Reward priming of temporal preparation

Clayton Hickey[a] & Sander A. Los[b]

[a] Center for Mind/Brain Sciences (CIMeC), University of Trento, Trento, Italy

[b] Cognitive Psychology, VU University Amsterdam, Amsterdam, The Netherlands
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Clayton Hickey[1] and Sander A. Los[2]

[1]Center for Mind/Brain Sciences (CIMeC), University of Trento, Trento, Italy
[2]Cognitive Psychology, VU University Amsterdam, Amsterdam, The Netherlands

Recent studies have demonstrated a strong impact of reward on the expectancy of future target locations or features. In this study, we examined whether reward would have similar effects on temporal preparation. In two experiments, participants completed a reaction time task with a variable interval between a warning stimulus and the target stimulus. After each trial they were awarded either low or high reward which was converted to cash after the experiment. Crucially, reward magnitude was assigned randomly and was unrelated to task performance. Nevertheless, across experiments, the results revealed that reward modified future temporal preparation, especially in participants that could be identified as highly motivated. These findings generalize the principles of reward priming to the temporal domain.

Adaptive behaviour relies on the ability to predict and prepare for the occurrence of future events. This kind of temporal prediction has been extensively studied in the lab using simple cueing paradigms in which a warning stimulus precedes a subsequent target. A core observation in this literature is that when the intervening interval is varied randomly across a set number of durations, responses to targets will become faster and more accurate as the interval between stimuli increases. Eventually performance reaches an asymptote that is thought to reflect optimal preparation. The interval between warning and target is known as the foreperiod (FP) and this general finding is accordingly known as the FP effect.

Please address all correspondence to Clayton Hickey, Center for Mind/Brain Sciences (CIMeC), University of Trento, Trento, Italy. E-mail: clayton.hickey@unitn.it

Clayton Hickey and Sander A. Los contributed equally to this work.

Classic interpretations of the FP effect have suggested that it is strategic in nature, with the warning signal causing participants to deliberately induce a preparatory state at subsequent time intervals when the target might appear (Woodrow, 1914; see Niemi & Näätänen, 1981, for review). This has been likened in the literature to the deployment of selective attention in space: just as the deployment of attention to a location will benefit response to a target at the attended location, so will preparation for a temporal interval benefit response to a target at that time (e.g., Correa, Lupiáñez, Madrid, & Tudela, 2006; Coull & Nobre, 1998; Kristjánsson, Eyjólfsdóttir, Jónsdóttir, & Arnkelsson, 2010; Yashar & Lamy, 2010, 2013). In FP designs with equal probability at different intervals, the likelihood of target presentation increases over time (i.e., the slope of the hazard function increases) and participants accordingly are better prepared for the target at long FPs (Janssen & Shadlen, 2005; Näätänen, 1971; Vangkilde, Petersen, & Bundesen, 2013).

Experiments examining intertrial-contingencies in variable-interval FP paradigms, however, have demonstrated that the temporal preparation indexed in FP tasks is highly sensitive to the character of prior experience. This can be demonstrated by examining performance on any given trial (trial n) as a function of characteristics in the immediately preceding trial (trial $n-1$). Results show that manual response in a short FP trial—where the target rapidly follows the warning signal—will be consistently faster when the immediately preceding trial also had a short FP (Baumeister & Joubert, 1969; Drazin, 1961; Possamaï, Granjon, Reynard, & Requin, 1975). This pattern is hard to reconcile with the idea that FP preparation is solely strategic in nature because there is no motivation for increased preparation under these circumstances.

Alongside other results in the literature the observation of such sequential effects has motivated the development of new accounts of temporal preparation. In particular, Los and colleagues (Los & Heslenfeld, 2005; Los, Knol & Boers, 2001; Los & Van den Heuvel, 2001; see also Steinborn, Rolke, Bratzke, & Ulrich, 2009, 2010) have suggested that temporal preparation might be largely automatic and non-strategic in nature, relying on the learning mechanisms that underlie conditioned behaviour. As a starting point for this account, Los and Van Den Heuvel (2001) point to the close similarity between basic FP designs and experimental paradigms employed in the animal literature to study trace conditioning. Trace conditioning occurs when a conditioned stimulus (CS; e.g., a tone) is paired with an unconditioned stimulus (US; e.g., the provision of food) and these events are separated by one or more consistent time intervals. Results unambiguously demonstrate that the conditioned responses (CR; e.g., salivation) will be solidly time-locked to the onset of the CS, and the likelihood and frequency of this response will be maximal at those times where US likelihood was high during training (e.g., Moyer, Deyo, & Disterhoft, 1990). If one accepts that temporal preparation might constitute a type of conditioned response, the

pattern of behaviour observed in FP paradigms is effectively identical to that observed in trace conditioning.

