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The warning stimulus as retrieval cue: The role of associative memory in temporal preparation

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ABSTRACT

In a warned reaction time task, the warning stimulus (S1) initiates a process of temporal preparation, which promotes a speeded response to the impending target stimulus (S2). According to the multiple trace theory of temporal preparation (MTP), participants learn the timing of S2 by storing a memory trace on each trial, which contains a temporal profile of the events on that trial. On each new trial, S1 serves as a retrieval cue that implicitly and associatively activates memory traces created on earlier trials, which jointly drive temporal preparation for S2. The idea that S1 assumes this role as a retrieval cue was tested across eight experiments, in which two different S1s were associated with two different distributions of S1-S2 intervals: one with predominantly short and one with predominantly long intervals. Experiments differed regarding the S1 features that made up a pair, ranging from highly distinct (e.g., tone and flash) to more similar (e.g., red and green flash) and verbal (i.e., "short" vs "long"). Exclusively for pairs of highly distinct S1s, the results showed that the S1 cue modified temporal preparation, even in participants who showed no awareness of the contingency. This cueing effect persisted in a subsequent transfer phase, in which the contingency between S1 and the timing of S2 was broken - a fact participants were informed of in advance. Together, these findings support the role of S1 as an implicit retrieval cue, consistent with MTP.

1. Introduction

In experiments on human information processing, a trial commonly starts with a neutral warning stimulus followed by a target stimulus to which the participant is instructed to respond. Many researchers adopt this schema for pragmatic reasons. The warning stimulus serves as a time marker that enhances the participant's temporal preparation for the impending target, which in turn reduces noise in the behavioral data. When asked about the underlying mechanism of temporal preparation, most researchers would probably frame their answer in terms of maximizing alertness for processing the upcoming target or mobilizing resources for action at the expected moment. While such broad notions are not necessarily wrong, they are severely underspecified and fail to provide insight into the underlying processing dynamics.

In the present study, we provide evidence for a role of the warning stimulus as a retrieval cue – a view that is both more detailed and

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more compelling than prevailing notions. Our view is couched in multiple trace conceptions of long-term memory, which assume that experiences are stored as separate episodic memory traces (e.g., Hintzman, 1986; Logan, 1988, 1990; Nosofsky & Palmeri, 1997, 2015). A recent elaboration of this idea is that the warning stimulus retrieves memory traces associated with it, which in turn jointly prepare the organism for the impending target stimulus. Below, we first provide the details of this *multiple trace theory of temporal preparation* (MTP; Los et al., 2014, 2017) and show how it accounts for classic findings in human temporal preparation. Then we return to the idea that the warning stimulus acts as a retrieval cue, which leads up to the empirical contribution of this article.

1.1. A multiple trace theory of temporal preparation

Temporal preparation has been extensively studied in the variable-foreperiod paradigm. In this paradigm, the researcher varies, within a block of trials, the duration of the foreperiod between a warning stimulus (S1) and a target stimulus (S2), and measures the participant's response time (RT) with respect to S2. The classical finding is that, as the foreperiod increases, mean RT decreases toward an asymptote (e.g., Niemi & Näätänen, 1981; Woodrow, 1914), indicating a gradual growth of temporal preparation toward a maximum. Furthermore, whereas the RT – foreperiod function is relatively impervious to several experimental manipulations, such as the task set with respect to S2 (e.g., simple versus choice; Bertelson & Boons, 1960; Frith & Done, 1986; Steinborn & Langner, 2012) or the modality and intensity of S1 or S2 (e.g., Grabenhorst, Michalareas, Maloney, & Poeppel, 2019; Los & Van der Burg, 2013), it is strongly modified by the distribution of foreperiods. When the distribution of foreperiods is varied in different blocks of trials from negatively skewed (a preponderance of long foreperiods) via uniform to positively skewed (a preponderance of short foreperiods), the RT – foreperiod function becomes progressively less steep, while maintaining a stable asymptote (e.g., Baumeister & Joubert, 1969; Cravo, Rohenkohl, Santos, & Nobre, 2017). A benchmark condition is provided by the exponential ("nonageing") distribution, in which the frequency of consecutive foreperiods decreases according to a fixed rate (e.g., 8:4:2:1), and the RT – foreperiod function has been shown to be approximately flat (e.g., Los, Kruijne, & Meeter, 2017; Näätänen, 1970, 1971; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000).

To account for these and related findings, Los, Kruijne, and Meeter (2014) proposed MTP, which makes three main assumptions. The first assumption concerns within-trial processing dynamics. It holds that the detection of S1 prompts a preactivation of task relevant effectors, which is counteracted throughout the foreperiod by a process of continuous inhibition. Inhibition is lifted when S2 is presented, allowing activation to drive response execution (e.g., Los, 1996; Näätänen, 1971; Narayanan, Horst, & Laubach, 2006). A large and diverse body of evidence supports this point of view (e.g., Dankner, Shalev, Carrasco, & Yuval-Greenberg, 2017; Los, 2013; Narayanan & Laubach, 2006; Olmos-Solis, Van Loon, Los, & Olivers, 2017; Pavlov, 1927; Prut & Fetz, 1999; Toda et al., 2017). For instance, when transcranial magnetic stimulation is applied to human motor cortex, the motor evoked potential measured at the corresponding effector has been shown to be smaller during the foreperiod than at baseline, prior to S1 onset (Davranche et al., 2007; Duque & Ivry, 2009; Hasbroucq et al., 1999). Since this reduced activation has been found for all potential effectors in a choice reaction task, it has been argued to reflect a general mechanism of impulse control that prevents premature response (Davranche et al., 2007; Duque & Ivry, 2009; Jahfari, Stinear, Claffey, Verbruggen, & Aron, 2010; Prut & Fetz, 1999; for alternative interpretations, see Duque, Greenhouse, Labruna, & Ivry, 2017; Hasbroucq et al., 1999).

The second assumption is *trace formation*. It holds that a unique memory trace is created on each trial, which contains the temporal profile of inhibition (during the foreperiod) and activation (after S2 occurrence) experienced on that trial, along with representations of S1, S2, and the response to S2. As in other multiple trace theories, each new memory trace is added to an accumulating pool of memory traces created on earlier trials (e.g., Hintzman, 1986; Logan, 1988). Furthermore, these traces vary in strength. The strength of each trace is maximal upon its formation and gradually reduces toward an asymptotic value as it grows older (cf. Donkin & Nosofsky, 2012; Howard, Shankar, Aue, & Criss, 2015; Taatgen & Van Rijn, 2011; Wixted, 2004). At this stage of development, we do not commit to any mechanism of strength reduction, be it decay as a function of time (e.g., Baddeley, Thomson, & Buchanan, 1975; Barrouillet, Bernardin, & Camos, 2004; Hommel & Frings, 2020) or interference induced by new experiences (e.g., Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012; Polyn, Norman, & Kahana, 2009). Either mechanism would result in the gradual weight reduction we postulate.

The third assumption of MTP is *trace expression*. It holds that previously formed memory traces jointly determine the state of temporal preparation during the ongoing foreperiod. This process is initiated on each trial by the presentation of S1, which directly and simultaneously retrieves memory traces that contain a corresponding representation of S1 (e.g., Hintzman, 1986; Logan, 1988; Medin & Schaffer, 1978; Ratcliff, 1978). Next, as the foreperiod elapses, each retrieved trace contributes to preparation in accordance with its strength and its momentary value of activation or inhibition. Specifically, at each moment during the foreperiod the state of preparation is determined by the ratio of the weighted activation over inhibition values aggregated across memory traces. Figuratively, trace expression can thus be thought of as a temporal alignment and replaying of previously formed memory traces during the ongoing foreperiod.

Finally, we assume that the state of temporal preparation reached at the moment of S2 presentation determines RT according to an inversely proportional function. This relationship can be appreciated by conceiving the state of temporal preparation as the distance of potential neural excitability relative to a fixed motor-action limit (Näätänen, 1971; Niemi & Näätänen, 1981). However, we refrain from making a principled commitment here because a large body of research has failed to bring clarity on the processing governed by temporal preparation (see Rolke & Ulrich, 2010 for review). Although there seems to be consensus that preparation leaves decision processes unaffected (e.g., Bausenhart, Rolke, Hackley, & Ulrich, 2006; Bertelson & Boons, 1960; Jepma, Wagenmakers, Band, & Nieuwenhuis, 2009; Los & Schut, 2008), it remains to be resolved whether its main locus of influence concerns perceptual or motor processes (e.g., Correa, Lupiáñez, & Tudela, 2005; Hackley, Schankin, Wohlschlaeger, & Wascher, 2007; Mattes & Ulrich, 1997;

Müller-Gethmann, Ulrich, & Rinkenauer, 2003; Sanders, 1980; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004). In view of this state of affairs, MTP should be evaluated as a learning theory of temporal relationships rather than as a theory of the processes it governs.

Fig. 1 schematically illustrates how MTP explains the classic findings of foreperiod duration, varied at four levels, and foreperiod distribution. In the case of an anti-exponential distribution (Fig. 1A), where the consecutive foreperiods occur with a ratio of 1:2:4:8, temporal preparation is very low just after the presentation of S1 in view of the low ratio of activation over inhibition across memory traces. As time elapses during a long foreperiod, activation gradually takes over, and temporal preparation increases accordingly (Fig. 1C). These dynamics thus give rise to the typically observed steep RT – foreperiod function (Fig. 1E). In the case of an exponential distribution (Fig. 1B), where consecutive foreperiods occur with a ratio of 8:4:2:1, activation starts to dominate inhibition quickly after the presentation of S1. Thus, preparation is already close to ceiling by the time the shortest foreperiod has elapsed and it remains at that level if the foreperiod lengthens (Fig. 1D), yielding the characteristically flat RT – foreperiod function (Fig. 1E).

Before we consider alternative views of temporal preparation, we make a final comment on the activation profile shown in each memory trace of Fig. 1 (in black), which starts prior to the onset of S2 and continues for some time afterwards. This temporal profile can be reproduced by formal models that make use of the property of time cells (e.g., Bakhurin et al., 2017; Eichenbaum, 2014; Mello, Soares, & Paton, 2015; Pastalkova, Itskov, Amarasingham, & Buzsáki, 2008; Shankar & Howard, 2012). In these models, each time cell has a unique temporal activation profile, attaining its maximum firing rate at a different moment in time. Thus, when triggered by S1, the population activity of a bank of time cells indicates how much time has elapsed since the presentation of S1. Once S2 is presented, the time cells that are most active at that moment establish a strong association with this event by means of Hebbian learning (e.g., Los, Knol, & Boers, 2001; Machado, 1997). Because these time cells exhibit their period of strong activation surrounding the moment of S2 presentation, this results in the corresponding activation profile shown in Fig. 1.

1.2. Alternative views of temporal preparation

In this section we discuss two alternative views of temporal preparation, one based on the hazard function, the other based on trace conditioning. This exposition allows us to position MTP relative to these alternatives and to show what solutions it offers for otherwise problematic findings.

Explanations based on the hazard function. The hazard function specifies the conditional probability that S2 will be presented at the next possible opportunity during the ongoing foreperiod, given that it has not been presented yet (e.g., Luce, 1986; Nobre, Correa, & Coull, 2007; Vangkilde, Coull, & Bundesen, 2012, Vangkilde, Petersen, & Bundesen, 2013). It has long been recognized that, for any given foreperiod in any given distribution, mean RT tends to be shorter as hazard is higher, which has led to the wide-spread idea that hazard drives temporal preparation (e.g., Coull, 2009; Cui et al., 2009; Herbst, Fiedler, & Obleser, 2018; Janssen & Shadlen, 2005; Niemi & Näätänen, 1981; Trillenberg et al., 2000; Vallesi & Shallice, 2007; Woodrow, 1914). Specifically, the RT – foreperiod functions resulting from different foreperiod distributions, as described in the previous section, are all consistent with the hazard function

It has invariably (though often implicitly) been assumed that the hazard function is derived from the distribution of foreperiods that applies in a block of trials (e.g., Grabenhorst et al., 2019; Janssen & Shadlen, 2005; Trillenberg et al., 2000; Vangkilde et al., 2012). However, this view is problematic because it cannot account for an important class of phenomena based on trial history (Los et al., 2014, 2017). Short-term effects of trial history, also called sequential effects, reflect that the RT – foreperiod function is modified by the foreperiods of the immediately preceding trials (Niemi & Näätänen, 1981; Woodrow, 1914; see Los, 2010, for review). Specifically, RT on any trial n has been shown to be relatively long when the foreperiod on that trial is shorter than the foreperiod on trial n-1 but not when it is equally long or longer (e.g., Capizzi, Correa, Wojtowicz, & Rafal, 2015; Drazin, 1961; Langner, Steinborn, Eickhoff, & Huestegge, 2018; Los & Heslenfeld, 2005; Zahn, Rosenthal, & Shakow, 1963). Earlier trials, at least up to trial n-2, modify the effect of foreperiod on trial n in a similar way, albeit with much reduced effect size (e.g., Los et al., 2001; Steinborn & Langner, 2012).

Long-term effects of trial history have been demonstrated more recently. Los et al. (2017) presented two groups of participants with either the exponential or the anti-exponential distribution of foreperiods (cf. Fig. 1B and 1A, respectively) in an acquisition phase, and observed the typically flat and steep RT – foreperiod function, respectively. Both groups then received, after explicit instruction, the uniform distribution in a transfer phase of more than 200 trials. The data revealed a flatter RT – foreperiod function throughout the entire transfer phase for the group that had received the exponential distribution during acquisition than for the group that had received the anti-exponential distribution. Extending this finding, Mattiesing, Kruijne, Meeter, and Los (2017) showed that this transfer effect even held when the acquisition and test phase were separated by a full week, attesting to its long-term nature.

Temporal preparation thus comprises a family of phenomena, ranging from short-term (intertrial sequential effects) via medium-term (the effect of foreperiod distribution) to long-term (the transfer effect of foreperiod distribution). In its standard conceptualization, the hazard function is fully determined by the current distribution of foreperiods, so it should drive preparation identically on each trial. Whereas this version suffices to account for medium-term effects, it lacks flexibility to account for the short-term and long-term effects of the family. To accommodate short-term effects, it has been proposed that an additional process operates alongside hazard-driven preparation, resulting in a dual-process model (Vallesi & Shallice, 2007; Vallesi, Lozano, & Correa, 2013). However, the recent disclosure of long-term effects poses a new challenge to conventional hazard-based models on the other end of the time scale.

