Statistical Learning Emerges from Temporally Preparing What Action to Perform Where

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Abstract

Statistical learning is the ability to exploit regularities of our world to predict what will happen when. Recently, we developed the Whac-A-Mole (WAM) paradigm to study whether participants can capitalize upon regularities embedded in complex temporal structures. Although participants were unaware of any regularity in WAM, we found better performance for targets with regular versus irregular intervals. Under the framework of statistical learning, this performance benefit can be understood to arise from distilling these regular intervals and predicting regular target onsets in a manner impossible for irregular targets. Intriguingly, here we instead found that this performance benefit emerges from preparation to a range of other temporal properties that we initially considered to be random. Participants temporally prepared, in parallel, for different actions to perform and locations to attend, without evidence that regular targets were responded to differently than irregular ones. With more time to prepare, participants gave faster and more accurate responses. Using a recent model of temporal preparation, *f*MTP, we illustrate that such complex temporal adaptation can arise from the memory processes underlying temporal preparation. In a broader sense, our results closely relate to theoretical work showing that statistical learning can emerge from general memory processes.

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To cope with the flood of information unfolding in space and time, making up our everyday environment, we use statistical regularities to guide behavior. By extracting regularities embedded in the environment, known as 'statistical learning' (Saffran et al., 1996; Sherman et al., 2020), we are able to predict future events and adapt behavior accordingly. Statistical learning usually operates outside our awareness, and can be found in different domains (e.g., language: Saffran et al., 1996; visual search: Baker et al., 2004; Kruijne and Meeter, 2015; Zhao et al., 2011; temporal order: Brady and Oliva, 2008; Kidd et al., 2012; Turk-Browne et al., 2005.

An integral part of such predictive behavior is time. In this study, we investigate how statistical learning capitalizes upon regularities embedded in complex temporal structures. Although a wealth of timing studies has already shown that participants adapt to an experiment's temporal statistics (Acerbi et al., 2012; de Jong et al., 2021; Maaß et al., 2019; Nobre & Ede, 2018), these studies do not match the demands of natural worlds (see Salet et al., in press, for an extensive discussion). Laboratory experiments overlook two important aspects of timing behavior in uncertain, dynamic environments. First, in timing experiments, intervals to be timed are isolated in discrete trials, while the temporal information in our world is much more complex: We constantly face ongoing streams of actions and events that happen in a certain temporal order, last for some time, and have some time in between them. Second, intervals are rarely explicitly cued to be relevant for behavior as they commonly are in experiments. Instead, we only learn about their relevance after interacting with our environment, and we hardly ever become aware of the temporality of our behavior.

To start closing this gap, we recently developed the Whac-A-Mole (WAM) paradigm to study such implicit timing behavior in a complex environment (Salet et al., 2021a). WAM does not consist of discrete trials, but instead of simultaneous streams of

sudden-onset targets ('moles') that participants have to hit in order to collect points. The critical manipulation, unbeknownst to participants, is that one target consistently appears every 3000 ms while two other targets appear at random moments. We found that average responses to the regular targets were faster and more accurate compared to irregular targets, and interpreted this 'regularity benefit' as a reflection of statistical learning (Salet et al., 2021a).

An intriguing open question is how exactly this regularity is distilled from the WAM environment. We surmised that participants might have learned three things at regular target onsets: (1) where to direct their attention; (2) what motor action to prepare; or (3) both. We set out to answer this question in two similar, preregistered experiments (https://osf.io/3d6h8; https://osf.io/3b78x). We introduced a color-response mapping in the WAM task (Figure 1), such that the moles would appear in one of three colors, each coding for a unique action that had to be executed (a button press with the index, middle, or ring finger). In the 'location' condition, the regular targets appeared in a fixed location, but had a random color and were thus linked with random actions. In the 'action' condition, the regular targets required a fixed action (i.e., all regular targets had the same color), but appeared in a random location. Finally, in the 'action=location' condition, target color and location were coupled as in the original study (i.e., regular and irregular targets appeared in fixed locations requiring a fixed action). In this way, we aimed to assess to what extent statistical learning results from learning the regular location and/or action.

In contrast with our preregistered hypotheses, however, new analyses showed that our findings resemble a phenomenon known as 'temporal preparation' (see also Addendum to Salet et al., 2021a: Salet et al., 2021b). The reoccurring finding in temporal preparation studies is that in blocks with variable target intervals, longer intervals allow more time for preparation, resulting in faster responses (Los et al., 2014; Niemi & Näätänen, 1981; Nobre & Ede, 2018). Similarly, we found performance to improve as more time passed since a target's previous onset, as if targets that did not come on screen for a while were expected

to come soon. Intriguingly, this was observed for both location and action, suggesting that participants monitored the timing of three features in these two dimensions in parallel.

We show that the 'regularity benefit' only emerges as a consequence of such temporal preparation. This finding is in stark contrast with our previous interpretation that this benefit arises from a statistical learning mechanism in which solely the regular interval is extracted (Salet et al., 2021a, 2021b). Using a recent model of temporal preparation (fMTP, Salet et al., 2022), we derive insights from which cognitive principles the observed behavior might emerge. In fMTP, preparation is determined by associative learning between timing circuits that monitor the timing of the targets and motor circuits initiating specific responses. We show that adaptive learning in fMTP tunes preparation to WAM's temporal properties. Additionally, just as we observed in the empirical data, the qualitative dynamics of the model show that the 'regularity benefit' emerges from temporal preparation.

Results

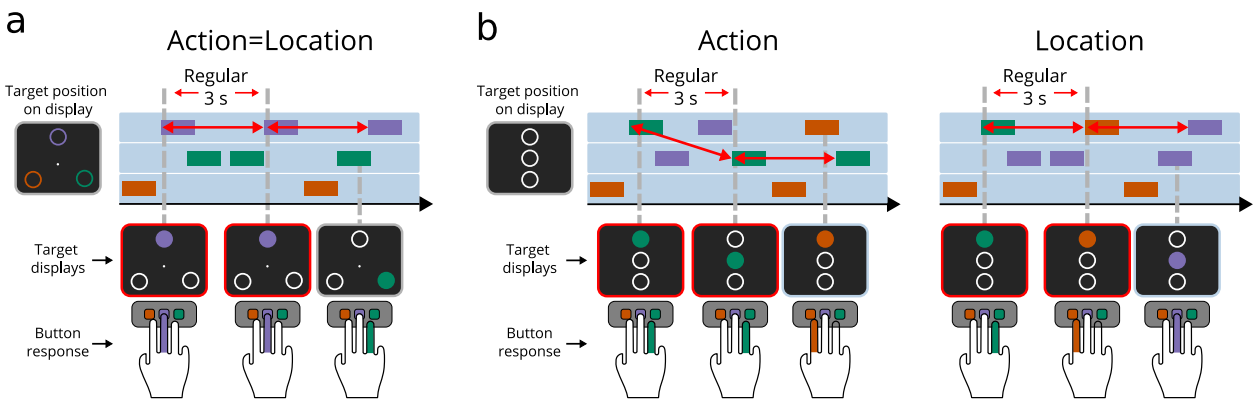
54 Participants scored as many points as possible by pressing the correct button as soon as the corresponding target came on screen (Figure 1). Points were scored by 'hitting' targets within 1000 ms after their onsets. Points were deducted if participants were too late (1250 ms after target onset) or pressed an incorrect button. Note that targets were presented in a continuous stream that was not divided into discrete trials, and multiple targets could be presented simultaneously.

Each participant completed three conditions (Figure 1) in separate phases of the experiment. In the 'action=location' condition, the targets were placed at the three corners of an equilateral triangle. Each target color corresponded to a particular location and action. One of these was the regular target, which appeared every 3000 ms (Figure 1a, red arrows). The other two targets appeared at pseudorandomly generated intervals.

In the 'action' and 'location' conditions, the direct mapping between location and

Figure 1

Experimental conditions.



Note. Segments of a series of target presentations in WAM. (a) In the 'action=location' condition, action and location were directly coupled and every 3000 ms a regular action was performed in a fixed location (red arrows). (b) In the 'action' and 'location' conditions, the direct mapping between location and action was removed. In the 'action' condition, the regular action was performed every 3000 ms in a random location. In contrast, in the 'location' condition, the regular location appeared every 3000 ms responded to with a random action. The red arrows represent the regular interval, the other events appeared at pseudorandom time points. A video of the task is available at: https://osf.io/2ca8h/.

