4A-left; paired-samples *t*-test, $p < 0.0001$, $t = 16.90$). Importantly, the time difference was shorter than the duration of the pause (mean difference in DTs ± SEM: 0.173 ± 0.123 s *vs.* 0.3 s), indicating that pause time is effectively used in the decision-making process. Otherwise, a difference in DTs between conditions equivalent to the duration of the pause would be expected. Therefore, during the pause, the decision-making process does not freeze but continues to evolve.

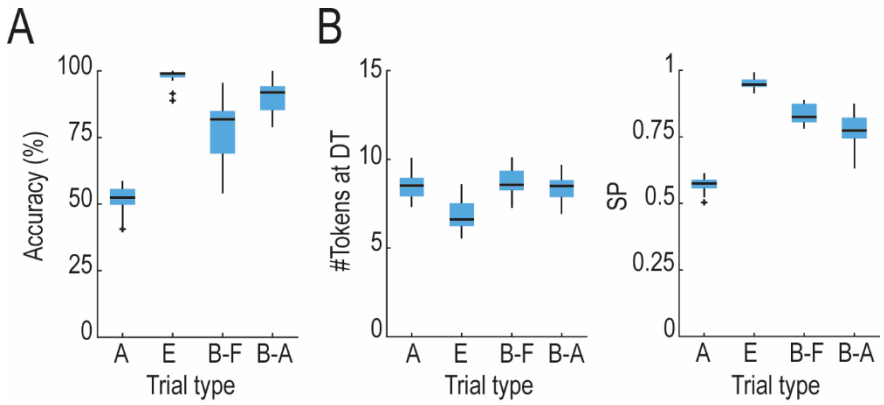

Figure 3. Behavior for subjects for specific trial's profiles. (A) *Accuracy across ambiguous (A), easy (E), bias-for (B-F) and bias-against (B-A) trials.* ***(B)*** *Number of tokens at DT (Left panel) and SP (Right panel) across correct ambiguous, easy, bias-for and bias-against trials.*

Despite the prolonged DTs observed during pause trials, this increase in DTs did not directly correlate with an increase in the amount of information used to make the decision. On the contrary, decisions were made with fewer tokens when a pause was present in the trial (Fig 4A-middle; paired-samples *t*-test, $p < 0.0001$, $t = 10.31$). Thus, choices were made with less SP for pause than no-pause trials (mean SP ± SEM: 0.80 ± 0.01 and 0.82 ± 0.01 for no-pause and pause trials, respectively; paired-samples *t*-test, $p < 0.0001$, $t = 5.89$). Interestingly, such reduction in both the number of tokens required for decision making and the SP at DT did not lead to a decrease in performance, as there was no significant difference in accuracy between conditions (Fig 4A-right; paired-samples *t*-test, $p > 0.05$). A Bayes factor of 0.25 (< 1/3) confirmed this result. Indeed, as expected, accuracy and SP were high and significantly correlated in both cases (R = 0.86 and

R=0.91, p < 0.0001, for no-pause and pause conditions, respectively), with similar linear fitted slope, but the offset of the linear curve was higher for pause than no-pause conditions (Fig 4B).

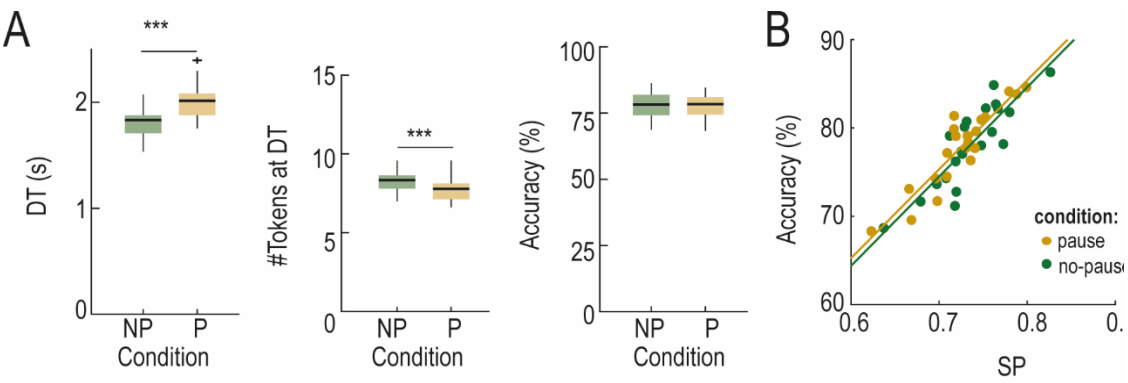

Figure 4. Behavior for subjects for pause and no-pause trials. (A) *DTs (Left panel), number of tokens at DTs (Middle panel) and accuracy (Right panel) divided into no-pause (NP) and pause (P) trials (paired t-test, *** = p < 0.0001).* ***(B)*** *SP Vs accuracy for all correct and incorrect trials divided into pause and no-pause conditions.*

Since decision made before the 4th token could potentially lead to misinterpretation of the results due to the pause occurring between the 3rd and 4th token, we repeated the analysis only for trials where decisions were made after the 4th token (98% and 96% of trials for no-pause and pause conditions, respectively). Same results in accuracy and number of tokens at DTs were observed (paired-samples *t*-test, p > 0.05 for accuracy and p < 0.0001, t = 10.13 for number of tokens at DT). The result confirmed that behavioral modulation was directly associated to the presence of the temporal gap.