By contrast, MTP naturally accounts for effects of trial history. It accounts for short-term effects by its assumption that memory

¹ In a recent contribution, Grabenhorst et al. (2019) obtained results that were quantitatively inconsistent with the hazard function, which led them to favor a model based on the reciprocal probability density function. However, from the present perspective, this model meets the same problems as hazard-based models in that it does not specify how people learn the appropriate probability density function, while it cannot account for effects of trial history.

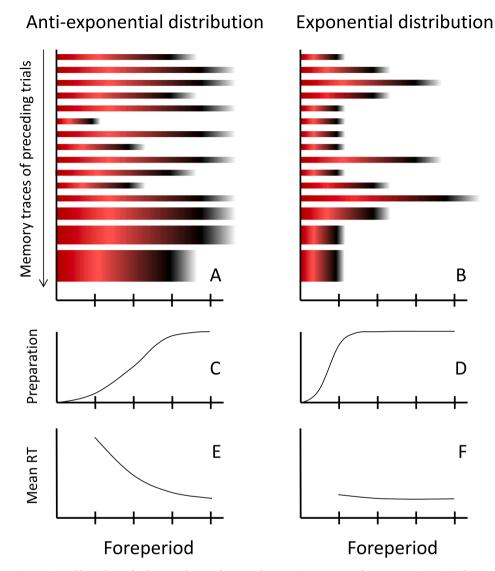


Fig. 1. Schematic overview of how the multiple trace theory of temporal preparation accounts for response time (RT) data under two different distributions of four different foreperiods (specified by tick marks on the horizontal axis). In the anti-exponential distribution (left), the ratio of foreperiods is 1:2:4:8; in the exponential distribution (right), the ratio is 8:4:2:1. A, B. The bars represent memory traces, created over 15 trials. In each bar, inhibition is indicated by red and activation by black. The thickness of the bars represents the relative weight of the memory traces as they contribute to current preparation. C, D. Development of preparation during the foreperiod, driven by the ratio of activation and inhibition aggregated across memory traces. E, F. Predicted mean RT as a function of Foreperiod. From "Hazard versus history: Temporal preparation is driven by past experience," by S.A. Los, W. Kruijne, & M. Meeter, 2017, *Journal of Experimental Psychology: Human Perception and performance*, 43, 78–88. Copyright 2017 by the American Psychological Association. (For the color version of this figure, the reader is referred to the online article.)

traces decrease in strength as they grow older (represented by the thickness of the traces in Fig. 1). Thus, when the foreperiod on trial n is shorter than on trial n-1, S2 is presented under the strong inhibitory expression of the most recently formed memory trace, which delays response. By contrast, when the foreperiod on trial n is equally long or longer than the foreperiod on trial n-1, S2 is presented when the inhibitory expression of the most recently formed memory trace is over, thereby leaving response unaffected. MTP also accounts for long-term effects because it denies artificial boundaries between experimental blocks or sessions. As a result, in a transfer phase with a uniform distribution of foreperiods, S1 will still prompt the retrieval of memory traces created during the earlier acquisition phase in which another (e.g., exponential or anti-exponential) distribution applied. Preparation will therefore reveal the influence of these older experiences, even if they occurred a week before, consistent with empirical findings (Mattiesing et al., 2017).

Incidentally, this analysis suggests how a hazard-based approach might be reconciled with the complete family of phenomena in temporal preparation. To do so, the hazard function should be derived, not from the current distribution of foreperiods, but from a memorized distribution of foreperiods that is incrementally updated upon every trial, with a stronger weighting of the most recent trials. In effect, such a 'memory hazard' model would stretch hazard to the point that it approaches MTP. But even so, an important

difference remains: According to MTP a complete preparatory state emerges from the retrieval of memory traces, whereas a memory hazard view would still need to specify how preparation results from a hazard informed expectancy.

Trace conditioning. To account for short-term effects in temporal preparation, Los (1996; Los & Van den Heuvel, 2001) proposed a trace-conditioning model, which is in many ways akin to MTP. However, instead of assuming that a new memory trace is created on every trial, this model assumes that a single memory trace is continuously updated by inhibition during the foreperiod ("extinction") and by activation upon the presentation of S2 ("reinforcement"). A formal version of this model (based on Machado, 1997) accurately accounts for the asymmetry of (higher-order) sequential effects (Los, 2013; Los et al., 2001).

The trace-conditioning model was originally intended as a general account of the phenomena of temporal preparation, based on the idea that medium-term effects would result from a propagation of short-term effects. For instance, favorable short-short sequences occur much more frequently under the exponential than under the uniform distribution, which therefore must contribute to the reduced slope of the RT – foreperiod function under the exponential distribution. However, a direct test of this idea revealed that this propagation of short-term effects is far too modest to account for the full-fledged effect of foreperiod distribution (Los & Agter, 2005; see Vallesi & Shallice, 2007; Vallesi et al., 2013 for additional criticisms). By extension, the more recently disclosed long-term effects are obviously way out of reach of the trace-conditioning model.

MTP corrects the myopia of the trace-conditioning model by assuming that all experiences are stored in separate memory traces. While the higher strength of recent memory traces still allows MTP to account for short-term effects, the relative frequency and longevity of all traces allow it to account for medium-term and long-term effects in addition. Thus, the system is flexible in prioritizing recent information relevant to the task at hand, while being stable by taking into account information that proved successful in the more distant past (see Los et al., 2014, for a comprehensive discussion).

1.3. The present study

An important insight ensuing from MTP is that S1 serves as a retrieval cue that prompts its associated memory traces to drive temporal preparation. This mechanism hinges on the assumption that a representation of S1 is stored in each newly created memory trace, making it addressable when the same S1 is presented on a future trial.

In the present study, we tested this assumption. We used the variable-foreperiod paradigm, with two different S1 cues, denoted as $S1_A$ and $S1_E$, and two different distributions of foreperiods, the anti-exponential and exponential distribution. During an acquisition phase, $S1_A$ was associated with the anti-exponential distribution (Fig. 1A), while $S1_E$ was associated with the exponential distribution (Fig. 1B). Participants were not informed of this contingency (with the exception of Experiments 4 and 5). All trials started equiprobably with $S1_A$ or $S1_E$, followed by a foreperiod randomly sampled from the associated distribution. In the subsequent transfer phase, the contingency between the S1 cue and the distribution of foreperiods was broken, and $S1_A$ and $S1_E$ were both associated with the uniform distribution —a fact participants were explicitly informed of.

According to MTP, the presentation of $S1_A$ or $S1_E$ should lead to the selective retrieval of its associated subset of memory traces. That is, $S1_A$ mainly retrieves memory traces representing long-foreperiod trials whereas $S1_E$ mainly retrieves memory traces representing short-foreperiod trials. As a result, the RT – foreperiod functions for $S1_A$ and $S1_E$ should diverge during the acquisition phase, as these S1 cues retrieve more and more memory traces corresponding to their associated distributions. Since this selective retrieval cannot be undone by explicit instruction, the RT – foreperiod functions should only gradually converge again during the transfer phase, as the newly formed memory traces under the uniform distribution come to dominate.

These predictions of MTP obviously rely on the assumption that the total pool of newly created memory traces is separable in two subsets, which are selectively addressable by $S1_A$ and $S1_E$. If this condition is not met, there will be a strong overlap between the memory representations linked to both S1 cues, and the resulting RT – foreperiod functions for $S1_A$ and $S1_E$ become indistinguishable. This consideration motivated a further goal of the present study: After a successful demonstration in Experiment 1 that the RT – foreperiod function is modified by S1 cue ($S1_A$ or $S1_E$), we explored the boundaries of this effect in seven follow-up experiments, in which we used different stimulus features to create the S1-pairs.

We finally note that although the verification of the predicted cueing effect would support MTP, it would not necessarily rule out alternative views on temporal preparation. Specifically, the finding of a cueing effect could lead one to propose a mechanism that allows participants to simultaneously learn two hazard functions, contingent on the presented S1. Alternatively, it could be considered a specific case of discrimination learning, which is a standard finding in the conditioning literature (e.g., McLaren & Mackintosh, 2002; Rescorla & Wagner, 1972). However, these considerations should not obscure the fact that MTP is the only account of temporal preparation to date from which the cueing effect derives as a principled prediction. Other views would need to postulate additional mechanisms to accommodate it.

2. Experiment 1

Experiment 1 served as a proof of principle that participants can implicitly learn the contingency between different S1s and the associated distribution of foreperiods. Therefore, we started out with a pair of highly dissimilar S1s: a tone and a flash.

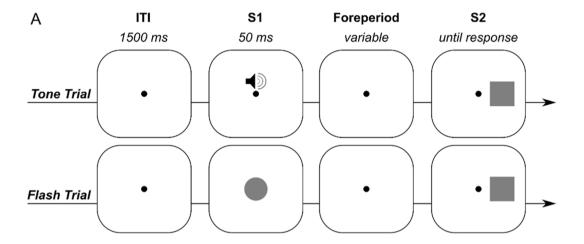
2.1. Method

<u>Participants.</u> Twenty students (14 females; mean age 22.5 years) participated for course credits or a payment of ϵ 8 in a single session of roughly 60 min. The data sets of two additional participants were discarded because more than 10% of their responses were

longer than 1000 ms in several conditions. All participants gave informed consent at the start of the experiment. Our sample size was motivated by the effect size of the interaction between foreperiod and foreperiod distribution in our earlier studies, with partial η^2 typically ranging between 0.15 and 0.30 (Los et al., 2017; Mattiesing et al., 2017). Therefore, if our hypothesis is correct that the effect of foreperiod depends on S1 cue (S1_A or S1_E), a sample of 20 participants should be sufficient to reveal it with a probability that exceeds 0.90 (Mayr, Erdfelder, Buchner, & Faul, 2007).

<u>Procedure.</u> Experiment 1 was created using E-prime 2.0 (Schneider, Eschman, & Zuccolotto, 2002). It took place in a dimly-lit, air-conditioned cubicle, equipped with a personal computer, which was connected to a 22-inch, 120-Hz LCD screen and a standard QWERTY keyboard. Participants sat at a distance of 70 cm from the screen asserted by a chin rest, with the left index finger on the z key and the right index finger on the m key. They wore padded headphones.

Fig. 2A shows the course of events on single trials. Throughout an experimental block, a dark-grey, 0.16° central fixation point was visible against a uniform white background. Each trial started with the presentation of S1, which was equiprobably a visual or auditory stimulus. The visual S1 was a dark-grey 0.65° central circle, presented for 50 ms, giving the impression of a flash. The auditory S1 was a 50-ms pure tone of 1000 Hz and about 50 dBA. After the offset of S1, a foreperiod of 400, 800, 1200, or 1600 ms elapsed followed by the presentation of S2. S2 was a dark-grey, $1.0^{\circ} \times 1.0^{\circ}$ square, presented with equal probability 2.3° to either the left or the right of fixation (center to center). Participants were instructed to press the z key (left) when the square appeared left and the m key (right)



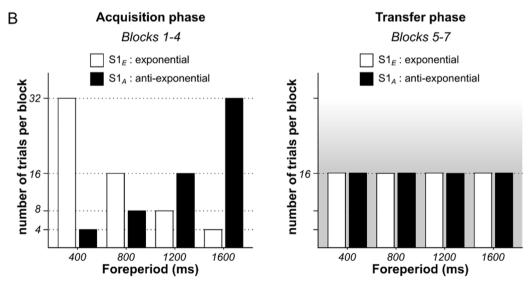


Fig. 2. Procedure and design of Experiment 1. A. Course of events on a 'tone trial' and a 'flash trial'. These trial types were randomized within blocks. Visual stimuli are not drawn to scale. B. Distributions of foreperiods during the acquisition phase and transfer phase of the experiment, separately for $S1_A$ and $S1_E$. For half of the participants $S1_A$ was the tone and $S1_E$ the flash; for the other half this mapping was reversed. Note that in the transfer phase, S1 cues are still labeled $S1_A$ and $S1_E$, in accordance with their history, even though both are now coupled with a uniform distribution of foreperiods. Experiments 1–8 all followed this block structure.

when it appeared right. The response led to the removal of S2, such that only the fixation point remained visible. The next trial started after a fixed intertrial interval of 1500 ms.

Fig. 2B shows the distribution of foreperiods associated with each S1 in an experimental session. Each session consisted of an acquisition phase and a transfer phase. In the acquisition phase, participants completed four blocks of 120 trials. For half of the participants, $S1_A$ was the tone and $S1_E$ the flash, whereas this was reversed for the other half of the participants. After $S1_A$, the foreperiod was randomly sampled from the anti-exponential distribution of foreperiods (4, 8, 16, and 32 trials with foreperiods of 400, 800, 1200, and 1600 ms, respectively), whereas after $S1_E$, the foreperiod was randomly sampled from the exponential distribution of foreperiods (32, 16, 8, and 4 trials with foreperiods of 400, 800, 1200, and 1600 ms, respectively). In the transfer phase, all participants completed three more blocks of 128 trials, in which, for both $S1_A$ and $S1_E$, the foreperiod was randomly sampled from the uniform distribution (16 trials with each foreperiod). After the completion of each block in both the acquisition and the transfer phase, mean RT and the percentage of correct responses of that block were shown on the screen. Participants copied these scores on a sheet of paper, to allow them to keep track of their performance throughout the session.

At the start of the experiment, participants were instructed to respond as quickly as possible to S2 while maintaining high accuracy. They were not informed of the variability of foreperiods nor of the contingency between the modality of S1 and the distribution of the foreperiods. After the completion of Block 4 (i.e., the last block in the acquisition phase), participants were queried whether the foreperiod following the tone was: (1) equally likely to be short or long; (2) more likely to be short than long; (3) more likely to be long than short. After selecting one of the three alternatives, the correct answer was revealed to them (alternative 2 or 3, depending on whether the tone was assigned to $S1_A$ or $S1_E$ for that participant). After the query it was emphasized that the contingency between the S1 cue and the distribution of foreperiods would no longer apply in the remaining three blocks (i.e., the transfer phase), and that short and long intervals would be equally likely after both the tone and the flash (i.e., a uniform distribution).