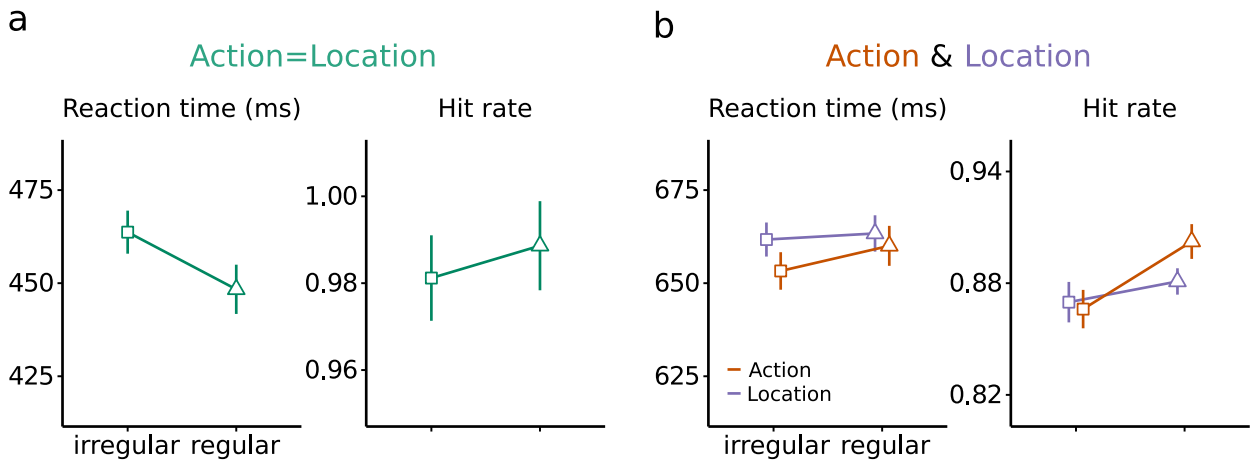
action was removed (Figure 1b). That is, the color corresponding to a certain action could appear in any location. To avoid Simon interference, the target positions were aligned vertically at the horizontal center of the screen. In the 'action' condition, one color, associated with a unique response finger, appeared every 3000 ms at a random location (Figure 1b, red arrows). Conversely, in the 'location' condition, a target appeared in one location every 3000 ms, but in a random color and was thus responded to with a random action. A video of the task is available at: https://osf.io/2ca8h/.

Regularity Benefit

For readability of the Results section, we relegated the details of statistical model selection to Appendix A.

Figure 2

Performance as a function of regularity.



Note. Mean RT and HR split on regularity with 95% within-subject confidence intervals (Cousineau, 2005; Morey, 2008) for the (a) 'action=location' condition and (b) 'action' and 'location' conditions. Note that the y-scale of 'action=location' condition differs from the 'action' and 'location' conditions.

A questionnaire indicated that only three participants were aware of the regularity. Those we subsequently replaced by new, unaware participants (see section Materials and Methods). The findings of the 'action=location' condition (Figure 2a) replicate our previous results of the 'regularity benefit' (Salet et al., 2021a): RT was lower and HR higher for the regular compared to irregular targets ($\Delta BIC > 15.7$, $BF > 1000$). A benefit that we have attributed to a statistical learning mechanism distilling the regular interval from the irregular environment (Salet et al., 2021a). For the 'action' and 'location' conditions (Figure 2b), the HR results align with these findings ($\Delta BIC > 28.0$, $BF > 1000$). However, we found no indication of faster responses to regular targets in the 'location' condition ($\Delta BIC = 8.9$, $BF = 83.6$) and even an inconclusive trend indicating slower responses to the regular target in the 'action' condition ($\Delta BIC = 1.1$, $BF = 1.7$). This inconsistency between HR and RT is surprising: As faster responses lead to higher HRs, we had expected RT to be the strongest driver of performance benefits (cf. Salet

et al., 2021a). In the following, we will show that a different explanation of the 'regularity benefit', rooted in temporal preparation, resolves this apparent inconsistency.

Temporal Preparation

[1]As the interval between irregular targets was highly variable (1250 – 14000 ms), we have thus far considered it unlikely that these intervals are monitored by participants and used to time responses. However, we came to realize that participants actually may anticipate irregular targets in a manner comparable to studies on temporal preparation.

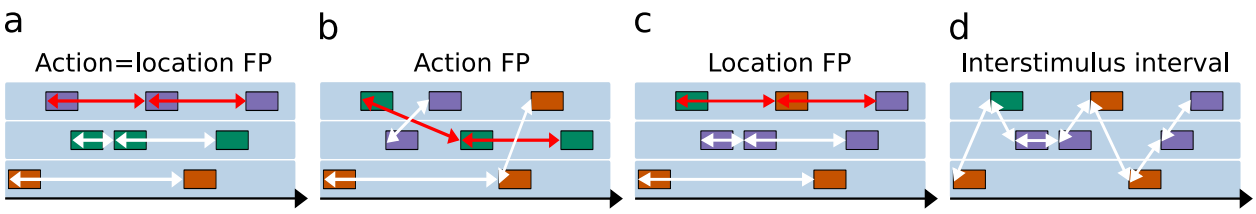
Preparing Irregular Targets

In this section, we test whether participants prepare for irregular targets, expressed by a decrease in RT as a function of the interval between each subsequent irregular onset (temporal preparation's signature: Los et al., 2014; Niemi & Näätänen, 1981; Nobre & Ede, 2018). From here on, we refer to this interval as the foreperiod (FP). Figure 3a illustrates the FP in the 'action=location' condition in which action was in correspondence with location. Note that the FP for the regular target was always 3000 ms by definition (Figure 3a, red arrows). In the 'action' and 'location' conditions, we define the FP as the time between two targets with the same action or location, respectively. That is, in the 'action' condition (Figure 3b), a FP was defined as the time between repeating actions (e.g., ring-to-ring finger). In the 'location' condition (Figure 3c), a FP marks the time between targets at the same location (e.g., top-to-top location). Figure 3d illustrates another interval; the interstimulus interval (ISI). This is the time between any subsequent target presentation, and is defined on a much smaller range (500 – 2500 ms) than FPs (1250 - 14000 ms). As explained in the Materials and Methods, the stimulus sequences have been generated using a stringent procedure that controls for differences in ISI between the targets. In Appendix A, we show that ISI has only an additive effect on RT and HR.

[1] All following analyses were not preregistered.

Figure 3

A multitude of temporal properties in WAM.



Note. Illustrating the foreperiod (FP) in the (a) 'action=location', (b) 'action', and (c) 'location' condition. The red arrows represent the timing of the regular target (constant FP of 3000 ms), the white arrows the irregular targets (FPs ranging from 1250 - 14000 ms). (d) The time between any subsequent target presentation is referred to as the interstimulus interval (ranging from 500 - 2500 ms).

To test whether FP duration modulated performance, we extended the statistical model of the section 'Regularity Benefit' (predicting RT and HR from 'regularity' and 'condition') to also include an effect of FP (as a continuous predictor) and its interaction with 'condition'. Of note, we transformed FP into $\frac{1}{FP}$ to better capture its curvilinear relation with RT and HR (see Figure 4). This vastly improved the models of both HR and RT compared to a linear relationship ($\Delta BIC > 1000$, $BF > 1000$). Figure 4 displays RT and HR as a function of binned FP together with model predictions[2]. Model comparisons revealed decreasing RT ($\Delta BIC > 1000$, $BF > 1000$) and increasing HR ($\Delta BIC = 482.7$, $BF > 1000$) as a function of FP, strongly suggestive of temporal preparation.

