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Motivation alters implicit temporal attention through sustained and transient mechanisms: A behavioral and pupillometric study

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Abstract

Temporal expectations aid performance by allowing the optimization of attentional readiness at moment of highest target probability. Reward enhances cognitive performance through its action on preparatory and reactive attentional processes. To elucidate how motivation interacts with mechanisms of implicit temporal attention, we studied healthy young adult participants (N = 73) performing a sustained attention task with simultaneous pupillometric recording, under different reward conditions (baseline: 0 c; reward: 10 c/fast response). Target timing was temporally unpredictable (variable foreperiod: 2-10 s, uniformly distributed), in which case implicitly formed timing expectations. Trials were binned according to current foreperiod (FP_n; short: 2–6 s; long: 6–10 s) and preceding foreperiod (FP_{n-1}; short: 2–6 s; long: 6-10 s). Overall, performance data showed the expected temporal attention effects, with slower responses after shorter FP_ns, particularly when they followed longer FP_{n-1}s. Moreover, these temporal effects were significantly reduced in the reward condition. While performance improved in all trial types, the largest benefit appeared in trials that were normally most disadvantaged by invalid temporal expectation. Furthermore, reward motivation was accompanied by an increase in sustained (prestimulus) and transient (poststimulus response) pupil diameter. The latter effect was particularly evident following short FP_ns. The current findings suggest that reward motivation can improve overall attentional performance and reduce implicit temporal bias, both through preparatory and reactive attentional mechanisms.

KEYWORDS

foreperiod, implicit timing, pupillometry, reward motivation, temporal attention

1 | INTRODUCTION

Reward motivation can shape an individual's cognitive performance in various domains, ranging from selective attention (Della Libera & Chelazzi, 2006; Kiss, Driver, & Eimer, 2009), conflict processing (Krebs, Boehler, Egner, & Woldorff, 2011), and working memory (Jimura, Locke, & Braver, 2010) to long-term memory (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006) and sustained attention (Esterman, Poole, Liu, & DeGutis, 2016; Massar, Lim, Sasmita, & Chee, 2016). Evidence from imaging studies suggests that this motivational improvement is typically established through alterations in the dynamics of control allocation (for a review, see Botvinick & Braver, 2015). Reward prospect can aid participants to prepare for upcoming task requirements and to more effectively allocate cognitive resources to the processing of relevant stimuli (Aarts et al., 2010; Krebs et al., 2011; Locke & Braver, 2008).

One cognitive domain for which such allocation of resources is particularly pertinent is temporal attention. Attending to relevant moments in time is a highly adaptive skill that is critical to many real-world behaviors (e.g., driving 2 of 11

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a car in traffic or anticipating a starting shot in competitive sports). Expectations about the timing of critical events help us to bias attention toward moments in time that have the highest likelihood of target occurrence (Coull & Nobre, 2008). This is thought to improve responsiveness by optimizing attentional readiness at important moments while preserving energy at less critical times. These temporal attentional biases have been found to influence performance on lab-based reaction time tasks (Coull & Nobre, 2008) as well as in real-world settings (e.g., sprinters' start times; Dalmaijer, Nijenhuis, & Van der Stigchel, 2015; Otsuka, Kurihara, & Isaka, 2017; see also Los, Hoorn, Grin, & Van der Burg, 2013).

In situations where the timing of relevant events is unpredictable, temporal predictions are formed implicitly, based on the passage of time. When the probability of target occurrence is equally likely at any moment in time (i.e., onset time is randomly drawn from a uniform distribution), responses become faster and more accurate when targets are preceded by longer lead times (foreperiod; FP) than when targets follow shorter foreperiods (Nickerson & Burnham, 1969; Niemi & Näätänen, 1981). This temporal bias is thought to reflect the increasing attentional readiness due to the mounting expectation of target appearance, given that a target has not occurred yet (conditional probability).

This FP effect is further modulated by temporal expectations set by the immediate history of FP durations in previous trials (Drazin, 1961). Expectations about the current trial's foreperiod (FP_n) are updated to resemble the previous trial's foreperiod (FP_{n-1}; Los, Knol, & Boers, 2001). Consequently, the effects of incomplete preparation (at short FPs) are particularly strong when the previous trial's FP was long. Whether the FP_n and FP_{n-1} effects reflect one singular or multiple underlying mechanisms is still a topic of debate (see, e.g., Capizzi, Correa, Wojtowicz, & Rafal, 2015; Los, Kruijne, & Meeter, 2014; Vallesi, Arbula, & Bernardis, 2014). However, it is clear that implicit attentional biases are formed based on the underlying temporal structure of the task (Coull & Nobre, 2008). These biases may facilitate an advantageous allocation of attention to specific points in time, but, conversely, they may leave us insufficiently prepared when expectations are invalid.