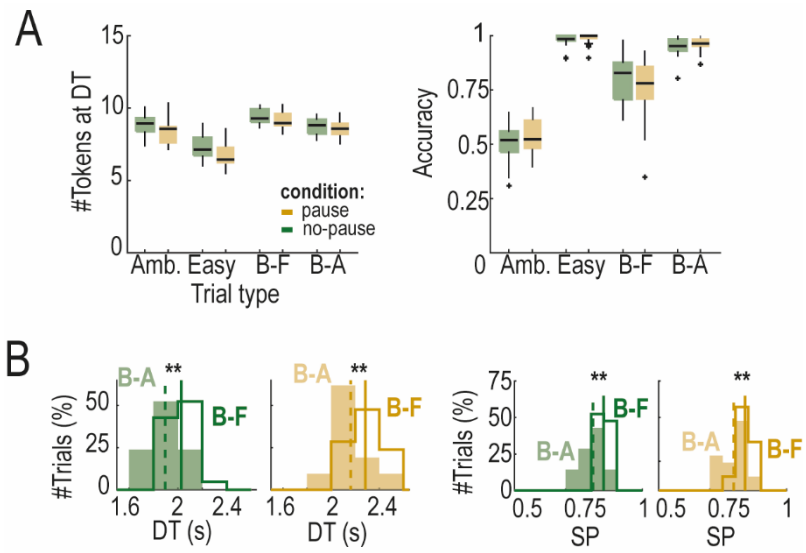

Figure 5. Behavioral modulation across trial types for pause and no-pause conditions. (A) *Number of tokens on the target at DT (Left panel) and accuracy across trial types (Right panel) for pause and no-pause conditions. In both cases, only correct trials with decisions made after the jump of the 4th token for ambiguous (Amb.) and easy trials and after the jump of the 7th token for bias-for (B-F) and bias-against trials (B-A) are considered.* ***(B)*** *Histograms of DTs (Left panels) and SPs (Right panels) observed in bias-against and bias-for trials for pause and no-pause conditions (paired-samples t-test, **= p < 0.001).*

Additionally, we examined the data by dividing it across different trial types to explore whether similar modulation of behavior could be observed when investigating specific trial profiles. To do this, we used trials with decisions made after the jump of the 4th token for easy and ambiguous trials, and after the jump of the 7th token for bias-for and bias-against trials. In these conditions, despite the overall reduction across trial types in the number of tokens at DT in the pause trials compared with the no-pause trials, there was not a significant difference between them (Fig 5A-left) and neither in accuracy (Fig 5A-right; two-way ANOVA, no interaction effect between trial type and condition, $p>0.05$). Nevertheless, there was a main effect in the number of tokens (pause/no-pause; two-way ANOVA, $p<0.01$, $F=73.6$ and $F=10.02$, respectively), but not in accuracy (two-way ANOVA, $p>0.05$). This is again consistent with a variation in the amount of perceptual information available at DT between conditions (pause/no pause trials) throughout the experiment, even when only trials with specific profiles are considered. Moreover, consistent with previous work (Ferrucci et al., 2021), we found a significant difference between DTs and SPs in bias-against compared to bias-for trials both, in no-pause trials (paired-samples t-test, $p < 0.001$, $t = 4.70$ for DTs and $p < 0.001$, $t = 4.17$ for SPs) and pause trials (paired-samples t-test, $p < 0.001$, $t = 4.11$ for DTs and $p < 0.001$, $t = 4.03$ for SPs), with longer DTs and higher SPs in bias-for than in bias-against trials (Fig 5B). This behavior is consistent with the idea of a working memory process that stores information that degrades during the course of the trial (Ferrucci et al., 2021).

