



## Static internal representation of dynamic situations reveals time compaction in human cognition



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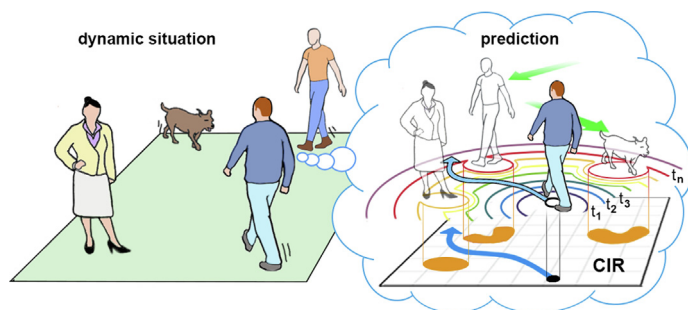
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### GRAPHICAL ABSTRACT



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### ABSTRACT

**Introduction:** The human brain has evolved under the constraint of survival in complex dynamic situations. It makes fast and reliable decisions based on internal representations of the environment. Whereas neural mechanisms involved in the internal representation of space are becoming known, entire spatiotemporal cognition remains a challenge. Growing experimental evidence suggests that brain mechanisms devoted to spatial cognition may also participate in spatiotemporal information processing.

**Objectives:** The time compaction hypothesis postulates that the brain represents both static and dynamic situations as purely static maps. Such an internal reduction of the external complexity allows humans to process time-changing situations in real-time efficiently. According to time compaction, there may be a deep inner similarity between the representation of conventional static and dynamic visual stimuli. Here, we test the hypothesis and report the first experimental evidence of time compaction in humans.

**Methods:** We engaged human subjects in a discrimination-learning task consisting in the classification of static and dynamic visual stimuli. When there was a hidden correspondence between static and dynamic stimuli due to time compaction, the learning performance was expected to be modulated. We studied such a modulation experimentally and by a computational model.

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**Results:** The collected data validated the predicted learning modulation and confirmed that time compaction is a salient cognitive strategy adopted by the human brain to process time-changing situations. Mathematical modelling supported the finding. We also revealed that men are more prone to exploit time compaction in accordance with the context of the hypothesis as a cognitive basis for survival.

**Conclusions:** The static internal representation of dynamic situations is a human cognitive mechanism involved in decision-making and strategy planning to cope with time-changing environments. The finding opens a new venue to understand how humans efficiently interact with our dynamic world and thrive in nature.

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## Introduction

Time is ubiquitous in our world and essential for understanding physical reality. But to what extent does our brain use it for interacting with the environment? An explicit encoding of time is critical for the proper structuring of episodic memory [1]. It is also mandatory for anticipating complex dynamic hazards, which has been hypothesized as the ultimate brain function [2]. Therefore, significant brain resources are devoted to the processing of spatiotemporal sensory information [3–5].

Neural bases and their cognitive correlates for processing static, i.e., purely spatial or time-invariant, situations are reasonably well established [6]. Current studies mainly focus on spatially selective neurons as place cells in the hippocampal formation, responsible for codifying the subject's position in space [7] and grid cells in the Entorhinal cortex, providing a spatial metric for the surrounding environment [8].

Nonetheless, there is little knowledge on the mechanisms underlying cognitive processing of time-changing situations. Growing experimental evidence suggests that brain mechanisms devoted to spatial cognition may also be involved in the processing of spatiotemporal information. At the neuronal level, temporal sequences of animal locations are encoded in the firing timing of place cells [9–11]. Moreover, these neurons are also involved in integrative processing of space and time, since some of them simultaneously behave as time cells [12]. Besides, these cells exhibit predictive activity during trajectory planning in path integration [13]. Thus, there are critical neural processes where time and space are deeply intertwined. Therefore, the relevant question is how this spatiotemporal entanglement is present in the brain at the functional level. An answer to this question may open novel venues for studying efficient survival behavior and decision-making in humans.

Mental navigation, though requiring specific processing of time, involves adaptive temporal mechanisms mediated by prospection of combined spatial representations [14]. In this sense, the interplay between time and space is particularly prominent in memory, where they act as crucial contexts for binding object information to support a cued recall [15]. This led to the conclusion that one of the critical areas shaping cognition, the hippocampus, must be involved in the general structuring of spatiotemporal experiences, far beyond the mere spatial domain, the function widely ascribed to it nowadays [16,17]. Therefore, converging experimental evidence suggests that coding and representation of space and time in the brain, far from being independent processes, are notably interweaved [18,19]. This spatiotemporal entanglement could be exploited in the context of generating complex behaviors since the time dimension introduces massive redundant information, which can impede fast and accurate processing of experiences. The latter is a paramount requirement for success during survival actions such as hunting, fighting, and escaping, which require real-time decision making in narrow time windows [20].

An effort for resolving the conflict “fast vs. complex” led to a theoretical hypothesis called *time compaction*, which exploits the

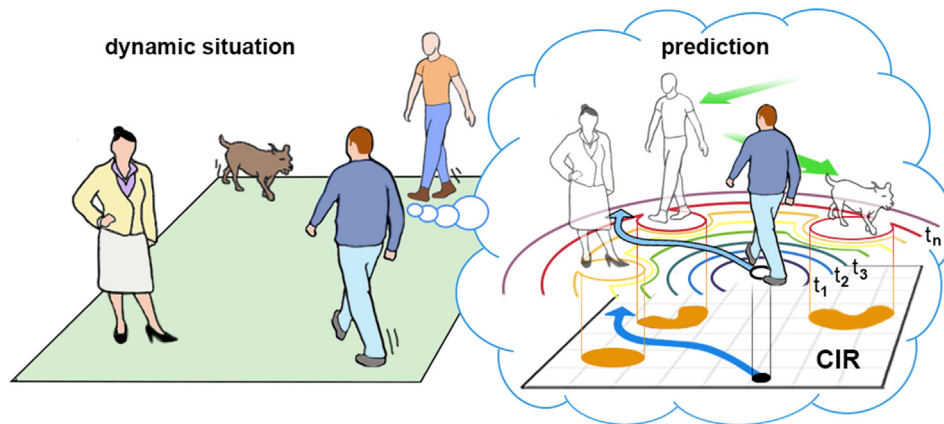
entanglement of space and time in the brain [21]. It states that when dealing with time-changing situations, *the brain does not encode time explicitly but embeds it into space*. Theoretically, time compaction can significantly decrease the complexity of internal representations and hence reduce brain resources involved in trajectory planning, e.g., when moving among multiple obstacles [22]. It also provides a natural framework for the cognitive processing of dynamic situations and serves as a building block for constructing episodic memory [23]. However, the experimental validation of this hypothesis has lacked until now. In this work, we focused on the behavioral aspect of the hypothesis, relevant for understanding survival behaviors. Our results show that humans use spatial (i.e., static) internal representations of the spatiotemporal (i.e., dynamic) situations as a cognitive strategy.

## Hypothesis of time compaction

Static situations (e.g., a room with furniture or a maze) described by the position of objects, their shapes, textures, colors, etc. can be extremely complicated. This complexity is further multiplied in time-evolving scenarios, which can also last rather long in time. Thus, it is highly unlikely that the brain encodes all dynamic situations explicitly. This constraint has dramatic consequences in situations when a subject's survival depends on making fast and reliable decisions, such as fighting, hunting, escaping, etc. In short, for survival, there is no time for time. Then, there must be specific mechanisms that could drastically reduce the amount of information contributed by the time dimension. The hypothesis of time compaction proposes a solution to the antagonism “complexity vs. velocity” by addressing the challenge of spatiotemporal cognition through *embedding time into space* [21].

According to the hypothesis, a dynamic situation is internally represented as a static map, called a compact internal representation (CIR). A CIR spatially arranges future interactions among the elements in the environment, eliminating (compacting) the time from the internal representation of the faced dynamic situation. Such a collapse or compaction of the temporal dimension can provide a remarkable reduction of information to be operated by the brain. The latter enables efficient processing and learning of time-changing situations and construction of sophisticated behaviors in real-time [23]. Therefore, time compaction proposes a paradoxical formula: to deal with time effectively, the brain eliminates time.

Let us illustrate the hypothesis on a simple example of a subject walking among other agents (Fig. 1). According to the hypothesis, the subject (pedestrian in the forefront) processes the situation by (1) predicting the evolution of the situation (moving man and dog, and standing woman), and (2) simulating his possible movements at successive time instants  $t_1, t_2, \dots, t_n$  (colored curves denote the possible future subject's positions). Both processes can be implemented in neural networks (for technical details and rigorous description see, e.g., [23]). Then, the coincidences between the subject's virtual positions and other parties correspond to future collisions. These locations (orange zones in Fig. 1, right)



**Fig. 1.** Hypothesis of time compaction. *Left:* Example of a dynamic situation. To move safely, the subject (forefront) generates a CIR of the situation. *Right:* The CIR is formed by predicting the behavior of other parties (green arrows) and simulating the subject’s positions at different times (colored curves for times  $t_1, t_2, t_3, \dots, t_n$ ). Coincidences between the subject’s virtual positions and the predicted locations of the pedestrians correspond to potential collisions, represented as virtual static obstacles in the CIR (orange areas). Then, the trajectory avoiding virtual obstacles in the CIR (blue arrowed curve) allows safe navigation in the real space (light blue arrowed curve).

are virtual or mental static obstacles since the subject cannot traverse them in the future [21]. Their spatial arrangement, according to the subject’s reference framework constitutes the CIR. For safe navigation, the subject can now simply avoid virtual static obstacles, as if they existed in reality (Fig. 1, right: blue arrowed curves in the CIR and real space). Thus, the brain internally reduces the dynamic situation to the static map, the CIR, which does not explicitly contain time. In other words, it would be like transforming a movie (the time-changing situation) into a single picture (the CIR) containing the relevant information to understand the film.

Earlier it has been hypothesized that interceptive actions are mediated by processing information related to time-to-collision (TTC) [24], as suggested by timing performance experiments [25]. This evidence has led many authors to focus on the importance of temporal dimension in the processes supporting interactive tasks, leaving apart the contribution of spatial dimension [26]. The paradigm shift discussed in this work is grounded on these ideas [21] and provides answers to critical challenges in the biology of complex behaviors [20]. Fig. 1 shows that time compaction uses TTC curves, but after that, the brain abandons the time dimension and works with the pure space domain.