Based on this insight and on empirical results, Los and Van den Heuvel (2001) suggested a handful of learning rules that might dictate trace conditioning of preparation in the FP paradigm. Two are of particular importance to the current paper. First is the idea that the act of responding to a target that appears at a critical moment (i.e., a potential moment of target occurrence) might reinforce the conditioned preparation for that moment. The strength of preparation for a target at an FP interval will accordingly be increased for the future when the target actually appears at that critical moment. Second is the corollary: withholding and suppressing a prepotent response when a critical moment fails to yield a target will result in extinction of the conditioned preparation for that FP. The strength of preparation for a target at this given critical moment will thus be reduced in the future.

It is important to note that these two rules generate an asymmetric pattern of influence in variable-interval FP paradigms. This is the case because the second of these rules proposes that preparation at a given FP will be decreased only when the critical moment for this FP is passed without the appearance of a target. Thus when a target fails to be detected at a short FP, but appears later, preparation for the short FP will be reduced in the future. But the reverse is not true: when the target appears at a short FP the trial effectively ends, and there is no need to inhibit response at longer FPs. Thus there is no reduction in preparation at these critical moments.

The idea that a rapid response to the target might act as a type of endogenous reinforcement of preparation is compelling and consistent with results in the FP literature (see Los, 2013, for review). However, other accounts for these results are possible (see Vallesi & Shallice, 2007, for a wholly strategic account of preparation) and it is not self-evident that target response would necessarily generate an endogenous reward signal or that such a signal would have the same impact as explicit reinforcement. The current study was thus designed to test the idea that asymmetric sequential priming in temporal preparation is sensitive to explicit reward feedback. Our reasoning was that if endogenous reinforcement signals underlie temporal preparation in the absence of feedback, then preparation should certainly be sensitive to an explicit manipulation of outcome quality through reward feedback.

To this end we had participants complete a simple FP task in which correct target detection immediately garnered high-magnitude or low-magnitude reward (see Figure 1). Reward took the form of points that had cash value but, importantly, the magnitude of reward was randomly determined for each correctly executed trial. This feature of the design was adopted in order to forestall the development of strategic preparatory biases. For example, if reward were consistently linked to a particular FP, participants would be very likely to place particular importance on this FP. Any resulting effect on preparation could be accounted for as a product of strategy (see Hickey, Chelazzi, & Theeuwes, 2010, for discussion of this issue in the context of attention to visual features). By randomizing reward magnitude we
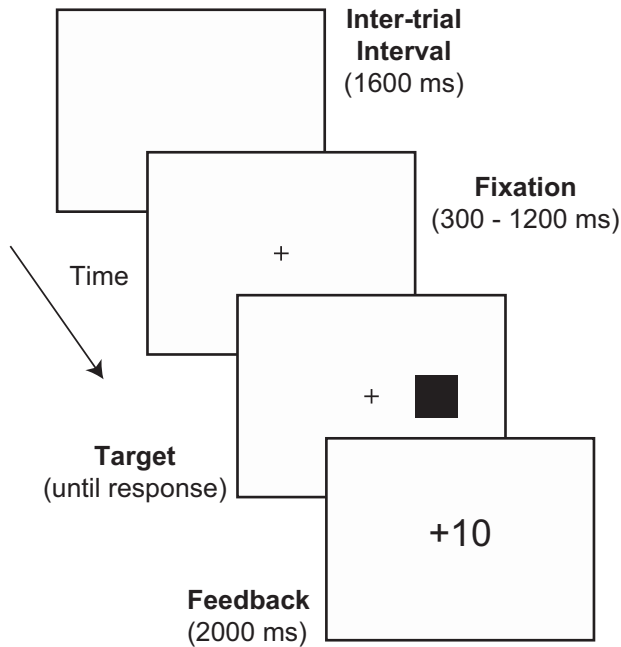
Figure 1.   Trial sequence.

created a situation where participants were provided neither the motivation nor opportunity to strategically prepare for any particular trial type. Any change in behaviour can thus be attributed unambiguously to low-level, non-strategic effects of explicit reinforcement.