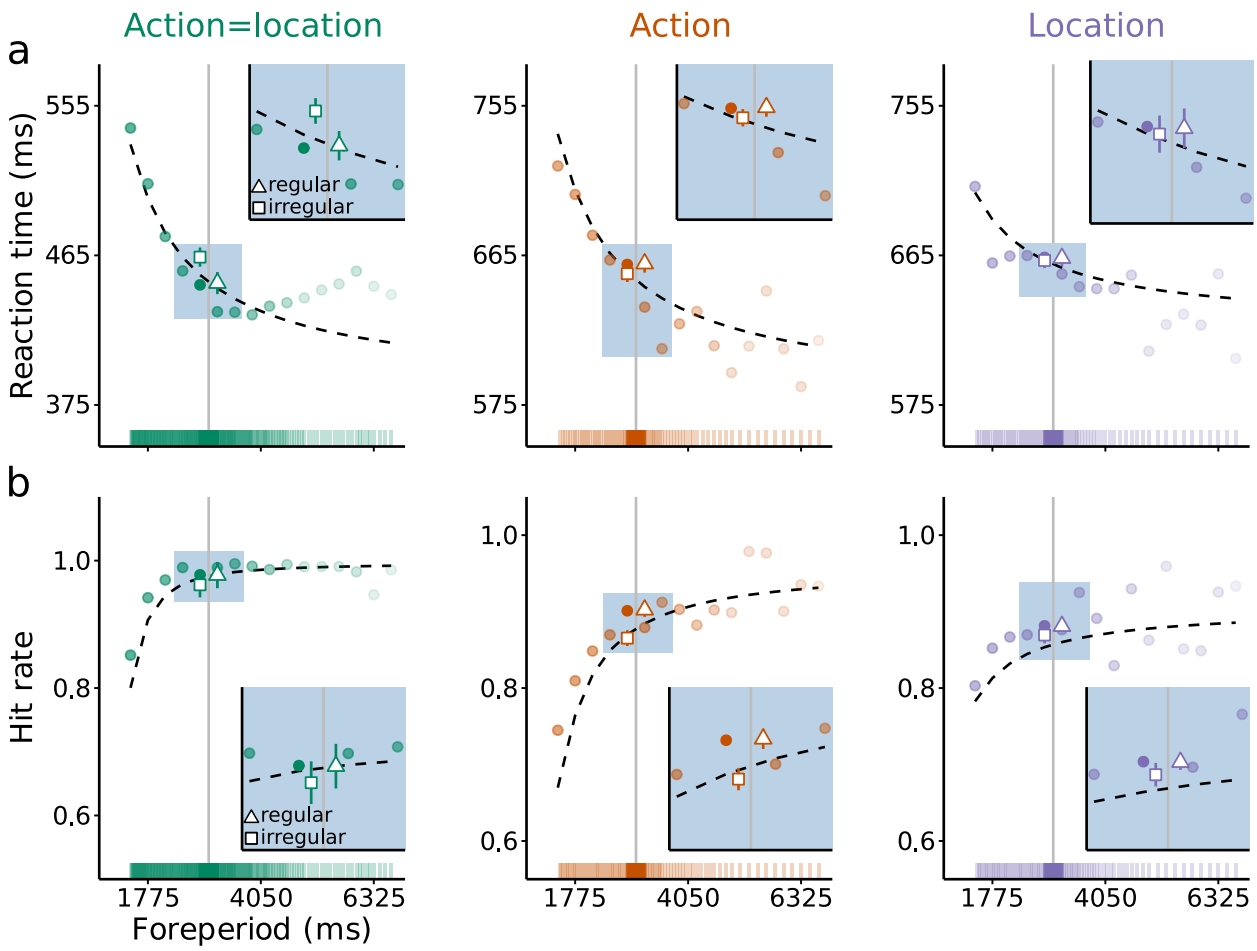
Is the Regularity Benefit an Illusion?

The inclusion of FP as predictor meant that the inclusion of the predictor 'regularity' was no longer warranted as fixed effect, for both RT ($\Delta BIC = 7.3$, $BF = 38.3$) and HR ($\Delta BIC = 10.5$, $BF = 193.0$). Additionally, the model only including FP vastly

[2] Note that statistical model predictions represent estimated marginal means (i.e., at the average level of other predictors) and not a least-squares fit to empirical data.

Figure 4

Temporal preparation.



Note. (a) Mean RT decreases and (b) HR increases as a function of foreperiod (FP), characteristic of temporal preparation effects for both regular and irregular targets. The points represent binned RT and HR (bin size = 350 ms), the dashed lines, the fit of the statistical model. For illustration purposes, we omitted 1% of the tail of the data (FP > 7200 ms). Opacity of the colored bar above the x-axis and the data points illustrate the amount of data per FP bin. Most data is around an FP of 3000 ms (solid vertical line). The open square and triangle in the inset plots are the same averages as plotted in Figure 2. Note that for RT the y-axis scale is the same for the 'action' and 'location' conditions, but differs from the 'action=location' condition.

outperformed the model including only regularity, for both RT ($\Delta BIC > 1000$, $BF > 1000$) and HR ($\Delta BIC = 488.8$, $BF > 1000$). In other words, what seemed to reflect statistical

learning can be better accounted for by temporal preparation for both regular and irregular targets. This is illustrated in Figure 4, which shows the average RT and HR as a function of regularity (as in Figure 2) and FP. For irregular targets, short FPs ($<$ 3000 ms) are characterized by high RTs and low HRs. Due to the strong asymptotic nature of preparation effects, long FPs ($>$ 3000 ms) are not affected to the same extent. This asymmetry leads to an apparent 'regularity benefit' when only considering the average RT and HR as a function of regularity. However, when observing performance as a function of FP, it can be seen that at FP = 3000 ms (Figure 4, insets), there is no apparent difference between regular and irregular targets.

Discussion

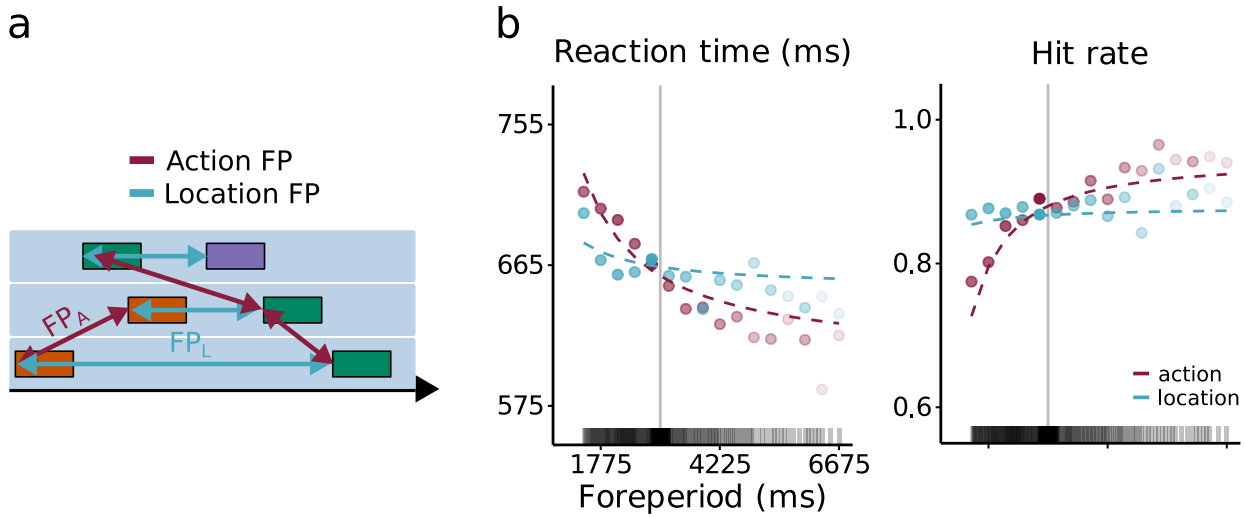
We found that participants temporally prepare for upcoming targets. Importantly, these findings go against our previous interpretation that participants only capitalize on the regularity embedded in WAM's complex temporal structure, giving rise to the 'regularity benefit' (Salet et al., 2021a, 2021b). Instead, participants show to temporally prepare, in parallel, for both regular and irregular targets.

Where and What is Next

Thus far, we have defined the FP in the 'action' condition as the time between repeating actions, and in the 'location' condition as the time between repeating locations (Figure 3b and 3c). This allowed us to evaluate whether FP effects could explain the 'regularity benefit' observed in these conditions. Note, however, that in 'action' and 'location' conditions, each target has both an 'action' and a 'location' FP (FP_A and FP_L; Figure 5a). It might be that participants exploit both FP types and prepare both what action (e.g., ring finger) and location comes next (e.g., top location). If so, we should find preparation curves for both FP types in each condition. Additionally, as these two conditions only differed in the assigned regularity (Figure 1b, action versus location) we expect the effect of both FP types to be similar in the 'action' and 'location' conditions.

Figure 5

Where and what is next.



Note. (a) Illustrates the two FP types: action FP and location FP in the same stimulus segment. (b) Mean RT and HR as a function of FP (plotted as in Figure 4).

To test this, we constructed new statistical models including the predictors FP_A and FP_L, and tested whether FP_A or FP_L interacted with 'condition'. Figure 5b displays preparation effects on RT, split on FP type, together with the statistical model's predictions. Model comparisons revealed an effect of FP_A on RT ($\Delta BIC = 592.3$, $BF > 1000$) and HR ($\Delta BIC = 270.3$, $BF > 1000$). For FP_L, an effect was found on RT ($\Delta BIC = 26.0$, $BF > 1000$), but evidence of absence for an effect on HR ($\Delta BIC = 6.8$, $BF = 30.3$). The models' steeper RT curves as a function of FP_A versus FP_L (slope coefficient 4.1 times larger for FP_A) and the absence of an effect of FP_L for HR suggests that preparation effects were more pronounced for action than for location. Finally, FP effects did not differ between the 'action' and 'location' conditions ($\Delta BIC > 13.9$, $BF > 1000$). Indeed, this confirms that the conditions govern similar preparation dynamics and are unaffected by the modality of the regularity (action versus location).