	ν	η	θ	L_e
Time-related	3,1073±0,1761	0,3384±0,0613	656,6393±3,6655	0,0036±0,0006
Event-related	2,9331±0,1643	0,2998±0,0611	655,4273±3,5266	0,0684±0,0102

Table 1. *Value of the free parameters estimated for the two models. The values are averaged across subjects (± SEM).*

Therefore, a temporal gap introduced within the course of some trials modulated DT of choices and the perceived amount of information. Surprisingly, this manipulation did not affect the accuracy of choices. Moreover, the gap did not alter the modulation of behavior in two trial types (bias-for/bias-against), characterized by contrasting information presented before the pause. Hence, a pivotal question emerges: what are the underlying dynamics of working memory that shape the decision-making process? In other words, does the retention of previously stored information degrade as a function of time or due to the arrival of new information?

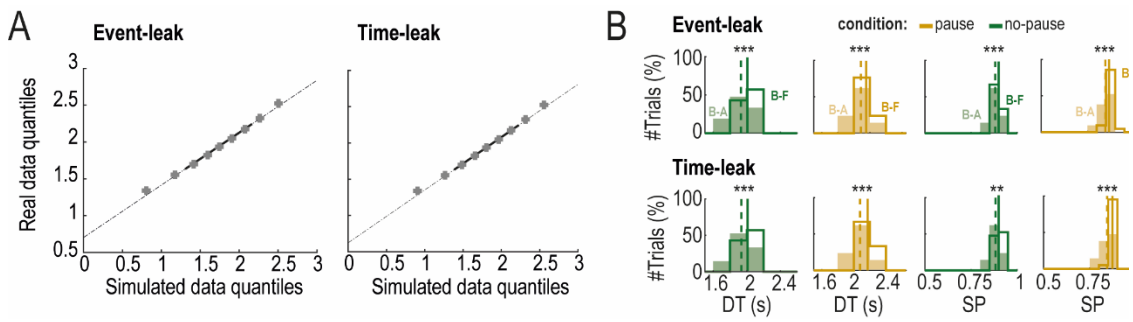

Figure 6. Quantile-quantile plot for DTs obtained from simulated and real data and reproduced DTs and SPs. (A) *The distribution of DTs obtained from experimental data is compared with that obtained from data simulated with event-related leak (Left panel) and time-related leak in working memory (Right panel). In both cases, the data points are linearly correlated ($R=0.99$, $p < 0.001$). For each dataset, correct and incorrect data are pooled together.* ***(B)*** *Histograms of DTs (Left panels) and SPs (Right panels) observed in bias-against and bias-for trials for pause and no-pause conditions and for the event-leak (Top panel) and the time-leak (Bottom panel) models (paired-samples t-test, **= $p < 0.001$).*

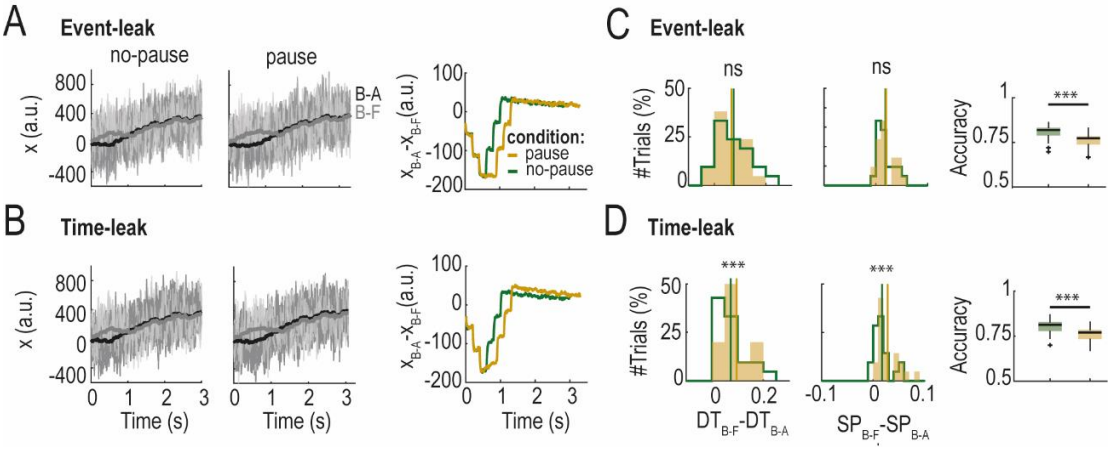

Figure 7. Activity of simulated data. (A) *Example of the simulated value of the activity across time of the event-related leak in working memory model. Left panel, example trials and mean activity for bias-against and bias-for trials in no-pause (top) and pause conditions (bottom). Dark colors show the mean activity over 1,000 trials. Right panel, mean difference of activity between bias-against and bias-for trials in no-pause and pause conditions.* ***(B)*** *Example of simulated value of activity across time of the time-related leak in working memory model for bias-for and bias-against trials. Right and left panels, same conventions as in (A).* ***(C)*** *Predictions of the event-related leak in working memory model. Top panel, difference in DTs (left) and SPs (right) between bias-against and bias-for trials between no-pause and pause conditions. Bottom panel, overall accuracy in no-pause and pause conditions (paired samples t-test, *** = $p < 0.0001$).* ***(D)*** *Predictions of the time-related leak in working memory model. Top and bottom panels, same conventions as in (C) (paired-samples t-test, *** = $p < 0.0001$).*