We approached the results with two core hypotheses, which are illustrated in Figure 2. If reinforcement underlies temporal preparation, correct detection of a target at a short FP should reinforce preparation at this critical moment and explicit reward should "boost" the effect (Figure 2a). Responses to targets at the short FP should accordingly be quicker following high-magnitude reward. On the other hand, when the target fails to occur at the short FP in our paradigm it becomes certain to appear at the long FP, and participants will presumably be maximally prepared for it. Thus response to a target at the long FP should have minimal effect on subsequent preparation at the long FP and preparation at this interval should not vary substantially as a function of prior reward. However, responses to targets at the short FP should be slower following rewarded trials where the target appeared at the long FP, reflecting the reinforcement of response suppression at the short FP (Figure 2b). Thus our expectation was that high-magnitude reward would primarily impact responses at the short FP, creating a response benefit when the prior trial also had a short FP and a detriment when the prior trial had a long FP.
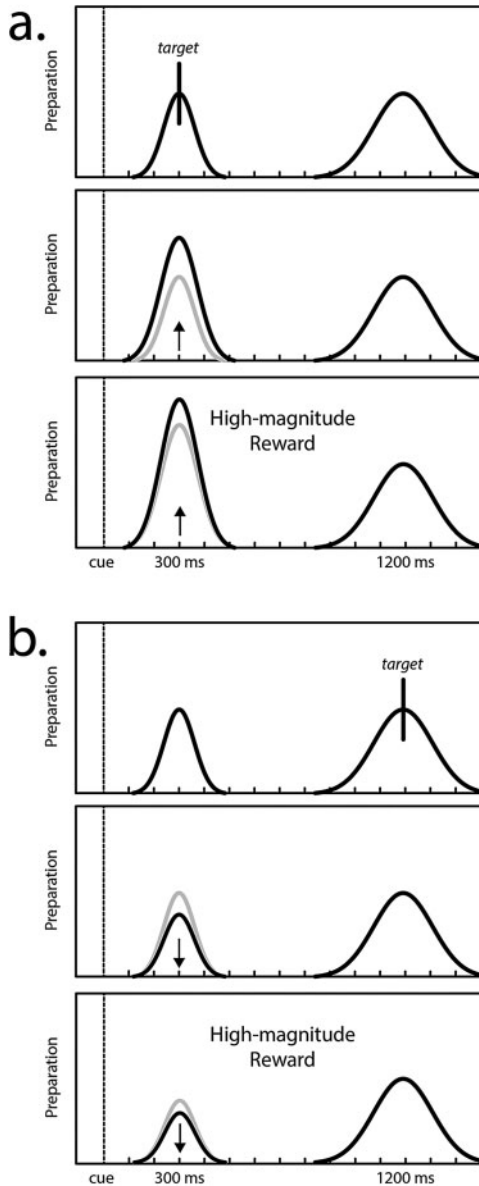
Figure 2. Schematic of expectations. (a) Reward modulation of preparation following trial with 300 ms SOA, and (b) reward modulation of preparation following trial with 1200 ms SOA. In both cases schematic reflects the influence of high-magnitude reward feedback. Black lines reflect current state of preparation. Grey lines are included for the purpose of illustrating change in preparation, and reflect the state of preparation from the immediately preceding panel. Thus in panel (a) response to a target at short FP (first panel) causes an increase in preparation at this critical moment (second panel) and explicit reinforcement of this state by high-magnitude reward feedback accentuates this preparatory state (third panel).

METHOD

Participants

Forty-nine student volunteers (mean age: 24 years, eight left handed, 18 men) with normal or corrected-to-normal vision gave written informed consent before beginning the experiment. All participants received a variable cash bonus based on the points accumulated during the experiment (max. €1.80 per 1/2 hour of participation) alongside a base pay (€3.50 per 1/2 hour of participation). One participant was excluded from analysis as an outlier (mean response time > 3 SD from group mean).