The focus of the current investigation is to determine how these temporal biases are altered by reward motivation. Thus far, very little is known about the interaction between motivation and temporal attention. From studies on motivation in other cognitive domains, it could be hypothesized that preparatory attention is increased when incentives are provided (Aarts et al., 2010; Krebs et al., 2011; Locke & Braver, 2008). Influential theoretical models describe this as a "proactive mode of control," where processing of oncoming target stimuli can be facilitated by active preparatory maintenance of goal-relevant information (Braver, 2012). In the domain of spatial attention, such motivated preparation has been found to improve performance and reduce the costs of invalid attentional expectations (invalid spatial cues; Engelmann, Damaraju, Padmala, & Pessoa, 2009).

In the temporal domain, it is still unknown whether motivation would similarly alter attentional biases. Particularly, it is not known whether motivation would be equally effective across all points in time, or whether some time points are systematically favored. A recent study using predictable target timing (i.e., fixed foreperiod design) demonstrated that a motivational manipulation (instruction to exert more effort) resulted in faster responses across different FPs (Steinborn, Langner, & Huestegge, 2017). An earlier study using a variable foreperiod design found that providing rewards resulted in a small reduction in temporal bias, in addition to an overall improvement (Los & van den Heuvel, 2001; exp. 1). However, this reduction failed to reach statistical significance, potentially due to a small sample size (N = 10).

The evidence to date therefore remains inconclusive. In this study, we aimed to elucidate how performance motivation interacts with implicit temporal attention to allocate resources across time. To this end, we measured temporal attentional bias in a large sample of subjects, with simultaneous performance and pupillometric recording (N = 73). Participants performed a sustained attention task with unpredictable target timing (variable FP). Reward motivation was manipulated across different runs by offering participants monetary incentive for fast performance. Following Los and van den Heuvel (2001), it was expected that motivation would result in an overall faster reaction time, and particularly a reduction of implicit attentional bias.

Pupil diameter is found to reflect modulations of attention (Kahneman & Beatty, 1966). In particular, prestimulus pupil diameter in anticipation of a target has been associated with proactive, preparatory attention, whereas phasic poststimulus pupil responses may reflect reactive attention (Chatham, Frank, & Munakata, 2009; Chiew & Braver, 2013). Prestimulus pupil diameter is found to increase prior to stimulus onset in predictable timing paradigms (Akdoğan & van Rijn, 2016; Unsworth, Robison, & Miller, 2018), reflecting attentional readiness. Moreover, reward manipulations have been shown to increase prestimulus pupil size (Chiew & Braver, 2013), possibly reflecting increased proactive attention. Following these studies, we expected to find increasing prestimulus pupil size with longer FP (increasing readiness), and overall larger prestimulus pupil size with reward motivation.

2 | METHODS

2.1 | Participants

Data from a previously reported study (Massar et al., 2016; exps. 2, 3; N = 48) were combined with an additional dataset (N = 25; previously unpublished), to obtain a large sample of

simultaneous behavioral and pupillometric data. The resultant data set comprised 73 participants (33 female) between the ages of 18 and 35 (M = 23.03, SD = 3.11). In all three experiments, participants performed an incentivized sustained attention task while undergoing pupillometry. Reimbursement was based on an individual's task performance. Participants gave informed consent in accordance with study procedures approved by the Institutional Review Board of the National University of Singapore.

2.2 | Task and procedure

Participants performed a sustained attention task (Psychomotor Vigilance Task: PVT; Dinges & Powell, 1985) under different reward conditions. Each task run started with the presentation of a fixation dot. At random interstimulus intervals (ISI = 2-10 s; uniformly distributed) a running millisecond counter appeared (see Figure 1). Participants were instructed to respond as fast as possible to the appearance of this target stimulus. Upon response, the millisecond counter stayed onscreen for 1 s displaying the reaction time as feedback. Subsequently, the next trial started with the presentation of a fixation dot. Each run lasted for 10 min, comprising approximately 80 trials. Participants first performed a baseline run (nonrewarded), followed by a rewarded run in which

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they earned additional bonus payout. Before the start of the reward run, participants were instructed that they would receive 10 cents for every response below a specified reaction time (RT) criterion (individual response criterion was determined as the median RT in baseline run). Similar to the baseline run, reaction time feedback was displayed after each response. As the individual RT criterion was explicitly stated before the reward run, the RT feedback could be used to infer whether the reward was earned on a given trial. A third reward condition varied between the different samples and is not reported here.