In general, the CIR potential goes beyond its role as a substrate for actions. CIR also provides a natural framework for learning and building memories of dynamic situations [23]. This paradigm allows storing previous experiences in a “library”. Then, such a CIR library can be used for fast navigation [23] and manipulation [27] by recalling the CIRs corresponding to given situations. Based on these features, we hypothesized that time compaction is a human cognitive mechanism mainly involved in survival-like decision-making, as attack or defense strategies during agonistic behaviors (fighting), trajectories generation (chasing and escaping), and coordination of actions among several agents (hunting). For instance, escape behaviors engage a wide range of processes from simple stimulus reactions (i.e., reflexes) to decision-making, and action selection [28,29]. The flexibility required to survive in dynamic environments ultimately comes from the cognitive control of these processes. A subject escaping from another one must quickly compute and decide between alternative trajectories [30,31], which can be attained by recalling CIRs.

We remark that a CIR is constructed by a simultaneous simulation of all possible subject’s actions [21]. Therefore, it contains different navigation strategies. For instance, in Fig. 1, the subject follows the trajectory marked by the blue arrow, which is not affected by the dog’s behavior. Nonetheless, the CIR comprises tra-

jectories (not shown for clarity), avoiding the dog in case of necessity. Therefore, CIRs would be fundamental building blocks of cognition. High-level behaviors taking into account motivation, goals, and planning are constructed on top of the CIRs.

## Methods

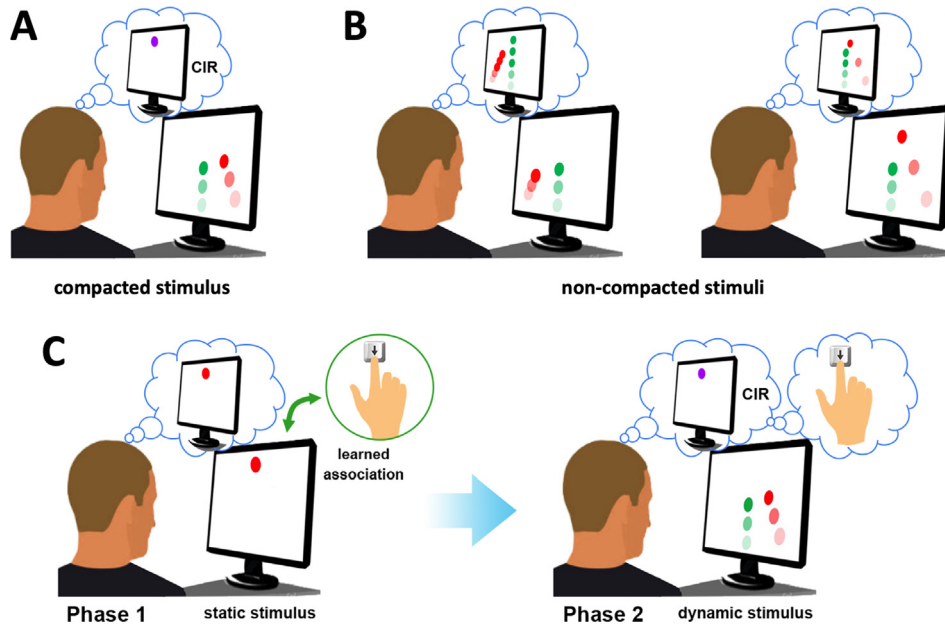
To reveal the existence of time compaction, we propose a behavioral methodology based on stimulus generalization [32,33] and inspired by classic experiments studying the cognitive processes involved in collision perception tasks [24,34].

### Design of experimental approach to test time compaction

Experimental validation of time compaction requires testing compacted versus non-compacted situations. The natural context of time compaction is when a subject takes part in a situation (as in Fig. 1). Under such egocentric scenarios, the subject is the agent who acts and affects the situation directly. Thus, there are always potential interactions leading to time compaction. Such ubiquity of the phenomenon creates a bias for its experimental testing since non-compacted situations are unlikely. We thus intentionally deviate from the natural context in searching for clear-cut evidence of time compaction.

The hypothesis states that time compaction must be a salient cognitive mechanism, independent of whether the subject participates in a situation or not. Therefore, we designed experiments using an allocentric perspective. The subject now is an observer and cannot influence the situations (see Discussion). We provide the participants with two types of visual stimuli.

1. Circles moving on a PC screen approaching in collision trajectories (Fig. 2A). Note that collision is not displayed on the screen, but the brain constructs it virtually. In this case, time compaction plays a role, thus, according to the hypothesis, the situation is compacted and represented in the brain by the colliding area only (CIR in Fig. 2A).
2. The same moving circles, but now collision is not expected (Fig. 2B). Then, the subject cannot compact the situation and resorts to represent it as a spatiotemporal structure (using initial positions, trajectories, velocities, etc.).



**Fig. 2.** From theory to experiments. *Time-compacted internal representation in allocentric context.* (A) Dynamic stimulus with future interactions is compacted and represented by its CIR (collision area). (B) Dynamic stimuli without collisions are not compacted but represented as spatiotemporal events. (C) Idea of the two-phase experiment. According to the hypothesis, in the brain a compacted dynamic stimulus and a static stimulus resembling its CIR will be closely related. Assume that in phase 1 (left), a subject has learned an association between a specific static stimulus and an arrow key (e.g., the down-arrow key). Then, in phase 2 (right), when the compacted dynamic stimulus is displayed, it will be represented by its CIR, whose resemblance with the static stimulus will elicit the same stimulus-key association, thus the subject will likely press the same arrow key (down-arrow key in the figure). Note that the moving circles are depicted as sequences of light-to-dark circles. Light and dark circles correspond to the initial and final positions of the circles, respectively. Besides, circle separation illustrates their speed: closer/further consecutive circles denote slower/faster movement (see also Supplementary Video).

Note that, following time compaction, for the brain, option 1 is less demanding than option 2.

*Experimentally verifiable predictions of time compaction*

We now exploit the similarity between the internal representations of dynamic and static situations by tailoring a two-phase experiment based on a stimulus generalization (Fig. 2C). The stimulus generalization appears when, after a behavioral response is associated with a specific stimulus, a similar novel stimulus triggers the same response [32]. During phase 1, a subject learns to associate static circles appearing at different positions on the screen (stimuli) with the up and down keyboard arrows (responses). For example, the static circle on the top-center of the screen can be associated with the down-arrow key (Fig. 2C, left). During phase 2, a subject is exposed to dynamic stimuli. According to time compaction, the situation with two circles moving in collision trajectories, even when such a collision is not displayed (Fig. 2C, right), will be internally represented as the static scene where the circle is on the top-center of the screen (Fig. 2A). Thus, following the stimulus generalization and time compaction, after the top-center circle stimulus is associated with pressing one of the arrow keys in phase 1, the presentation of the stimulus displaying colliding circles in phase 2 should trigger the pressing of the same arrow key. Note that the static and dynamic stimuli (here depicted as sequences of light-to-dark circles, see also Supplementary Video), similar under the time compaction hypothesis, differ significantly. Recent experimental findings confirm that the stimulus generalization is mediated by abstract representations [33], as the time compaction theory claims.

Therefore, if the hypothesis is correct (i.e., static and dynamic situations can be represented internally in a similar way), then prior learning of specific static scenes must accelerate or slow down the posterior learning of dynamic situations. The sign of

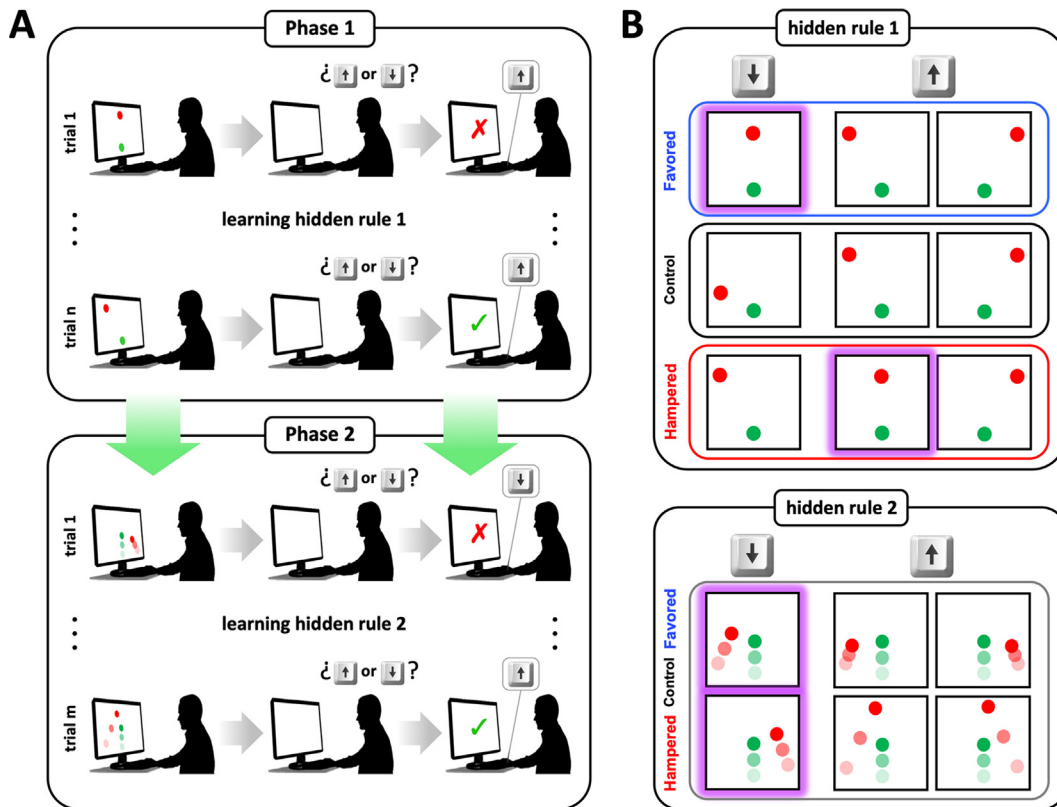
the effect will depend on the similarity/dissimilarity of the CIRs of static and dynamic situations.

*Overview of experiments*

To test time compaction predictions and rule out alternative explanations of the phenomenon, we designed different configurations of static and dynamic stimuli (see below). The participants were prompted to discover by trial-and-error two hidden rules relating the stimuli with the up- and down-arrow keys (Fig. 3A). The assignment of the keys was random for each participant. All participants were divided into four groups: (1) Control, (2) Favored, (3) Hampered, and (4) Validation.

*Experiments testing time compaction.* In this part, we deal with the first three groups of participants (the fourth group will be discussed below). During phase 1 (Fig. 3A, top panel), in each trial, a participant observes for 1.5 s one static stimulus, randomly chosen from a set of three static situations corresponding to his/her group (Fig. 3B, top panel). When the stimulus disappears, the participant presses either up- or down-arrow key. If the pressed key matches the key associated with the shown stimulus according to hidden rule 1, the participant receives positive feedback in the form of a green tick; otherwise, a red cross is displayed. This procedure is repeated until the participant figures out hidden rule 1, associating the keys with static situations.