Experimental stimuli and procedure

The experiment took place in a quiet, dimly-lit dedicated room. Experimental stimuli were presented against a white background on a standard 19″ CRT computer monitor located approximately 70 cm in front of the participant.

Stimuli and procedure are illustrated in Figure 1. The onset of a black 0.5 cm central fixation cross served as cue and preceded target onset by 300, 750, or 1200 ms (Experiment 1a), or 300 or 1200 ms (Experiment 1b), with SOA for each trial randomly selected from these possibilities with equal probability. The target was a black square with 1.2 cm sides that appeared 2.4 cm to the left or right of the fixation cross and sustained until response. Participants were instructed to respond as quickly as possible to a left-lateralized target by pushing the "z" key on a standard keyboard with their left index finger and to a right-lateralized target by pushing the "m" key with their right index finger. Correct response resulted in immediate reward feedback in green Arial font (42 pts; "+10" or "+1"). Incorrect or slow responses (> 600 ms) resulted in negative feedback ("–1" in the same font with red colour). Reward feedback was presented for 2000 ms and followed by a blank screen for 1600 ms Participants in Experiment 1a completed 14 blocks of 48 trials (~1 hour) and participants in Experiment 1b completed seven blocks of 48 trials (~1/2 hour). At the end of each block participants were informed of their average RT, accuracy, and the total number of points accumulated to that point in the experiment.

Instructions were provided to participants as a component of the experimental computer program. This conveyed that (1) accumulated points would determine the value of a cash bonus awarded at the end of the experiment, (2) points would be awarded only when response was accurate and quick, (3) the magnitude of reward could be 1 or 10 points, and (4) a single point would be lost when response was inaccurate or slow. The instructions provided no information about how to optimize outcome and reward magnitude was in fact randomly determined for each correctly completed trial.

Participants in Experiment 1a completed a short inventory after participation. This proposed six reward schedules that might have been adopted in the experiment and asked participants to rate their certainty that each of these schedules had been employed using a 4-point Likert scale (where 4 indicated complete disagreement and 1 complete agreement). The following options were listed: (1) correct responses garnered high reward, (2) left targets garnered high reward, (3) right targets garnered high reward, (4) long cue / target intervals garnered high reward, (5) short cue / target intervals garnered high reward, and (6) reward magnitude was random.

RESULTS

In order to identify the sequential FP effect and test for its modulation by prior reward we examined results as a function of three key factors: SOA in the current trial (SOA_n), SOA in the immediately preceding trial (SOA_{n-1}), and the magnitude of reward received in the immediately preceding trial. Analysis was limited to correct trials that had been preceded by a correct trial in the same block. Outlier RTs (>3 SDs from per-subject mean) were discarded from analysis, resulting in the exclusion of 1.5% +/− 1.8% trials per subject (mean +/− SD).

Response latencies from Experiments 1a and 1b are illustrated in Figures 3a and 3b, respectively. The two versions of the experiment were conducted in order to test a hypothesis regarding the efficacy of reward feedback with an increased number of FP intervals. However, as detailed below, results at the 300 and 1200 ms FPs were statistically indistinguishable across Experiments 1a and 1b, and we accordingly focus interpretation on the combined results illustrated in Figure 3c. The asymmetric sequential FP effect is primarily apparent as a speeding of response in short FP trials that were preceded by short FP trials rather than long FP trials. Responses in long FP trials were less sensitive to this intertrial contingency (see also Los & Van den Heuvel, 2001; Steinborn et al., 2010; Vallesi & Shallice, 2007). Accuracy was at ceiling across all conditions (~98%) and is not treated further.