Due to the random ISI distribution in the PVT, target timing is unpredictable. Previous studies using this task have demonstrated robust FP effects, showing that responses are reliably faster after longer ISIs (long FP) compared to shorter ISIs (short FP; Kong, Asplund, Ling, & Chee, 2015; Massar & Chee, 2015; Matthews et al., 2017; Tucker, Basner, Stern, & Rakitin, 2009). Here, we categorized trials into FP bins based on the ISI duration (ISI 2–6 s: short FP; ISI 6–10 s: long FP) in the current trial (FP_n) and the preceding trial (FP_{n-1}). For each combination of FP_n (short, long) and FP_{n-1} (short, long), median RTs were calculated after removal of premature responses (RT <150 ms), resulting in four RT scores per run. Median RT scores were statistically analyzed using a 2 (Reward Condition: baseline vs. reward) × 2 (FP_n:



FIGURE 1 (a) Task schematic of the psychomotor vigilance task. (b) Increasing readiness with longer FPs. (c) Expected pattern of behavioral performance

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short vs. long) × 2 (FP_{n-1}: short vs. long) repeated measures analysis of variance (ANOVA). Upon detection of significant interactions, foreperiod effects for the different reward and FP_{n-1} conditions were quantified following the equation below (Kong et al., 2015):

Foreperiod effect = median RT short FP_n – median RT long FP_n

2.3 | Pupilometry

Throughout the task, pupil size was continuously recorded using the Tobii X60 eye tracker (Tobii AB, Danderyd, Sweden) at a sampling rate of 60 Hz. Blinks and artifacts were corrected offline by linear interpolation. Prestimulus pupil diameter was calculated for each trial as the average in a 1,000-ms window prior to target onset. Resulting trial average scores were *z*-transformed across all conditions per subject. In the same manner as for the RT data, prestimulus pupil data were binned based on FP_n and FP_{n-1} and analyzed using a Reward × FP_n × FP_{n-1} repeated measures ANOVA. Follow-up foreperiod effects were calculated as follows:

Foreperiod effect = prestimulus pupil diameter short FP_n -prestimulus pupil diameter long FP_n

Poststimulus pupil responses were quantified in a 700– 1,500 ms post-target window (where post-target dilation was the largest). Prior to quantification, pupil data were *z*-transformed (over a window spanning from 1,000 ms prestimulus to 4,000 ms poststimulus) and corrected with reference to a 500-ms pretarget baseline. Average poststimulus pupil responses were binned based on FP_n and FP_{n-1} and analyzed using a Reward × FP_n × FP_{n-1} repeated measures ANOVA. Follow-up foreperiod effects were calculated as follows:

Foreperiod effect = poststimulus pupil response short FP_n -poststimulus pupil response long FP_n

3 | RESULTS

3.1 | Behavior

Median RTs following the different FP_n and FP_{n-1} combinations are plotted in Figure 2a (baseline) and 2b (reward). Repeated measures ANOVA demonstrated the typical foreperiod effect (FP_n main effect: F(1, 72) = 171.82, p < 0.001, $\eta_p^2 = 0.705$) and the influence of the preceding trial's foreperiod (FP_n × FP_{n-1} interaction: F(1, 72) = 55.47, p < 0.001, $\eta_p^2 = 0.435$; indicating increased foreperiod effect following a long FP_{n-1}). Moreover, there was a significant main effect of reward, F(1, 72) = 45.69, p < 0.001, $\eta_p^2 = 0.388$. Pairwise comparison indicated that RTs were faster with reward across all foreperiod bins (Table 1).

Central to our investigation, a significant Reward × FP_n × FP_{n-1} three-way interaction suggested that reward did not reduce RTs uniformly across all foreperiod bins, F(1, 72) = 7.18, p = 0.009, $\eta_p^2 = 0.091$. Analysis of the foreperiod effects in the separate FP_{n-1} bins for each reward condition (see Figure 2c) demonstrated that the FP_n effect (which is driven by short FP_n trials) was reduced by reward motivation, when trials followed a long FP_{n-1}, t(72) = 2.58, p = 0.012, but not following a short FP_{n-1}, t(72) = -0.688, p = 0.493. These data show that time points that are normally most affected by incomplete attentional preparation show the strongest improvement with motivation.