2.2. Results

The first trial of each block was discarded, as were trials with erroneous key presses (1.65%) and trials on which RT was shorter than 150 ms or longer than 1000 ms (0.13%). These percentages were low and not analyzed any further. Mean RT was calculated on the basis of the remaining trials.

Fig. 3 shows mean RT as a function of block, foreperiod, and S1 cue $(S1_A \text{ or } S1_E)$. We applied a mixed analysis of variance (ANOVA) on the RT data of each block separately, with foreperiod and S1 cue as within-subjects variables, and group $(S1_A \text{-tone}, S1_E \text{-flash or vice versa})$ as a between-subjects variable. In this and all subsequent analyses, foreperiod was included as a (1 df) linear factor, to allow an unambiguous interpretation of a possible modifying effect of S1 cue on the slope of the RT – foreperiod function in the acquisition or transfer phase. Alpha was set at 0.05.

The main effect of foreperiod was significant in all blocks, minimal F(1,18)=15.94, p=.001, partial $\eta^2=0.47$, reflecting that mean RT decreased as foreperiod increased. Furthermore, the main effect of S1 cue was significant in all blocks, minimal F(1,18)=8.31, p=.01, partial $\eta^2=0.32$, indicating that mean RT was longer for S1_A than for S1_E. Crucially, the interaction between foreperiod and S1 cue was also significant in all blocks, both in the acquisition phase, minimal F(1,18)=9.00, p=.008, partial $\eta^2=0.33$, and in the transfer phase, minimal F(1,18)=23.71, p<.001, partial $\eta^2=0.57$. In all blocks, the RT – foreperiod function was steeper after S1_A than after S1_E. Apparently, the contingency between S1 and the distribution of foreperiods was learned during the acquisition phase and it persisted for at least three 128-trial blocks in the transfer phase. Finally, the factor group (S1_A-tone, S1_E-flash or vice versa) was involved in a significant interaction with S1 cue in Block 1, F(1,18)=8.50, p=.009, partial $\eta^2=0.32$, and Block 3, F(1,18)=5.67, p=.029, partial $\eta^2=0.24$, indicating that the effect of S1 cue was stronger when S1_A was the flash and S1_E the tone than vice versa. However, since such an interaction was not seen in any of the other blocks, its relevance seems limited.

In the query after Block 4, twelve participants reported the correct contingency between the S1 cue and the distribution of foreperiods, one participant reported the reverse contingency, and the remaining seven participants reported no contingency. This performance is better than expected by chance, $\chi^2(2) = 9.1$, p = .005. Importantly, though, the pattern of mean RTs in the eight

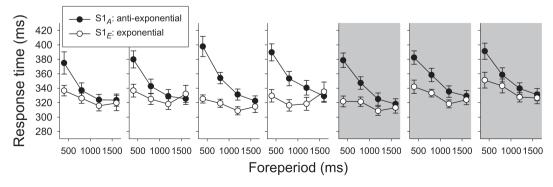


Fig. 3. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 1 (visual or auditory S1). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

participants who did not correctly report the contingency was not different from the pattern shown in Fig. 3. In particular, even in this small subsample, the critical interaction between foreperiod and S1 cue was significant in all blocks of the acquisition phase, minimal F (1, 6) = 7.36, p = .035, partial η^2 = 0.549, and transfer phase, minimal F (1, 6) = 10.51, p = .018, partial η^2 = 0.637.

2.3. Discussion

The results of Experiment 1 clearly showed the cueing effect predicted by MTP (Los et al., 2014, 2017). In all blocks of the acquisition phase, the RT – foreperiod function was steeper for $S1_A$ than for $S1_E$ trials, and this effect persisted throughout the transfer phase. Two additional findings indicate that the underlying learning process was implicit and not dependent on the participant's awareness of the contingency between S1 and the distribution of foreperiods. First, even the participants who failed to report the correct contingency after Block 4 showed a clear modifying effect of S1 cue on the RT – foreperiod function. Second, this modifying effect persisted in the transfer phase even though participants were explicitly informed that the contingency would no longer apply. These findings are all consistent with the predictions of MTP. According to MTP, $S1_A$ selectively retrieves memory traces corresponding to the anti-exponential distribution, leading to a steep RT – foreperiod function, whereas $S1_E$ selectively retrieves memory traces corresponding to the exponential distribution, leading to a much flatter RT – foreperiod function.

3. Experiment 2

To ensure that the findings of Experiment 1 are not strictly tied to auditory-visual S1 pairs, we aimed for a replication in Experiment 2, in which we replaced the auditory stimulus by a tactile stimulus.

3.1. Method

A new sample of 20 students participated (12 females; mean age 23.5 years). The method was identical to that of Experiment 1, except that the auditory stimulus was replaced by a tactile stimulus, which was delivered by a vibrator. The vibrator was removed from a cell phone and inserted in a hard plastic cylinder of about 5 cm long and 1 cm in diameter. It was attached about 1 cm above the participant's navel with some tape. To prevent that participants could hear the vibration, they wore a combination of earplugs and sound attenuating ear muffs throughout the experimental session. Independent testing, with the vibrator hand-held by the experimenter close to the participant's navel, confirmed that none of the participants was able to hear the vibration.

Because of technical malfunction, the vibration lasted longer than the intended 50 ms and it varied across trials, occasionally exceeding a full second. To minimize the impact of this issue, we excluded all trials in which the vibration lasted longer than 500 ms (5.2% of the trials with the tactile S1). The duration of the vibration on the remaining trials ranged between 62 and 500 ms (M = 128 ms, S = 101 ms). It is important to note though, that this anomaly did not threaten the validity of the experiment, because the foreperiod always started at the offset of S1, and its duration was uncorrelated with the duration of S1 (Pearson's S = 1000).

3.2. Results

The percentages of trials with incorrect key presses (1.4%) or with responses outside the 150–1000 ms range (0.2%) were low and not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1.

Fig. 4 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed a significant main effect of foreperiod in each block, minimal F(1, 18) = 21.32, p < .001, partial $\eta^2 = 0.54$, reflecting that RT decreased as the foreperiod increased. The main effect of S1 cue was also significant in all blocks, minimal F(1, 18) = 8.67, p = .009, partial $\eta^2 = 0.33$, indicating that mean RT was

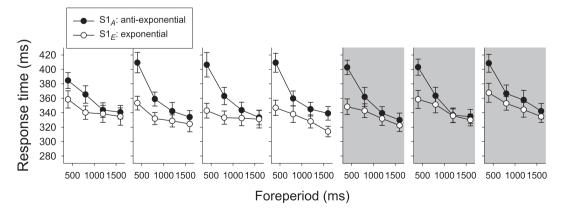


Fig. 4. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 2 (visual or tactile S1). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

shorter for $S1_E$ than for $S1_A$. Crucially, the interaction between S1 cue and foreperiod approached significance in Block 1, F(1, 18) = 3.86, p = .065, partial $\eta^2 = 0.18$, and was significant in all the remaining blocks, minimal F(1, 18) = 4.73, p = .043, partial $\eta^2 = 0.21$. This interaction reflects that the RT – foreperiod function was flatter for $S1_E$ than for $S1_A$, indicating that participants, as in Experiment 1, learned the contingency between S1 and the distribution of foreperiods. The factor group ($S1_A$ -flash, $S1_E$ -vibration or vice versa) modified the effect of foreperiod in Block S, F(1, 18) = 7.83, P = .012, partial $\eta^2 = 0.30$, and the effect of S1 cue in Blocks $S1_E$ and $S1_E$ minimal $S1_E$ ($S1_E$) and $S1_E$ than in the group with the flash as $S1_E$ and the vibration as $S1_E$ than in the group with the reverse contingency.

In the query after Block 4, eight participants reported the correct contingency between S1 and the distribution of foreperiods, four participants reported the reverse contingency, and the remaining eight reported no contingency between S1 and the distribution of foreperiods. Although this performance does not significantly deviate from chance, $\chi^2(2) = 1.6$, p = .22, we repeated the ANOVA on the RT data, including only those twelve participants who did not correctly report the contingency. The pattern of mean RTs in this subsample was very similar to the pattern shown in Fig. 4. The interaction between foreperiod and S1 cue failed to reach significance in Block 1, F(1, 10) < 1 and Block 4, F(1, 10) = 1.56, p = .22, partial $\eta^2 = 0.135$, but it was significant in the other five blocks, minimal F(1, 10) = 6.71, p = .027, partial $\eta^2 = 0.402$.

3.3. Discussion

The data of Experiment 2 showed that the RT – foreperiod function was steeper for $S1_A$ than for $S1_E$, both in the acquisition phase and in the transfer phase. This finding replicates the findings of Experiment 1 for a visual-tactile S1 pair, and confirms that participants learn the contingency between S1 cue and the distribution of foreperiods. The data also confirmed that the underlying learning process is implicit, because few if any participants became aware of the prevailing contingency during acquisition. In addition, there was no difference in the cueing effect of the participants who did and who did not report the correct contingency after the acquisition phase. These findings were all predicted by MTP, which posits that S1 serves as a selective retrieval cue for associated memory traces formed on preceding trials.

4. Experiment 3

The cueing effect observed in Experiments 1 and 2 provides a proof of principle that participants implicitly learn the contingency between the S1 cue and the distribution of foreperiods when the members of the S1 pair come from different stimulus modalities. In Experiment 3, we attempted to replicate the cueing effect for an S1 pair within the visual modality, using a red or green flash. We expected that this should be feasible, given that discrimination learning with color cues has been well established in both appetitive and aversive conditioning research (e.g., Guttman & Kalish, 1956; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Schmidt, Belopolsky, & Theeuwes, 2015; Terrace, 1963).

4.1. Method

A new sample of 20 students with normal color vision participated (16 females; mean age 21 years). The method was identical to that of Experiment 1, except that S1 was always the 50-ms visual flash of a saturated red or green color.

4.2. Results

The percentages of trials with incorrect key presses (1.8%) or with responses outside the 150–1000 ms range (0.2%) were low and not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as

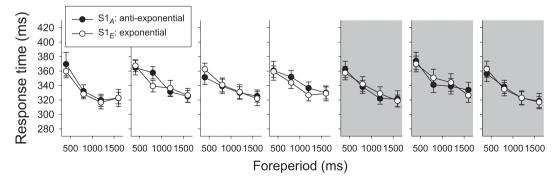


Fig. 5. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 3 (red or green S1). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

that of Experiment 1.

Fig. 5 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed a significant main effect of foreperiod in each block, minimal F(1, 18) = 16.76, p = .001, partial $\eta^2 = 0.48$, reflecting that RT decreased as the foreperiod increased. In contrast with the previous experiments, neither the main effect of S1 cue, maximal F(1, 18) = 2.42, p = .137, partial $\eta^2 = 0.12$, nor the interaction between foreperiod and S1 cue, maximal F(1, 18) = 1.48, p = .24, partial $\eta^2 = 0.08$, reached significance in any one of the seven blocks. As is clear from Fig. 5, the RT – FP functions for both S1 cues were very similar throughout the experiment. Evidence for the absence of the critical interaction between S1 cue and foreperiod was subsequently quantified in a Bayesian ANOVA using the BayesFactor package in R (Morey & Rouder, 2018; Rouder, Morey, Speckman, & Province, 2012). Bayes Factors (BFs) were computed for each block by fitting different model objects using the 'lmBF' function with default prior distributions on model coefficients. Different model objects implemented the full interaction between S1 cue and foreperiod, or implemented simpler nested models that only implemented two, one, or none of the main effects. Posterior distributions for each model were constructed based on 250,000 samples. In all blocks, the preferred model was one with only foreperiod as a main effect, which was preferred over all other models with BFs greater than 20.0. Thus, this indicates strong evidence for the absence of such an interaction. Finally, the ANOVA revealed a significant interaction between group and foreperiod in Blocks 3, F(1, 18) = 10.38, P = .005, partial P = 0.37 and a significant interaction between group and S1 cue in Blocks 4 and 5, minimal P = 0.08, P = .004, partial P = 0.25. Because these effects did not exhibit a systematic pattern across blocks, we did not analyze them in greater detail.

In the query after Block 4, nine participants reported the correct contingency between S1 and the distribution of foreperiods, one participant reported the reverse contingency, and the remaining ten reported no contingency between S1 and the distribution of foreperiods. This performance deviates significantly from chance, $\chi^2(2) = 7.3$, p = .013. Importantly, though, the pattern of mean RTs in the nine participants who correctly reported the contingency was not different from the pattern shown in Fig. 5. In particular, in this subsample, the interaction between foreperiod and S1 cue did not reach significance in any of the seven blocks, maximal F(1, 7) = 2.58, p = .15, partial $\eta^2 = 0.27$.

4.3. Discussion

The findings of Experiment 3 stand in stark contrast with those of Experiments 1 and 2. Whereas the between-modality S1 features examined in Experiments 1 and 2 caused the associated RT – FP functions to diverge from the first block onward, the within-modality features of Experiment 3 completely failed to do so. This finding is surprising in view of convincing demonstrations of discrimination learning in Pavlovian conditioning paradigms, in which one color is associated with an appetitive or aversive consequence whereas another color is not (e.g., Guttman & Kalish, 1956; Koster et al., 2004; Schmidt et al., 2015; Terrace, 1963). Of course, it is possible that, in Experiment 3, a longer acquisition phase would have ultimately led to a behavioral expression of the contingency, but even in that case, the learning rate would be much lower than in the between-modality conditions examined in the previous experiments. In Experiments 7 and 8 we further explored this discrepancy. At this point, we emphasize that the present findings do not contradict MTP's mechanism that S1 acts as a retrieval cue for memory traces created on earlier trials. They only suggest that retrieval was not selective, with the different S1s retrieving memory traces regardless of their contingency with the distribution of foreperiods.

Another important finding of Experiment 3 was that even the nine participants who correctly reported the contingency between S1 color and the distribution of foreperiods exhibited indistinguishable RT – foreperiod functions for $S1_A$ and $S1_E$. This finding constitutes a remarkable counterpart of the finding of Experiments 1 and 2 that participants who *failed* to notice the contingency still exhibited clearly distinguishable RT – foreperiod functions in both the acquisition and transfer phase. Together, these findings suggest that awareness of the contingency between S1 and the distribution of foreperiods is neither a necessary nor a sufficient condition for its expression in temporal preparation. Experiments 4–6 were designed to further test this view.