Leakage of information depends on the arrival of new information

To characterize the dynamics of memory during the decision-making process, we simulated an urgency-gating model featuring two types of memory. One involves gradual leakage of information over time, while the other involves information leakage related to the presence of new events (Materials and Methods). In both cases, the working memory is responsible of remembering past information and updating it with new one. Then, this information is projected into a decision-making process that ultimately decides which choice to make. We used a differential evolution algorithm to fit the experimental data with the two computational models, using the experimental data from easy, ambiguous, bias-for and bias-against trials. The estimated parameters for each model are shown in Table 1. Overall, the two models were able to fit the data with similar precision (Fig 6A), with a simulated distribution similar to the real one across the two scenarios. Moreover, both reproduce significant differences between DT and SP for bias-for and bias-against trials in the two conditions (Fig 6B; event-related leak: paired samples t-test, $p < 0.0001$, $t = 5.74$ and $t = 5.56$, $t = 5.29$ and $t = 5.29$ for DTs and SPs and no-pause and pause conditions, respectively; time-related leak: paired samples t-test, $p < 0.001$, $t = 5.81$ and $t = 6.89$, $t = 4.84$ and $t = 6.15$ for DTs and SPs and no-pause and pause conditions, respectively).

The critical difference between the models lies on the predictions they made concerning the difference in DTs and SPs in bias-for and bias-against trials for no-pause and pause conditions. Therefore, the profile of these trials becomes crucial in discerning between event-related or time-related information leakage. The reason is that the only divergence between the two trial types occurs in the initial six tokens with a reversal point after the 3th token (Fig 1C-right). The introduction of a temporal gap immediately at such point has the potential to either modify or leave unaffected the observed behavioral disparity between these two trial types (Ferrucci et al., 2021). Specifically, in the event-related leak model, the difference in activity of the decision-making model between bias-for and bias-against pause trials becomes equivalent to that in the no-pause condition after the pause concludes (0.9 s after the start of the trial; Fig 7A). In other words, before the jump of the 4th token, the difference in activity between the two trials' profile

across conditions becomes identical but delayed in time. Conversely, in the time-related leak, the pause amplifies the difference in activity between bias-for and bias-against trials and this difference persists for the rest of the trial (Fig 7B). As a consequence, these distinct dynamics yield differing testable predictions. On the one hand, the event-related leak predicts no significant difference between the modulation of DT and SP for bias-for and bias-against trials in pause and no-pause conditions (Fig 7C). On the other hand, the time-related leak model predicts a significant difference between DT and SP, with the modulatory effect between trial types being magnified by the presence of the pause. None of them, however, reproduced no differences in accuracy between pause and no-pause trials, in contrast to the real data (Fig 4A-right). We explore the possible explanation for this later.

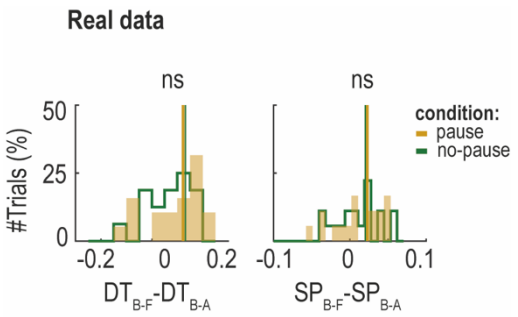

Figure 8. Lack of modulatory effect of pause in behavior of specific trial profiles. *Histograms of the difference between DT (Left panel) and SP (Right panel) in bias-for and bias-against trials in pause and no-pause conditions.*

The experimental data corroborated the predictions made by the event-leak model (Fig 8), with subjects showing no differences in the modulation of behavior between bias-for and bias-against in pause *vs*. no-pause conditions (paired-samples t-test, $p > 0.05$). This result was further support by a Bayes factor of 0.26 (< 1/3). Thus, our results suggest that information stored in working memory leaks away due to the arrival of new perceptual information, thereby influencing behavior when this information is processed by a decision-making module. This is supported by the fact that the time-leak model predicts changes on the difference between DT and SP on specific trial types across conditions, a prediction that diverges from the experimental findings.