While the analysis based on FP bins showed a clear influence of FP_n (faster RT after long FP_n) and FP_{n-1} (longer RT with long FP_{n-1}), the division in dichotomous bins does not fully examine the underlying continuous FP distribution. In order to confirm these findings, utilizing the whole distribution, we performed a general linear model (GLM) analysis. Trial by trial, FP_n and FP_{n-1} were used as predictors and fitted to RT data. This resulted in regression coefficients (β), indicating how strongly RT is influenced by each of the



FIGURE 2 Median RT as a function of the current foreperiod (FP_n) and the immediately preceding foreperiod (FP_{n-1}) in baseline (a) and rewarded (b) conditions. (c) Foreperiod effects as a function of motivation and FP_{n-1}. Error bars represent standard error of the mean. *p < 0.05

TABLE 1 Pairwise comparison of variables in baseline and reward conditions

RT (ms)	Baseline M (SD)	Reward M (SD)	$\frac{t}{df = 72}$	p
Short FP _{n-1} and short FP _n	310.92 (34.01)	303.46 (31.39)	2.83	0.006
Short FP_{n-1} and long FP_n	298.99 (31.71)	289.62 (27.32)	4.76	< 0.001
Long FP_{n-1} and short FP_n	335.75 (36.94)	317.80 (31.23)	6.66	< 0.001
Long FP_{n-1} and long FP_n	305.83 (34.34)	294.29 (29.34)	5.63	< 0.001

Note. RT = reaction time; FP_n = current foreperiod; FP_{n-1} = preceding foreperiod.

predictors. Data were fitted for each subject separately, and at the second level, resulting β coefficients were tested for significance using *t* tests (see Figure 3). Significant negative β coefficients were found for FP_n, confirming that longer FP_n was associated with faster RTs (baseline: *t*(72) = -18.25, *p* < 0.001; reward: *t*(72) = -14.76, *p* < 0.001), and significant positive β coefficients were found for FP_{n-1} (baseline: *t*(72) = 10.56, *p* < 0.001; reward: *t*(72) = 9.46, *p* < 0.001), indicating that longer FP_{n-1} led to slower RTs. These findings confirm that RT is subject to the temporal attentional biases as described earlier. Crucially, when comparing β coefficients between the baseline and reward runs, we found that the influence of both FP_n, *t*(72) = -5.07, *p* < 0.001, and FP_{n-1}, *t*(72) = 3.02, *p* = 0.004, were reduced during the rewarded run.

3.2 | Prestimulus pupil diameter

Prestimulus pupil diameter under the different FP_n and FP_n 1 combinations are depicted in Figure 4. Overall, the most prominent effect of reward on prestimulus pupil diameter was a significant increase in pupil size during the reward runs compared to baseline (reward main effect: F(1, 72) =48.59, p < 0.001, $\eta_p^2 = 0.403$), which was present in all FP_n and FP_{n-1} conditions. Pupil size was further characterized by a significant Reward \times FP_n interaction, F(1, 72) = 9.77, p = 0.003, $\eta_p^2 = 0.119$. Further inspection of this interaction pattern by post hoc comparisons revealed a significant FP_n effect in baseline runs. However, contrary to our expectation, prestimulus pupil diameter was decreased, rather than increased, at long FP_ns compared to short FP_ns (see Figure 4b,c; FP_n effect at short FP_{n-1}: t(72) = 2.98, p = 0.004; long FP_{n-1} : t(72) = 2.78, p = 0.007). During reward runs, this decrease in pupil diameter with longer FP_n was no longer present. Prestimulus pupil size was stable across all FP_n and FP_{n-1} conditions (*ps*>0.68, Figure 4b,c). Finally, no significant $\text{FP}_{n} \times \text{FP}_{n-1}$ interaction (p = 0.950) or Reward $\times \text{FP}_{n} \times$ FP_{n-1} interaction (p = 0.950) were found.