5. Experiment 4

It is interesting to compare the findings of Experiments 1–3 to those reported in the literature on temporal orienting (e.g., Coull & Nobre, 1998, 2008; Nobre & Van Ede, 2018). The design of temporal orienting studies is very similar to the current design, except that participants are informed of the contingency between S1 and the distribution of foreperiods at the start of the experiment. The typical finding is that of a pronounced cueing effect for short but not for long foreperiods, similar to the findings of Experiments 1 and 2 (e.g., Coull & Nobre, 1998; Denison, Heeger, & Carrasco, 2017; Kingstone, 1992, Experiment 4; Los & Van den Heuvel, 2001; Mo & Kersey, 1980; Nobre, 2001; Zahn, 1970). This finding has been interpreted as evidence for a controlled influence on timing behavior, which hinges on the idea that participants must be aware of the meaning of the cue regarding the most likely impending foreperiod (e.g., Nobre, 2001).

The present data challenge this view. The findings of Experiments 1 and 2 were very similar to those in temporal orienting studies, even in participants that were unaware of the contingency. Conversely, in Experiment 3 the contingency failed to have an effect on temporal preparation, even in participants who were presumably aware of the contingency. It is possible, though, that the "aware" participants of Experiment 3 discovered the contingency late during the acquisition phase, or that they guessed correctly when prompted by the query. In either case, this may have reduced the cueing effect, and obscured a possible mediating role of awareness. In Experiment 4, we tested this possibility by turning the design of Experiment 3 into a full-fledged temporal orienting design by informing participants of the contingency at the start of the experimental session.

5.1. Method

A new sample of 20 students with normal color vision participated (14 females; mean age 22.5 years). The method was identical to that of Experiment 3, except that participants were explicitly instructed at the start of the experiment of the contingency between the color of S1 and the distribution of foreperiods. Specifically, for the participants assigned to the $S1_E$ -red, $S1_A$ -green group, the instruction was: "When the flash is RED: The interval is mostly SHORT (and sometimes long); when the flash is GREEN: The interval is mostly LONG (and sometimes short)." This instruction was reversed for the participants assigned to the other group. Participants were encouraged to use the information conveyed by S1 to prepare for the impending target stimulus. The query was presented twice, not only after block 4 (as in all previous experiments) but also after Block 1 to make sure that participants were aware of the contingency between S1 and the distribution of foreperiods that applied during the acquisition phase. After they completed the first query, participants were once more reminded of the prevailing contingency before starting Block 2.

5.2. Results

The percentages of trials with incorrect key presses (1.0%) or with responses outside the 150–1000 ms range (0.7%) were low and not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1.

Fig. 6 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed that foreperiod approached significance in Block 3, F(1, 18) = 4.02, p = .06, partial $\eta^2 = 0.18$, and was significant in all other blocks, minimal F(1, 18) = 9.64, p = .006, partial $\eta^2 = 0.35$, reflecting that RT decreased as the foreperiod increased. There was a main effect of S1 cue in Block 2, F(1, 18) = 12.83, p = .02, partial $\eta^2 = 0.42$, indicating that RT was shorter in the S1_E condition than in the S1_A condition. This effect was not significant in any of the other blocks, maximal F(1, 18) = 1.28, p = .27, partial $\eta^2 = 0.07$. Crucially, there was no significant interaction between foreperiod and S1 cue, neither in the acquisition phase, maximal F(1, 18) = 2.24, p = .15, partial $\eta^2 = 0.11$, nor in the transfer phase, maximal F(1, 18) = 0.98, p = .34, partial $\eta^2 = 0.05$. In the same manner as for Experiment 3, the absence of this interaction was assessed via Bayesian model comparisons. Again, the analyses revealed strong support for models with only a main effect of foreperiod over other models, including the model with the interaction between S1 cue and foreperiod (all BF > 11.3). In this respect, the findings of Experiment 4 were consistent with those of Experiment 3, but not with those of Experiments 1 and 2. Finally, the ANOVA revealed an interaction between distribution and group in Block 2, F(1, 18) = 6.22, p = .023, partial $\eta^2 = 0.26$, indicating that the shorter RT for S1_E than for S1_A trials was greater in the group with the red flash associated with the exponential distribution and the green flash with the anti-exponential distribution than in the other group. No other effects were significant.

In the query after Block 4, seventeen out of twenty participants correctly reported the contingency between S1 and the distribution of foreperiods; the remaining three participants reported no contingency. Clearly, this performance deviated significantly from chance, $\chi^2(2) = 24.1$, p < .001 and it was also better than performance in Experiment 3, where participants were not informed of the contingency at the start of the experiment, $\chi^2(2) = 7.23$, p = .013. The pattern of mean RTs in the seventeen participants who correctly reported the contingency in Experiment 4 was not different from the pattern shown in Fig. 6. In particular, in this subsample, the interaction between foreperiod and S1 cue did not reach significance in any of the seven blocks, maximal F(1, 15) = 2.25, p = .16, partial $\eta^2 = 0.13$.

In a final analysis, we contrasted the findings of Experiments 3 and 4 (color cues, contingency either instructed or not instructed; Figs. 5 and 6). To maximize power, we collapsed the data of each experiment across the five blocks of the acquisition phase and the three blocks of the transfer phase. Separate ANOVAs were performed on both phases, with Experiment (3 or 4) as between-subjects variable and S1 cue and foreperiod as repeated measures. Crucially, neither ANOVA yielded any evidence for an interaction between S1 cue and foreperiod, F < 1 in both phases, nor for a three-way interaction involving foreperiod, S1 cue and Experiment, F < 1 in both phases. Furthermore, in the ANOVA of the acquisition phase, two effects involving the factor Experiment approached significance. First, the main effect of Experiment, F (1, 38) = 3.62, P = .065, partial P = 0.087, reflects that mean RT tended to be longer in Experiment 3 (P = 3.99 ms, P = 3.9

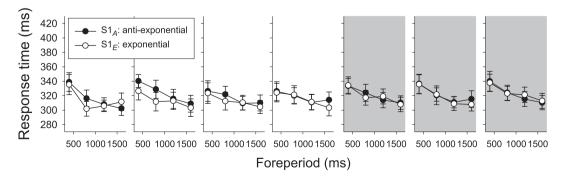


Fig. 6. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 4 (red or green S1; instructed contingency). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

interaction, F(1, 38) = 3.35, p = .075, partial $\eta^2 = 0.81$, reflects that the RT – FP function was somewhat steeper in Experiment 3 then in Experiment 4. In the ANOVA of the transfer phase. The only significant effect involving Experiment was the Experiment by foreperiod interaction, F(1, 38) = 6.19, p = .017, partial $\eta^2 = 0.14$, again reflecting a steeper RT – FP function in Experiment 3.

The frequentist ANOVA gave no indication that Experiment 3 and 4 differed with respect to the effects of the S1 cue. We confirmed this by means of Bayesian Model comparisons, contrasting all possible models with predictors Experiment, foreperiod (as a continuous predictor) and S1 cue. For both the Acquisition as well as the Transfer phase, the model with only Experiment and foreperiod as main effects was preferred. The relevant model comparisons indicated that, in both phases, there was evidence against a main effect of S1 cue (both BF > 6.38), against an interaction between foreperiod and S1 cue (both BF > 89.51), and against a three-way interaction between foreperiod, S1 cue, and Experiment (both BF > 1000.0).

5.3. Discussion

The method of Experiment 4 deviated from that of Experiment 3 in that participants were informed of the contingency between S1 color and the distribution of foreperiods from the start of the experimental session. This change clearly resulted in greater awareness among participants of the contingency as revealed by the query at the end of the acquisition phase. By contrast, this change did not result in a cueing effect: Like in Experiment 3, the RT – FP functions for $S1_E$ and $S1_A$ were very similar in both the acquisition and the transfer phase. Therefore, the findings of Experiment 4 strengthen the conclusion that awareness of the contingency is not a sufficient condition for its behavioral expression.

The comparison of the data of Experiment 4 to those of Experiment 3 revealed that, if anything, advance knowledge of the contingency had the global effect of flattening the RT – FP function regardless of the contingency. This suggests that, in the present paradigm, advance knowledge of the contingency brought about a general awareness in participants of the different foreperiods and the imperfectness of the S1 cue to predict them. In turn, this may have prompted participants to orient early foreperiods even when the cue predicts a long foreperiod, such that a relatively high preparatory state is reached early after S1. Whatever the merit of this suggestion, it does not compromise our more important claim that, by itself, awareness of the contingency does not lead to its behavioral expression.

6. Experiment 5

To provide a more definitive test of our claim that awareness of the contingency is an insufficient condition for its behavioral expression, we conducted Experiment 5, where S1 was a pair of word cues that directly referred to the associated foreperiod distribution. That is, S1 was either the word "SHORT", in which case the subsequent foreperiod was drawn from an exponential distribution, or "LONG", in which case it came from the anti-exponential distribution. Participants were informed of the meaning of the S1 cue at the start of the experiment.

6.1. Method

Experiment 5 was conducted online because of the Covid-19 pandemic. Using Prolific, 30 participants between 18 and 30 years old signed up and were paid about 7 euro for their services. We obtained complete data sets from 26 participants. Three participants responded faster than 150 ms or slower than 1000 ms on more than 10% of the trials; one participant made erroneous responses on more than 10% of the trials. The data sets of these participants were excluded, leaving a final sample of 22 participants (10 males; mean age 22.7 years).

The experiment was created in OpenSesame 3.3.3 (Mathôt, Schreij, & Theeuwes, 2012) using OSweb and performed using Jatos (Lange, Kühn, & Filevich, 2015). Participants were instructed to perform the experiment on a laptop or PC in a quiet environment while turning off all possible sources of distraction. The procedure was identical to that of Experiment 4, except for the following changes. First, instead of a red or green flash, S1 was the word "SHORT" or "LONG", written in black capital letters (mono, point size 32). As in all experiments of this study, S1 was presented in the middle of the screen for 50 ms, allowing for a comfortable identification of the (unmasked) word. Second, the meaning of the word cue was fixed for all participants. Participants were instructed that the interval following the word "SHORT" was mostly short but sometimes long, whereas the interval following the word "LONG" was mostly long but sometimes short. Participants were encouraged to use this information to prepare for the impending S2. There were no queries about the meaning of the word cue anytime during the experiment. After the acquisition phase, participants were informed that the contingency no longer applied in the three remaining blocks of the transfer phase.

6.2. Results

The percentages of trials with incorrect key presses (1.71%) or with responses outside the 150–1000 ms range (1.53%) were not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1, except that there was no between subjects variable because the contingency between the word cues and the distribution of foreperiods was identical for all participants.

Fig. 7 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed that foreperiod was significant in Block 1, F(1, 21) = 5.42, p = .030, partial $\eta^2 = 0.21$, but not in any of the other blocks during acquisition, maximal F(1, 21) = 2.73, p = .11, partial $\eta^2 = 0.12$, obtained in Block 2. By contrast, the effect of foreperiod was significant in all blocks of the transfer phase, minimal F(1, 21) = 0.12, obtained in Block 2.

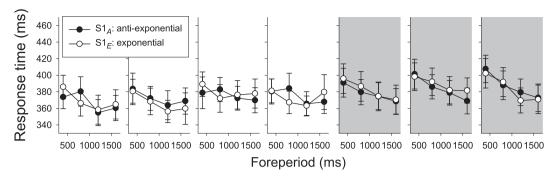


Fig. 7. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 5 (word cues, online). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

(1, 21) = 14.97, p = .001, partial $\eta^2 = 0.42$, obtained in Block 5. Whenever significant, the effect of foreperiod reflected that RT decreased as foreperiod increased. No other effects were significant in any of the ANOVAs. Notably, the interaction between foreperiod and S1 cue failed to reach significance in any of the seven blocks, maximal F(1, 21) = 2.26, p = .15, partial $\eta^2 = 0.10$, obtained in Block 6. In the same way as for Experiments 3 and 4, we used Bayesian model comparisons for data from each block to quantify the evidence for the absence of the Cue type by Foreperiod interaction. Again, we found compelling evidence against such an interaction (all BF > 14.7).

6.3. Discussion

The findings of Experiment 5 provided further evidence that awareness of the contingency between S1 and the distribution of foreperiods is an insufficient condition for its behavioral expression. Whereas in Experiment 4, awareness of the contingency required participants to actively interpret the color of S1 to anticipate the most likely impending foreperiod, this possibly effortful cognitive step was eliminated in Experiment 5. Indeed, it is difficult to think of a more direct way to express this contingency than by verbal labels, which are processed automatically and are hard to ignore (e.g., MacLeod, 1991; Snell, Declerck, & Grainger, 2018). Nevertheless, the behavioral outcomes were not any different from those of Experiment 4: There was no sign of a cueing effect in the RT data, neither during acquisition nor during transfer. In addition, the RT – foreperiod function during acquisition was again flatter than in any of the other experiments of this study, suggesting that awareness of the fallibility of the S1 cue prompts participants to compensate the otherwise low temporal preparation in the beginning of the foreperiod.

7. Experiment 6

In Experiment 5, we found that direct verbal cues that were informative of the upcoming foreperiod did not modulate preparation effects. However, this experiment was conducted online, in a less controlled setting than Experiments 1–4. To obviate the objection that suboptimal experimental control in Experiment 5 may have prevented the manifestation of the cueing effect, we performed an online replication of Experiment 1 (auditory and visual S1 cues).

7.1. Method

Experiment 6 was an online replication of Experiment 1. We obtained 26 complete data sets from 30 participants who signed up on Prolific. One participant reported not to have heard the sound during the experiment; three other participants responded faster than 150 ms or slower than 1000 ms on more than 10% of the trials. The data sets of these participants were excluded, leaving a final sample of 22 participants (14 males; mean age 22.8 years). For eight participants the tone was associated with the exponential distribution and the flash with the anti-exponential distribution during acquisition; the remaining 14 participants received to the reversed contingency. The imbalance of the group sizes was the result of asymmetric attrition.