Temporal gap modulates urgency

An intriguing observation from our experimental data is the absence of a discernible impact of the temporal gap on participants' overall accuracy. This phenomenon defies explanation within the framework of the two models we employed, in which we assumed that the parameters remained constant across trials, regardless of the experimental condition (Materials and Methods). It appears that the assumption of parameter stability may not hold true; instead, it seems that certain decision-making parameters could be influenced by the unique dynamics of individual trials. We posit a hypothesis: the temporal gap may exert a modulatory effect on the urgency signal's value, diminishing it due to the absence of token jumps during the pause. Such modulation could potentially increase the amount of information perceived, by transiently attenuating the urgency to respond, thereby augmenting the likelihood of correct responses. To explore this possibility, we conducted an additional series of simulations. Our findings revealed that a change in the level of urgency during the pause could potentially normalize accuracy between conditions (Fig 9A-left). This phenomenon persists even if the number of tokens at DT is lower for pause than no-pause conditions (Fig 9A-right). In other words, the effect remains even if the value of urgency is still higher before the 4th token for pause than no-pause conditions. Additionally, the lack of variation in the difference in DT and SP between bias-for and bias-against trials remains unaffected by the modulation of urgency (Fig 9B). Hence, our results indicate a potential influence of the temporal gap on participants' sense of urgency, offering a plausible explanation of the observed experimental outcomes.

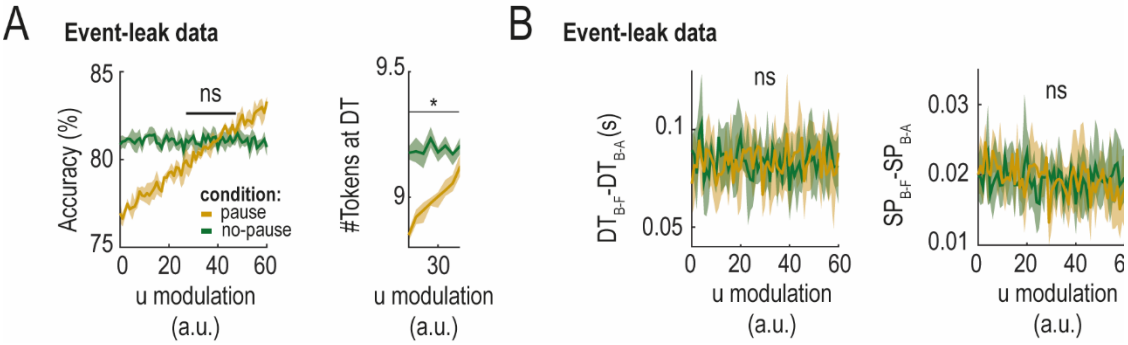

Figure 9. Modulation of urgency by pause onset. (A) *Simulated accuracy and number of tokens at DT for pause and no-pause conditions across different levels of urgency modulation (paired samples t-test corrected for multiple comparisons, * = p < 0.01; ns, non-significant difference). Shaded colors indicate the interquartile range.* ***(B)*** *Difference between DT and SP for bias-for and bias-against trials in pause and no-pause conditions. Same conventions as in (A).*

Discussion

Our findings challenge the notion of a static decision-making state during temporal gaps of information, revealing a continued evolution of the decision-making process in the absence of sensory evidence, resulting in observable behavioral modulations. Additionally, our results demonstrate that information stored in memory leaks away due to the arrival of new perceptual information but remains stable between events. During decision making, the mnemonic information is combined with an urgency signal that reflects the internal need to make a choice and that continues to evolve even in the absence of sensory evidence. Overall, our study provides compelling evidence of a decision-making process that not only evaluates perceptual information but also considers the "pressure" to make a decision as a critical variable to guide behavior.

In recent decades, various decision-making theories have emerged. The prevailing view in the literature suggests that decisions are made by accumulating sensory evidence until it reaches a decision boundary (Stone, 1960; Van Zandt et al., 2000; Brown and Heathcote, 2008; Churchland et al., 2011; Bollimunta et al., 2012; Cassey et al., 2014; Dutilh et al., 2019). Although this framework could explain many behavioral and neuronal observations, it fails to explain behavior when information continuously fluctuates (Cisek et al., 2009; Ferrucci et al., 2021) (Winkel et al., 2014; Holmes et al., 2016; Trueblood et al., 2021), as it commonly occurs in natural conditions. Under these circumstances, decisions cannot be made instantaneously, and thus a memory is necessary to build a representation of non-present information and to update it with upcoming one. Therefore, memory needs to be stable enough to retain information across time, but flexible enough to be updated when new information in available. Here, we have proposed a basic equation to model this process, where previous information is retained but degrades when new information arrives. How this computation is implemented by neuros in the distributed memory network remains unaddressed. One plausible explanation is that a combination of cells with heterogeneous excitability interact with each other, generating stable yet adaptable dynamics (Marcos et al., 2019). Nevertheless, to provide a definitive answer to this question, further experiments involving animals and electrophysiology are imperative.