As prestimulus pupil size in the shortest FP_n trials could be influenced by phasic pupil responses from the preceding trial, we repeated the above analysis, including only trials



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FIGURE 3 Regression coefficients indicating the influence of FP_n and FP_{n-1} on reaction time. ${}^{**}p < 0.01$; ${}^{***}p < 0.001$

with $FP_n > 3$ s. This did not significantly change the results (see online supporting information).

3.3 | Poststimulus pupil response

Changes in reactive attention were quantified as the poststimulus pupil response (see Figure 5a, b). There was neither a main effect of reward condition nor a main effect of FP_{n-1} on post-stimulus pupil response (p = 0.098, p = 0.171, respectively). However, there was a significant main effect of FP_n on post-stimulus pupil response, F(1, 72) = 9.64, p = 0.003, $\eta_p^2 = 0.118$, and a Reward × FP_n interaction, F(1, 72) = 5.86, p = 0.018, $\eta_p^2 = 0.075$. Follow-up analyses showed a significant foreperiod effect in the rewarded condition (FP_n effect at short FP_{n-1}: t(72) = 2.83, p = 0.006; long FP_{n-1}: t(72) = 3.88, p < 0.001; see Figure 5c) that was absent in the baseline condition (ps > 0.23, Figure 5c). This finding suggests that reward increased reactive attention, particularly at short foreperiod trials.

Because increased poststimulus pupil responses may reflect a reaction to errors (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005), we reanalyzed the data in the



FIGURE 4 Pupillometric data for (a) pupil traces plotted as a function of current foreperiod (FP_n) and immediately preceding foreperiod (FP_{n-1}) in baseline (gray) and high reward (green) conditions. Time = 0 indicates target onset. (b) Prestimulus pupil diameter extracted from a 1-s window prior to stimulus onset. (c) Foreperiod effects (pupil diameter at short FP_n – long FP_n)



FIGURE 5 Poststimulus pupil response in (a) baseline, and (b) reward conditions. (c) The foreperiod effects as a function of motivation and FP_{n-1} . Error bars represent standard error of the mean. **p < 0.01; ***p < 0.001

reward condition, excluding all trials in which RTs were slower than the response time criterion (i.e., RT feedback indicates failure to gain reward). In this control analysis, all effects persisted, including the Reward × FP_n interaction, F(1, 71) = 6.18, p = 0.015, $\eta_p^2 = 0.080$ (also see supporting information). This indicates that the increased poststimulus pupil response after short foreperiods did not just reflect increased error monitoring in the rewarded condition.

3.4 | Correlational analysis

To examine whether there were any associations between the changes in performance due to reward and reward-induced pupil changes, difference scores between the reward and baseline runs were calculated for RT and for pre- and poststimulus pupil diameter (reward – baseline), for each FP_n and FP_{n-1} bin. Four subjects were identified as outliers on one of these scores (> mean $\pm 3 \times SD$) and were excluded from the respective correlational analyses. Results showed that RT benefit was not correlated with prestimulus pupil diameter increase in any of the FP bins (ps > 0.12; see Table 2). In contrast, increases in poststimulus pupil response were negatively correlated with RT difference scores in all except the long FP_{n-1} llong FP_n bin (Table 2). This indicates that subjects with larger increases in poststimulus pupil response during the reward run showed the strongest performance improvement (RT reduction).



	Prestimulus pupil Reward effect		Poststimulus pupil	Poststimulus pupil Reward effect	
			Reward effect		
	r	р	r	р	
Reward effect RT (ms)					
Short FP_{n-1} and short FP_n	-0.03	0.82	-0.24	0.04	
Short FP_{n-1} and long FP_n	0.03	0.80	-0.30	0.01	
Long FP_{n-1} and short FP_n	0.01	0.97	-0.30	0.01	
Long FP_{n-1} and long FP_n	-0.20	0.10	-0.16	0.19	

Note. Bold-faced values indicate statistical significance at p < 0.05. RT = reaction time; FP_n = current foreperiod; FP_{n-1} = preceding foreperiod.

4 | DISCUSSION

Findings in this study demonstrate that reward motivation can interact with implicit biases in temporal attention to alter patterns of behavioral performance. Reward improved overall performance, as evident from faster RTs in all time bins. However, this improvement was not uniform across the different time bins. The largest benefits were found in time bins that are normally characterized by the lowest target expectation (short FP_n preceded by long FP_{n-1}). Pupillometric data suggest that these behavioral effects were supported both by overall enhanced preparatory attention (prestimulus) and by a boost in poststimulus pupil responses.