The procedure was identical to that of Experiment 1, except for the following changes. First, the experiment was performed online, using the software specified in the method section of Experiment 5. Second, at the start of the experiment, participants were presented with three tones (1000 Hz, 50 ms) that they could hear either via the computer audio or via earphones. They were requested to set the sound volume at a comfortable level (neither too soft nor too loud) and not to adjust it afterwards. Third, since Experiments 1 and 2 already revealed that awareness of the contingency did not modify the behavioral data pattern, we abstained from assessing this directly via a query after Block 4 (the last block of the acquisition phase). Otherwise, the instructions were identical to those of Experiment 1. That is, the contingency was not instructed anytime during the acquisition phase. At the start of the transfer phase, participants were told that the contingency, which they might have discovered during the acquisition phase, would no longer hold in the remaining blocks.

7.2. Results

The percentages of trials with incorrect key presses (1.57%) or with responses outside the 150–1000 ms range (1.67%) were not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1.

Fig. 8 shows mean RT as a function of block, foreperiod and S1 cue. The ANOVA of these data revealed a main effect of foreperiod in all blocks, minimal F(1,20)=6.95, p=.016, partial $\eta^2=0.23$, obtained in Block 2, reflecting that RT decreased as the foreperiod increased. The main effect of S1 cue was also significant in all blocks, F(1,20)=4.86, p=.039, partial $\eta^2=0.20$, obtained in Block 1, reflecting that RT was shorter on S1 $_E$ trials than on S1 $_A$ trials. Crucially, whereas the interaction between S1-cue and foreperiod was not significant in Block 1, F(1,20)=0.23, p=.64, it was significant in all subsequent blocks in both the acquisition phase and the transfer phase, minimal F(1,20)=6.99, p=.016, partial $\eta^2=0.26$, reflecting that the RT – FP function was steeper when S1 specified the antiexponential distribution than when it specified the exponential distribution. Finally, the effect of the grouping variable (tone exponential, flash anti-exponential or vice versa) was not involved in any significant effect.

In a follow-up analysis, we contrasted the findings of Experiment 6 with those of Experiments 1 (Fig. 3), after collapsing the data of each experiment across the five blocks of the acquisition phase and the three blocks of the transfer phase. In the ANOVA of the acquisition phase, the main effect of Experiment F(1, 40) = 13.31, p = .001, partial $\eta^2 = 0.250$ was significant, reflecting that mean RT was shorter in Experiment 1 (M = 335 ms, SE = 7.06) than in Experiment 6 (M = 377 ms, SE = 8.83). There was a strong interaction between S1 cue and foreperiod, F(1, 40) = 51.75, p < .001, partial $\eta^2 = 0.564$. This interaction may have been slightly stronger in Experiment 1 than in Experiment 6, although the corresponding three-way interaction failed to reach significance, F(1, 40) = 3.55, p = .067, partial $\eta^2 = 0.082$, nor was any other effect involving Experiment significant. The results of the ANOVA of the transfer phase were similar. Mean RT in Experiment 1 (M = 339 ms, SE = 6.87) was shorter than in Experiment 6 (M = 369 ms, SE = 9.86), F(1, 40) = 6.10, p = .018, partial $\eta^2 = 0.132$. There was a strong interaction between S1 cue and foreperiod, F(1, 40) = 93.73, p < .001, partial $\eta^2 = 0.701$, but this was not significantly modified by Experiment, F(1, 40) = 2.90, p = .096, partial $\eta^2 = 0.068$. Other interaction effects involving Experiment were also not significant.

In the same way as for Experiments 3 and 4, we used Bayesian Model comparisons to confirm the apparent absence of a difference in cueing effects across experiments. In line with our main conclusions, we found that in both the acquisition phase and the transfer the preferred model included an effect of foreperiod and S1 cue, as well as their interaction. In addition to these terms, there was strong evidence for a main effect of Experiment (both BF > 1000). Most critically, comparisons yielded no evidence for a three-way interaction involving foreperiod, S1 cue, and Experiment (both BF > 891.06).

7.3. Discussion

The results of Experiment 6 replicated those of Experiment 1 in an online setting: The RT – foreperiod functions for the S1 cues gradually diverged during acquisition and gradually converged again during transfer. Furthermore, the combined analysis with the data of Experiment 1 did not reveal any interaction involving the factor Experiment, indicating that the cueing effect for an audiovisual S1 is a robust phenomenon that is not critically dependent on controlled lab conditions. By extension, this finding indicates that the absence of a cueing effect in Experiment 5 cannot be attributed to the online setting, and rather reflects an ineffectiveness of word cues to evoke it.

To summarize the main findings of this study so far, the cueing effect predicted by MTP was clearly observed when the members of the S1 cue differed in modality (Experiments 1, 2, and 6) but not when they differed in color or verbal content (Experiment 3, 4, and 5). Furthermore, if a cueing effect was observed, it was found to be equally strong in those participants who were and who were not able to report the contingency at the end of the acquisition phase (Experiment 1, 2), and it persisted during the transfer phase after participants had been informed that the contingency would no longer hold (Experiments 1, 2, 6). By contrast, if no cueing effect was observed, this could not be induced by fully informing participants beforehand about the predictive nature of the S1 cues (Experiments 4, 5). Together, these findings clearly show that awareness of the contingency is neither a necessary nor a sufficient condition for its behavioral expression.

8. Experiment 7

If awareness does not mediate the behavioural expression of the contingency between the S1 cue and the distribution of fore-periods, then, what does? One notable dissociation in the experiments presented thus far is that a cueing effect emerged when the S1 cues were each presented via a different stimulus modality, whereas no cueing effect emerged when the cues were presented in the same modality. This suggests that modality differences are necessary for the observation of a cueing effect. However, this proposal is difficult to reconcile with effective within-modality cueing demonstrated in related paradigms (e.g., Koster et al., 2004; Schmidt et al., 2015). In Experiments 7 and 8, we therefore explored the possibility of obtaining a contingency effect for within-modality S1 pairs that were subjectively highly dissimilar. These experiments were both performed in the lab.

In Experiment 7, S1 was either a central flash (as used in Experiments 1–4 and 6) or a wide rectangular frame surrounding the central fixation point. Although these stimuli are both visual, they are potentially more dissimilar than the red and green S1 cues in Experiment 3 and 4 as they greatly differ in shape and the retinal regions they stimulate. This, we hypothesized, might allow for the formation and retrieval of distinct memory traces for $S1_A$ and $S1_E$, thereby giving rise to a cueing effect.

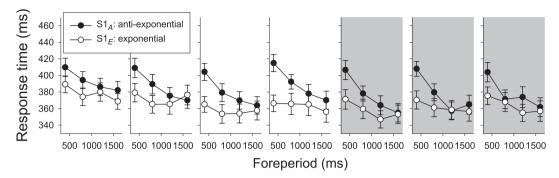


Fig. 8. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 6 (auditory or visual S1, online). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

8.1. Method

A new sample of 20 students (14 females; mean age 22.8 years) participated. The method was identical to that of Experiment 1, except that the auditory stimulus was replaced by a visual frame. The frame was an unfilled, horizontally oriented, $4.68^{\circ} \times 3.12^{\circ}$ rectangle with a dark-grey outline of three pixels wide (0.08°) surrounding the fixation point (cf. Los & Van der Burg, 2013). Like in Experiment 1, the flash was the dark-grey circle with a diameter of 0.65°. Both S1s were presented for 50 ms.

8.2. Results

The percentages of trials with incorrect key presses (1.1%) or with responses outside the 150–1000 ms range (0.53%) were low and not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1.

Fig. 9 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed that foreperiod was significant in each block, minimal F(1,18)=37.23, p<.001, partial $\eta^2=0.67$, reflecting that RT decreased as the foreperiod increased. The main effect of S1 cue was not significant in Block 1, F<1, but significant in all subsequent blocks, minimal F(1,18)=4.49, p=.048, partial $\eta^2=0.20$. The interaction between foreperiod and S1 cue was not significant in Blocks 1–3, maximal F(1,18)=2.46, p=.14, partial $\eta^2=0.12$ (attained in Block 3), it was significant in Blocks 4–6, minimal F(1,18)=5.63, p=.029, partial $\eta^2=0.24$, and became nonsignificant again in Block 7, F(1,18)=1.65, p=.22, partial $\eta^2=0.08$. As is clear from Fig. 7, the RT – FP functions for S1_A and S1_E gradually diverged during the acquisition phase and gradually converged again during the transfer phase. Finally, there were several interactions involving group. Group significantly interacted with S1 cue in all blocks, minimal F(1,18)=5.64, p=.029, partial $\eta^2=0.24$ except for Block 6, F(1,18)=4.01, p=.06, partial $\eta^2=0.18$. Furthermore, there was a one-off significant three-way interaction in Block 1, F(1,18)=4.48, p=.049, partial $\eta^2=0.20$. Generally, these interactions indicate that the contingency effect (or its modifying influence on the RT – foreperiod function) was more pronounced for the group with the flash as S1_E and the frame as S1_A than for the group with the reverse contingency.

In the query after Block 4, nine participants reported the correct contingency between S1 and the distribution of foreperiods, six reported the reverse contingency, while the remaining five participants reported no contingency between S1 and the distribution of foreperiods. This performance does not significantly deviate from chance, $\chi^2(2) = 1.3$, p = .26.

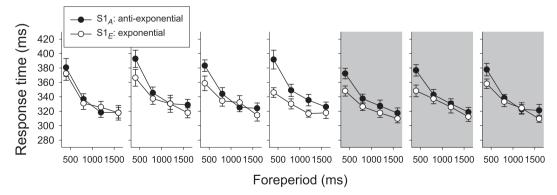


Fig. 9. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 7 (central flash or wide frame). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

8.3. Discussion

The results of Experiment 7 showed that the RT – FP functions corresponding to $S1_A$ and $S1_E$ gradually diverged in the course of the acquisition phase and then gradually converged again in the course of the transfer phase. This finding demonstrates that the contingency between S1 and the distribution of foreperiods may find expression in temporal preparation even when both S1s are from the same modality. This contingency effect seemed weaker than for the between-modality S1 pairs used in Experiment 1, 2, and 6, where a behavioral contingency effect was observed in every block (except for Block 1 in Experiments 2 and 6). For the present within-modality S1 pair, it attained significance only in the last block of the acquisition phase and was no longer significant in the last transfer block. Nevertheless, the evidence for a behavioral contingency effect was clear, which implies that the absence of this effect for color cues (Experiment 3 and 4) or word cues (Experiment 5) cannot be attributed to the use of within-modality S1 cues per se. Furthermore, the present data again confirmed the implicit nature of the contingency effect, because there was no evidence that participants became aware of the contingency during the acquisition phase, while the clear transfer effect was obtained after participants were instructed that the contingency would no longer hold.

Another noteworthy finding of Experiment 7 is that, in nearly all blocks, the modification of temporal preparation was stronger when the frame was $S1_A$ and the flash $S1_E$ than for the reverse contingency. This finding can be explained when it is assumed that both S1 and foreperiod vary on a common dimension expressing 'distance' (see Kornblum, Hasbroucq, & Osman, 1990). On this dimension, the central flash signifies 'nearby' whereas the frame signifies 'far away', which would make the flash – exponential, frame – anti-exponential contingency easier to learn than the reverse contingency. This tentatively suggests that a preexisting semantic relationship could facilitate or impede the expression of the contingency in temporal preparation. This view will be further elaborated in the General Discussion section.

9. Experiment 8

Experiment 8 served to confirm the findings of Experiment 7 within the auditory modality. S1 was either a high-pitched or a low-pitched tone. Since these tones are subjectively highly dissimilar, we expected that the contingency between the pitch of S1 and the distribution of foreperiods could come to expression in temporal preparation.

9.1. Method

A new sample of 20 students (15 females; mean age 22.5 years) participated in Experiment 8. The method was identical to that of Experiment 1, except that two easily discriminable auditory tones of about 50 dBA were used, one low-pitched tone of 600 Hz and one high-pitched tone of 1200 Hz.

9.2. Results

The percentages of trials with incorrect key presses (1.13%) or with responses outside the 150–1000 ms range (0.69%) were low and not further analyzed. Mean RT was calculated on the basis of the remaining trials. The statistical analysis followed the same schema as that of Experiment 1.

Fig. 10 shows mean RT as a function of block, foreperiod, and S1 cue. The ANOVA revealed that foreperiod was significant in each block, minimal F(1,18)=17.97, p<.001, partial $\eta^2=0.50$, reflecting that RT decreased as the foreperiod increased. The main effect of S1 cue was significant in Block 5, F(1,18)=8.17, p=.01, partial $\eta^2=0.31$, but not in any other block, maximal F(1,18)=2.02, p=.17. The interaction between foreperiod and S1 cue reached significance in Blocks 2, 3, and 5, minimal F(1,18)=4.95, p=.039, partial $\eta^2=0.22$, but not in any of the other blocks, all F(1,18)<1. As is clear from Fig. 10, the RT – FP function in Blocks 2, 3, and 5 was less steep for S1_E than for S1_A. Finally, group exhibited a significant main effect in Block 5, F(1,18)=4.59, p=.046, partial $\eta^2=0.20$, and

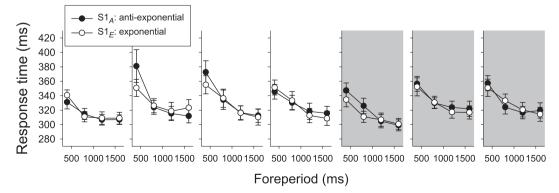


Fig. 10. Mean response time as a function of block, foreperiod, and S1 cue in Experiment 8 (high or low pitched tone). The first four blocks are from the acquisition phase; the last three blocks (shaded) from the transfer phase. Error bars represent \pm 1 SE of the condition mean.

was involved in a three-way interaction with S1 cue and foreperiod in Block 7, F(1, 18) = 4.87, p = .041, partial $\eta^2 = 0.213$. These effects were small and incidental.

In the query after Block 4, five participants reported the correct contingency between S1 and the distribution of foreperiods, seven reported the reverse contingency, while the remaining eight participants reported no contingency between S1 and the distribution of foreperiods. This performance does not significantly deviate from chance, $\chi^2(2) = 0.7$, p = .35.

9.3. Discussion

The results of Experiment 8 showed that the contingency between the pitch of S1 and the distribution of foreperiods came to expression in temporal preparation. The RT – foreperiod function was steeper for $S1_A$ than for $S1_E$ in two acquisition blocks and in the first transfer block. This effect was clearly not as strong as that obtained for the between-modality S1 pairs examined in Experiments 1, 2, and 6, and it also exhibited an unexpected discontinuity in Block 4. Nevertheless, it corroborates the finding of Experiment 7 that a cueing effect can be observed for same-modality S1 cues. The underlying learning process was again found to be implicit, since performance in the query did not differ from chance.