The experimental task used in this study relies on non-noisy sensory information. A potential concern about our findings might be their extension to scenarios involving noisy sensory evidence (Roitman and Shadlen, 2002; Kiani et al., 2013; Marcos et al., 2015). However, a previous study using a task similar to ours but with noisy stimuli revealed no discernable difference in decision-making dynamics compared to those observed with non-noisy stimuli (Cisek et al., 2009; Thura et al., 2012; Ferrucci et al., 2021). Building upon these findings, it is reasonable to infer that if no distinctions emerge at the decision-making level, a similar principle likely applies to the dynamics of memory. Although we believe that the alternative scenario is

highly improbable, this claim needs to be confirmed through additional experiments where memory is necessary to keep track of noisy information.

Our results indicate that participants have the ability to measure time, and not only evidence, as a reference to respond. Indeed, both non-human and human animals are capable of monitoring the timing of their decisions. For example, studies have revealed that rats accurately assess and report the magnitude of their timing errors in self-generated intervals (Kononowicz et al., 2022). Neuronal activity in the lateral intraparietal cortex, which is closely associated with decision-making processes (Huk and Shadlen, 2005), has been shown to encode elapsed time when non-human primates must decide based on it (Leon and Shadlen, 2003; Janssen and Shadlen, 2005). Similarly, in humans engaged in tasks where a cue prompts a response, there is evidence supporting the existence of a decision bound that concludes the decision-making process before such a cue is presented (Smith and Ratcliff, 2004; Gold and Shadlen, 2007; Waskom and Kiani, 2018).

In contrast to previous studies, our results show an effect of a temporal gap of information on behavior (Kiani et al.; Waskom and Kiani, 2018; Tohidi-Moghaddam et al., 2019; Azizi and Ebrahimpour, 2023). It is important to note that our experimental design differs significantly from those studies in key aspects. On the one hand, in all previous cases the task included a go signal that instructed the participants to make a choice. By contrast, in our experimental task participants were allowed to respond at their own discretion, potentially enabling them to manage their speed-accuracy trade-off, through a growing urgency signal (Cisek et al., 2009). On the other hand, the perceptual evidence presented in our task is dynamic and, thus, changes continuously throughout the entire duration of a trial. Overall, our findings emphasize the importance of considering both accuracy and decision times as behavioral measures to fully understand the decision-making process. Furthermore, it is crucial to include time-varying information into the experimental designs, mimicking real-world scenarios, to understand perceptual decisions in more natural contexts.

The urgency signal, a time-varying signal reflecting the imperative need to commit to a choice, has gained increasing attention in recent experimental and theoretical studies (Carland et al., 2016). The neural mechanisms of such urgency have been widely studied (Hanks et al., 2014; Thura and Cisek, 2014; Braunlich and Seger, 2016; van Maanen et al., 2016; Thura and Cisek, 2017). For instance, during decision making, neural activity in specific brain areas, such as the dorsal premotor and primary motor cortex, exhibit signatures of tracking sensory information while combining it with an urgency signal (Thura and Cisek, 2014). Signatures of such urgency can be found in the basal ganglia (Thura and Cisek, 2017). Various models have approached the influence of urgency on decision dynamics differently. Some models propose that perceptual signals are gained modulated by urgency, while others suggest that urgency directly affects decision bounds, causing them to converge with time (Ditterich, 2006b, a; Churchland et al., 2008; Cisek et al., 2009; Hawkins et al., 2015; Carland et al., 2016; Murphy et al., 2016; Ferrucci et al., 2021). In this study, we have proposed that an urgency signal gain modulates perceptual evidence in an additive manner. The rationale for this choice is to maintain the neutrality of urgency in the decision process, allowing us to study working memory dynamics without additional influencing factors. This is particularly important when comparing between specific trial types in cases of a temporal gap or of the absence of it, where time has passed differently. For instance, if a multiplicative combination of perception and urgency were employed, it would result in a differential enhancement of the difference between trial types across conditions. This could lead to predicted behavioral differences directly tied to the specific manner in which the two signals are combined.

Our results suggest that a temporal gap between streams of information modulates the urgency to make decisions. One possible explanation for this modulation is that the system, upon encountering an interruption in the flow of information, slows down to gather additional information before committing to a choice. This directly connects SP with urgency and aligns with the concept of adjusting the speed-accuracy trade-off by modulating urgency (Thura et al., 2014; Carland et al., 2016). This modulation is sufficient to explain the absence of differences in

accuracy between pause and no-pause conditions in our experiment, even though decisions are still made with lower SP (Fig 4B). This could be attributed to SP being substantially above chance at the time of choice, with little additional information gained from waiting longer.