Once phase 1 has been fulfilled (i.e., hidden rule 1 has been discovered), the participant goes through phase 2 (Fig. 3A, bottom panel), which is similar to the previous phase but now the stimuli are randomly taken from a set of six dynamic situations (Fig. 3B, bottom panel). In phase 2, all experimental groups are exposed to the same set of stimuli. Then, the participants should discover the hidden rule 2 associating stimuli with up- and down-arrow keys.



**Fig. 3.** Experimental procedure. (A) Participants go consecutively through phases 1 and 2. In each phase, they discover by trial and error a hidden rule relating the up- and down-arrow keys with the stimuli shown on the screen. In each trial, a participant receives feedback depending on whether the pressed key matches the hidden rule or not. (B) Hidden rule 1 associates the up- and down-arrow keys with the three static stimuli (a green circle located at the middle bottom part of the screen, and a red circle is at the upper part of the screen for the Favored and Hampered groups, and located laterally above the green one for the Control group). For each participant, the arrow key assignment is randomly established at the beginning of the experiment. This rule differs among Favored, Control, and Hampered groups. Note, the green circle does not carry information and is intended as a spatial reference to clearly distinguish center from sides. Hidden rule 2 is the same for all these groups. It associates the up- and down-arrow keys with the six dynamic stimuli, two dynamic matching (DM), and four non-dynamic matching (non-DM) stimuli (all dynamic stimuli show the green circle moving upwards vertically, and the red one displacing upwards diagonally). The static and dynamic matching stimuli (SM and DM) are highlighted in purple. The picture shows one of the two possible assignments of arrow keys; in the other one, the up-arrow key is changed by the down-arrow key and vice versa (dynamic stimuli are represented by sequences of light-to-dark circles as in Fig. 2, see also Supplementary Video).

During the experiments, we recorded the sequence of responses of each participant and several other measures (see below). We then expected that, according to the hypothesis, the classification performance in phase 2 was modulated by phase 1 (different among the experimental groups; Fig. 3B, top).

*Validation experiments.* To discard any potential bias inherent to phase 2 that could interfere with the learning of the hidden rule 2, we recruited new subjects. These subjects tackle phase 2 directly (skipping phase 1). We then measure their learning performance during stimulus classification as in time compaction experiments. Hence, any internal discrepancy between phase 2 in the validation and time compaction experiments would be due to previous exposure to phase 1.

*Stimulus combinations for different groups of participants: Expected learning performance*

To test the predicted modulation of the learning performance, we designed specific static and dynamic stimuli. Each static situation comprises one green and one red circles, placed at different locations of a PC screen (Fig. 3B, top panel). There are three sets of static stimuli specific for each experimental group. In phase 2, all groups receive the same set of dynamic stimuli consisting of six videos displaying two moving circles: one always moving following the same upwards vertical trajectory, and the other one

moving upwards diagonally (Fig. 3B, bottom panel). Note that no movie shows a collision of the circles, i.e., they disappear before crossing or collision. These dynamic scenes presented during phase 2 are similar to the stimuli employed to study the cognitive mechanisms used by humans in collision situations [24,34].

The hypothesis of time compaction is based on the functional similarity of the internal representation of static and dynamic situations. We thus have one static and two dynamic stimuli that are supposed to be identical from this point of view (Fig. 3B, highlighted in purple). They correspond to stimuli shown in Fig. 2. We call them static matching (SM) and dynamic matching (DM) stimuli. The experimental groups differ by the use of SM and hidden rules.

*Control group.* Among the static stimuli, there is no SM (Fig. 3B, top panel, Control). Therefore, the CIRs for static and dynamic stimuli are different, and hence no connection between hidden rules 1 and 2 exists. Thus, learning in phase 2 is independent of phase 1. We use the results of this group as the control for monitoring the performance of other groups of participants.

*Favored group.* In this case, the SM (Fig. 3B, top panel, Favored; highlighted in purple) and two symmetric DM (Fig. 3B, bottom panel; highlighted in purple) are displayed in phases 1 and 2, respectively. Let us now assume that for a given participant, both the SM and DMs are associated with the down-arrow key, as shown in Fig. 3B. Then, according to time compaction, a match

exists between hidden rules 1 and 2. During learning the hidden rule 1, the subject creates the association: “SM-down key”. Then, time compaction predicts that when the DM appears during phase 2, the subject will recall its CIR, which is similar to the SM, and hence he/she will likely press the down key, which is the correct choice. Thus, subjects in this group will learn faster during phase 2, compared to the other groups.

*Hampered group.* This group is similar to the Favored group, but now in hidden rule 1, the SM and one non-SM are interchanged (Fig. 3B, top panel, Hampered). Thus, hidden rules 1 and 2 relate the SM and DM to opposite keys and, following the example, SM and up key will be linked. In this case, a subject after learning hidden rule 1 will be stacked at the presentation of the DM, since the “logical” response “up key” will produce an error. Then, an effort to “forget” the previous association and establish a new one will be required. Thus, subjects in this group will learn slower during phase 2.

### Conceptual experimental constraints

The experimental procedure described above was intended to uncover time compaction as a salient cognitive mechanism for dealing with dynamic situations. We recall that CIR serves as a cognitive substrate for motivation, planning, etc. In other words, time compaction is a primary mechanism that takes place independently on such high-level processes. Thus, no special instructions or training of the participants prior to the experiment are necessary. We then made sure that before the experiment, all participants were not aware of (1) the nature of the experiment, (2) a possible relationship between static and dynamic stimuli, and (3) the importance of collisions.

### Subjects

We engaged in the study 410 university students and graduates (adults). None of them reported prior attentional problems. All subjects had normal or corrected-to-normal vision, were naïve to the study purpose, and had no experience with the tasks and stimuli used here. Mean age of the participants was 21.08 years for women and 22.46 for men (95% confidence intervals [19.98, 22.17] and [21.08, 23.84]; no significant difference, Welch test  $p = 0.12$ ).

Experiments were conducted over randomly composed groups of men and women. The final sample of  $n = 261$  subjects (135 women and 126 men) for Control (35 women, 40 men), Favored (52 women, 48 men) and Hampered (48 women, 38 men) groups comprised participants who fulfilled the task showing a stable performance (see [Supplementary Material](#)), i.e., with the learning lengths not exceeding 46 trials (82% out of a sample of 318). Most subjects completed the experiment within 10 min. The other 92 participants (50 women and 42 men) were assigned to the Validation group.

### Procedure

Participants were subjected to a computer-based trial and error training. The experiment in the Control, Favored, and Hampered groups consisted of two phases: static conditioning (phase 1) followed by dynamic testing (phase 2) (Fig. 3A). The Validation group was tested in phase 2 only (i.e., skipping the phase 1). All subjects completed the procedure individually, as no interaction between them was allowed.

The experimental protocol was implemented on PCs by using MATLAB v17 (MathWorks). Static and dynamic situations were shown on the PC screen for 1.5 s and contained either two static or two moving circles of a diameter of 1 cm colored in red and

green and presented on a white background (Fig. 3B). Circles were chosen to avoid prior cognitive bias [35]. In the static situations, a green circle was added as a geometric reference to facilitate the distinction between stimuli with the lateral and central red circles (compare Figs. 2 and 3B). It also helped to pass from the static to the dynamic phase (all the time showing two circles). During phase 2, the green circle always moved upwards vertically with a velocity of 4.5 cm/s. The red circle moved upwards diagonally with one of the three velocities: 1/3, 2/3, and 4/3 of the speed of the green circle. The initial position of the red circle was chosen in such a way that the velocity ratio 2/3 corresponds to circle collision, i.e., to the DM stimuli. In the DMs, collision is not shown on the screen but would take place 1 s after the circles disappear (recall that circles were displayed during 1.5 s).

Before each experiment, a researcher read aloud a brief instruction to be followed by the participants, which was also shown on the PC screen. Any question asked by the participants was answered by citing the instructions again. There was no mention of the connection between phases. The structure of the instruction was as follows. First, it says that the experiment consists of a static stage, followed by a dynamic stage. The objective is to find out the relationship between the displayed situations and the up/down arrow keys. In the static stage, the instruction specified that the green circle is located at the bottom in the center of the image, whereas the red circle appears randomly at the upper left, center, or right of the screen. In the dynamic stage, both green and red circles move along straight lines at a constant velocity. While the green circle always starts from the bottom center and moves upwards vertically, the red circle changes its movement from trial to trial randomly, and can appear at the bottom left or the bottom right of the screen. Therefore, the participants were not aware of possible collisions between the moving circles and of the relation between static and dynamic stimuli.

There was no time limit to complete both phases 1 and 2. However, there was a maximum of 80 trials per phase. A subject was considered to have learned the hidden rule if he/she gave at least 18 correct responses in the last 20 trials. In this case, the experiment was stopped, and the trial at which the participant reached the criterion was considered the learning length. Note that a 20-trial range corresponds to the expectation of the number of trials such that every situation appears at least twice (for further details on the task complexity and stimulus difficulty see [Supplementary Material](#) and Figs. S2 and S3).

After completing phases 1 and 2, participants were prompted to write down the underlying association rule, which in their opinion, best explain the relationships between the displayed situations and the arrow keys. At the end of the experiment, the participants filled out a form containing information about age and gender. All subjects provided informed consent for their anonymous participation in accordance with the experimental procedures, approved by the Institutional Review Board (Committee of Bioethics, National Distance Education University). All experiments were performed following the guidelines and regulations set forth by the Declaration of Helsinki.

### Statistical analysis of data

*Estimation of time-to-event curves.* A time-to-event function represents the probability that a certain proportion of individuals had learned hidden rule 2 at a given trial. It was obtained through the Kaplan-Meier nonparametric estimator [36]. To assess whether gender and experiment might simultaneously affect the time-to-event curves estimation, a multivariate Cox proportional-hazards regression model was fitted [37]. The model assumptions were checked via the Schoenfeld test [38,39] and residuals plots against time for each covariate (Figs. S4A, S4B). This procedure helped

identify two potential cutoffs at learning lengths 20 and 46, which may hamper the proportional-hazards assumption. We extended the Cox model to allow for time-dependent coefficients [40] using a step function, dividing the sample into three learning length intervals: < 20, 20–46, and > 46 (Figs. S4C, S4D). The revised fit revealed that the effect of the experiment was mainly limited to the first two intervals.

*Estimation of learning curves.* General estimating equations (GEE) were used to model the probability of success at a given trial since it allows taking into account different correlation structures in the data [41–43]. Binomial “logit” was used as a link function given the dichotomous nature of the response variable (either fail a trial or not). A backward stepwise elimination procedure was followed to select the minimal set of variables with a significant explanatory power. Variables taken into account were gender, group, trial number, and their interactions. Successive nested models were compared using the F-test and the Quasilikelihood Information Criterion (QIC) [44]. The interaction terms were interpreted separately for gender and experiment. To ensure that the model characterized the learning phase, we considered the set of trials with a mean success rate lower or equal to 0.99. A factor representing the different researchers that conducted experiments was introduced in the model, and no significant effect was found (F-test,  $p = 0.21$ ). Thus, there was no detectable bias introduced in the results by the researcher, which confirms the reproducibility of the experimental approach.