10. General discussion

In this study, we examined the hypothesis that the warning signal that initiates temporal preparation (S1) does so by serving as a retrieval cue for associated memory traces. This hypothesis follows from the assumption of MTP that each trial leaves a trace in memory with representations of the events that occurred on that trial along with a temporal profile of inhibition during the foreperiod (Los et al., 2014, 2017; cf. Fig. 1). The presentation of S1 leads to the retrieval of its associated memory traces, which in turn jointly determine the level of preparation during the foreperiod.

To test this hypothesis, we performed eight experiments in which two different S1 cues, $S1_A$ and $S1_E$, were associated with an anti-exponential and exponential distribution of foreperiods during an acquisition phase, and with the uniform distribution during a subsequent transfer phase. MTP predicts that $S1_A$ predominantly retrieves memory traces corresponding to the anti-exponential distribution of foreperiods (Fig. 1A) whereas $S1_E$ predominantly retrieves memory traces corresponding to the exponential distribution (Fig. 1B). As a result, the RT – foreperiod functions corresponding to $S1_A$ and $S1_E$ should diverge during the acquisition phase as these S1 cues become associated with more and more memory traces corresponding to the anti-exponential and the exponential distribution, respectively. In the course of the transfer phase, these functions should converge again as the newly formed memory traces from the uniform distribution gradually come to dominate.

To assess this pattern, Table 1 summarizes the effect size for the interaction between S1 cue and foreperiod in each block of each experiment. In this table, we rearranged the order of experiments in accordance with the strength of the interaction effect. Our findings are consistent with the predicted pattern. That is, whenever the S1 cue was found to modify the RT – FP function (Experiments 1, 2, 6, 7, and 8), this modifying effect tended to increase during the acquisition phase and decrease again during the transfer phase. The effect sizes also illustrate that learning was strong for between-modality S1 pairs (Experiments 1, 2, and 6) and weaker (Experiments 7 and 8) or even absent (Experiment 3, 4, and 5) for within-modality S1 pairs. Clearly, the behavioral expression of the contingency is not all or

Table 1 Overview of the effect sizes (partial η^2) of the interaction term between S1 cue and foreperiod in all blocks of each experiment. Shaded cells signify p < .05.

	Acquisition blocks					Transfer blocks			
Experiment; S1 dimension	1	2	3	4	· _	5	6	7	
1. Modality (flash, tone)	.33	.54	.60	.50		.72	.68	.57	
2. Modality (flash, vibration)	.18	.37	.54	.21		.62	.55	.44	
6. Modality (flash, tone), online	.01	.38	.26	.37		.33	.53	.27	
7. Shape (flash, frame)	.06	.08	.12	.36		.27	.24	.08	
8. Tone pitch (high, low)	.03	.26	.22	.05		.54	.01	< .01	
3. Color (green, red)	.02	.02	.08	<.01		.02	.01	.03	
4. Color (green, red), instructed	.11	.08	< .01	.08		.07	.05	.04	
5. Verbal ("short", "long"), online	< .01	.03	< .01	.05		.03	.10	< .01	

none, but constitutes a gradient depending on the specifics of the S1 pair. This finding will be further elaborated below.

Another main conclusion of this study is that the observed cueing effect relies on an implicit learning mechanism, which argues against the view that temporal preparation is a controlled process (e.g., Gottsdanker, 1975; Vallesi & Shallice, 2007). Several observations support this conclusion. First, if present, the cueing effect was not weaker in participants who failed to report the contingency between the S1 cue and the distribution of foreperiods than in participants who successfully reported it. Second, if a cueing effect was found during acquisition, it was also present in at least the first block of the transfer phase (see Table 1), after it was emphasized that the contingency would no longer hold. Third, for colored and verbal S1 pairs, which did not modify the RT – foreperiod function, it did not matter whether participants were (Experiment 4 and 5) or were not (Experiment 3) informed of the contingency at the start of the acquisition phase. Together, these findings make a compelling case that awareness of the contingency between S1 and the distribution of foreperiods is neither a necessary nor a sufficient condition for its behavioral expression.

10.1. Stimulus discrimination and generalization

A central finding of the present study was that of a cueing gradient: The cueing effect was much stronger for some S1 pairs than for others and even absent for S1s that differed in color and verbal content. A similar cueing gradient has been obtained in studies on short term effects in temporal preparation. Thus, Steinborn et al. (2009, 2010) presented participants with a uniform distribution of foreperiods along with two nonpredictive S1s (e.g., a flash and a tone). The data revealed the typical asymmetric sequential effect described in the Introduction. Crucially, in most experiments, this effect was stronger when S1 repeated from trial n - 1 to trial n + 1 to the strong memory trace created on the last trial than an alternated S1. However, similar to the findings of the present study, this modifying influence showed a gradient: It was relatively strong for S1s of different modalities (Steinborn, Rolke, Bratzke, & Ulrich, 2009), and weaker or absent for S1s of the same modality (Steinborn, Rolke, Bratzke, & Ulrich, 2010).

As noted previously, a gradient in cueing effectiveness of different S1 pairs is not problematic for MTP, as long as at least some S1 pairs show a cueing effect consistent with the idea of associative learning. However, the observed gradient speaks to the fundamental problem of stimulus discrimination versus generalization, which deserves closer consideration in itself.

One perspective consistent with both the present gradient (Table 1) and the findings of Steinborn et al. (2009, 2010), is that the cueing effect is determined, not by whether the members of the S1 pair are subjectively discriminable, but by the distinctiveness of the neural activation they evoke (see also Adam, Hommel, & Umiltà, 2003; Adam & Koch, 2014). Indeed, stimuli of different modalities activate clearly distinct brain areas from the first moment of their presentation, whereas considerable overlap exists in brain areas activated by stimuli of the same modality. This corresponds with the stronger cueing effect for S1s of different modalities than for S1s of the same modality. In turn, when comparing S1 pairs within the visual modality, neural distinctiveness is stronger for stimuli occupying different areas of the visual field, such as the flash and the frame in Experiment 7, than for stimuli that merely differ in color (Brouwer & Heeger, 2009, 2013; Harvey & Dumoulin, 2011; Larsson & Heeger, 2006) or verbal content. This corresponds with the modest cueing effect in the former case, but an absence of it in the latter case. Finally, in the auditory domain, pitch is known to be analyzed by different neural populations from the basilar membrane onwards (Greenwood, 1990), which is consistent with the modest cueing effect observed in Experiment 8.

Although an explanation in terms of neural distinctiveness is broadly consistent with the data of Table 1 and the data observed by Steinborn et al. (2009, 2010), it is puzzling at the same time. Since the seminal work of Shepard (1958, 1987), it has been generally acknowledged that the problem of stimulus discrimination exists in psychological space. According to this view, a pair of cues (or other stimuli) may be perceived as highly distinct even when they share many features in neural space and thus need to be distinguished on the basis of the distributed neural patterns they evoke. This view of distinctiveness in psychological space has subsequently been adopted by successful formal theories of stimulus categorization (e.g., Medin & Schaffer, 1978; Nosofsky & Palmeri, 1997; Sanders & Nosofsky, 2020). With an explanation of the present cueing gradient in terms of neural distinctiveness, MTP would therefore lose its natural connection with this theoretical framework.

Furthermore, from an empirical point of view, it should be noted that the experimental literature is replete with examples of robust cueing effects elicited by stimuli that are highly distinct in psychological space but not in neural space. Specifically, both in appetitive and aversive conditioning, effective discrimination learning of differently colored conditioned stimuli has been well established (e.g., Guttman & Kalish, 1956; Koster et al., 2004; Schmidt et al., 2015; Terrace, 1963). In addition, in temporal orienting, a paradigm that comes close to the present paradigm, enhanced visual detection has been reported at the moment predicted by a color cue (Rohenkohl, Gould, Pessoa, & Nobre, 2014). In view of these results, our failure to observe any cueing effect of colored S1s may have been caused by the specific characteristics of our design, some of which will be examined below (see subsection Implications for Temporal Orienting).

In view of these considerations, our explanation in terms of neural distinctiveness should be considered tentative and in need of further testing. The number of data points along our hypothetical neural gradient is still sparse, and future research may aim at adducing additional data points to come to a more balanced assessment.

 $^{^2}$ Our design was not well suited to verify this modifying effect of S1 transition because of the rare occurrence of some foreperiods during acquisition and the small number of blocks during transfer. Nevertheless, in Experiments 1 and 2, we qualitatively replicated the findings of Steinborn and colleagues in the transfer phase, although the data were too noisy to reproduce the significant three-way interaction among fore-period on trial n, foreperiod on trial n-1 and S1 transition.

10.2. Implications for theoretical perspectives on temporal preparation

Elsewhere we have noted that a natural relationship exists between human temporal preparation and trace conditioning in the animal timing literature (Los & Heslenfeld, 2005; Los & Van den Heuvel, 2001). This relationship comes most clearly to the fore at the design level upon recognizing the equivalence between S1 and the conditioned stimulus (CS), between S2 and the unconditioned stimulus (US), and between the foreperiod and the trace separating the CS and the US in time. Beyond the design level, the phenomena in both literatures also bear close similarity. The present findings are a case in point: It has been shown that animals can learn to synchronize the conditioned response with the moment predicted by an auditory or visual CS (e.g., Matell, De Corte, Kerrigan, & DeLussey, 2016; Roberts, 1981; Swanton, Gooch, & Matell, 2009). However, at the theoretical level a clear divide exists between these literatures. Whereas research into animal timing has a long tradition in associative learning approaches, most work on human temporal preparation has been based on the hazard function without regard to the underlying learning processes.

Although the present findings have revealed a critical role of associative learning in temporal preparation, extant formal association learning models cannot easily accommodate them. A variety of seminal models have been developed to account for either the selection (discrimination learning; e.g., McLaren & Mackintosh, 2002; O'Reilly et al., 2007; Rescorla & Wagner, 1972) or the timing (trace conditioning; e.g., Gibbon, 1977; Grossberg & Schmajuk, 1989; Staddon & Higa, 1999; Machado, 1997; Miall, 1989; for review, see Matell & Meck, 2004) of the conditioned response, but we are not aware of any model that integrates these processes, as our findings require. The challenge posed by the present findings is added to the multiple time-scale problem specified in the Introduction, which also has no obvious solution within current association learning theories.

The hazard-based approach is also not directly applicable to the findings of the present study. As argued in the Introduction, this approach may account for the multiple time-scale problem, provided that the representation of the distribution of foreperiods is incrementally updated after every experienced trial with a stronger weighting of the most recent experiences. The present findings require that the cognitive system can keep track of two such representations simultaneously, by updating and utilizing them separately for each S1. Doing so would pose a considerable challenge to the cognitive system. It has been argued that the computation of the hazard function is complex and numerically unstable (Grabenhorst et al., 2019), and the requirement to derive the hazard function from one of two changeable distributions is likely to compound this problem.

Meanwhile, MTP offers a computationally simple solution for the multiple time-scale problem that also predicts the cueing effect of the present study. This is essentially the case because MTP stores individual experiences instead of abstractions from experiences, as is done by reinforcement models and hazard-based approaches. As recently argued by Gershman and Daw (2017), any approach that abstracts summary statistics from the environment will face computational complexities and has difficulties accounting for behavioral consequence of unique experiences. This insight led them to argue for a more prominent role of episodic memory in the reinforcement learning literature. MTP can be considered as a principled instantiation of this proposal.

10.3. Implications for temporal orienting

As pointed out earlier, the design of the present study is similar to the design used in studies of temporal orienting (e.g., Coull & Nobre, 1998; Denison et al., 2017; Los & Van den Heuvel, 2001; Nobre, 2001; Zahn, 1970; Nobre & Van Ede, 2018). The main difference is that the contingency between S1 and the distribution of foreperiods is explicitly instructed at the start of the experimental session in studies of temporal orienting but only afterwards in the present study (with the exception of Experiments 4 and 5). In a typical temporal orienting study (cf. Nobre, 2001), there are two foreperiods (e.g., 600 and 1400 ms), preceded by one of two possible S1s (e.g., one of two concentric circles turning bold). At the start of the experiment, participants are informed that S1 predicts the impending foreperiod with high (e.g., 80%) validity. Typical findings are very similar to those of the present Experiments 1, 2, and 6, in that there is a cueing effect on short-foreperiod trials but not on long-foreperiod trials (for reviews see Nobre, 2001; Nobre & Van Ede, 2018).

In the standard account of temporal orienting (e.g., Nobre, 2001), it is assumed that this asymmetric cueing effect hinges on a correct interpretation of the meaning of S1, leading the participant to initially expect a short foreperiod after a short-foreperiod cue (S1 $_E$ in our design) and a long foreperiod after a long-foreperiod cue (S1 $_A$ in our design). On short-foreperiod trials, this differential expectancy finds expression in RT, reflecting a misalignment of the attentional focus in the case of an invalid long-foreperiod cue. By contrast, on long-foreperiod trials, the passage of time provides an additional cue, which allows for a readjustment of the attentional focus. In particular, on trials with an invalid short-foreperiod cue, the failure of S2 to occur after a short foreperiod causes a breach of expectation (Nobre, Coull, Frith, & Mesulam, 1999), which prompts the participant to shift attention to a later moment in time. As a result, when S2 is ultimately presented, it is equally expected regardless of the preceding cue, which explains the absence of a cueing effect on RT.

MTP accounts for the asymmetric cueing effect in a fundamentally different way. According to it, temporal preparation is implicitly driven by the subset of memory traces retrieved by S1 regardless of the duration of the foreperiod. Thus, if S1 predominantly retrieves memory traces with a short-foreperiod profile (S1 $_E$; Fig. 1 right), temporal preparation peaks earlier than if S1 predominantly retrieves memory traces with a long-foreperiod profile (S1 $_A$; Fig. 1 left), explaining the cueing effect on short-foreperiod trials. However, by the time the longest foreperiod has expired, preparation obtains the same maximum level for S1 $_E$ and S1 $_A$, explaining the absence of a cueing effect on long-foreperiod trials. According to this explanation, the subset of memory traces selected by S1 implicitly drives temporal preparation throughout the foreperiod until the onset of S2. That is, participants do not have to be aware of the contingency between S1 and the distribution of foreperiods, nor do they experience a breach of expectation when the foreperiod is longer than predicted by S1.