4.1 | Reward motivation reduces implicit temporal bias in reaction time

Behavioral findings clearly showed temporal attention effects as related to FP duration, which were further modulated by the preceding trial's FP. Responses were slower after a short compared to a long FP, particularly when the preceding trial's FP was long. These effects describe the typical pattern of attentional performance in tasks with unpredictable FP timing (Nickerson & Burnham, 1969; Niemi & Näätänen, 1981). In the rewarded condition, this pattern was reduced but not fully abolished, suggesting that temporal expectations exert a robust influence on attentional processes (Kong et al., 2015). While reaction times improved in all FP bins, the most pronounced changes were found in the short FP_nllong FP_{n-1} trials. These trials are normally disadvantaged as expectations based on both the passage of time in the current trial and expectations set by the previous trial's FP are stacked against these time points. In a way, this reduction in temporal bias resembles the effects of reward in reducing the costs of invalid expectations in other cognitive domains (e.g., spatial cuing; Engelmann et al., 2009).

It should be noted that the incentive structure in the current study was different from situations where reward is provided based on specific target features or, unpredictably, in a trial-by-trial manner (Braem, Verguts, Roggeman, & Notebaert, 2012; Hickey, Chelazzi, & Theeuwes, 2010). A recent study that used an unpredictable reward scheme in a variable foreperiod task found enhanced implicit temporal biases on trials following high reward compared to low reward (Hickey & Los, 2014). Importantly, as reward was randomly assigned after each trial (random feedback), it was not contingent on performance. Therefore, reward could only act by influencing post-trial adaptation processes (e.g., reinforcement of temporal expectation; Los et al., 2001). In our study, the reward implementation (i.e., blocked reward conditions, with explicit RT criterion) allowed participants to prepare for speeded target detection in a proactive, strategic manner (Chiew & Braver, 2016; Krebs & Woldorff, 2017).

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As outlined in the dual mechanisms of control (DMC) theory (Braver, 2012), motivation can act to increase preparatory control processes (Chiew & Braver, 2013; Krebs et al., 2011). Although such proactive control can facilitate the processing of upcoming events, it is thought to be metabolically costly and is therefore minimized in nonmotivated conditions (Braver, 2012). In motivated conditions, the presumed costs of control may be offset by increased incentives (Kool, Shenhav, & Botvinick, 2017). Consequently, proactive control may be applied in a more continuous manner (Esterman et al., 2016; Jimura et al., 2010; Locke & Braver, 2008).

One way in which such motivated control might work is by stabilizing performance and minimizing the occurrence of attentional lapses (as evidenced from occasional very long RTs; Sanders, 1983). Such lapses are among the most sensitive indicators of impaired performance on the psychomotor vigilance task under suboptimal conditions such as sleep deprivation (Lim & Dinges, 2008) and can be partially countered by motivation (Massar, Lim, Sasmita, & Chee, 2018). The current analysis suggests that such long RT trials are more probable at time points of lowest temporal expectancy. By increasing attentional readiness, Steinborn et al. (2017) showed that performance improvement is achieved particularly by reducing the frequency of these long RT trials.

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Another issue regarding the reward structure is that the order of conditions was fixed (i.e., baseline always preceded reward runs). While practice effects can therefore not be excluded, it should be noted that, generally, repeated exposure does not reduce foreperiod effects. A study by Langner, Steinborn, Chatterjee, Sturm, and Willmes (2010) demonstrated that, over the course of a 1-hr task, overall RT increased with time on task. In contrast, there were no changes in the foreperiod or sequential effects with longer time on task.¹ In fact, given that the temporal features of the task environment are learned over time (Los et al., 2001, 2014), repeated exposure is more likely to increase temporal biases rather than to reduce them (Los, Kruijne, & Meeter, 2017).

4.2 | Pupil diameter is increased in sustained and transient manners under motivation

Following predictions from the DMC theory, we expected reward to impact on performance through increased proactive attention. In line with this idea, we found a marked increase in prestimulus pupil diameter during reward runs. Previous studies have similarly found that motivated conditions are accompanied by increased pupil size in the period prior to target onset, suggesting enhanced preparatory control (Chiew & Braver, 2013). In contrast to our expectations, however, prestimulus pupil diameter did not increase with longer FPs, as would be expected based on temporal preparation. In fact, in the baseline condition, pupil size was slightly smaller after long FPs. This reduction was no longer present in the reward condition. Although these findings would support the idea that preparatory control can be applied in a sustained manner under motivated conditions (Braver, 2012), they do not align well with the notion that attentional readiness should increase over longer FPs (Coull & Nobre, 2008). The increase in prestimulus pupil diameter with reward therefore reflects a sustained, nontime-specific increase in attentional readiness (Jimura et al., 2010).