*Association rule verbalization and response time.* Potential relationships between the verbalization of the association rules found by the participants and the learning length were explored by using a Generalized Linear Model (GLM) with a binomial “logit” link function. Regarding verbalization, 96.2% of participants (251 from 261) expressed the dynamic rules in two main categories: in ‘collision’ terms (containing words as collision, crash, finding, etc.) or in ‘velocity’ terms (with words as velocity, speed, etc.). The remaining participants (10 from 261 or 3.8%) wrote the dynamic rule by mixing ‘collision’ and ‘velocity’ terms or using spatially related descriptions based on directions, positions, etc. The learning lengths were divided into four groups: less or equal to 20 trails, [21,30,31,40], and [40,46]. The differences in response time due to experiment or gender were checked by fitting a GEE with a gaussian “identity” link function and considering the response time as a continuous response variable.

Table S1 (Supplementary Material) provides a comprehensive description of all statistical contrasts (sample size, test, sample statistic value, p-value). All statistical calculations were performed in R v3.3.1, using the packages survival [45], survminer [46], geepack [47], stats, base [48], and dplyr [49].

*Probabilistic model of time compaction*

The model describes the process of finding hidden rule 2 in phase 2. It quantifies the probability of a successful answer at each trial, based on the following assumptions:

- The association key-stimulus is learned at the first stimulus presentation (if the pressed key is not correct, then the opposite one is correct). Thus, the wrong answers to the same stimulus are due to a faulty recall.
- The probability of a correct recall decays exponentially with the trial. The decay rate depends on the number of times the same stimulus has appeared and does not depend on the specific stimulus.

Besides, in experiments, we observed the probability of 0.97 and 0.88 for men in Favored and Hampered groups, respectively,

and 0.91 considering together women and Control men. Thus, we introduce additional, data-driven assumption:

- If a stimulus has appeared four or more times, then the recall probability reaches 1, and hence the pressed key will always be correct.

Time compaction is taken into account through the associations between situations and keys to be learned during phase 2 after the previous conditioning training in phase 1. We can assume that the Favored group learns associations for two DM situations in phase 1. Then, the remaining four non-DMs have to be learned. The Hampered group must re-elaborate the two associations for DMs since they were “wrongly” assigned during phase 1.

The model describes the probability of a successful answer at each trial  $T$  for the Favored, Control, and Hampered groups by:

$$P_F = 1 - \frac{1}{3} \left(\frac{5}{6}\right)^{T-1} [1 + \alpha(a, T) + \beta(b, T)]$$

$$P_C = 1 - \frac{1}{2} \left(\frac{5}{6}\right)^{T-1} [1 + \alpha(a, T) + \beta(b, T)]$$

$$P_H = 1 - \frac{1}{2} \left(\frac{5}{6}\right)^{T-1} \left[\frac{4}{3} + \alpha(a, T) + \beta(b, T)\right]$$

where  $\alpha$  and  $\beta$  stand for the recalling terms for the second and third appearance of a stimulus, respectively, and  $a$  and  $b$  denote the corresponding recalling rates (see Supplementary Material for details).

The model comprises the analytical description of the population learning process and the computational simulation of the individual learning performance. Probabilistic model parameters were estimated from the sample learning rates by the trust-region-reflective least-squares fitting. In the beginning, each participant’s answer vector was padded with ones (success) to get an identical length of 46 trials. Initially, the model was fitted to data from the groups of women and the Control of men taken together. Bootstrapped confidence intervals were obtained for the model parameters. Then, the model was fitted to data of men in the Favored and Hampered groups constraining the first recalling rate values to the interval range found in Control, as we expect that the first repetition of any stimulus contains similar information among conditionings. Final values of the pair of recalling decay rates for the Favored, Control, and Hampered groups were:  $(a, b) = (0.1797, 0), (0.2194, 0.0549),$  and  $(0.0832, 1.2166),$  respectively.

To computationally simulate the individual learning performance according to the model, we proceeded through the following steps.

1. For each real participant, we identified the sequence of stimuli he/she received during the experiment.
2. Since his/her learning length is shorter than the maximum length of stimulus sequence, the sequence was padded with random stimuli until reaching a length equal to 80. We generated  $10^3$  extended stimulus sequences from the real stimulus sequence for this participant.
3. Each extended stimulus sequence was then introduced  $10^3$  times into the simulation.
4. We obtain  $10^6$  sequences of possible answers from this participant, leading to  $10^6$  learning lengths.
5. Steps 1 to 4 are repeated for all participants from each group.

We thus got a set of learning lengths that were used to approximate the distribution of the experimental learning lengths (Fig. 7).

Model fitting and experiment simulation were programmed in MATLAB v17 (MathWorks) [50] and R v3.3.1, package nlstools [51].

## Results

We engaged 261 participants (135 women and 126 men), distributed between Control, Favored and Hampered groups, and other 92 participants (50 women and 42 men) assigned to the Validation group (see Methods). Participants of the first three groups classified the static stimuli, discover the hidden rule 1, and then classified the dynamic stimuli trying to reveal the hidden rule 2 (Fig. 3A). The learning performance in phase 2 was then assessed: (1) at the population level as the average number of successful answers per trial, leading to the *success rate*, and (2) at the individual level as the number of trials required by each participant to learn the rules, named as *learning length* (Fig. S1). These two metrics were also used to quantify the learning performance of subjects in the Validation group.

### Existence of time compaction

The analysis of the population learning was performed by fitting the rate of successful answers to logistic regressions. The independent variables were trial, gender, group, and researcher (the person who conducted the experiment). We included gender as a factor to test whether time compaction is represented differently in men and women in line with other cognitive sex-biases known in the literature (see Discussion). Only gender and group factors were found significant. Fig. 4A shows the success rate per trial separately for men and women and different groups. As predicted by time compaction, population learning in men was significantly faster/slower for Favored/Hampered groups compared to Control. Surprisingly, women showed no significant difference among Favored, Hampered, and Control groups. Moreover, their performance was identical to men in the Control group.

To characterize the individual learning performance, we evaluated the *learning length* of each participant as the number of trials required to figure out hidden rule 2 (Fig. 4B). As expected, men from Favored/Hampered groups had a significantly higher/lower probability of learning compared to men in the Control group (Fig. 4B, inset). On the contrary, phase 1 did not affect individual learning in women. Again, no significant difference was found for all groups of women against men in the Control group.

These findings reveal an intrinsic cognitive relationship between SM and DM stimuli in men suggesting that men internally represent dynamic situations primarily by the static representation of relevant interactions. The lesser salience of time compaction in women reported in our experiments and the absence of differences between the groups of women and the Control group of men point to that women may rely on time compaction in conjunction with a broad range of decision-making strategies, as has been reported by other authors [52,53] (see Discussion).

### Salience of time compaction within phase 2

As shown above, the previous exposure to phase 1 alters the learning performance in phase 2. Let us get an insight into this process.

Fig. 5A shows a typical random sequence of dynamic stimuli. Learning hidden rule 2 involves two opposite mechanisms. On the one hand, the accumulation of information with each trial facilitates the discovery of the association rule. On the other hand, the distance (in trials) between consecutive appearances of a stimulus promotes the forgetting of the associations found before. Thus, we can guess that in control conditions (no previous information is

available), a subject randomly answers to the first presentation of, e.g., stimulus DM<sub>2</sub> at trial 3. The feedback obtained allows deducing the correct association. For example, if the pressed key is wrong, the opposite one must be right. Then, if DM<sub>2</sub> appears, say, at trial 7 (after four trials), the three intermediate stimuli will interfere in the recalling of the association learned for DM<sub>2</sub>.

Time compaction predicts that phase 1 should have an effect on the forgetting of learned associations within phase 2. We thus explore this claim by analyzing the probability of successful answers as a function of the distance between stimulus appearances and the trial in different groups. Fig. 5B summarizes the population results.

At trial 5, the majority of stimuli were repeated only once (Fig. 5B, left, inset), and hence learning has barely begun. A close repetition of the same stimulus (distance < 5) causes a successful answer with a high probability (>0.75) in all groups of subjects (Fig. 5B, left). Nonetheless, participants in the Favored group have a significantly higher probability than the other subjects for all distances. The latter supports time compaction since, according to this hypothesis, participants from the Favored group have acquired previous CIR knowledge in phase 1, which helps answer correctly in phase 2. At trial 13, most of the stimuli have been repeated 1–3 times (Fig. 5B, middle, inset). At this point in the learning process, the curves for Favored/Hampered participants are less/more affected by distance, so these subjects are more/less resilient to forget the learned associations than Control participants, as predicted by time compaction. Finally, trial 20 represents the final learning stage, showing the above-discussed learning differences (Fig. 4).

Therefore, this analysis suggests two processing mechanisms involved in learning modulation during the experiments: the previously acquired information and the resilience to forgetting, which are both compatible with the connection between phases 1 and 2 hypothesized by time compaction.

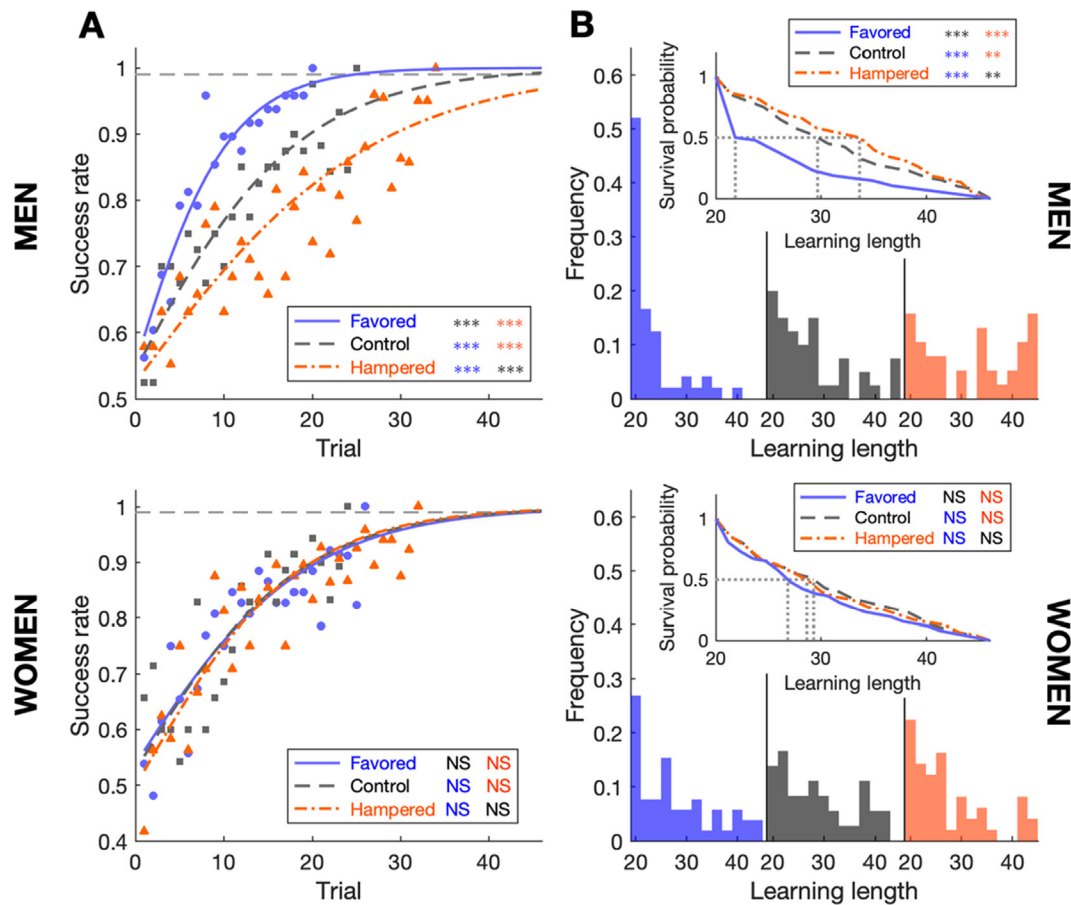
### Rule verbalization corroborates gender-wise salience of time compaction