Discussion

Here we show that in the 'action' and 'location' conditions, participants temporally prepare, in parallel, what action to perform and what location to attend. Furthermore, we found indications that the effect of 'action' preparation (FP_A) is more pronounced than 'location' preparation (FP_L).

Replication

In Appendix B, we present results of a very similar experiment with 54 participants. Analyses point to exactly the same conclusions as presented so far.

*f*MTP: A Computational Account of Preparation

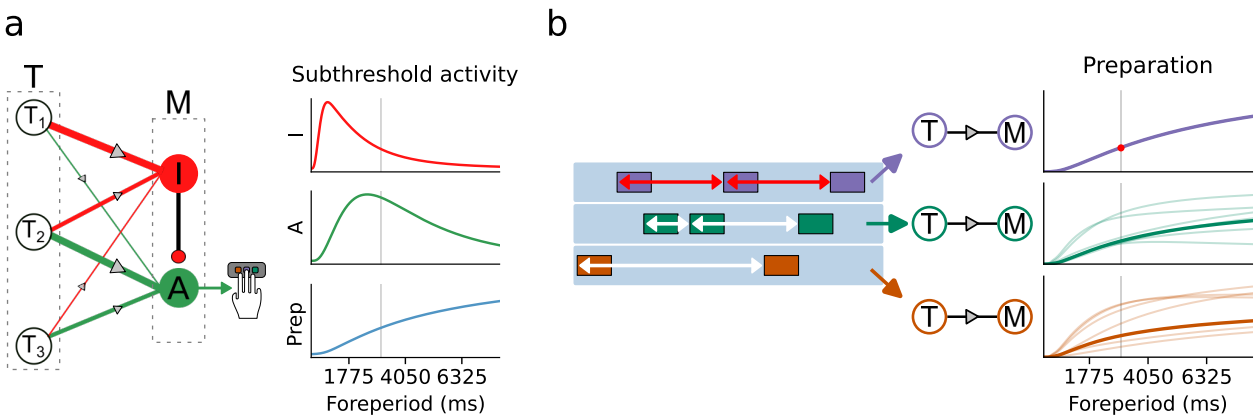
When considering all temporal information embedded in WAM (Figure 3), we find behavioral effects that appear to reflect temporal preparation (Figure 4 and 5). In this section, we use a model of temporal preparation (*f*MTP, Salet et al., 2022) as a proof of concept to strengthen the link between our empirical findings and temporal preparation. To do so, we focus on the 'action=location' condition and, in particular, on two key aspects of the data. First, does using WAM's stimulus sequence as input to the model lead to the same preparation curves as observed in the data? Second, does the average RT computed from these preparation effects give rise to an apparent 'regularity benefit'?

Model Architecture

A detailed (mathematical) description of *f*MTP can be found in Salet et al. (2022). In short, *f*MTP is a neural network consisting of a motor circuit and a timing circuit (Figure 6a). The motor circuit consists of an activation and inhibition node, and their interplay resembles the initiation of a motor plan (i.e., a button press corresponding to the target on screen). During the FP, activation is suppressed by inhibition (Davranche et al., 2007; Duque & Ivry, 2009; Greenhouse et al., 2015; Hasbroucq et al., 1999; Prut & Fetz,

Figure 6

fMTP.



Note. Illustration of *f*MTP's underlying dynamics. (a) Trace formation. In the motor circuit (M), inhibition (I) controls activation (A) to prevent premature responses during the FP. Each node in the timing circuit (T; three example nodes are drawn) projects to both I and A. The thickness of the connections represents the association strength after a sequence of FPs. These associations determine the subthreshold fluctuations in I and A determining preparation (Prep) on the next trial. (b) In WAM, each target (unique location and action) triggers a unique preparation circuit. A constant FP (purple) leads to similar preparation on each trial. As the regular FP is always 3000 ms (solid vertical line), the model's predicted preparation is only observed at that specific FP (red dot). For the irregular targets (green and orange, varying FPs) preparation fluctuates. Transparent lines represent preparation of different target presentations, the non-transparent line represents average preparation across all presentations. Note that I and A are plotted in arbitrary units, but their ratio (preparation) directly scales to RT.

1999; Sinclair & Hammond, 2008), enabling the staging of a motor plan without executing it, akin to an athlete awaiting the start signal before taking off. At target presentation, however, the inhibition node is suppressed, and the activation node is triggered, initiating the response.

Trace Formation

This interplay between the inhibition and activation node during the FP is driven by a timing circuit (Figure 6a, Shankar & Howard, 2012): An array of neuronal units that convey information about the passage of time during the FP (Eichenbaum, 2014; MacDonald et al., 2011; Pastalkova et al., 2008). Different time points during the FP are encoded by different nodes in the timing circuit. Each node in the timing circuit projects to the motor circuit, and their simultaneous firing leads to Hebbian learning (see Gallistel & Gibbon, 2000; Machado, 1997; Mauk & Ruiz, 1992, for similar rules used for learning to time). In this way, specific points in time get associated with either inhibition or activation; just as a ringing bell becomes associated with food in Pavlovian conditioning.

The Hebbian associations between the timing and motor circuit are stored in 'memory traces' on each FP trial. A simplified example of this process is illustrated in the left panel of Figure 6a, depicting three example nodes in the timing circuit: T_1 encodes early time points before target onsets, T_2 encodes time points around target onsets, and T_3 late time points after target onsets. Through Hebbian learning caused by simultaneous firing of the timing, inhibition, and activation nodes, T_1 primarily forms associations with inhibition (thick red line, it is too soon to respond), T_2 with activation (thick green line, it is time to respond), and T_3 neither with inhibition nor activation (thin connection lines, target has already passed). These Hebbian associations define the 'memory trace' at each trial.

Memory

Critically, fMTP postulates that preparation is determined by the collective contribution of traces formed on previous trials, retrieved from memory. Due to forgetting, traces contribute according to their recency with traces of remote trials contributing less strongly than recent traces (Wixted, 2004; Wixted & Ebbesen, 1991). It is the contribution of memory traces by which the network's state tunes to the temporal properties of the

environment. The right panel of Figure 6a visualizes the result of this 'tuning' after a sequence of multiple FPs between 2500 and 3000 ms. Early points in time (FP $<$ 2500 ms) become strongly associated with inhibition, whereas points in time close to target onset (FP ~2750 ms) become more strongly associated with activation. These subthreshold fluctuations in the balance between activation and inhibition during the FP reflect preparation (Figure 6a, blue line). For later time points (FP $>$ 3000 ms), as activation started to decrease later than inhibition, preparation gradually increases. This gives rise to the asymptotic nature of preparation effects.

*f*MTP and WAM

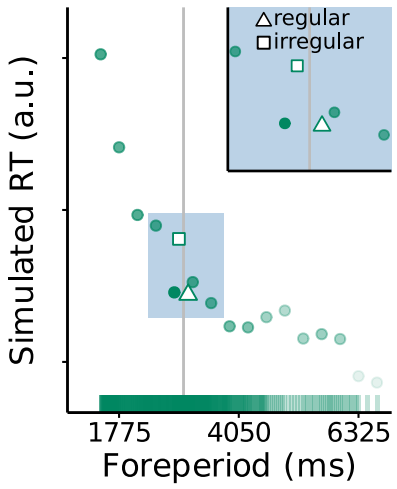
Originally, *f*MTP was developed and tested as a model of experiments in which FPs (range of 300 - 5500 ms) are presented in isolated trials (Salet et al., 2022). To model the more complex WAM task with three continuous streams of target onsets and a wide range of FPs (1250 – 14000 ms), we extend the model such that each target triggers a unique preparation circuit existing of timing and motor circuits (Figure 6b). With this, we assume specificity of preparation. That is, each target elicits its associated timing circuit that projects to a corresponding motor circuit, representing a specific response. Aside from this assumption, we keep all other aspects of *f*MTP the same and directly adopt the default parameter values reported in Salet et al. (2022). Below, we discuss the implications of this 'specificity' assumption, but first we evaluate the model's predictions.

Simulation

To arrive at RT, we formalize the interplay of inhibition and activation in *f*MTP (i.e., preparation) as the I/A ratio. High levels of inhibition increase the I/A ratio and slow down responses, and vice versa for high levels of activation. We focus the simulation on the goodness of the qualitative predictions of *f*MTP (i.e., simulated RT). Salet et al. (2022) showed that this simulated RT provides a simple measure that linearly relates to RT. For each preparation circuit, one for each target, the simulation returns a simulated RT for

Figure 7

fMTP: simulated RT.