For poststimulus pupil responses, reward elicited an increase, particularly after short FPs. This increased poststimulus response may reflect a reactive boost in attention upon target presentation (Chatham et al., 2009). While target expectancy may be optimal at longer FPs, implicit temporal expectations would leave us vulnerable to incomplete preparation at short foreperiods. The lack of readiness that results from these expectations may be partially countered by a compensatory mobilization of attentional resources. Although much of the literature on motivated cognition focuses on the proactive effects, several studies have shown that motivation can enhance reactive processes (Boehler, Schevernels, Hopf, Stoppel, & Krebs, 2014; Engelmann et al., 2009). Similar to the current study, fMRI studies have found increased reactive activation especially in situations where the occurrence of relevant events cannot be predicted (e.g., in a stop-signal task; Boehler et al., 2014) or when predictions are violated (e.g., invalid spatial cues; Engelmann et al., 2009). Likewise, strongest behavioral improvements have been found in conditions that are most disadvantaged by invalid expectations in baseline conditions.

4.3 | Pupil-performance associations

While both performance and pupil data showed interesting patterns of time-based and reward-based alteration, they did not always line up completely. As mentioned above, prestimulus pupil data did not show the expected pattern of temporal preparation with longer FPs. In addition, reward-related prestimulus increases were not correlated with behavioral improvement. This casts doubts on the exact mechanisms that are reflected in the prestimulus pupil size. With regard to temporal preparation, several studies have found increased pupil diameter prior to target onset in fixed foreperiod tasks with predictable target timing (Akdoğan & van Rijn, 2016; Unsworth et al., 2018; Van der Molen, Boomsma, Jennings, & Nieuwboer, 1989). In contrast, prestimulus pupil increase in variable foreperiod paradigms is either smaller compared to fixed foreperiod tasks (Jennings, Molen, & Steinhauer, 1998) or unreported (Unsworth et al., 2018). It may therefore be possible that prestimulus pupil diameter mostly reflects explicit temporal preparation (predictable timing) and not implicit temporal preparation.

Several notes of caution need to be made with respect to the prestimulus pupil findings. Most pertinently, as pupil responses are rather slow, they can have influence up to several seconds after a relevant event. Therefore, prestimulus diameter on trial n could be influenced by pupil responses from earlier trials (n–1 or earlier). An inherent issue with variable foreperiod designs is that short FP trials are more likely to be affected by such residual pupil effects carried over from previous trials. Although we attempted to minimize this effect in our supporting analysis (by excluding trials with very short FPs), it is not possible to fully exclude the carryover effects from preceding trials as a potential factor in our data.

Another issue that needs to be highlighted is that prestimulus pupil diameter may reflect factors that are not functionally related to attentional performance. A study by Chiew and Braver (2014) demonstrated that positive emotional arousal increased overall pupil diameter, in a similar way as reward

¹A relevant observation in the study by Langner et al. (2010) is that subjects' self-reported motivation (task engagement) significantly decreased with time on task, without affecting temporal preparation. One reason for the discrepancy with the current study may lie in the nature of the incentive structure implemented here (i.e., instruction to respond below RT criterion), explicitly pushing for fast RTs.

motivation did. In a recent study, blocked reward manipulation (in contrast to trial-by-trial reward cueing) resulted in increased prestimulus pupil size, without any improvement in performance (Kostandyan et al., 2018). Reward-related arousal may therefore act to increase pupil size without necessarily impacting on attentional mechanisms (but see Massar et al., 2016, exp. 3). The exact mechanisms by which prestimulus pupil size relates to attentional readiness, and its alteration with reward motivation, therefore remain elusive. To disentangle the effects of successive trials, future studies could benefit from allowing longer delays between trials as well as measuring faster physiological responses (e.g., EEG/ ERP).