Special interest has been placed on persistent activity as a way of representing information that is no longer present in the environment (Fuster and Alexander, 1971; Wilson et al., 1993; Tsujimoto et al., 2008; Genovesio and Tsujimoto, 2014; Marcos et al., 2019). In the prefrontal cortex, neurons encoding the previous outcome exhibit persistent activity with some decline (Marcos et al., 2016). In most cases, neuronal firing decline is related with the passage of time, with a minority of them being associated with the presence of a new event. Here, we showed that information in working memory seems to mainly decline due to the arrival of new information. However, it is also possible that the passage of time has an impact on the dynamics of memory in some circumstances, and that a mixture of both factors needs to be considered. For instance, in cases in which the working memory capacity is pushed to its limit, any new information to be stored could replace the previously stored one while being also weaken by the passage of time (Zhang and Luck, 2008; Fukuda et al., 2010). How the two leakage processes – time-leak and event-leak - interact with each other is an open question.

Materials and Methods

Participants

Twenty-one participants performed the experimental task (aged 23-42; all right-handed except one; ten females). All experimental procedures were in accordance with the ethical standards of the university research committee, with the Code of Ethics of the World Medical Association (Declaration of Helsinki, 1964) and its later amendments. The experimental protocol was approved by the Ethics Committee of the Miguel Hernández University/CSIC/Institute of Neurosciences of Alicante. Before performing the tasks, all participants provided written consent.

Experimental task

Each participant performed five blocks of perceptual decision-making trials that contained pause and no-pause trials in a random order. To avoid random guessing, the participant had to make 100 correct trials to complete each block. The experimental paradigm was based on the modified version of (Cisek et al., 2009) presented in (Ferrucci et al., 2021). A BENQ GL2580 monitor (24.5’’) was used to display the visual stimuli for the task and a mouse was used as an interface between the participants and the computer. The participants sat in front of the screen at approximately 60 cm.

At the beginning of each trial, three circles with white outlines were displayed on a black screen, each measuring 2.5 cm in diameter (Fig 1A). The central circle, positioned at the center of the screen, contained 15 tokens randomly distributed within its area. Two additional circles, designated as targets, were placed 5 cm on either side of the central circle. To initiate a trial, the participant was required to place the mouse cursor inside the central circle. Subsequently, the tokens began to jump to one of the two peripheral circles every 200 ms, disappearing just before the subsequent token’s jump. Participants were free to report their decision at any moment before the last token’s jump, and were instructed to report their choice by moving the cursor inside one of the peripheral circles. Following their selection, the outline of the chosen circle changed from white to green for correct choices and to red for incorrect choices. After feedback, the remaining tokens jumped to one of the peripheral circles every 20 ms. Consequently, participants could save time by making rapid choices, encouraging the participants to respond before the trial concluded. If the choice was not made before the last token’s jump, no feedback was provided. A time interval of 500 ms separated the end of a trial from the beginning of the next.

Two conditions were introduced in the sequence of jumps: trials with a 300 ms temporal gap before the jump of the fourth token, termed *pause trials*, and trials without such a gap, termed *no-pause trials*. The temporal gap consisted of a period where no jumps occurred and no

information was available on the screen. The specific position of the temporal gap within the token's sequence was selected to maximize its potential effect on behavior (see below). Within each block, half of the trials were pause trials and both conditions were randomly interleaved within the block.

At each time in the trial, the success probability (SP) to select target 1 over target 2 could be calculated as (Cisek et al., 2009; Ferrucci et al., 2021):

$$P(C|N_1, N_2, N_r) = \frac{N_r!}{2^{N_r}} \sum_{k=0}^{\min(N_r, 7-N_2)} \frac{1}{k!\,(N_r - k)!}$$

where $P(C|N_1,N_2,N_r)$ was the chance that target 1 was correct (C) when there were N_1 tokens in target 1, N_2 tokens in target 2, and N_r tokens still remaining in the central circle. SP is calculated with respect to the chosen target.

In each of the five blocks, we included five trial types, in equal proportion (20%): "random", "easy", "ambiguous", "bias-for" and "bias-against" (Cisek et al., 2009; Ferrucci et al., 2021). In random trials, the direction of token jumps was randomly determined. Easy trials involved most tokens jumping to the correct target while ambiguous trials featured an even distribution of tokens between the two targets until just before the trial's end (Fig 1C-left). The bias-for and bias-against trials were particularly effective in discerning between leakage in memory during decision making (Ferrucci et al., 2021). The reason is that these two trial types differ solely in the direction of the first six tokens' jumps, which is completely opposite, with the highest divergence occurring after the 3rd token jump (Fig 1C-right). Introducing a temporal gap immediately after this jump has to potential to significantly alter the behvioral differences between the two trial types. Random trials were included to prevent subjects from anticipating the trial pattern.