Note. Mean simulated RT (arbitrary units, a.u.) as a function of FP (plotted as Figure 4 and 5).

each experienced FP corresponding to that target. These simulated RTs are subsequently analyzed exactly like the empirical data (see Figure 4a). Of note, we do not simulate HR but hold the rationale that faster RT leads to higher HR, a relation found across all empirical data (Figure 4 and 5).

Figure 7 shows the model predictions. Using the WAM sequence as input to the model leads to a similar RT pattern as observed in the data. The RT curve for the irregular targets arises from *f*MTP's memory principles as earlier time points become, through Hebbian learning, primarily associated with inhibition, whereas for later time points activation is more pronounced. This changing balance, shifting in favor of activation as time passes, yields increasing preparation as a function of FP (see Figure 6), resulting in the downward sloping RT curve. Interestingly, in line with the empirical data, simulated RT for the regular target which is always presented at a FP of 3000 ms, is similar to simulated RT for irregular targets with this FP. Due to the asymmetric nature of preparation effects, averaging across regularity leads to an apparent 'regularity benefit' (Figure 7, inset), just as we observed in the empirical data.

Discussion

Our simulations show *f*MTP to capture the two key aspects of the data. Guided by *f*MTP, we can make assumptions about the cognitive mechanisms from which our findings might arise. That is, responses in WAM are governed by associative learning between timing circuits that monitor the timing of the targets and motor circuits initiating specific responses. This target-by-target learning process drives preparation during the interval between targets, governing the readiness to respond. In this way, by interacting within WAM, participants adapt their behavior to WAM's temporal properties.

To account for the multiple response options in WAM, we made a 'specificity' assumption that each response option is independently prepared for. This assumption contrasts with how we had proposed *f*MTP in Salet et al. (2022). That is, we implemented preparation as a non-specific process, independent of the response. A non-specific implementation of *f*MTP where each response was tied to the same neural circuit failed to capture the empirical data (Appendix C, Figure C1).

Interestingly, these results fit with a range of behavioral and neurophysiological studies which have addressed the (non)specificity of preparation. Traditionally, the finding that inhibition also applies to task-irrelevant effectors has led to the view that preparation comes with widespread non-specific inhibition of the entire motor system (Hasbroucq et al., 1999; Prut & Fetz, 1999). This is how we had implemented *f*MTP (Salet et al., 2022), and aligns with the observation that preparation effects are qualitatively highly similar in simple- versus choice RT tasks (Bertelson & Boons, 1960; Frith & Done, 1986; Los & van den Heuvel, 2001; Steinborn & Langner, 2012).

In contrast with this 'non-specific' view, however, studies have also found higher inhibition of the selected compared to the non-selected effector of the response, suggesting at least some specificity of inhibition (Davranche et al., 2007; Duque & Ivry, 2009; Greenhouse et al., 2015). This finding has led to the 'gain modulation hypothesis' that proposes that inhibition enhances the specificity of selected responses (Duque et al., 2017;

Greenhouse et al., 2015). The specificity of inhibition can be illustrated by imagining an 'inhibition spotlight' centered around response representations (Greenhouse et al., 2015). A narrow focus, increasing specificity, solely inhibits the selected response, while a broad focus also inhibits non-selected responses. Interestingly, the focus – and thereby specificity – is hypothesized to be context dependent. In tasks with a single response option (e.g., simple RT task), the focus is more broad and therefore also inhibits non-selected responses. However, with multiple response options (e.g., choice RT task), its focus narrows to enhance the separation between the response representations; thereby decreasing the probability of selecting the incorrect response.

In WAM, participants had three response options, and continuously risked a penalty for incorrect choices. From the view of the gain modulation account, it might be that these task demands narrowed the spotlight of inhibition, thereby characterizing preparation as a specific process. A range of behavioral studies has similarly shown that preparation can, at least in some contexts, be specific for the selected response (Langner et al., 2018), target identity (Thomaschke et al., 2016; Thomaschke et al., 2011; Wagener & Hoffmann, 2010), and target location (Wagener & Hoffmann, 2010). These findings align with the specificity assumption in *f*MTP (Figure 6b). However, to what extent and under which circumstances preparation reflects a (non)specific process remains a question that requires more research.

In sum, our simulations (under the assumption of specificity) served as a proof of concept to show that our results arise from the underlying memory processes of temporal preparation. However, it is fair to recognize that the current implementation is a simplification of the WAM task. On the one hand, it can be considered a strength that a previous implementation of *f*MTP (Salet et al., 2022), fit to preparation experiments with a different range of FPs, directly translates to this paradigm. On the other hand, this implementation ignores various aspects of the data. For example, we did not directly model hits and misses, and only focused on the 'action=location' condition. Although we leave the development of a complete model of WAM open for future work, the present

implementation demonstrates the promise of conceiving adaptive behavior in WAM as a result of general memory processes underlying temporal preparation.

General Discussion

Statistical learning is a phenomenon signified by a 'regularity benefit' (e.g., lower RT, higher HR) for regular versus irregular properties of the environment (e.g., Fiser & Aslin, 2001; Olson & Chun, 2001; Turk-Browne et al., 2009; Yu & Zhao, 2015; Zhao et al., 2013). This benefit is commonly interpreted as arising from "*...the ability to extract regularities from the environment over time*" (p. 15, Sherman et al., 2020). In line with this view, we surmised that the 'regularity benefit' observed in WAM is a reflection of a statistical learning mechanism that extracts the regularity (i.e., single regular interval; Salet et al., 2021a). Intriguingly, we found that the 'regularity benefit' originates from parallel preparation to a multitude of temporal properties that we initially considered to be random.

Statistical Learning: What is it?

Statistical learning research has convincingly shown the 'regularity benefit' to be a very robust finding across different domains (e.g., Fiser & Aslin, 2001; Olson & Chun, 2001; Saffran et al., 1996; Turk-Browne et al., 2009; Yu & Zhao, 2015; Zhao et al., 2013). The theoretical construct of statistical learning, however, has been argued to be underspecified (Frost et al., 2019; Thiessen, 2017). That is, mechanistic explanations of what is exactly learned in these paradigms lag behind the robust empirical phenomena (Frost et al., 2019).

Problem of Inadequate Contrasts

Our results demonstrate an issue that might arise when interpreting empirical observations without the guidance of a precise theoretical construct. The overall contrast between regular and irregular targets (Figure 2) provided the misconception of statistical learning of the regular, but not irregular targets (see also Salet et al., 2021b). However,

this difference actually originated from the preparation of a range of other temporal properties of both regular and irregular events. This is not to say that solely observing the average split on regular versus irregular events always provide such an illusion. We do argue, however, that 'regularity benefits' might not always do justice to the complexity of adaptive behavior. Statistical learning might be more powerful than solely extracting the regularity from the experiment (see Thiessen, 2017, for similar reasoning).

Our results speak to an issue that is prevalent in experimental designs intended to study statistical learning. That is, it can be particularly difficult to introduce a (statistical) regularity in isolation without introducing other factors that may affect performance. An example of this issue has been highlighted for 'probability cueing' (Jiang, 2018; Shaw & Shaw, 1977), a common visual search paradigm where targets are more likely to be found in certain locations than others. Performance benefits can be observed for regular targets over irregular targets, but it has been argued that for a large part this may be attributed to repetition priming (Maljkovic & Nakayama, 1994; Rabbitt et al., 1979). By having targets appear more frequently at certain locations, they will almost invariably have appeared more recently at that location as well. Repetition priming can often account for most, if not all 'regularity benefits' observed in a task, without assuming that any long-lasting learning takes place (Kabata & Matsumoto, 2012; Maljkovic & Martini, 2005; Walthew & Gilchrist, 2006). Later studies have argued that learning in such designs is better assessed through so-called 'transfer phases', studying the lasting effects of a regularity in subsequent experimental blocks in which the regularity no longer holds (Sha et al., 2017, Jiang et al., 2016, Kruijne and Meeter, 2015; see also Los et al., 2017).

In the temporal domain, this issue might be particularly critical, as introducing a temporal regularity almost invariably introduces other temporal and non-temporal aspects of the task. For example, our WAM sequences have been generated via a procedure that equates the number of regular and irregular targets, while controlling for any differences in ISI (Salet et al., 2021a). This procedure was intended to ensure that regular and irregular

targets only differed with regards to their timing, making this regularity the only factor that participants would be able to exploit. Here we show that participants nevertheless still timed the intervals between irregular targets. As it might be impossible to design tasks ruling out timing to such variable intervals, they are important to consider in any temporal task. For example, such 'irregular' timing might similarly play a role in recent work that found visual search to be facilitated for regular versus irregular spatiotemporal patterns (Boettcher et al., 2022). This performance benefit, expressed as average RT and HR split on regularity, was interpreted to arise from learning the spatiotemporal pattern that guides attention in visual search. However, as in WAM, their stimulus sequence embeds a multitude of other temporal properties (including ISI and FP). Therefore, as in our study, 'statistical' learning might be even more powerful than merely learning the regular spatiotemporal pattern.