In the present study, awareness of the contingency was neither necessary nor sufficient for the emergence of a cueing effect, which argues against the standard account of temporal orienting. This finding does not mean, however, that awareness of the contingency, and an ensuing controlled contribution, is ruled out in general. Several issues may be worth considering in this respect. First, in typical studies of temporal orienting (e.g., Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999), there are only two highly distinct foreperiods, which are cued by S1 with high validity. In the present study, the foreperiods were more numerous, less spaced over time, and less conspicuously associated with S1. In typical temporal orienting studies, it must therefore be relatively easy to develop and maintain awareness of the contingency between S1 and the distribution of foreperiods, which in turn may help participants to deliberately allocate attention to the relevant moments in time. Second, as compared to the present study, typical temporal oriental studies employ more meaningful cues with respect to the duration of the foreperiod they predict (e.g., a bold inner circle predicting a short foreperiod and a bold outer circle predicting a long foreperiod). It is conceivable that such a compatible space-time relationship (cf. Kornblum et al., 1990) fosters awareness as to when action is required and encourages participants to deliberately prepare accordingly.

What complicates the latter argument is that semantic relationships may also influence behavior in an implicit way, as has been demonstrated in several areas of human performance. Experiment 7 of the present study provides a case in point. Here, the cueing effect was stronger in the group in which the central flash was associated with the exponential distribution and the wide frame with the anti-exponential distribution than in the group that experienced the reverse contingency. This modifying influence may have resulted from a semantic space-time correspondence, with the central flash representing nearby (cueing short intervals) and the frame representing far away (cueing long intervals). Crucially though, participants performed at chance level when asked about this contingency in the query after the acquisition phase, indicating that semantic modification, if any, occurred implicitly. Therefore, the finding of a sematic modification of the cueing effect does not imply an explicit or controlled nature of the underlying processing dynamics.

The question of whether or under what circumstances temporal orienting relies on awareness of the contingency between S1 and the distribution of foreperiods is probably a difficult one that deserves closer investigation. What the present findings indicate, though, is that the common assumption of a mediating role of awareness, and ensuing cognitive control, is premature and that the possibility of an implicit learning mechanism should be taken seriously.

10.4. Beyond temporal preparation

The present work has further established that the phenomena of temporal preparation should be understood as expressions of long-term memory (Los et al., 2014, 2017; Mattiesing et al., 2017). In doing so, this work connects research on temporal preparation to a vastly growing literature that shows the role of long-term memory in other domains of human performance. For instance, in a paradigm that mirrors the present paradigm, it has been shown that the passage of time can be used as a retrieval cue for an associated S2 (Thomaschke & Dreisbach, 2013, 2015; Wagener & Hoffmann, 2010; Wendt & Kiesel, 2011). Furthermore, in paradigms of visual perception and attention, it has been shown that associations among nontemporal features of the task environment may likewise come to expression in performance measures (e.g., Chun & Jiang, 1998; Geng & Behrmann, 2005; Turk-Browne, Jungé, & Scholl, 2005; Wang & Theeuwes, 2018).

To account for such expressions of statistical learning, the multiple trace view (or episodic memory view) has become increasingly more common over the past decade. Multiple trace theories were initially developed to account for traditional memory findings in categorization, recall, and recognition (Hintzman, 1986; Howard & Eichenbaum, 2013; Medin & Schaffer, 1978; Nosofsky & Palmeri, 1997, 2015), and they were subsequently extended to account for the automatization of skill in human performance (Logan, 1988, 1990). In recent years, the multiple trace view has further extended its scope to account for adaptive behavior across various domains, including visual attention (Kruijne & Meeter, 2015, 2016a, 2016b), interval reproduction (Taatgen and Van Rijn, 2011), reinforcement learning (Doll, Shohamy, & Daw, 2015; Bornstein, Khaw, Shohamy, & Daw, 2017) and cognitive control (Bejjani, Zhang, & Egner, 2018; King, Korb, & Egner, 2012). Combined with the present work, these developments inspire confidence in the feasibility of a unified multiple trace theory of spatiotemporal statistical learning.

11. Conclusions

The present study has yielded evidence for the view that, in the variable foreperiod paradigm, S1 serves as a cue for the selective retrieval of detailed representations of past experiences. These representations include information about the foreperiod as well as feature specific information about S1, S2 and the response. The data revealed several properties of the retrieval process triggered by S1, characterizing it as selective, associative and implicit. The retrieval process is selective because highly dissimilar S1s retrieve different memory traces. It is associative because it reflects the contingencies that apply in the (experimental) world. It is implicit because the contingencies find behavioral expression without mediation of awareness. These properties are at the core of MTP, and allow it to account for a wide range of phenomena in temporal preparation.

References

Adam, J. J., Hommel, B., & Umiltà, C. (2003). Preparing for perception and action (I): The role of grouping in the response-cuing paradigm. *Cognitive Psychology*, 46, 302–358.

Adam, J. J., & Koch, I. (2014). Response-repetition effects depend on motor-set: Evidence for anatomical coding in response selection. *Human Movement Science*, 33, 172–184.

Baddeley, A. D., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of Verbal Learning and Verbal Behavior*, 14, 575–589.

Bakhurin, K. I., Goudar, V., Shobe, J. L., Claar, L. D., Buonomano, D., & Masmanidis, S. C. (2017). Differential encoding of time by prefrontal and striatal network dynamics. *Journal of Neuroscience*, 37, 854–870.

Barrouillet, P., Bernardin, S., & Camos, V. (2004). Time constraints and resource sharing in adults' working memory. *Journal of Experimental Psychology: General, 133*, 83–100

Baumeister, A. A., & Joubert, C. E. (1969). Interactive effects on reaction time of preparatory interval length and preparatory interval frequency. *Journal of Experimental Psychology*, 82, 393–395.

Bausenhart, K. M., Rolke, B., Hackley, S. A., & Ulrich, R. (2006). The locus of temporal preparation effects: Evidence from the psychological refractory period paradigm. *Psychonomic Bulletin & Review*, 13, 536–542.

Bejjani, C., Zhang, Z., & Egner, T. (2018). Control by association: Transfer of implicitly primed attentional states across linked stimuli. *Psychonomic Bulletin & Review*, 25, 617–626.

Bertelson, P., & Boons, J.-P. (1960). Time uncertainty and choice reaction time. Nature, 187, 531-532.

Bornstein, A. M., Khaw, M. W., Shohamy, D., & Daw, N. D. (2017). Reminders of past choices bias decisions for reward in humans. *Nature Communications*, 8, 15958. Brouwer, G. J., & Heeger, D. J. (2009). Decoding and reconstructing color from responses in human visual cortex. *Journal of Neuroscience*, 29, 13992–14003.

Brouwer, G. J., & Heeger, D. J. (2013). Categorical clustering of the neural representation of color. Journal of Neuroscience, 33, 15454–15465.

Capizzi, M., Correa, A., Wojtowicz, A., & Rafal, R. D. (2015). Foreperiod priming in temporal preparation: Testing current models of sequential effects. *Cognition*, 134, 39–49.

Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology, 36*, 28–71. Coull, J. T. (2009). Neural substrates of mounting temporal expectation. *PLoS Biology, 7*, Article e1000166.

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *Journal of Neuroscience*, 18, 7426–7435.

Coull, J. T., & Nobre, A. C. (2008). Dissociating explicit timing from temporal expectation with fMRI. Current Opinion in Neurobiology, 18, 137–144.

Correa, A., Lupiáñez, J., & Tudela, P. (2005). Attentional preparation based on temporal expectancy modulates processing at the perceptual level. *Psychonomic Bulletin & Review, 12,* 328–334.

Cravo, A. M., Rohenkohl, G., Santos, K. M., & Nobre, A. C. (2017). Temporal anticipation, based on memory. *Journal of Cognitive Neuroscience*, 29, 2081–2089. Cui, X., Stetson, C., Montague, P. R., ... Eagleman, D. M. (2009). Ready...Go: Amplitude of the fMRI signal encodes expectation of cue arrival time. *PLoS Biology*, 7, Article e1000167.

Dankner, Y., Shalev, L., Carrasco, M., & Yuval-Greenberg, S. (2017). Prestimulus inhibition of saccades in adults with and without attention-deficit/hyperactivity disorder as an index of temporal expectations. *Psychological Science*, 28, 835–850.

Davranche, K., Tandonnet, C., Burle, B., Meynier, C., Vidal, F., & Hasbroucq, T. (2007). The dual nature of time preparation: Neural activation and suppression revealed by transcranial magnetic stimulation of the motor cortex. European Journal of Neuroscience, 25, 3766–3774.

Denison, R. N., Heeger, D. J., & Carrasco, M. (2017). Attention flexibly trades off across points in time. Psychonomic Bulletin & Review, 24, 1142-1151.

Doll, B. B., Shohamy, D., & Daw, N. D. (2015). Multiple memory systems as substrates for multiple decision systems. *Neurobiology of Learning and Memory, 117*, 4–13. Donkin, C., & Nosofsky, R. M. (2012). A power-law model of psychological memory strength in short-term and long-term recognition. *Psychological Science, 23*, 625–634.

Drazin, D. H. (1961). Effects of foreperiod, foreperiod variability, and probability of stimulus occurrence on simple reaction time. *Journal of Experimental Psychology*, 62, 43–50.

Duque, J., & Ivry, R. B. (2009). Role of corticospinal suppression during motor preparation. Cerebral Cortex, 19, 2013-2024.

Duque, J., Greenhouse, I., Labruna, L., & Ivry, R. B. (2017). Physiological markers of motor inhibition during human behavior. *Trends in Neurosciences*, 40, 219–236. Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, 13, 732–744.

Frith, C. D., & Done, D. J. (1986). Routes to action in reaction-time tasks. Psychological Research Psychologische Forschung, 48, 169–177.

Geng, J. J., & Behrmann, M. (2005). Spatial probability as an attentional cue in visual search. Perception & Psychophysics, 67, 1252-1268.

Gershman, S. J., & Daw, N. D. (2017). Reinforcement learning and episodic memory in humans and animals: An integrative framework. *Annual Review of Psychology*, 68, 101–128.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, 84, 279–325.

Gottsdanker, R. (1975). The attaining and maintaining of preparation. In P. M. A. Rabbitt, & S. Dornic (Eds.), Attention and Performance V (pp. 33–49). London: Academic Press.

Grabenhorst, M., Michalareas, G., Maloney, L. T., & Poeppel, D. (2019). The anticipation of events in time. *Nature Communications*, 10, 5802. https://doi.org/10.1038/s41467-019-13849-0.

Grossberg, S., & Schmajuk, N. A. (1989). Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks, 2*, 79–102. Greenwood, D. D. (1990). A cochlear frequency-position function for several species—29 years later. *The Journal of the Acoustical Society of America, 87*, 2592–2605. Guttman, N., & Kalish, H. I. (1956). Discriminability and stimulus generalization. *Journal of Experimental Psychology, 51*, 79–88.

Hackley, S. A., Schankin, A., Wohlschlaeger, A., & Wascher, E. (2007). Localization of temporal preparation effects via trisected reaction time. *Psychophysiology*, 44, 334–338.

Harvey, B. M., & Dumoulin, S. O. (2011). The relationship between cortical magnification factor and population receptive field size in human visual cortex: Constancies in cortical architecture. *Journal of Neuroscience*, 31, 13604–13612.

Hasbroucq, T., Osman, A., Possamaï, C.-A., Burle, B., Carron, S., Dépy, D., ... Mouret, I. (1999). Cortico-spinal inhibition reflects time but not event preparation: Neural mechanisms of preparation dissociated by transcranial magnetic stimulation. *Acta Psychologica*, 101, 243–266.

Herbst, S. K., Fiedler, L., & Obleser, J. (2018). Tracking temporal hazard in the human electroencephalogram using a forward encoding model. *eNeuro*, 5, 1–17. Hintzman, D. L. (1986). "Schema abstraction" in a multiple trace model. *Psychological Review*, 93, 411–428.

Hommel, B., & Frings, C. (2020). The disintegration of event files over time: Decay or interference? Psychonomic Bulletin & Review, 27, 751–757.

Howard, M. W., & Eichenbaum, H. (2013). The hippocampus, time, and memory across scales. Journal of Experimental Psychology: General, 142, 1211–1230.

Howard, M. W., Shankar, K. H., Aue, W. R., & Criss, A. H. (2015). A distributed representation of internal time. Psychological Review, 122, 24-53.

Jahfari, S., Stinear, C. M., Claffey, M., Verbruggen, F., & Aron, A. R. (2010). Responding with restraint: What are the neurocognitive mechanisms? *Journal of Cognitive Neuroscience*, 22, 1479–1492.

Janssen, P., & Shadlen, M. N. (2005). A representation of the hazard rate of elapsed time in macaque area LIP. Nature Neuroscience, 8, 234–241.

Jepma, M., Wagenmakers, E.-J., Band, G. P. H., & Nieuwenhuis, S. (2009). The effects of accessory stimuli on information processing: Evidence from electrophysiology and a diffusion-model analysis. *Journal of Cognitive Neuroscience*, 21, 847–864.

King, J. A., Korb, F. M., & Egner, T. (2012). Priming of control: Implicit contextual cuing of top-down attentional set. *Journal of Neuroscience, 32*, 8192–8200. Kingstone, A. (1992). Combining expectancies. *Quarterly Journal of Experimental Psychology, 44A*, 69–104.

Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus-response compatibility - a model and taxonomy. *Psychological Review*, 97(2), 253–270.

Koster, E. H. W., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion, 4*, 312–317. Kruijne, W., & Meeter, M. (2015). The long and the short of priming in visual search. *Attention, Perception & Psychophysics, 77*, 1558–1573.

Kruijne, W., & Meeter, M. (2016a). Implicit short- and long-term memory direct our gaze in visual search. Attention, Perception, & Psychophysics, 78, 761–773.

Kruijne, W., & Meeter, M. (2016b). Long-term priming of visual search prevails against the passage of time and counteracting instructions. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 42*, 1293–1303.

Lange, K., Kühn, S., & Filevich, E. (2015). "Just Another Tool for Online Studies" (JATOS): An easy solution for setup and management of web servers supporting online studies. *PlosOne*, 10(6), Article e0130834.