To estimate decision times (DTs), participants performed an additional set of 40 trials where only one token jumped to one of the targets, randomly. The interval from the token's arrival at the target to the moment the mouse cursor left the central circle to report the choice established the subject's baseline reaction time (RT). The baseline RT was subtracted from the RT recorded from the main task. The RT in the main task was estimated by subtracting the trial's start time from the time of maximum acceleration of the cursor. By employing this method, we mitigated the influence of trials in which participants moved the cursor from the central circle but experienced delays in making their selection (~10% of trials). Number of tokens and success probabilities were then computed based on the estimated DT.

Unless otherwise stated, all analyses are performed on correct trials.

We controlled the lack of awareness of either the temporal gap or the trial types with a questionnaire, provided at the end of the experimental session. Only one participant reported the presence of the gap.

Computational model

Sensory evidence. The perceptual evidence in working memory was estimated as:

$$\frac{de_{leak}}{dt} = \frac{de}{dt} - L_e e_{leak}$$

where L_e represents a leakage term for perceptual information stored in memory and $\frac{de}{dt}$ is the change in the perceptual evidence displayed on the screen. Specifically, $\frac{de}{dt}$ is defined as:

$$\frac{de}{dt} = \delta_{t,t_R} - \delta_{t,t_L}$$

where the delta functions represent the jump of a token to either right ($\delta_{t,t_R} = 1$) or left ($\delta_{t,t_L} = 1$).

Throughout a trial, the value of L_e is different from 0 when simulating leakage in working memory associated with the passage of time (*time-leak* model). On the contrary, L_e differs from 0 exclusively when a new event occurs – a token jump - in cases related to information leakage resulting from the arrival of new events (*event-leak* model).

Urgency-gating model. The computational model simulated in this study is an urgency-gating model with the following dynamics:

$$x_{t+\Delta t} = \frac{\tau}{\tau + \Delta t} x_t + \frac{\Delta t}{\tau + \Delta t} (\nu e_{t+\Delta t} \Delta t + s\xi\sqrt{\Delta t})$$

where x describes the state of the process at time t and t+Δt, ν is the drift rate, Δt is the step size of the simulation, e is the sensory evidence provided by memory, s is a scaling factor and ξ is an independent and identically distributed random sample taken from a standard normal distribution. In each trial, the drift rate ν was sampled from a normal distribution with mean ν and standard deviation η. The leaky term was implemented using as a low-pass filter with a time constant denoted as τ(10 ms). An urgency signal, which increases with the time elapsed since the initiation of the decision-making process ($u_t = u_{sign} \cdot t$), was added to the instantaneous value of the accumulation of evidence. The sign (u_{sign}) of the urgency signal favored the sign of the accumulation. The decision was considered to be made when $x_{t+\Delta t} + u_{t+\Delta t} > \theta$ or $x_{t+\Delta t} + u_{t+\Delta t} < -\theta$ and the corresponding decision time was estimated as $t - \frac{\Delta t}{2}$.

In the two models of working memory, parameters ν, η, θ and L_e are free parameters that were estimated with a fitting procedure that optimized the goodness of fit. The step size Δt was set to 10 ms and the scaling factor s was arbitrarily set to 100.

To illustrate the dynamics of the two computational models, we performed simulations with the mean value of the best set of fitted parameters. We ran 10,000 trials and randomly selected 1,000 of them to show the individual and mean activity of some example trials, as well as the models' predictions.

To modulate the urgency signal, we included an offset that was subtracted from the instantaneous value of u_t at pause onset, in the pause condition. Then, the urgency value increased following the same rate as before.

Estimation of model parameters

The free model parameters (ν, η, θ and L_e) were estimated independently for each model to fit the participants' data. We used the quantile maximum products estimation (QMPE) (Heathcote et al., 2002; Ferrucci et al., 2021), dividing DTs into quantiles for correct and error trials. The QMPE estimates the similarity between simulated and real data by comparing the proportion of data within each quantile. We used a differential evolution algorithm to maximize the goodness of fit (Mullen et al., 2011; Ardia et al., 2013), with broad parameters boundaries and executing 100 particles for 500 search iterations. To mitigate the risk of local minima, this parameter estimation process was repeated five times for each model and participant's data. Model predictions were assessed through Monte Carlo stimulation, generating 10,000 replicates for each experimental condition. Upon termination of the search, data was simulated using the parameters set that yielded the highest goodness of fit.

The data fitting procedure was performed using all trials, including correct and errors, across easy, ambiguous, bias-for and bias-against trial types and pause and no-pause conditions.

Statistical tests

The normality of datasets was tested using the Shapiro–Wilk test.

Bayes Factors (Rouder et al., 2009) were calculated using a Cauchy distribution with a scale factor of 0.707. A Bayes Factor lower than 1/3 indicates evidence for the null hypothesis (Jeffreys, 1961).

Data and code availability

The data and code for computational modelling used in this study, as well as any additional information are available from the corresponding author upon request.

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