What is Learned?

Various computational models have shown that statistical learning can naturally arise from memory processes, without the need for a specialized module performing statistical computations (French et al., 2011; Kruijne & Meeter, 2015; Mareschal & French, 2017; McClelland & Elman, 1986; Perruchet & Pacton, 2006; Perruchet & Vinter, 1998; Schapiro et al., 2017; Thiessen & Pavlik Jr., 2013). Although these theories have their differences, conceptually they work from two main principles of memory: activation and a forgetting process modeled as decay or interference. In these memory models, each presented item is automatically stored in a memory trace that decays over time. Trace activation increases as an item is repeated, while other items may cause interference and decrease trace activation. In this way, repeating items in the environment (i.e., regularities) gain dominance in memory through associative learning between incoming input and internal memory traces. The application of these models has provided support that such memory processes can lead to adaptation to the environment's statistics, commonly

interpreted as statistical learning.

Our findings, demonstrating that statistical learning effects can emerge from temporal preparation, instantiate this perspective in the temporal domain. Similar to these memory models of statistical learning, Salet et al. (2022) demonstrated that temporal preparation can naturally emerge from associative memory processes, without the need for a system that calculates hazards (Janssen & Shadlen, 2005; Trillenberg et al., 2000) or tracks probabilities (Grabenhorst et al., 2021; Grabenhorst et al., 2019). As a proof of concept, we showed that *f*MTP's associative learning rules indirectly give rise to 'regularity benefits' in WAM (Figure 6).

Temporally Structured World

Ample evidence from interval timing studies has already shown that behavior adapts to the temporal statistics embedded in experiments (Acerbi et al., 2012; de Jong et al., 2021; Maaß et al., 2019; Nobre & Ede, 2018). However, typical timing studies explicitly cue the relevant intervals for behavior in isolated trials. This deviates from behavior in the natural world in two important ways. First, the temporal structure of our world is much more complex than simple, isolated intervals. Second, intervals are hardly ever explicitly cued, and we only learn about their relevance after interacting with our environment, while we are hardly ever aware of the temporality of our behavior. We initially hypothesized that, in complex environments like WAM, participants would simplify the complex temporal structure by only adapting to regular intervals. Instead, we found that behavior was driven by a multitude of temporal properties which we had initially thought to be irrelevant.

One way to interpret the present findings is that participants continuously tracked six different intervals (three actions and three locations) in parallel to prepare what action to perform where. What timing mechanisms could give rise to such complex temporal preparation? In such complex scenarios, it is simply undoable to keep track of multiple overlapping intervals with a single (neural) timekeeper. At the same time, recruiting a new

timekeeper for each new interval in the environment will likely burden cognitive resources. Interestingly, it has been argued that time comes as a free by-product of dynamic neural activity elicited by incoming stimuli, a view known as the 'intrinsic' view of timing (Buonomano & Laje, 2010; Karmarkar & Buonomano, 2007; Mauk & Buonomano, 2004). In this view, tracking multiple, overlapping intervals may be feasible if these events trigger at least partly a set of non-overlapping neurons. A recent 'intrinsic-adaptive' view on timing has emphasized the computational power of linking such intrinsic timing properties with associative learning rules to capitalize upon nature's temporal structure (Salet et al., in press).

With *f*MTP, combining timing circuits with associative learning, we showed this to be a promising concept. The demonstration that our findings can arise from a common temporal preparation process opens new directions for future investigations of timing behavior in complex, dynamic environments like WAM. For example, a common finding is that temporal preparation is sensitive to variations in the distribution of FPs (Los et al., 2014; Trillenberg et al., 2000). Similarly, in a WAM design in which target presentations follow a distribution of FPs instead of a single regular FP (i.e., 3000 ms), behavior might adapt to the type of distribution. In that regard, if preparation is indeed specific as we implemented into *f*MTP (Figure 6a), an interesting question is whether multiple distributions, paired with different targets, can be learned simultaneously.

Conclusion

We found, across two experiments, temporal adaptation to be much more powerful than we previously thought. Initially, we had assumed that participants would capitalize on WAM's complex temporal structure through a statistical learning mechanism extracting a single regular interval. Instead, we found behavior to be driven by a multitude of other temporal properties, which we first considered impossible to be learned. Guided by *f*MTP, a computational model of temporal preparation, we illustrated that such complex temporal

adaptation might emerge from general learning mechanisms underlying temporal preparation.

Materials and Methods

Preregistration

This study's planned sample size, included variables, hypotheses, and planned analyses were preregistered on Open Science Framework (OSF) prior to any data being collected (https://osf.io/3b78x). Experiment files, analysis scripts and the full dataset can also be found on OSF (https://osf.io/9bjmy).

Participants

59 First-year psychology students of the University of Groningen were recruited for the experiment and received course credits in compensation for their participation. Participants gave informed consent prior to participation. The experiment was approved by the Ethics committee of the Faculty of Behavioral and Social Sciences (PSY-1920-S-0360).

Stimuli and Task

The experiment was implemented in OpenSesame (Mathôt et al., 2012) using the PsychoPy backend (J. Peirce, 2009; J. Peirce et al., 2019; J. W. Peirce, 2007). Participants were seated in a dimly lit room at approximately 60 cm viewing distance from a 22" LCD monitor (100 Hz, Iiyama MA203DT) and were instructed to score as many points as possible by reacting to sudden-onset targets with the correct button press. A video of the task is available at: https://osf.io/2ca8h/.

Target positions were indicated by unfilled circles (r = 1.5 cm), and their onsets were indicated by filling the circles with one of three colors, spaced equidistantly (120°) in CIELab space (orange, L*a*b*: [54.0, 56.4, 47.2]; green, L*a*b*: [54.0, -31.4, 17.1]; purple, L*a*b*: [54.0, -43.1, -31.4]) for 1000 ms. Participants' task was to press the corresponding

color-button on a conventional keyboard (colored stickers were placed on the left, right and down arrow keys) using their right hand. They were instructed to leave their response fingers (index, middle and ring finger) on the three buttons at all times.

In the 'action=location' condition, the three targets were placed at three corners of an equilateral triangle (sides = 24 cm). In this condition, each target color corresponded to one particular location, and the color-mapping was such that the index finger responded to the color of the left target, the middle finger responded to the color of the top target, and the ring finger responded to the color of the right target (Figure 1a). A white fixation dot (r = 0.24 cm) was presented centrally, and upon each button press a rectangle in the associated color appeared around the fixation dot, serving as visual feedback for the participants.

In each block, all three targets locations were presented twenty times. One of the locations/colors was used for the regular targets, which appeared every 3000 ms. The other two targets appeared at pseudorandomly generated intervals, and the order of target presentation was random. For each participant and block, a unique sequence of intervals for the irregular targets was generated. In these sequences, the interval between two subsequent targets in the same location was minimally 1250 ms (250 ms between offset and new onset), and there was always at least one irregular target between two regular targets. Additionally, the interval between the onset of a target and the onset of any next target (ISI) was controlled for, such that the distributions of ISI's preceding regular and irregular targets are equated (see section 'Interstimulus Interval' at https://osf.io/3d6h8 for more details).

In the 'action' and 'location' conditions, targets were aligned vertically at the center of the screen (distance between targets = 10.5 cm). This vertical alignment aimed to prevent any Simon interference, that is, performance detriments when responding to lateralized targets with the contralateral response finger (e.g., a left-sided target with the ring finger). To indicate which button participants pressed, a rectangle in the associated

color appeared around all three targets. In each block, targets were presented twenty times at each of the three locations and in each of the three colors, leading to a total of sixty target presentations per block. In the 'action' condition, there was no temporal regularity in the location of the targets, but one color, associated with one response action, appeared every 3000 ms at a random location (Figure 1b). Conversely, in the 'location' condition a target appeared at one of the locations every 3000 ms, but in a random color (Figure 1c). The temporal sequences of irregular targets were the same as in the 'action=location' condition.

Participants scored points if they hit a target within 1000 ms after its onset. Each hit was rewarded with five points and accompanied by the sound of a dropping coin. If participants were too late (250 ms after target offset) or pressed an erroneous button, five points were deducted as a penalty.