To explore to what extent time compaction manifests itself at a conscious level, we asked participants to verbalize the hidden rule 2 they figured out in phase 2. We then analyzed the written answers and separated them into “collision-related” (i.e., CIR related) and “others” (see Methods). Fig. 6A shows the probability of “collision-related” responses as a function of the learning length. The generalized linear model with logit link function revealed that fast-learning men show a significant tendency to answer in terms of a “collision” regardless of the experimental group.

Moreover, the more learning time they required, the more they resorted to alternative strategies based on other criteria, such as, e.g., circles’ velocities. Women had no such tendency. About 45% of them responded in terms of a collision regardless of the learning length. It means, in particular, that in the group of participants with learning length within [40,46] trials, women more frequently identified the correct “collision rule” than men. This result further supports the conclusion mentioned above on the broad range of decision-making strategies used by women.

The analysis of population and individual learning performance during phase 2 has revealed differences caused by phase 1. To explore whether these differences could also be explained by changes in the difficulty of the association task (see [Supplementary Material](#)), we studied the response time (i.e., the time elapsed from the disappearance of the displayed situation until the participant pressed a key; see Methods). Fig. 6B shows the regression analysis of the response time, which for women and men shows no significant differences regarding the experimental group. Thus, this suggests that all participants had similar difficulty in resolving the test regardless of their previous conditioning. This conclusion is in line





**Fig. 4.** Modulation of learning performance in phase 2. Top and bottom rows correspond to men and women, respectively; blue, black, and orange colors stand for Favored (F), Control (C), and Hampered (H) groups respectively (F: 48 men, 52 women; C: 40 men, 35 women; H: 38 men, 48 women). (A) Population learning process as success rate per trial (considered up to 0.99 level, dashed lines). Men in Favored/Hampered group learned the testing association rule faster/slower than men in Control group (F vs. C:  $p = 3e-04$ ; F vs. H:  $p = 9.8e-13$ ; C vs. H:  $p = 2.5e-04$ ). Population learning process in women showed no dependence on the direction of conditioning (F vs. C:  $p = 0.28$ ; C vs. H:  $p = 0.93$ ). Men from the Control group and women from all groups showed no significant differences ( $p = 0.23$ ,  $n = 40$  vs. 135). Curves describe the logistic regression of the corresponding population learning (circles, squares, and triangles correspond to Favored, Control, and Hampered groups respectively). (B) Individual learning performance. The histograms show the distributions of the learning length (from left to right: Favored, Control, and Hampered). It is significantly more/less likely for men in Favored/Hampered groups to learn the association rule than in Control condition (F vs. C:  $p = 7.2e-04$ ; F vs. H:  $p = 3.5e-8$ ; C vs. H:  $p = 5.8e-03$ ). This effect was not observed in women (F vs. C:  $p = 0.98$ ; F vs. H:  $p = 0.67$ ; C vs. H:  $p = 0.76$ ). Men from the Control group and women from all groups did not show significant differences ( $p = 0.95$ ,  $n = 40$  vs. 135). Insets show Cox survival curves quantifying differences in the individual learning performance. Dotted lines mark the learning length for the learning probability of 0.5.

with the findings previously discussed (Fig. 5), supporting that observed differences lie in the information managed during phase 2 more than in an alteration of the task difficulty.

*Probabilistic modeling of time compaction*

The reported experimental results reveal a time compaction-based mechanism involved in human decision-making. To get an insight into how this mechanism works, we developed a probabilistic model describing the participant's behavior during the experiment. Since men were more prone to exploit time compaction, the model will be compared with their results (Fig. 4, top row).

The model introduces the probability  $P$  of a successful answer of a participant at each trial  $T$  in phase 2 of the experiment. It assumes a recalling exponential decay, i.e., the forgetting rate [54,55]. Thus, the probability can be expressed as

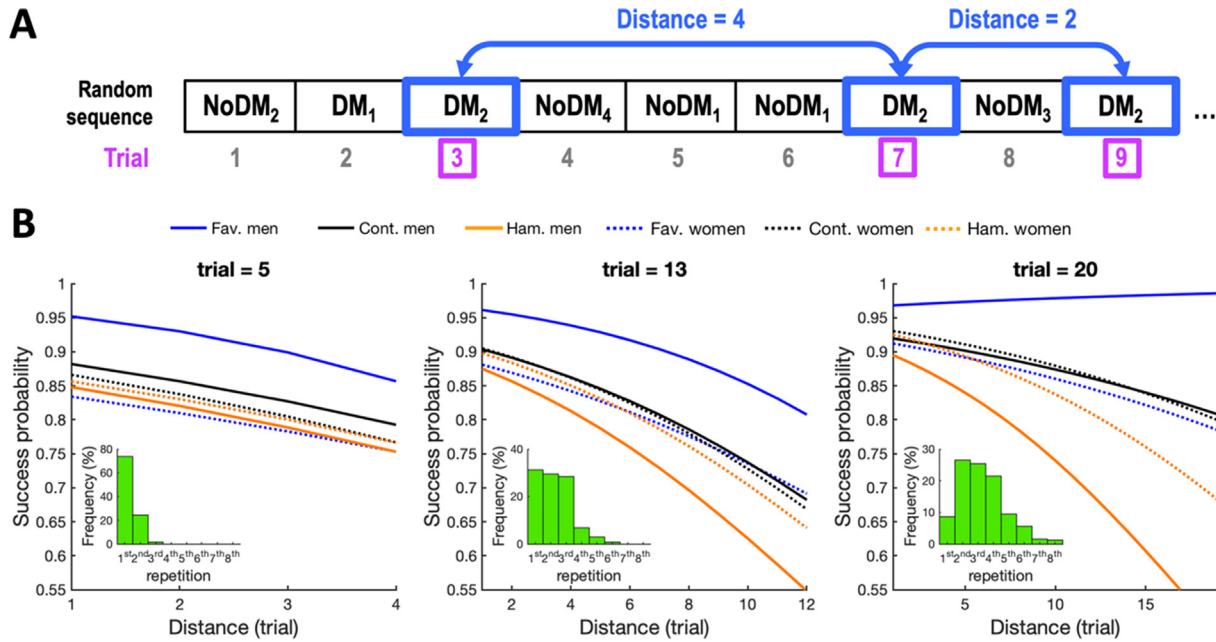
$$P(T, G) = 1 - \gamma_G(T)\delta^T$$

where  $\delta$  is the decay exponent and  $\gamma_G(T)$  is the decay rate that depends on the trial and, more importantly, on phase 1 or group  $G$ . Time compaction introduces biases for Favored and Hampered groups relative to the Control one. Favorably conditioned partici-

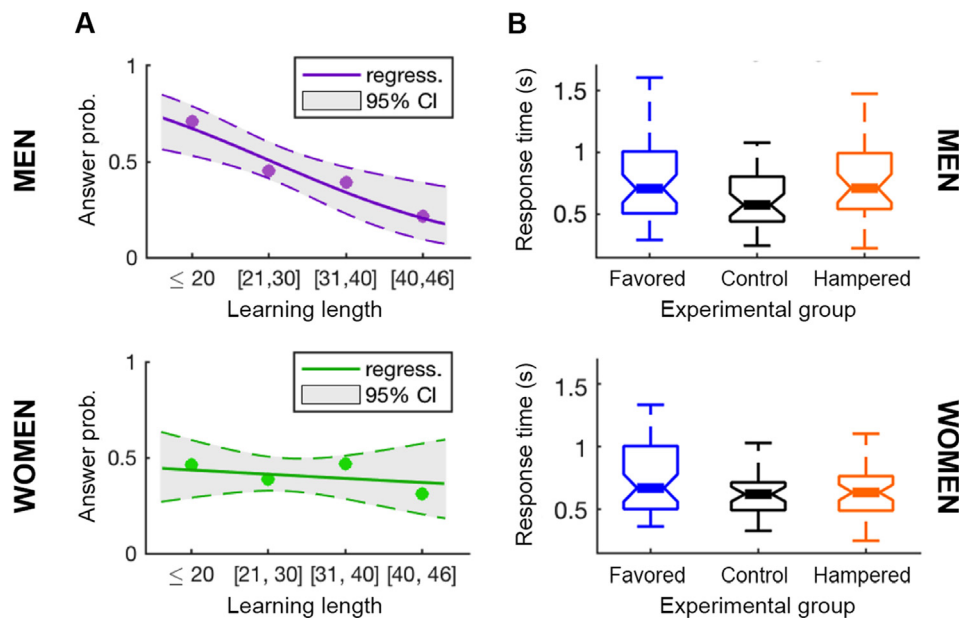
pants start phase 2 with a set of associations already learned, whereas hampered participants need to re-elaborate the hidden rule 2 (Supplementary Material). Thus, the decay rate is different for different experimental groups:  $\gamma_F < \gamma_C < \gamma_H$ , whose parameters were adjusted by fitting the experimental data (see Methods).

The simulation of the learning process during phase 2 was performed by creating a set of virtual participants “responding” to the same input sequences used in the experiments with human subjects. Fig. 7 compares experimental results with simulations, showing a notable agreement between learning data and theoretical predictions for Favored and Control groups. Thus, the model, through the description of the mechanisms behind participant's behavior, provides additional support for time compaction.