Statistical analysis began with an omnibus repeated-measures analysis of variation (RANOVA) based on the combined results illustrated in Figure 3c. This had within-subject factors for SOA_n (300 vs. 1200 ms), SOA_{n-1} (300 vs. 1200 ms), and prior reward (high vs. low), as well as a between-subject factor for experiment (1a vs. 1b), and revealed an interaction between SOA_n and SOA_{n-1} [$F(1,46) = 34.82$, $p < 10^{-5}$, $\eta_p^2 = 0.431$] that indexes the asymmetric sequential FP effect. Critically, this 2-way interaction further varied as a function of prior reward, as reflected in a reliable 3-way interaction [$SOA_n \times SOA_{n-1} \times$ reward: $F(1,46) = 4.6$, $p = .037$, $\eta_p^2 = 0.091$]. This did not differ between Experiment 1a and 1b [4-way interaction: $F < 1$]. Additional main effects of SOA_n
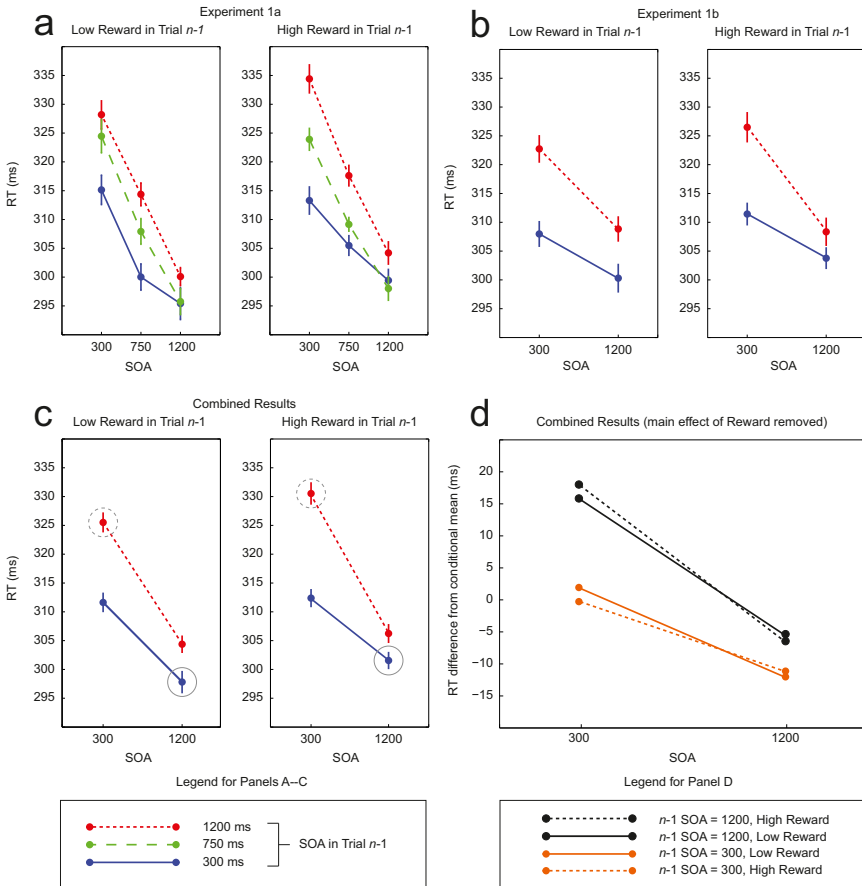
Figure 3. Results for (a) Experiment 1a, (b) Experiment 1b, (c) both experiments combined, and (d) both experiments combined with the main effect of reward removed. Error bars reflect within-subject standard error (Cousineau, 2005).

$[F(1,46) = 55.41, p < 10^{-7}, = 0.546]$, SOA_{n-1} $[F(1,46) = 123.31, p < 10^{-12}, \eta_p^2 = 0.728]$, and reward $[F(1,46) = 6.19, p = .017, = 0.119]$ were detected, as well as a 2-way interaction between SOA_n and experiment $[F(1,46) = 6.61, p = .018, \eta_p^2 = 0.116$; $SOA_n \times SOA_{n-1} \times$ experiment: $F(1,46) = 1.30, p = .260, = 0.27$; all other Fs < 1]. Planned contrasts across the reward manipulation revealed a slowing of response in trials following high magnitude reward when the SOA differed from that on the preceding trial (1) when the SOA was 300 ms and the preceding SOA was 1200 ms (identified by broken circles in Figure 2c; $t(47) = 2.07, p = .044$) and (2) when the SOA was 1200 ms and the preceding SOA was 300 ms (identified by unbroken circles in Figure 2c; $t(47) = 2.92, p = .005$). No

corresponding effects were observed when the current SOA matched that of the preceding trial ($ps > 0.3$).