Procedure

The experiment comprised three conditions, each comprising eight experimental blocks. A block lasted approximately 1 minute, and was followed by feedback on the total score, the number of hits and misses, and the high-score. Participants always began the experiment with the 'action=location' condition, preceded by one practice block with no regularity. The regular color and location in the 'action=location' condition was counterbalanced across participants. After the 'action=location' condition, participants performed four practice blocks with vertically aligned targets where target locations and colors were no longer coupled, without any regularities. The order of the following 'action' and 'location' conditions was counterbalanced across participants. The features of the regular targets in the 'action' and 'location' conditions changed with respect to the 'action=location' condition (e.g., if the regular targets were green in 'action=location', they changed to orange or purple in the 'action' condition). However, we added the constraint that the middle finger response was never tied to the regularity in the 'action'

condition, and that the regularity was never in the middle location in the 'location' condition. This was done to prevent positive response biases (i.e., generally faster responses with the middle finger and/or attention bias towards the center of the screen). When comparing responses to the 'middle' irregular target to the other irregular target, we indeed found an advantage of middle finger and middle target responses (Appendix A) and therefore discarded these responses from further analyses. Note that our conclusions are still supported when we include these responses.

Questionnaire

At the end of the experiment, participants answered seven questions to assess their awareness of the temporal regularity: (1) They were asked an open question in which they were asked whether they had observed anything noteworthy during the experiment; (2) after being informed about the temporal regularity in the 'action=location' condition, they were asked whether they had noticed this regularity (Yes/No); (3) They were presented with a forced choice question to indicate (or guess) which target location/color had been the regular one; (4) after having been informed of the existence of the temporal regularities in the 'action' and 'location' condition, they were presented with questions to indicate whether they had noticed these (Yes/No); (5) They were asked a question to indicate in what order the regularities had been presented; and they were presented with two more forced choice questions to indicate (or guess) the color (6a) and location (6b) of the temporal regularity.

Inclusion Criteria

None of the participants reported the regularity in question 1. Nevertheless, we excluded and replaced the data from three participants who indicated having been aware of one of the regularities in question 2 or 4, and chose the correct location/color in question 3, 6a or 6b. We additionally excluded data from blocks in which the hit rate for one of the three targets was less than 25%, suggesting that a participant might not have divided their

attention across all targets. Two more participants were excluded because more than three out of eight blocks in one condition had to be discarded. Subsequently, we identified RT outliers in two steps: First, we set a global cutoff (across-participant) to remove extreme outliers (only including 150 ms $<$ RT $<$ 1500 ms). Second, we removed RTs that exceed the median -/+ three times the median absolute deviation (computed after the global cutoff) for each participant (within-participant cutoff). All RTs not identified as outliers, are defined as a hit.

Data Analysis

Analyses were conducted in Python 3.8.5 and R 3.6.1 and assessed participants' responses expressed by RT and HR. We analyzed log-transformed RT using linear mixed models (LMMs Baayen et al., 2008; Bates et al., 2015) and HR by general (G)LMMs with a logistic link function.

For both RT and HR, we included 'participant' as a random intercept. The main interest of the study was whether regularity of targets (regular versus irregular), foreperiod (FP), and their possible interaction with condition ('action=location', 'action', versus 'location') affected performance. These predictors are reported in the Results section. To investigate order effects, we additionally assessed whether these predictors interacted with the order of condition presentation ('action $\rightarrow$ location' versus 'location $\rightarrow$ action'; note that condition 'action=location' was always presented first). Furthermore, we considered the effect of previous response (hit versus miss) and practice effects (time-on-task, indexed by block number). Tests for these additional predictors are reported in Appendix A.

We tested the contribution of each of these predictors by means of model comparisons, based on Bayes factors (BF) estimated from BIC scores (Wagenmakers, 2007). To quantify statistical evidence for or against a predictor term, we compare the best statistical model that includes this predictor against the best model without it. The analysis of condition order and practice effects did not reveal any effects on RT or HR.

Appendix A offers a complete report of the statistical procedure.

Competing Interests

The authors declare no competing interests.

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Appendix A

Full Statistical Report

Here, we provide all details of the statistical procedure for the model selection of the (General) Linear Mixed Models (G)LMM to analyze response time (RT) and hit rates (HR). Statistical evidence for or against an effect of interest was quantified by comparing the best statistical model (in terms of BIC) with this effect against the best model without this predictor term. For some comparisons, this means that the compared models can differ in terms of other predictors as well. In the R-notebooks on our OSF repository (https://osf.io/2ca8h/) we list full tables with all possible models ranked by BIC, which determines which models were compared.

Middle Bias

As documented in our preregistration (https://osf.io/3b78x), we suspected a 'middle bias' in the 'action' and 'location' conditions. That is, we hypothesized there would be a benefit of (1) detecting targets in the middle location, which was in the center of the screen and (2) a facilitation of middle finger responses compared to the index and ring finger responses. For this reason, these responses were never associated with any regularity by design.

Model comparisons indeed revealed a middle bias: RT was lower and HR higher for middle finger responses ($\Delta BIC = 13.4$, $BF = 801.0$) and for responses towards the middle location (RT: $\Delta BIC = 51.0$, $BF > 1000$; HR: $\Delta BIC = 114.3$, $BF > 1000$). Only for the HR of the middle finger responses, evidence for such a bias was inconclusive ($\Delta BIC = 1.6$, $BF = 2.2$). The best RT models also included a random slope for the effect of 'middle action' and 'middle location' for each participant. For this reason, all analyses in the main text exclude targets presented at the central location or requiring a middle finger response. We note, however, that analyses including those 'middle' responses yielded the same conclusions.

Regularity Benefit

Questionnaire

At the end of the experiment, participants answered a questionnaire (see Materials and Methods) to assess their awareness of the regularity. In the open question, none of the participants reported to be aware of the regularity. In the forced-choice yes/no questions, 5.5% ('action=location' condition) and 13.0% ('action' and 'location' conditions) indicated to have been aware of the regularity. However, only 30.0% ('action=location' condition) and 34.0% ('action' and 'location' conditions) of participants were able to correctly identify the regular color and/or location, closely in line with a guessing rate of 33.3%. Three participants were replaced because they both indicated to have been aware of the regularity, and had correctly identified the regular color and/or location.

Reaction Time

Model comparisons revealed that there was an interaction between 'condition' and 'regularity' (ΔBIC = 75.7, $BF > 1000$). This interaction entailed that in the 'action=location' condition RT was lower for regular compared to irregular targets (ΔBIC = 15.8, $BF > 1000$); in the 'location' condition RT did not differ (ΔBIC = 8.9, BF = 83.6); and in the 'action' condition we found an inconclusive trend indicating higher RT for regular targets (ΔBIC = 1.1, BF = 1.7). In addition, there was support for the fixed effect 'condition' (ΔBIC = 213.6, $BF > 1000$). Figure 3 in the main text, indicate that RT was lower in the 'action=location' blocks. However, we did not perform post-hoc tests to further explore their differences. Finally, there was support for predictor 'previous response' (hit/miss) (ΔBIC = 142.1, $BF > 1000$). The coefficient of 'previous response' entailed that RTs were higher when the preceding trial ($n - 1$) was missed compared to when it was a hit. Of note, for all following reports of the 'previous response' predictor, the direction of the effect was in the same direction: RT was higher and HR lower when $n - 1$ was a miss. The random effects structure of the model included a random intercept for

each participant and random slopes for the effect of 'regularity', 'condition', and 'practice effects' (time-on-task indexed by block number).

Hit Rate

Model comparisons indicated that HR was overall higher for regular than for irregular targets ($\Delta BIC = 28.2$, $BF > 1000$), but we found no interaction between regularity and condition ($\Delta BIC = 7.3$, $BF = 38.4$). Besides support for 'regularity', as reported in the main text, we found support for 'condition' ($\Delta BIC > 1000$, $BF > 1000$) and 'previous response' ($\Delta BIC = 449.6$, $BF > 1000$). The random effects structure of the best model contained only a random intercept per participant.

Temporal Preparation

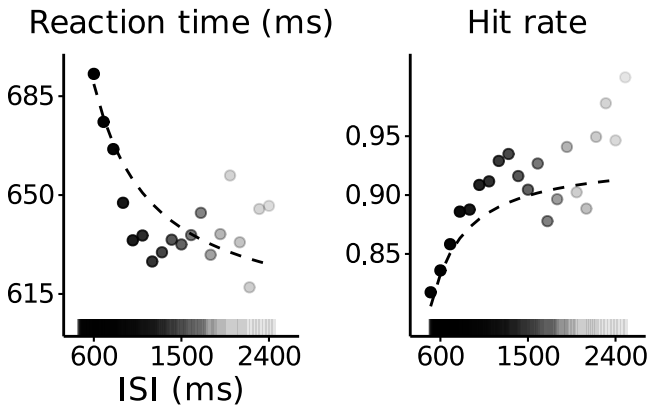
In addition to the support for the fixed effects reported in our article ('FP' and removal of 'regularity'), there was support for an interaction between 'condition' and 'FP' (RT: $\Delta BIC = 172.4$, $BF > 1000$; HR: $\Delta BIC = 100.9$, $BF > 1000$) and 'previous response' (hit/miss) (RT: $\Delta BIC = 142.1$, $BF > 1000$; HR: $\Delta BIC = 213.6$, $BF > 1000$). The interaction between 'condition' and 'FP' entails that the preparation curves have different slopes (see Figure 4 main text). However, we did not perform post-hoc tests to explore this interaction further. The random effects structure of the best RT model included, besides an intercept for each participant, a random slope for the interaction between 'regularity' and 'condition', and the effect of 'practice effects' (uncorrelated). The HR model only included an intercept for each participant.