Langner, R., Steinborn, M., Eickhoff, S. B., & Huestegge, L. (2018). When specific action biases meet nonspecific preparation: Event repetition modulates the variable-foreperiod effect. *Journal of Experimental Psychology: Human Perception and performance*, 44, 1313–1323.

Larsson J. & Heeger, D. J. (2006). Two retinal visual areas in human lateral visual cortex. Journal of Neuroscience, 26, 13124–13128.

Logan, G. D. (1988). Toward an instance theory of automatization. Psychological Review, 95, 492-527.

Logan, G. D. (1990). Repetition priming and automaticity: Common underlying mechanisms? Cognitive Psychology, 22, 1-35.

Los, S. A. (1996). On the origin of mixing costs: Exploring information processing in pure and mixed blocks of trials. Acta Psychologica, 94, 145-188.

Los, S. A. (2010). Foreperiod and the sequential effect: Theory and data. In A. C. Nobre, & J. T. Coull (Eds.), Attention and Time (pp. 289–302). Oxford: Oxford University Press.

Los, S. A. (2013). The role of inhibition in temporal preparation: Evidence from a go/no-go task. Cognition, 129, 328-344.

Los, S. A., & Agter, F. (2005). Reweighting sequential effects across different distributions of foreperiods: Segregating elementary contributions to nonspecific preparation. *Perception & Psychophysics*, 67, 1161–1170.

Los, S. A., & Heslenfeld, D. J. (2005). Intentional and unintentional contributions to nonspecific preparation: Electrophysiological evidence. *Journal of Experimental Psychology: General*, 134, 52–72.

Los, S. A., Knol, D. L., & Boers, R. M. (2001). The foreperiod effect revisited: Conditioning as a basis for nonspecific preparation. *Acta Psychologica, 106*, 121–145. Los, S. A., Kruijne, W., & Meeter, M. (2014). Outlines of a multiple trace theory of temporal preparation. *Frontiers in Psychology, 5*, 1058.

Los, S. A., Kruijne, W., & Meeter, M. (2017). Hazard versus history: Temporal preparation is driven by past experience. *Journal of Experimental Psychology: Human Perception and Performance*, 43, 78–88.

Los, S. A., & Schut, M. L. J. (2008). The effective time course of preparation. Cognitive Psychology, 57, 20-55.

Los, S. A., & Van den Heuvel, C. E. (2001). Intentional and unintentional contributions to nonspecific preparation during reaction time foreperiods. *Journal of Experimental Psychology: Human Perception and Performance, 27, 370–386.*

Los, S. A., & Van der Burg, E. (2013). Sound speeds vision through preparation, not integration. *Journal of Experimental Psychology: Human Perception and Performance*, 39, 1612–1624.

Luce, R. D. (1986). Response Times. New York: Oxford University Press.

Machado, A. (1997). Learning the temporal dynamics of behavior. Psychological Review, 104, 241-265.

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. Psychological Bulletin, 109, 163-203.

Matell, S. M., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Cognitive Brain Research*, 21, 139–170. Matell, M. S., De Corte, B. J., Kerrigan, T., & DeLussey, C. M. (2016). Temporal averaging in response to change. *Timing & Time Perception*, 4, 223–247.

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. Behavior Research Methods, 44,

Mattes, S., & Ulrich, R. (1997). Response force is sensitive to the temporal uncertainty of response stimuli. Perception & Psychophysics, 59, 1089-1097.

Mattiesing, R. M., Kruijne, W., Meeter, M., & Los, S. A. (2017). Timing a week later: The role of long-term memory in temporal preparation. *Psychonomic Bulletin & Review, 24,* 1900–1905.

Mayr, S., Erdfelder, E., Buchner, A., & Faul, F. (2007). A short tutorial of GPower. Tutorials in Quantitative Methods in Psychology, 3, 51–59.

McLaren, I. P. L., & Mackintosh, N. J. (2002). Associative learning and elemental representation: II. Generalization and discrimination. *Animal Learning and Behavior*, 30, 177–200.

Medin, D. L., & Schaffer, M. M. (1978). Context theory of classification learning. Psychological Review, 85, 207-238.

Mello, G. B. H., Soares, S., & Paton, J. J. (2015). A scalable population code for time in the striatum. Current Biology, 25, 1113-1122.

Miall, R. C. (1989). The storage of time intervals using oscillating neurons. Neural Computation, 1, 359–371.

Miniussi, C., Wilding, E. L., Coull, J. T., & Nobre, A. C. (1999). Orienting attention in time: Modulation of brain potentials. Brain, 122, 1507-1518.

Mo, S. S., & Kersey, R. (1980). Foreperiod effects on time estimation and simple reaction time in schizophrenia. Journal of Clinical Psychology, 36, 94–99.

Morey, R. D., & Rouder, J. N. (2018). BayesFactor: Computation of Bayes factors for common designs. R package version 0.9.12-4.2. https://CRAN.R-project.org/package=BayesFactor.

Müller-Gethmann, H., Ulrich, R., & Rinkenauer, G. (2003). Locus of the effect of temporal preparation: Evidence from the lateralized readiness potential. Psychophysiology, 40, 597–611.

Näätänen, R. (1970). The diminishing time-uncertainty with the lapse of time after the warning signal in reaction-time experiments with varying fore-periods. *Acta Psychologica*, 34, 399–419.

Näätänen, R. (1971). Non-aging fore-periods and simple reaction time. Acta Psychologica, 35, 316-327.

Narayanan, N. S., Horst, N. K., & Laubach, M. (2006). Reversible inactivations of rat medial prefrontal cortex impair the ability to wait for a stimulus. *Neuroscience*, 139, 865–876.

Narayanan, N. S., & Laubach, M. (2006). Top-down control of motor cortex ensembles by dorsomedial prefrontal cortex. Neuron, 52, 921-931.

Niemi, P., & Näätänen, R. (1981). Foreperiod and simple reaction time. Psychological Bulletin, 89, 133-162.

Nobre, A. C. (2001). Orienting attention to instants in time. *Neuropsychologia*, 39, 1317–1328.

Nobre, A. C., Correa, A., & Coull, J. T. (2007). The hazards of time. Current Opinion in Neurobiology, 17, 465-470.

Nobre, A. C., Coull, J. T., Frith, C. D., & Mesulam, M. M. (1999). Orbitofrontal cortex is activated during breaches of expectation in tasks of visual attention. *Nature Neuroscience*, 2, 11–12.

Nobre, A. C., & Van Ede, F. (2018). Anticipated moments: Temporal structure in attention. Nature Reviews Neuroscience, 19, 34-48.

Nosofsky, R. M., & Palmeri, T. J. (1997). An Exemplar-Based Random Walk Model of Speeded Classification. Psychological Review, 104, 266-300.

Nosofsky, R. M., & Palmeri, T. J. (2015). An Exemplar-Based Random-Walk Model of Categorization and Recognition. In J. T. Townsend, & J. R. Busemeyer (Eds.), *The Oxford Handbook of Computational and Mathematical Psychology* (pp. 142–164). New York: Oxford.

Oberauer, K., Lewandowsky, S., Farrell, S., Jarrold, C., & Greaves, M. (2012). Modeling working memory: An interference model of complex span. Psychonomic Bulletin & Review, 19, 779–819.

Olmos-Solis, K., Van Loon, A. M., Los, S. A., & Olivers, C. N. L. (2017). Oculomotor measures reveal the temporal dynamics of preparing for search. *Progress in Brain Research*, 236, 1–23.

O'Reilly, R. C., Frank, M. J., Hazy, T. E., & Watz, B. (2007). PVLV: The primary value and learned value Pavlovian learning algorithm. *Behavioral Neuroscience*, 121, 31–49.

Pastalkova, E., Itskov, V., Amarasingham, A., & Buzsáki, G. (2008). Internally generated cell assembly sequences in the rat hippocampus. *Science*, 321, 1322–1327. Pavlov, I. P. (1927). *Conditioned reflexes*. London: Oxford.

Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review, 116,* 129–156.

Prut, Y., & Fetz, E. E. (1999). Primate spinal interneurons show pre-movement instructed delay activity. Nature, 401, 590-594.

Ratcliff, R. (1978). A theory of memory retrieval. Psychological Review, 85(2), 59-108.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black, & W. F. Prokasy (Eds.), Classical conditioning II: Current research and theory (pp. 64–99). New York: Appleton-Century-Crofts.

Roberts, S. (1981). Isolation of an internal clock. Journal of Experimental Psychology: Animal Behavior Processes, 7, 242–268.

Rohenkohl, G., Gould, I. C., Pessoa, J., & Nobre, A. C. (2014). Combining spatial and temporal expectations to improve visual perception. *Journal of Vision, 14*, 1–13. Rolke, B., & Ulrich, R. (2010). On the locus of temporal preparation: Enhancement of premotor processes? In A. C. Nobre, & J. T. Coull (Eds.), *Attention and Time* (pp. 227–241). Oxford: Oxford University Press.

Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, *56*, 356–374. Sanders, A. F. (1980). Some effects of instructed muscle tension on choice reaction time and movement time. In R. S. Nickerson (Ed.), *Attention and Performance VII* (pp. 59–74). Hillsdale, NJ: Erlbaum.

Sanders, C. A., & Nosofsky, R. M. (2020). Training deep networks to construct a psychological feature space for a natural-object category domain. *Computational Brain & Behavior*, 3, 229–251.

Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2015). Attentional capture by signals of threat. Cognition and Emotion, 29, 687-694.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). E-Prime User's Guide. Pittsburgh: Psychology Software Tools Inc.

Shankar, K. H., & Howard, M. C. (2012). A scale-invariant internal representation of time. Neural Computation, 24, 134-193.

Shepard, R. N. (1958). Stimulus and response generalization: Deduction of the generalization gradient from a trace model. Psychological Review, 65, 242–256.

Shepard, R. N. (1987). Toward a universal law of generalization for psychological science. Science, 237, 1317–1323.

Snell, J., Declerck, M., & Grainger, J. (2018). Parallel semantic processing in reading revisited: Effects of translation equivalents in bilingual readers. *Language, Cognition and Neuroscience, 33*, 563–574.

Staddon, J. E. R., & Higa, J. J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior, 71*, 215–251.

Steinborn, M. B., & Langner, R. (2012). Arousal modulates temporal preparation under increased time uncertainty: Evidence from higher-order sequential foreperiod effects. *Acta Psychologica*, 139, 65–76.

Steinborn, M. B., Rolke, B., Bratzke, D., & Ulrich, R. (2009). Dynamic adjustment of temporal preparation: Shifting warning signal modality attenuates the sequential foreperiod effect. *Acta Psychologica*, 132, 40–47.

Steinborn, M. B., Rolke, B., Bratzke, D., & Ulrich, R. (2010). The effect of a cross-trial shift of auditory warning signals on the sequential foreperiod effect. *Acta Psychologica*, 134, 94–104.

Swanton, D. N., Gooch, C. M., & Matell, M. S. (2009). Averaging of temporal memories by rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 35, 434-439.

Taatgen, N., & Van Rijn, H. (2011). Traces of times past: Representations of temporal intervals in memory. Memory & Cognition, 39, 1546-1560.

Terrace, H. S. (1963). Discrimination learning with and without "errors". Journal of the Experimental Analysis of Behavior, 6, 1-27.

Thomaschke, R., & Dreisbach, G. (2013). Temporal predictability facilitates action, not perception. Psychological Science, 24, 1335–1340.

Thomaschke, R., & Dreisbach, G. (2015). The time-event correlation effect is due to temporal expectancy, not to partial transition cost. *Journal of Experimental Psychology: Human Perception and Performance*, 41, 196–2018.

Toda, K., Lusk, N. A., Watson, G. D. R., Kim, N., Lu, D., Li, H. E., ... Yin, H. H. (2017). Nigrotectal stimulation stops interval timing in mice. *Current Biology, 27*, 1–8. Trillenberg, P., Verleger, R., Wascher, E., Wauschkuhn, B., & Wessel, K. (2000). CNV and temporal uncertainty with 'ageing ' and 'nonageing' S1–S2 intervals. *Clinical Neurophysiology, 111*, 1216–1226.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General*, 134, 552–564. Vallesi, A., Lozano, V. N., & Correa, A. (2013). Dissociating temporal preparation processes as a function of the inter-trial interval duration. *Cognition*, 127, 22–30. Vallesi, A., & Shallice, T. (2007). Developmental dissociations of preparation over time: Deconstructing the variable foreperiod phenomena. *Journal of Experimental Psychology: Human Perception and Performance*, 33, 1377–1388.

Van der Lubbe, R. H. J., Los, S. A., Jaśkowski, P., & Verleger, R. (2004). Being prepared on time: On the importance of the previous foreperiod to current preparation, as reflected in speed, force, and preparation-related brain potentials. *Acta Psychologica*, 116, 245–262.

Vangkilde, S., Coull, J. T., & Bundesen, C. (2012). Great expectations: Temporal expectation modulates perceptual processing speed. *Journal of Experimental Psychology: Human Perception and Performance, 38*, 1183–1191.

Vangkilde, S., Petersen, A., & Bundesen, C. (2013). Temporal expectancy in the context of a theory of visual attention. *Philosophical Transactions of the Royal Society B*, 368(1628), 20130054.

Wagener, A., & Hoffmann, J. (2010). Temporal cueing of target-identity and target-location. Experimental Psychology, 57, 436-445.

Wang, B., & Theeuwes, J. (2018). Statistical regularities modulate attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 44, 13–17.

Wendt, M., & Kiesel, A. (2011). Conflict adaptation in time: Foreperiods as contextual cues for attentional adjustment. *Psychonomic Bulletin & Review, 18*, 910–916. Wixted, J. T. (2004). On common ground: Jost's (1897) law of forgetting and Ribot's (1881) law of retrograde amnesia. *Psychological Review, 111*, 864–879. Woodrow, H. (1914). The measurement of attention. *Psychological Monographs, 17*(5, whole no. 76), 1–158.

Zahn, T. P. (1970). Effects of reductions in uncertainty on reaction time in schizophrenic and normal subjects. *Journal of Experimental Research in Personality, 4*, 135–143

Zahn, T. P., Rosenthal, D., & Shakow, D. (1963). Effects of irregular preparatory intervals on reaction time in schizophrenia. *Journal of Abnormal and Social Psychology*, 67, 44–52.