The main effect of reward detected in the omnibus RANOVA may stem from effects that are not the focus of this paper. For example, reward may have a broad impact on motivation or cognitive control (e.g., Braem, Verguts, Roggeman, & Notebaert, 2012; Braem, Hickey, Duthoo, & Notebaert, 2014) that would influence performance across all SOA conditions. To gain some perspective on this possibility and to more clearly examine the interactive impact of reward in the data we removed the mean RT observed across all SOA conditions in each of the high and low magnitude reward conditions separately. This preserved all variance caused by reward interactions while removing the main effect of reward, and the resulting data pattern is illustrated in Figure 3d. The pattern suggests that reward's impact on the asymmetric sequential FP effect primarily occurred at the 300 ms SOA. Prior reward appears to speed response in short SOA trials when the preceding trial was also a short SOA trial, but slows response when the preceding trial was a long SOA trial.

The impact of reward on the sequential FP effect is unarguably small: the summed deviation in response latency between results illustrated in the two panels of Figure 3c is only 11.7 ms, and this reduces to 5.9 ms when the main effect of reward is removed from each condition (see Figure 3d). However, this should be interpreted within the experimental context. First, the statistical effect size is not negligible. Partial eta squared constitutes a ratio of variance accounted for by the effect compared to the summed variance of the effect and its error term. Thus the observed value of 0.091 indicates that the effect accounts for 9.1% of total variance at this level of the general linear model. Second, responses in the experiment are exceedingly quick. Average RT collapsed across all conditions is 311.5 ms, meaning that 5.9 ms corresponds to 1.9% of total RT. Third, the magnitude of reward's impact on the sequential FP effect reported here is comparable in size to that created by other manipulations in the literature (e.g., Steinborn et al., 2009, Experiments 2 and 3). And finally, large effects of reward are common only in paradigms where reward feedback can be used to guide strategic preparation. Where this is not the case reward effects are commonly much smaller (e.g., Hickey et al., 2010; Hickey, Kaiser, & Peelen, 2015).

We approached the experiment with the ancillary hypothesis that reward feedback would guide temporal preparation most effectively in those who were conscientiously engaged in the task and actively preparing for the target stimuli. To test this we conducted a final correlational analysis of results. For each participant we first calculated an index of raw FP effect by subtracting RTs observed in conditions with a 1200 ms FP from RTs observed in conditions with a 300 ms FP. Positive values reflect a response benefit in conditions with a long SOA, indexing participant preparation following the warning signal. In a second step we calculated an index of the modulating impact of reward on the sequential FP effect. To do so we calculated a point estimate of the three-way interaction

among SOAn, SOAn–1, and reward for each participant. Specifically, we calculated the sequential FP effect for each of the reward conditions by subtracting results observed when the current SOA matched that in the previous trial from results observed when this was not the case, subsequently calculating the difference in this measure between reward conditions. As illustrated in Figure 4a, these measures strongly correlated [$r = 0.424$, $p = .003$]. When participants prepared, as evident in a strong FP effect, this preparation was increasingly sensitive to the quality of reward feedback in the immediately preceding trial.

To further investigate this individual variability in the data we conducted a median split, separating subjects into high-FP and low-FP groups (see Figures 4a and 4b). Note in these results that RT in the high-FP group could be as quick as 290–295 ms. The 300 to 310 ms responses in the low-FP group thus do not appear bound by a strong floor effect: there is room for further improvement. However, a general caveat should be attached to this correlation analysis. We have explicitly interpreted variance in the FP effect as reflecting variance in preparation. This is consistent with the broad literature on the FP effect, where variability in the effect has, for example, been linked to arousal and motivation indexing ERP components like the contingent negative variation (Leuthold, Sommer, & Ulrich, 2004) and stimulus-locked lateralized readiness potential (Los & Heslenfeld, 2005). However, there are viable alternative interpretations, such as the possibility that differences in the FP effect could stem from variability in the quality of time perception.

Participants in Experiment 1a completed a questionnaire at the end of the experiment that was designed to gain insight into their beliefs about the reward schedule. Participants rated their agreement with six statements suggesting different schedules that may have been used in the experiment. A "1" response indicated complete agreement and a "4" indicated complete disagreement. Results suggest that participants were quite sure that the reward schedule was not contingent on location (mean rating: 3.50 +/− 0.77 SD) or response speed (mean: 3.16 +/− 0.80 SD), but less certain that SOA did not play a determining role (mean 2.84 +/− 0.85 SD). When asked if they thought the reward schedule was random, 17% of respondents were certain this was the case, but 13% were completely convinced that this was not the case, with the remainder unsure (mean: 2.16 +/− 0.85 SD). We examined this last measure to determine if it predicted the impact of reward on performance, but found no hint of a reliable relationship (all rs < 0.15, ps > .5).