Nonetheless, for the Hampered group, there is a deviation between the theoretically predicted histogram of individual learning and experimental data, i.e., the model does not capture accurately specific behavior of this group. A possible reason can be related to the model assumptions. For example, the learning of hampered participants could require more than two stimulus appearances, while the model is based on two parameters only. However, a more likely reason is the influence of exogenous factors not included in the model, such as motivation, frustration, tiredness, etc. (see Supplementary Material).



**Fig. 5.** Saliency of time compaction within phase 2. (A) Typical sequence of six dynamic stimuli (two DMs and four non-DMs) in phase 2. The distances between successive appearances of e.g., stimulus DM<sub>2</sub> influence its learning. (B) Population probability of answering successfully at the next appearance of DM stimulus for different groups of subjects at trial 5 (left, beginning of learning), 13 (middle, the intermediate stage of learning), and 20 (right, the final stage of learning). Insets show the frequency of N repetitions of the stimuli in a sequence as in (A). Solid and dashed colored curves depict the success probability fitted by logistic regression (GLM, logit link). The repetition distance and trial association differ significantly between experimental groups for men (between distance, trial and group  $p = 5e-4$ ; pairwise distance and trial for Favored group  $p = 1e-4$ , for Control Group  $p = 0.028$  and for Hampered group  $p = 1e-3$ ) but not for women (between distance, trial and group  $p = 0.08$ ; pairwise distance and trial for Favored group  $p = 0.06$ , for Control Group  $p = 0.54$  and for Hampered group  $p = 0.92$ ).

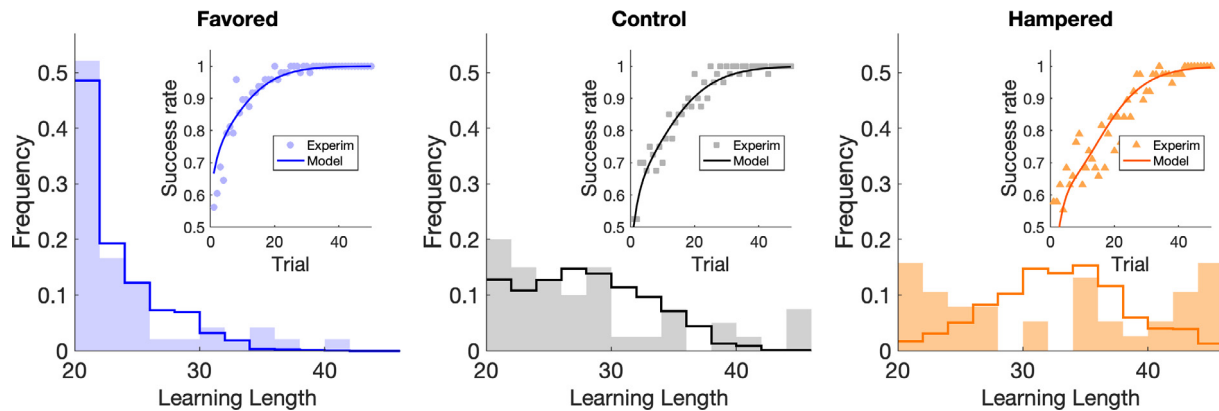


**Fig. 6.** Rule verbalization and response time (top and bottom rows correspond to men and women, respectively). (A) Rule verbalization in terms of ‘collision’ has a probability above 0.7 for men who quickly learned the rule regardless of the experimental group. The probability decreases with the learning length. No correlation is observed for women (thick curves and grey areas denote logistic regression and confidence intervals at 95%, respectively; men:  $p = 1.2e-3$ ,  $n = 126$ ; women:  $p = 0.67$ ,  $n = 135$ ). (B) Response time shows no differences among groups (GEE with linear link function, F vs. C:  $p = 0.13$ ,  $n = 100$  vs. 75; F vs. H:  $p = 0.45$ ,  $n = 100$  vs. 86; C vs. H:  $p = 0.42$ ,  $n = 86$  vs. 75) and for gender ( $p = 0.4$ ,  $n = 126$  men vs. 135 women). \*\*\*,  $< 0.001$ ; \*\*,  $< 0.01$ ; \*,  $< 0.05$ ; NS: No significant difference.

*Validation of time compaction against alternative hypotheses*

The above-described results establish a connection between mental abstraction of static and dynamic situations. In the framework of time compaction (Figs. 1 and 2), such a link is due to the

hypothesized similarity between internal representations of specific static and dynamic stimuli. To validate time compaction as the only plausible mechanism explaining the data, we now explore alternative interpretations that could be compatible with the experimental findings.



**Fig. 7.** Probabilistic modeling of time compaction. *Main panels:* Histogram and stair-like curve correspond to experimental and simulated individual learning performance, respectively (Favored in blue, Control in black, and Hampered in orange). *Insets:* Population learning process. Different markers correspond to experimental data, while curves show the model predictions, i.e., the successful answer probabilities  $P(T, \gamma)$ .

*No unexpected spatial compatibility between static and dynamic stimuli.* The experiment revealed differences between learning compacted and non-compacted dynamic stimuli, DM and non-DM, respectively. Time compaction focuses on the relationship between SM and DM stimuli to explain the results. However, there may be a relationship between non-SM and non-DM stimuli, also explaining the learning differences. Let us provide a rationale for discarding this option.

On the one hand, Favored and Control groups differ by a single static stimulus: the SM stimulus and a third non-SM stimulus for Favored and Control subjects, respectively (Fig. 3B). Thus, a potential unexpected spatial compatibility between the other non-SMs and non-DM stimuli must be the same for both groups. Therefore, its effect cannot explain the learning differences (Fig. 4). On the other hand, the spatial information “contained” in dynamic stimuli, such as initial positions of circles and their trajectories, is common. The only difference is the final positions of the red circle. Then, by assuming a link between the final positions of the red circle in dynamic stimuli and its locations in static stimuli, we end up with a learning process inconsistent with the experimental results (see [Supplementary Material](#) and Fig. S8). Besides, if the final positions play a role, it should be reflected in the rules written by the participants after the experiment. However, the participants answered in terms of collision or velocities and did not refer to the final positions.

Another issue may be a possible transfer of spatial information not explicitly displayed in the stimuli. The most relevant is the possible relationship between the locations of the red circle in static stimuli with the predicted final positions in dynamic stimuli. When circles in non-DM stimuli disappear, each participant mentally continues and finishes the movement differently, hence the extracted “final” positions changes from subject to subject. Therefore, the transfer of a stable rule relating non-SM to non-DM stimuli is unlikely. Moreover, time compaction uses collision as the limit unique for DM stimuli. Thus, time compaction emerges as the most plausible explanation of the reported results.

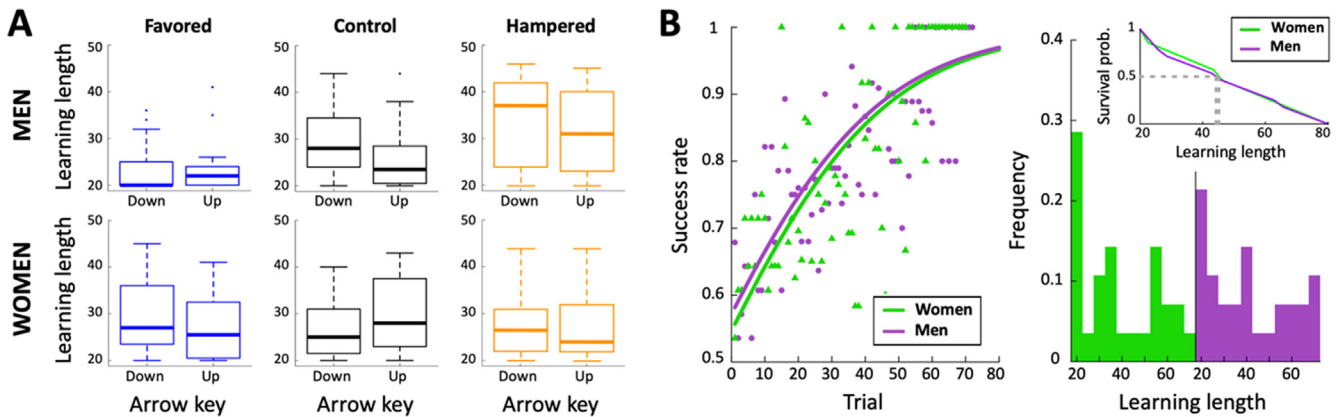
*No crosstalk due to possible stimulus–response compatibility.* One of the most ubiquitous sources of information transfer, and hence a possible connection between phases 1 and 2, is the stimulus–response compatibility (SRC) [56]. It addresses the question: How much of the response can be inferred from the stimulus? The stimuli used in the experiments (Fig. 3B) contain spatial information that could be shared with the response, i.e., the keyboard buttons. For the experiments, we choose vertical-arrow keys to minimize potential bias due to handedness, possible meanings linked to letter keys, finger use preferences, etc. (see [Supplementary Material](#)).

To avoid any information transfer between the up-arrow key and the top position or movement direction of the circles, up and down arrow keys were counterbalanced. We randomly assigned them for each participant (as an example, in Fig. 3B SM and DM stimuli were assigned to down-arrow key). Furthermore, to discard any crosstalk, we analyzed whether the assignment of the up- or down-arrow key had any influence on the learning performance. The analysis revealed that the key assignment explains no variability across gender and experimental group in terms of the learning length (Fig. 8A). One of the main signatures of SRC is the alteration of the response time, i.e., the time the participant takes to relate the stimulus with the response [56]. We found no such bias between experimental groups (Fig. 6B), as well as related to the key assignment (Fig. S9, [Supplementary Material](#)). This points SRC as an unfeasible cause of crosstalk that could explain the obtained results.

*No crosstalk due to implicit bias in dynamic stimuli.* We now address the following question: Do the dynamic stimuli pose any implicit bias in the results? The laterality in circles positions and directions of movement could potentially introduce a preference of some stimuli against the others [57]. However, the symmetry in the setup design avoids the bias of the DMs over non-DM stimuli. Red and green circles move along different trajectories (neither opposite nor parallel) and velocities (Fig. 3B). This discards that some stimuli were, by themselves, differently processed than others [58]. Regarding other visual information presented during the experiment, the feedback provided during learning in the form of a tick or a cross does not transfer any information, artificially linking SM and DMs (see details in [Supplementary Material](#)).

*No gender-related bias in the setup.* One of our most relevant results is the gender differences in the salience of time compaction in favor of men. It is widely known that men outperform women in specific tasks related to spatial perception, as, e.g., in the rod-and-frame and the water level tests [59]. Such processing is based on spatial (static) perception and mental rotation [60]. Nevertheless, in our experiments, these cognitive mechanisms were barely involved in phase 1 only, where no differences between men and women were found, whereas learning performance was measured in the dynamic phase.