Poststimulus pupil responses showed a pattern that was more in line with behavioral findings. While showing no effects of temporal preparation in baseline, an increase in poststimulus pupil response was found in the reward run particularly after short FP_ns. Moreover, this reward-related increase in poststimulus pupil response was correlated with performance improvement. While we interpret this as reflecting a reactive attentional mechanism in an attempt to compensate for not being ready at shorter FPs, this interpretation must be taken with caution. Similarly, as with prestimulus pupil diameter, poststimulus pupil responses do not uniquely reflect attentional processes. Poststimulus dilation has been associated with attentional processes (Kostandyan et al., 2018), but also with error detection (Crichtley et al., 2005), emotional arousal (Bradley, Miccoli, Escrig, & Lang, 2008; Chiew & Braver, 2014), and surprise (Knapen et al., 2016). All of these factors may interact with reward motivation to boost the physiological responses (although error processing did not seem to be a sufficient explanation from our supporting analysis). Given the clear link between reward-related pupil response and performance, we think it is plausible that reactive, compensatory mechanisms are at play. Such mechanisms are likely much faster than the slow dynamics reflected in the poststimulus pupil response, but they may rely on shared underlying processes that enable the mobilization of necessary resources (e.g., phasic noradrenergic firing; Aston-Jones & Cohen, 2005).

4.4 | Conclusion

In conclusion, the influence of implicit temporal biases on attentional deployment is reduced under motivated conditions. This is accompanied by increased pre- and poststimulus pupil diameter, suggesting both proactive and reactive attentional processes. Alternative explanations need to be acknowledged, but potentially the combined influence of these mechanisms may support behavioral improvement. This resulted in faster responses at all time points, but PSYCHOPHYSIOLOGY

particularly at moments that are normally most vulnerable to incomplete preparation.

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SUPPORTING INFORMATION

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Pre-stimulus pupil size excluding the shortest FP's

To account for the potential influence of post-stimulus pupil response on trial n-1 on the calculation for pre-stimulus pupil size on trial n, we re-analysed the pre-stimulus pupil size excluding trials with the shortest foreperiod length (trials with foreperiod < 3s). As in the main analysis, pre-stimulus pupil size was characterized by a significant main-effect of reward [F(1,72) = 46.83, p < .001, partial $\eta^2 = .394$], and a significant Reward x FPn interaction [F(1,72) = 4.12, p = .046, partial $\eta^2 = .054$]. Further testing of this interaction showed that pupil size significantly decreased with longer FPn's in the baseline condition, but not in the reward condition.



Supplementary Figure 1. Prestimulus pupil diameter for all trials excluding trials following foreperiod (FPn) length less than 3seconds plotted as a function of current foreperiod (FPn) and the immediately preceding foreperiod (FPn-1; A) and the foreperiod effect (B) in baseline and rewarded conditions. *p < .05, **p < .01, error bars represent standard error of the mean.

Post-stimulus pupil response exclusion of error trials

In the current study, reward acquisition was contingent on meeting a response time criterion. Therefore, it is likely to associate instances with failure to meet the response time criterion as errors. In a previous study, errors have been shown to elicit increases in pupil response (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005). As the short FP_n is a period where performance is most often impaired, it is possible for errors to occur most often in this time-bin, rendering the driver of pupil response we observe in this study ambiguous. To circumvent this, we re-analysed the pupil response including only trials with responses meeting the response time criteria (Supplementary figure 1). We excluded one participant who had 0 trial that met the response criterion for one of the FP_n and FP_{n-1} combination.

Analysis on the remaining 72 participants revealed a non-significant main effect of FPn [F(1,71) = 2.69, p = .106, partial $\eta^2 = .036$] and non-significant main effect of either reward or FPn-1 (p = .232 and p = .346, respectively). This finding corroborates with the pattern of observation reported in the main text.

Importantly, with this restricted sample, we also found a significant reward x FP_n interaction (*F*(1,71) = 6.18, *p* = .015, partial η^2 = .080). Follow-up analysis showed significant foreperiod effect in the rewarded condition [short FPn-1: *t*(72) = 2.55, *p* = .013; long FPn-1: *t*(71) = 2.19, *p* = .032] that is absent in the baseline condition (*ps* > .90, Figure 2E).



Supplementary Figure 2. Pupillary response exclusively in trials where the response criterion was met, plotted as: stimulus locked pupil size as a function of current foreperiod (FP_n) and the immediately preceding foreperiod (FP_{n-1}) in baseline (A) and rewarded (B) conditions and the foreperiod effect of mean pupil response (0.7 – 1.5 s post-stimulus onset) as a function of reward (C). *p < .05, error bars represent standard error of the mean.