DISCUSSION

Temporal preparation has traditionally been interpreted as purely strategic in nature, reflecting a deliberate preparatory response to a warning signal. However,
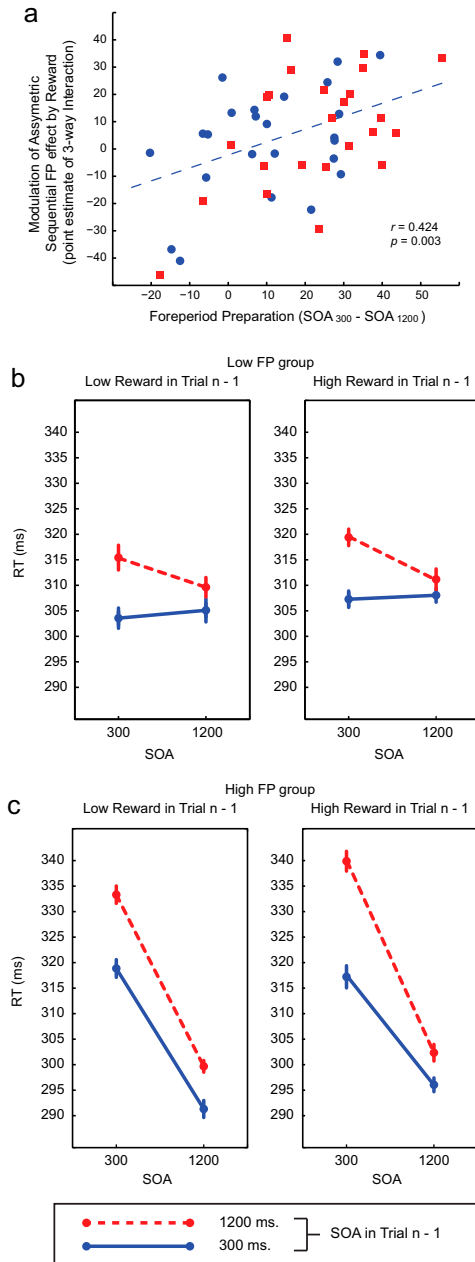
Figure 4. (a) Correlation between raw preparation and the modulation of preparation by prior reward. Red markers reflects participants from Experiment 1a and blue markers participants from Experiment 1b. (b) Results from median split. Participants with smaller FP effect. (c) Participants with larger FP effect.

the observation of sequential effects on preparation has motivated the development of accounts that emphasize the role of automatic and non-strategic factors. One example is the *trace conditioning model* of Los and colleagues (Los & Heslenfeld, 2005; Los et al., 2001; Los & Van den Heuvel, 2001). At the core of this account is the idea that rapid response to a target at a given FP creates an endogenous reward signal that reinforces preparation for the corresponding critical moment.

If preparation is sensitive to implicit, endogenous reward, it should presumably also be sensitive to explicit, exogenous reward, and the current study was designed to test this prediction of the trace conditioning model. Our results show that reward feedback will have an impact on preparation. This was in spite of the fact that reward in our task was randomly determined for each correctly completed trial, and thus provided no strategic information that could be used to optimize performance. When the specific effect of reward on preparation was examined (see Figure 3d), participants were found relatively faster to response at short FPs when the preceding trial had a short FP and high-magnitude reward was received, but were relatively slower to response at short FPs when the preceding trial had a long FP and high-magnitude reward was received. This pattern closely followed those motivated in the introduction from the trace conditioning model of temporal preparation (see Figure 2).

Further analysis demonstrated that this non-strategic impact of reward on temporal preparation could be predicted by a general index of preparation, namely the FP effect itself. Those participants who showed a strong improvement in performance in long FP trials were also those who showed the greatest sensitivity to reward feedback. Therefore, it seems that the influence of reward on subsequent temporal preparation is predicated on the willingness of the participant to prepare for a fast response to the impending target.