Therefore, more complex mechanisms beyond the mere spatial perception should be considered. These include (1) spatial visualization and mental management of information for establishing the stimulus-key relationship (when visual information disappears, and a key must be pressed) and (2) mental animation detected in subjects who verbalized the rule in terms of ‘collision’. On the one hand, no significant differences exist between men and



**Fig. 8.** Exploration of alternative hypotheses. (A) Statistical tests of the influence of arrow keys (down and up) on the learning length in different groups of subjects. All associations are not significant (between gender, experimental group, and arrow key  $p = 0.17$ ; pairwise interactions gender and arrow key:  $p = 0.91$  for men,  $p = 0.29$  for women; group and arrow key:  $p = 0.23$  for Favored,  $p = 0.34$  for Control, and  $p = 0.76$  for Hampered). (B) Learning in phase 2 without previous exposure to phase 1. No significant differences between women (green) and men (purple) were found in population (left,  $p = 0.59$ ) and individual (right,  $p = 0.48$ ) learning performances.

women when performing spatial visualization tasks [59]. On the other hand, spatial memory is strongly involved in the rule learning, since participants must memorize and recall previous stimulus-key associations to correctly answer after each stimulus presentation. In this regard, given the dynamic nature of the stimuli and the simplicity of circles' trajectories, a plausible way of coding them, an alternative to time compaction, is through circles' initial and final positions. It is also equivalent to coding in terms of velocities (see Section 'Rule verbalization' and Fig. 6). Such a processing demand spatial memory of the object location, which shows gender bias in favor of women [61]. The use of circles also positively biases the woman's performance during object location memory tasks [61]. In consequence, there are several cognitive mechanisms involved in the processing of the dynamic stimuli here considered, but in general, without clear gender bias (or even more favorable to women). This conclusion is consistent with our findings, which show no difference between women and men in the Control group.

*Validation group discards gender bias in phase 2 other than time compaction*

The previous arguments suggest that known mechanisms that could be involved in the dynamic stimuli processing cannot explain the gender differences here reported. Nonetheless, to discard any other factors inherent to the dynamic stimuli by themselves, which could not have been considered above, we conducted experiments with the Validation group consisting of additional 92 subjects (50 women and 42 men). The participants of this group skipped the conditional phase and took part in phase 2 only.

We performed the same analysis of the population and individual learning performances, as described in Fig. 4. The results show no gender bias during the classification of the dynamic stimuli according to hidden rule 2 (Fig. 8B). Therefore, we discard phase 2 by itself as the origin of the reported sex bias. This result confirms that observed learning differences between men and women arise when phase 2 is linked to phase 1 according to time compaction.

**Discussion**

Survival in nature forces spatial and temporal restrictions on the animal's attack and defense behaviors, which elicits challeng-

ing questions addressed in this work. (1) How does the brain coordinate sophisticated strategies? (2) What are the functional mechanisms involved in the computation of behaviors? The hypothesis of time compaction offers a solid framework to deal with these questions. In this paper, we have reported the first experimental evidence of its existence as a mechanism of human cognition.

Predation and evasion behaviors share neuronal mechanisms [20], which helps different animals to act as a predator or prey depending on the circumstances. Elementary defensive interactions are mainly encoded by temporal information, as answers to threatening looming objects, which are mediated by computing time-to-collision [62,63]. However, experiments with the interception of virtual balls in different gravity conditions have confirmed the importance of spatial prediction versus the predominance of the temporal dimension in these non-trivial, though simple, situations [26]. These results are not only compatible with the concept of time compaction but are in its basis.

Our results have shown that time compaction is a salient functional strategy, exploited even when the subject is not involved or explicitly interested in interacting with the environment. On the one hand, this suggests that human brain uses time compaction as a central strategy in dynamic scenarios. On the other hand, time compaction can serve as a vehicle for acquiring knowledge through observation, so there is no need to experience potentially dangerous situations critical for surviving [64].

Time compaction explains how fast and accurate responses to complex scenarios are generated in narrow time windows. The representation of lived experiences as static maps containing the relevant information to deal with them, allows constructing 'memories.' Then the experiences can be efficiently learned, stored, recalled, compared, and structured by managing their CIRs [23]. Thus, when the subject must respond in real-time, it can rapidly recall the corresponding CIR from memory. Moreover, the cognitive architecture based on time compaction [23] provides an operational mechanism for the coexistence of the so-called model-based (MB) and model-free (MF) computations [65].

MB computation reflects prospective simulation of future actions and outcomes, which corresponds to the 'conscious' construction of the CIRs. In contrast, the MF process is faster and uses previously learned experiences, which will be consistent with the CIR recalling, to elicit rapid and effective 'subconscious' responses. These responses are often structured as sequences of actions, constructed considering their semantic content, i.e., the meaning of

such actions in the context of the global task, which is a compulsory requirement to chain movements and behaviors into sophisticated strategies. The action representation supported by time compaction allows encapsulating the semantic of each potential response [27].

One of the most relevant cognitive dimensions emerges in situations that engage the subject with other cognitive beings in a circular relationship. Then, mutual decisions affect the cognitive beings recursively [66], which is a particular case of the theory of mind. Time compaction offers a context where this challenge can be tackled from an operational perspective [22]. This could help unravel that cognitive entanglement, e.g., between two fighters in combat, is decisive to understand survival interactions in humans.

Time compaction was conceived initially as a primary gender-independent cognitive mechanism, however we have found a significant sex bias during our experiments. The salience of time compaction was statistically significant in men but not in women. Notably, the learning performance was the same for all groups of women and the control group of men. Moreover, the proportion of women (about 45%), verbally relating the experiments with time compaction (responses in terms of collision), was independent of the learning length, whereas men exhibited a strong decay from about 70% to 20%. Thus, our data suggest that women do rely on time compaction but in combination with other decision-making strategies.

The gender differences found here are in agreement with other studies. Men frequently use holistic strategies, gathering information about spatial relations among stimuli. In contrast, women often use a segmentary approach, focusing on particular aspects of the relevant elements and less on their relationships [52,53]. Thus, men outperform women in mental transformations of objects (image integration, rotation, projection, etc.), a skill that may have decisively contributed to their ability to anticipate trajectories of preys or thrown objects during agonistic encounters [67]. At the same time, women show a better performance in tests related to object location memory, compatible with their predominant role in foraging, where memorizing locations of relevant items is a significant advantage [61,68]. This way, a plausible explanation for our gender-biased results is coherent with sex differences reported in the literature related with hunter-gatherer hypothesis [61]: the preferred participation of males in survival tasks as hunting, chasing, and fighting is consistent with the salience of time compaction as a cognitive process optimizing real-time interactions in complex dynamic situations. On the other hand, the postulated role of women as gatherers would be in line with our findings, which show that, in the circumstances elicited by the experimental setup, they do not primarily invoke time compaction among other cognitive strategies, though, as commented, it also belongs to female's cognitive repertoire.

The design of conducted experiments and found gender differences suggest that CIRs of dynamic situations work at the cognitive level, beyond visual substrate and primary mechanisms as time compression [69] and visual extrapolation [70,71]. We note that time compaction provides a functional generalization of the internal representation of static situations, which suggests that the notion of CIR resonates with the concept of cognitive maps [6]. Cognitive map theory argues that the hippocampus is involved in the navigation to unmarked locations, defined by their relationships with the environment, but not in the navigation to visible static goals [72]. Nevertheless, avoidance of visible, dynamic objects does rely on the hippocampus [73]. This finding is coherent with time compaction, where a CIR appears from the forecasted interactions, and so the relationships, among elements in a time-changing environment. This increases the likelihood that cognitive maps and CIRs share neurobiological mechanisms.

Thus, we hypothesize that specific cell populations responsible for physical object encoding, as recently characterized object-vector cells [74], may also be involved in the encoding of virtual objects in a CIR representing future interactions. This perspective may reveal time compaction as the central part of a general framework unifying spatial and spatiotemporal cognition.

## Conclusion

In this work, we have shown that humans internally represent time-changing situations as static abstractions consisting of the spatial arrangement of future interactions. Our experimental and mathematical findings have confirmed the predictions made by the time compaction hypothesis. Thus, compact internal representations, or CIRs, would be among the central mechanisms underlying the human ability of making reliable decisions for fast interaction with dynamic environments. Our results also uncovered a preference of men to use time compaction for coping with dynamic situations, whereas women rely on a broader range of strategies. This gender bias is compatible with earlier reported sex differences related to role separation in humans to strengthen survival opportunities. Thus, the reported findings support the potential importance of time compaction as a cognitive strategy central for survival interactions at the levels of action and abstraction.

## Compliance with Ethics Requirements

*All procedures followed were in accordance with the ethical standards of the responsible committee on human experimentation, approved by the Institutional Review Board, Committee of Bioethics, National Distance Education University, Madrid, Spain, and according to the Helsinki Declaration of 1975, as revised in 2008. Informed consent was obtained from all patients for being included in the study.*

*This document is accompanied by the Ethical Committee Approval (Committee of Bioethics, National Distance Education University, Madrid, Spain).*

## Declaration of Competing Interest

None.

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## Author contributions

J.A.V-A., C.C.T., S.D-H., and A.S-J. designed, performed and analyzed experiments, and wrote the manuscript. S.L., N.K., and A.M. performed and analyzed experiments. G.L.T. and R.P. designed

and performed experiments. V.A.M. designed the experiments and wrote the manuscript.

### Data and materials availability

The data and custom code are available upon request from J.A. V-A.

### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jare.2020.08.008>.