Where and What is Next

Besides the support for the fixed effects 'FP_A', 'FP_L', (main text) and 'ISI' (reported below), there was support for an effect of 'previous response' (RT: $\Delta BIC = 27.1$, $BF > 1000$; HR: $\Delta BIC = 393.5$, $BF > 1000$). The random effects structure of the RT model included, besides an intercept for each participant, a random slope for the effect of

Figure A1

Interstimulus interval.



Note. Mean reaction time and hit rate as a function of ISI (plotted as in Figure 4 and 5, but now with bin size = 100 ms).

'previous response' and 'ISI' (uncorrelated). The HR model only includes an intercept for each participant.

Interstimulus Interval

As mentioned in the main text, we analyzed the effect of ISI on behavior (Figure 3d). Similarly to FPs, it might be that longer ISIs result in speeded responses (Figure A1). Indeed, model comparison supported including ISI as an additive predictor (RT: ΔBIC = 72.3, BF > 1000; HR: $\Delta BIC = 99.4$, $BF > 1000$). We did not find evidence that ISI interacted with either of the two FP types (RT: $\Delta BIC = 19.3$, $BF > 1000$; HR: ΔBIC = 14.2, $BF > 1000$), implying that ISI and both FPs independently affect preparation.

Taken together, these results suggest that, on top of both FP_A and FP_L, ISI drives preparatory behavior. However, ISI effects might not only be caused by preparation over time. As displayed in Figure A1, the effect of ISI on RT and HR is mainly driven by ISIs shorter than 1000 ms (first two data points of FigureA1). Whenever the ISI is below 1000 ms, it reflects a situation where multiple targets are on screen simultaneously, and responses to the second of two overlapping targets are likely affected by the resulting conflict.

Appendix B

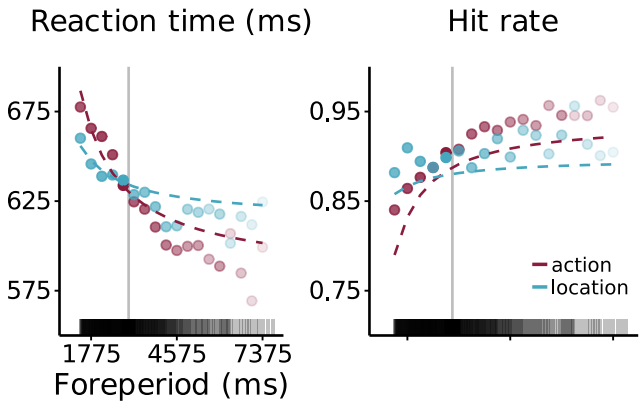
Replication

The experiment we discussed in the main text is a follow-up of an earlier preregistered experiment (https://osf.io/3d6h8). In this experiment, we presented participants with 'action' and 'location' conditions. Following Salet et al. (2021a), all targets were arranged in an equilateral triangle, and this experiment did not include an 'action=location' condition. In all other respects, the two experiments were identical. As we found no indication of a 'regularity benefit' in either condition of this experiment, and we ran the experiment in the main text as a follow-up, reasoning that the absence of a 'regular benefit' might have been a consequence of Simon interference obscuring any small 'regularity benefits'.

Here, we assess whether the FP effects reported in the main text could similarly be identified in the data of this experiment. As displayed in Figure B1, RT and HR in this experiment were also modulated by FPs. Model comparisons revealed that we replicated all critical effects: We found an effect for both RT and HR of FP_A (RT: $\Delta BIC = 81.6$, $BF > 1000$; HR: $\Delta BIC = 326.9$, $BF > 1000$), FP_L (RT: $\Delta BIC = 130.6$, $BF > 1000$; HR: $\Delta BIC = 7.2$, $BF = 37.4$), and ISI (RT: $\Delta BIC = 60.6$, $BF > 1000$; HR: $\Delta BIC = 22.8$, $BF > 1000$). Additionally, for HR, we found an interaction between FP_A and ISI ($\Delta BIC = 12.5$, $BF = 614.1$). As such, this experiment provides further support of our findings in the section 'Temporal Preparation' of the main text. Finally, we again found support for the fixed effect 'previous response' (hit/miss) ($\Delta BIC = 36.2$, $BF > 1000$; HR: $\Delta BIC = 98.7$, $BF > 1000$). The random effects structure of the model included a random intercept per participant and a random slope for 'FP_A' (for RT only, not for HR), 'previous response', and 'ISI'.

Figure B1

Replication.



Note. Mean reaction time and hit rate as a function of action and location FP. Plotted as in Figure 5b.

Appendix C

*f*MTP, non-specific implementation

All implementation details of the model can be found in the Python code (https://osf.io/eu7sd/, accompanied by a step-by-step tutorial). Salet et al. (2022) offers a detailed mathematical description of *f*MTP. Here, we only provide a qualitative description of the models as applied to WAM.

Non-specific Preparation

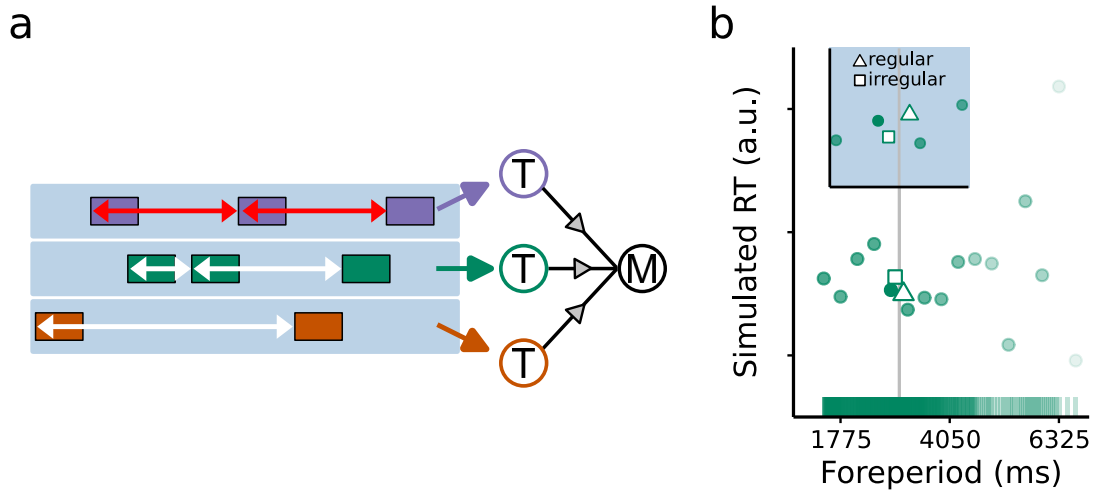
In the main text, we characterized preparation in WAM as a specific process, meaning that each target presentation triggers its associated timing circuit that projects to a corresponding motor circuit representing a specific response (Figure 6b, main text). Here, we present a version of the model that characterizes preparation as a nonspecific process (Figure C1a). In this implementation, as for the specific implementation, each target onset still triggers one of three independent, timing circuits. However, the 'non-specific' motor circuit reflects inhibition and activation of *any* response. In both versions of the model, simultaneous activity in the timing and motor circuits drives Hebbian learning. In the 'specific' implementation, such learning only occurred between the two corresponding timing and motor circuits. The critical difference is that, since the 'non-specific' motor circuit represents preparation for any response option, such learning happens simultaneously for all three timing circuits.

Simulation

At each target presentation, the three timing circuits affect activity in the motor circuit. The amount of preparation for this target is determined as the summed preparation brought forth by the three timing circuits and directly translated to RT as explained in the main text. Figure C1a shows the model's predicted RT as a function of FP. Clearly, for this model, there is no indication that RT decreases as a function of FP as observed in the data.

Figure C1

fMTP: non-specific implementation.



Note. (a) *f*MTP characterizing preparation as a non-specific process. Each of the timing circuits projects to the same motor circuit. (b) Mean simulated RT (arbitrary units, a.u.) as a function of FP (plotted as in Figure 7).