This conclusion gives rise to further reflections on the relationship between automatic and controlled processes in temporal preparation. According to the trace-conditioning view, temporal preparation is by and large an automatic process, driven by elemental rules of extinction and reinforcement. Paradoxically, though, the correlational analysis suggests that the influence of reward is modified by the willingness of participants to prepare for the upcoming target stimulus, which seems to implicate a controlled state of mind. One way out of this conundrum is to assume that, ultimately, participants control arousal and motivational state to comply with the task instruction to respond to the target as quickly as possible. Crucially, whereas this state does not pertain to the temporal dimension itself, it is a prerequisite for the application of the rules of conditioning that govern temporal preparation. Thus, high preparation should indirectly lead to a relatively large effect of FP, and by extension to relatively strong impact of reward on the future preparatory state, consistent with the observed correlation. According to this view temporal preparation is a conditionally automatic process (Bargh, 1989): Once a crucial control setting is

in place (i.e., preparation to respond quickly to the target) all other processes (i.e., those responsible for the fluctuations of preparation over time) proceed automatically (see Los, 2013, for further discussion of this point of view).

As noted in the Introduction, temporal preparation has been characterized in the literature as similar in nature to spatial attention: just as a spatial cue will benefit response to a target that appears at the cued location, so will a temporal cue benefit response to a target that appears at the cued time (e.g., Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999). In this context, the current results add to a developing literature suggesting a low-level, non-strategic role for reward in the priming of perception and selective attention (see Chelazzi, Perlato, Santandrea, & Della Libera, 2013, for review). For example, the attentional suppression of distracting stimuli that underlies negative priming is observed only following high-magnitude reward, being effectively abolished after sub-optimal outcome (Della Libera & Chelazzi, 2006, 2009). In visual search, the receipt of reward following target selection will prioritize visual processing of features that happened to characterize the target. Subsequent objects with these features will draw attention to their location (Anderson, Laurent, & Yantis, 2011), even when participants are aware that stimuli colour is task irrelevant (Kristjánsson, Sigurjónsdóttir, & Driver, 2010) or when the reward-primed colour is very unlikely to characterize a target (Hickey et al., 2010). The eyes are more likely to be misallocated to the location of reward-primed stimuli during search for a target (Hickey & van Zoest, 2013) and such objects cause deviation in the saccadic path even when the eyes are correctly deployed (Hickey & van Zoest, 2012).

The similarity between current results and those observed in the context of visual search are particularly striking in the case of Hickey, Chelazzi, and Theeuwes (2014). These authors find that the receipt of reward following selection of a visual search target will speed response to subsequent targets appearing at the same location. More surprising, reward additionally acts to facilitate the suppression of salient distractor locations. As a result, responses to targets appearing at prior distractor locations are slow and inaccurate following reward, much as responses to targets appearing at a suppressed critical moment were slower following reward in the current results. Thus reward's impact in time is mechanistically similar to its impact in space: in both cases it acts both to potentiate subsequent processing of trial characteristics associated with the target and to inhibit trial characteristics that were task irrelevant.

Recent results from neurophysiological work with humans and non-human primates suggest the existence of neural circuitry necessary for the translation of reward outcome to temporal preparation in the visual domain. Dopaminergic activity in the midbrain is well known to index temporal predictions of reward outcome, much larger in magnitude when reward occurs at unexpected rather than expected times (Schultz, 2002) and at intervals where uncertain reward might occur (Fiorillo, Tobler, & Schultz, 2003). Moreover, similar temporal

predictions can be observed in non-dopaminergic cells in rat primary visual cortex. This was demonstrated by Shuler and Bear (2006) who had rats complete a task where two types of visual input were conditioned to reward outcome. One type of cue indicated that reward would be available after a short period of work, the other that it would be available after more effort and more time, and results showed a ramping of activity in V1 cells at the reward interval predicted by visual input even when no reward was forthcoming. Temporal expectation of reward thus can impact visual processing from the very earliest of stages.

It has been suggested elsewhere that the reward-priming of visual features and locations might reflect low-level mechanisms with evolutionary origins (Hickey et al., 2010, in press). By this, dopaminergic signals in the midbrain might act to guide resources toward objects that have acted as valid reward cues in the past (Berridge & Robinson, 1998; Ikemoto & Panksepp, 1999; Toates, 1986). Here we demonstrate that reward plays a similar role in the temporal domain. Reward appears to prime vision not only for features and locations, but times as well.

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