### References

- Eichenbaum H, Fortin N. Episodic memory and the hippocampus: It's about time. *Curr Dir Psychol Sci* 2003;12(2):53–7.
- Llinás RR. *I of the Vortex: From neurons to self*. MIT Press; 2001.
- Rao S, Mayer A, Harrington D. The evolution of brain activation during temporal processing. *Nat Neurosci* 2001;4:317–23.
- Livesey AC, Wall MB, Smith AT. Time perception: manipulation of task difficulty dissociates clock functions from other cognitive demands. *Neuropsychologia* 2007;45:321–31.
- Kraus BJ, Robinson RJ, White JA, Eichenbaum H, Hasselmo ME. Hippocampal "time cells": time versus path integration. *Neuron* 2013;78:1090–101.
- Epstein R, Patai EZ, Julian J, Spiers H. The cognitive map in humans: Spatial navigation and beyond. *Nat Neurosci* 2017;20:1504–13.
- O'Keefe J. Place units in the hippocampus of the freely moving rat. *Exp Neurol* 1976;51:78–109.
- Fyhn M, Molden S, Witter MP, Moser EI, Moser MB. Spatial representation in the entorhinal cortex. *Science* 2004;305:1258–64.
- Skaggs WE, McNaughton BL, Wilson MA, Barnes CA. Theta phase precession in hippocampal neuronal populations and the compression of temporal sequences. *Hippocampus* 1996;6:149–72.
- Jeewajee A, Barry C, Douchamps V, Manson D, Lever C, Burgess N. Theta phase precession of grid and place cell firing in open environments. *Philos Trans R Soc Lond B Biol Sci* 2014;369(20120532).
- O'Keefe J, Recce ML. Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus* 1993;3:317–30.
- Eichenbaum H. Time cells in the hippocampus: a new dimension for mapping memories. *Nat Rev Neurosci* 2014;15:732–44.
- Pfeiffer BE, Foster DJ. Hippocampal place-cell sequences depict future paths to remembered goals. *Nature* 2013;497(7447):74–9.
- Arnold A, Iaria G, Ekstrom AD. Mental simulation of routes during navigation involves adaptive temporal compression. *Cognition* 2016;157:14–23.
- Manohar SG, Pertzov Y, Husain M. Short-term memory for spatial, sequential and duration information. *Curr Opin Behav Sci* 2017;17:20–6.
- Rueckemann JW, Buffalo EA. Spatial responses, immediate experience, and memory in the monkey hippocampus. *Curr Opin Behav Sci* 2017;17:155–60.
- Quiroga RQ. Neural representations across species. *Science* 2019;363:1388–9.
- Kraus BJ, Brandon MP, Robinson RJ, Connerney MA, Hasselmo ME, Eichenbaum H. During running in place, grid cells integrate elapsed time and distance run. *Neuron* 2015;88(3):578–89.
- Bubic A, Von Cramon DY, Schubotz R. Prediction, cognition and the brain. *Front Hum Neurosci* 2010;4:25.
- Evans DA, Stempel AV, Vale R, Branco T. Cognitive control of escape behaviour. *Trend Cogn Sci* 2019;23(4):334–48.
- Villacorta-Atienza JA, Velarde MG, Makarov VA. Compact internal representation of dynamic situations: neural network implementing the causality principle. *Biol Cybern* 2010;103:285–329.
- Villacorta-Atienza JA, Calvo C, Makarov VA. Prediction-for-CompAction: Navigation in social environments using generalized cognitive maps. *Biol Cybern* 2015;109(3):307–20.
- Villacorta-Atienza JA, Makarov VA. Neural Network Architecture for Cognitive Navigation in Dynamic Environments. *IEEE Trans Neural Netw Learn Syst* 2013;24:2075–87.
- Tresilian JR. Perceptual and cognitive processes in time-to-contact estimation: Evaluating the role of cognitive processes in arrival-time judgements (Doctoral dissertation). Texas Tech University; 1997.
- Novak JLB. Judgments of absolute time-to-contact in multiple object displays: Evaluating the role of cognitive processes in arrival-time judgements (Doctoral dissertation). Texas Tech University; 1997.
- Russo M, Cesqui B, La Scaleia B, Ceccarelli F, Maselli A, Moscatelli A, et al. Intercepting virtual balls approaching under different gravity conditions: evidence for spatial prediction. *J Neurophysiol* 2017;118(4):2421–34.
- Calvo Tapia C, Villacorta-Atienza JA, Diez-Hernando S, Khoruzhko M, Lobov SA, Potapov I, et al. Semantic knowledge representation for strategic interactions in dynamic situations. *Front Neurobot* 2020;14(4).
- Roberts AC et al. Habituation of the C-start response in larval zebrafish exhibits several distinct phases and sensitivity to NMDA receptor Blockade. *PLoS ONE* 2011;6:e29132.
- Qi S, Hassabis D, Sun J, Guo F, Daw N, Mobbs D. How cognitive and reactive fear circuits optimize escape decisions in humans. *Proc Natl Acad Sci USA* 2018;115(12):3186–91.
- Cooper WEJ, Blumstein DT, editors. *Escaping from predators: An integrative view of escape decisions*. Cambridge University Press; 2015.
- Ellard CG, Eller MC. Spatial cognition in the gerbil: computing optimal escape routes from visual threats. *Anim Cogn* 2009;12:333–45.
- Ghirlanda S, Enquist M. A century of generalization. *Anim Behav* 2003;66(1):15–36.
- Pfeuffer CU, Hosp T, Kimmig E, Moutsopoulou K, Waszak F, Kiesel A. Defining stimulus representation in stimulus–response associations formed on the basis of task execution and verbal codes. *Psych Res* 2018;82(4):744–58.
- Law DJ, Pellegrino JW, Mitchell SR, Fischer SC, McDonald TP, Hunt EB. Perceptual and cognitive factors governing performance in comparative arrival-time judgments. *J Exp Psychol Hum Percept Perform* 1993;19(6):1183.
- Reed CL, Vinson NG. Conceptual effects on representational momentum. *J Exp Psychol Hum Percept Perform* 1996;22:839–50.
- Peterson AV. Expressing the Kaplan–Meier estimator as a function of empirical subsurvival functions. *J Am Stat Assoc* 1977;72:854–8.
- Jahn-Eimermacher A, Lasarzik I, Raber J. Statistical analysis of latency outcomes in behavioral experiments. *Behav Brain Res* 2011;221:271–5.
- Schoenfeld DA. Sample-size formula for the proportional-hazards regression model. *Biometrics* 1983;39:499–503.
- Abeysekera W, Sooriyachchi M. Use of Schoenfeld's global test to test the proportional hazards assumption in the Cox proportional hazards model: an application to a clinical study. *J Natl Sci Found Sri* 2009;37:41–51.
- Saegusa T, Di C, Chen YQ. Hypothesis testing for an extended Cox model with time-varying coefficients. *Biometrics* 2014;70:619–28.
- Hanley JA, Negassa A, Edwards Deb MD, Forrester JE. Statistical analysis of correlated data using generalized estimating equations: An orientation. *Am J Epidemiol* 2003;157:364–75.
- Hardin JW. Generalized estimating equations (GEE). *Encycl Stat Behav Sci* 2005.
- Hin LY, Wang YG. Working-correlation-structure identification in generalized estimating equations. *Stat Med* 2009;28:642–58.
- Pan W. Akaike's information criterion in generalized estimating equations. *Biometrics* 2001;57:120–5.
- Therneau T. A package for survival analysis in R. <URL: CRAN.R-project.org/package=survival>; 2015.
- Kassambara A, Kosinski M. *Survminer: Drawing survival curves using 'ggplot2'*. <URL: CRAN.R-project.org/package=survminer>; 2017.
- Halekoh U, Hojsgaard S, Yan J. The R Package geeepack for generalized estimating equations. *J Stat Soft* 2006;15:1–11.
- R Core Team. R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria. <URL: r-project.org/>; 2016.
- Wickham H, Francois R, Henry L, Müller K. *Dplyr: A grammar of data manipulation*. 2017. <URL: CRAN.R-project.org/package=dplyr>.
- MATLAB 17.0. The MathWorks, Inc., Natick, Massachusetts, United States.
- Baty F et al. A toolbox for nonlinear regression in R: The package nlstools. *J Stat Soft* 2015;66:1–21.
- Peña D, Contreras MJ, Shih PC, Santacreu J. Solution strategies as possible explanations of individual and sex differences in a dynamic spatial task. *Act Psychol* 2008;128:1–14.
- Picucci L, Caffo A, Bosco A. Besides navigation accuracy: Gender differences in strategy selection and level of spatial confidence. *J Env Psych* 2011;31:430–8.
- Nemhard D, Osothsilp N. An empirical comparison of forgetting models. *IEEE Trans Eng Managem* 2001;48:283–91.
- Averell L, Heathcote A. The form of the forgetting curve and the fate of memories. *J Math Psychol* 2011;55:25–35.
- Kornblum S, Hasbroucq T, Osman A. Dimensional overlap: cognitive basis for stimulus-response compatibility-a model and taxonomy. *Psycholog Rev* 1990;7(2):253–70.
- Maass A, Suintner C, Deconchy JP. *Living in an asymmetrical world: How writing direction affects thought and action*. Psychology Press; 2014.
- Murray DJ. *Gestalt psychology and the cognitive revolution*. Univ of Georgia Press; 1995.
- Voyer D, Voyer S, Bryden MP. Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychol Bull* 1995;117(2):250–70.
- Linn MC, Petersen AC. Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Develop* 1985;56:1479–98.
- Voyer D, Postma A, Brake B, Imperato-McGinley J. Gender differences in object location memory: A meta-analysis. *Psychon Bull Rev* 2007;14(1):23–38.
- Wang Y, Frost BJ. Time to collision is signaled by neurons in the nucleus rotundus of pigeons. *Nature* 1992;356:236–8.
- Yilmaz M, Meister M. Rapid innate defensive responses of mice to looming visual stimuli. *Curr Biol* 2013;23:2011–5.
- Zentall TR. Imitation: definitions, evidence, and mechanisms. *Anim Cogn* 2006;9(4):335–53.
- Mobbs D, Headley DB, Ding W, Dayan P. Space, time, and fear: survival computations along defensive circuits. *Trend Cogn Sci* 2020;24(3):228–41.
- Vernon D, Lowe R, Thill S, Ziemke T. Embodied cognition and circular causality: on the role of constitutive autonomy in the reciprocal coupling of perception and action. *Front Psych* 2015;6:1660.
- Lawton CA, Hatcher DW. Gender differences in integration of images in visuospatial memory. *Sex Roles* 2005;53(9–10):717–25.

- [68] Silverman I, Eals M. Sex differences in spatial abilities: Evolutionary theory and data. In: Barkow J, Cosmides I, Tooby J, editors. *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press; 1992. p. 533–49.
- [69] Ekman M, Kok P, de Lange FP. Time-compressed preplay of anticipated events in human primary visual cortex. *Nat Commun* 2017;8:15276.
- [70] Delle Monache S, Lacquaniti F, Bosco G. Differential contributions to the interception of occluded ballistic trajectories by the temporoparietal junction, area hMT/V5+, and the intraparietal cortex. *J Neurophysiol* 2017;118:1809–23.
- [71] Russo M, Cesqui B, La Scaleia B, Ceccarelli F, Maselli A, Moscatelli A, et al. Intercepting virtual balls approaching under different gravity conditions: evidence for spatial prediction. *J Neurophysiol* 2017;118:2421–34.
- [72] Morris RG, Garrud P, Rawlins JN, O'Keefe J. Place navigation impaired in rats with hippocampal lesions. *Nature* 1982;297:681–3.
- [73] Telensky P, Svoboda J, Blahna K, Bureš J, Kubik S, Stuchlik A. Functional inactivation of the rat hippocampus disrupts avoidance of a moving object. *Proc Natl Acad Sci USA* 2011;108:5414–8.
- [74] Høydal ØA, Skytøen ER, Andersson SO, Moser MB, Moser EI. Object-vector coding in the medial entorhinal cortex. *Nature* 2019;568(7752):400–4.