Training-induced Changes in the Dynamics of Attention as Reflected in Pupil Dilation

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Charlotte Willems*, Atser Damsma*, Stefan M. Wierda, Niels Taatgen, and Sander Martens

Abstract

■ One of the major topics in attention literature is the attentional blink (AB), which demonstrates a limited ability to identify the second of two targets (T1 and T2) when presented in close temporal succession (200–500 msec). Given that the effect has been thought of as robust and resistant to training for over 2 decades, one of the most remarkable findings in recent years is that the AB can be eliminated after a 1-hr training with a color-salient T2. However, the underlying mechanism of the training effect as well as the AB itself is as of yet still poorly understood. To elucidate this training effect, we employed a refined version of our recently developed pupil dilation deconvolution method to track any training-induced changes in the amount and onset of attentional processing in response to target stimuli. Behaviorally, we replicated the original training effect with a color-salient T2. However, we showed that training without a salient target, but with a consistent short target interval, is already sufficient to attenuate the AB. Pupil deconvolution did not reveal any posttraining changes in T2-related dilation but instead an earlier onset of dilation around T1. Moreover, normalized pupil dilation was enhanced post-training compared with pretraining. We conclude that the AB can be eliminated by training without a salient cue. Furthermore, our data point to the existence of temporal expectations at the time points of the trained targets posttraining. Therefore, we tentatively conclude that temporal expectations arise as a result of training. ■

INTRODUCTION

In daily situations such as driving in heavy traffic or playing sports, the right timing of attentional allocation can be crucial. Unfortunately, mistakes are hard to prevent, because attentional allocation is not solely under conscious control. A phenomenon that presumably arises from this failure to control attention is the attentional blink (AB): the limited ability to identify the second of two targets when they are presented in close temporal succession (200–500 msec; Raymond, Shapiro, & Arnell, 1992). Despite 2 decades of research, no consensus has yet been reached on whether the AB originates from a limitation of resources (Dell'Acqua, Jolicœur, Luria, & Pluchino, 2009; Dux, Asplund, & Marois, 2008; Chun & Potter, 1995; Shapiro, Raymond, & Arnell, 1994) or is a detrimental side effect of an attentional strategy (Taatgen, Juvina, Schipper, Borst, & Martens, 2009; Wyble, Bowman, & Nieuwenstein, 2009; Olivers, van der Stigchel, & Hulleman, 2007; Nieuwenstein & Potter, 2006; Nieuwenstein, Chun, Van der Lubbe, & Hooge, 2005). On either side of the discussion, the AB has been thought of as robust and resistant to training (Dale & Arnell, 2013; Taatgen et al., 2009; Braun, 1998; Maki & Padmanabhan, 1994; for reviews, see Martens & Wyble, 2010; Dux & Marois, 2009). In contrast to

this view, a recent study has revealed that the AB can be eliminated by only 1 hr of training using a color-salient second target consistently presented at short time intervals (Choi, Chang, Shibata, Sasaki, & Watanabe, 2012). However, the underlying cause of this training-induced improved performance remains as of yet still unknown.

According to Choi et al. (2012), this enhanced temporal resolution might be the result of a fundamental improvement, which could be because of either top–down attentional processes or increased processing abilities. Choi and colleagues found that the training effect was generalizable to multiple time intervals between the targets, that is, lags, and persisted up to several months. In addition, performance was improved on a different, target-mask task with only a single target. They argued that the increased temporal resolution is most likely the result of fundamental attention-based improvements. This claim is supported by evidence from an fMRI experiment in which Choi et al. found differences in DLPF activity when comparing target processing at short lags with target processing at long lags posttraining. According to Choi et al., if the training induced a general enhancement in target processing, such differences would not be observed. It is questionable how strong the neuroimaging evidence supports this claim, given the limited temporal resolution of fMRI.

In contrast, Tang, Badcock, and Visser (2013) suggested that the effect of training is because of the strengthening

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of temporal expectations that arise from the fixed temporal locations of the targets during the training. This theory was evidenced by their finding that the training effect could be reduced by diminishing the temporal expectations with a more variable task or training. Furthermore, they found a decrease in performance at the longer lag after the color-salient training but an attenuation of this performance decrease at the longer lag after the variable task condition and the variable training condition. Because the color-salient training consisted of short-lag trials only, Tang et al. argued that the timing of the targets was trained as opposed to the explanation that a fundamental change in target processing had occurred (Choi et al., 2012). However, the temporal expectations account can neither explain why the effect of training was generalizable to multiple lags and another task (Choi et al., 2012), nor can it exclude that a variable training or task just needs a longer training duration to attain a similar improvement in performance.

To resolve these issues, we aimed to study training-induced changes in attentional allocation by measuring pupil dilation. Pupil dilation is thought to reflect changes in activity of the locus ceruleus: a nucleus that is the hub of the noradrenergic system (for reviews, see Laeng, Sirois, & Gredebäck, 2012; Sara, 2009). Given that phasic activity of the locus ceruleus is associated with the processing of task-relevant stimuli (Dayan & Yu, 2006; Aston-Jones & Cohen, 2005), task-evoked pupil dilation is thought to reflect changes in the attentional detection system (Privitera, Renninger, Carney, Klein, & Aguilar, 2008). Although pupillary responses have a delay of ~1 sec, it is possible to analyze a fast-paced task like the AB task (~10 Hz) by using our recently developed pupil dilation deconvolution method (Wierda, van Rijn, Taatgen, & Martens, 2012). This method assumes that the pupillary response reflects a summation of responses to separate events (Hoeks & Levelt, 1993), which makes it possible to deconvolve the pupil dilation signal into isolated attentional pulses that are associated with the processing of each of the two targets. A benefit of this deconvolution method is that it allows for the extraction of expectation effects, which can arise in the absence of an actual target (Wierda et al., 2012).

Using a refined version of this deconvolution method, our goal in the current article is to address the changes in target-related attentional allocation as a result of the color-salient training. Two additional training tasks will function as control conditions, which leaves us with three training conditions: First, the color-salient training condition, resembling the training of Choi et al. (2012), contains a red second target and only short-lag trials. Second, the Lag-2 training condition contains no salient target; thus, all stimuli are presented in black, and again, there are only short-lag trials (Choi et al., 2012). Third, the Lag-2&6 training is similar to the Lag-2 condition with the exception that the lags between the targets are variable, that is, a short lag and a long lag. On the basis of the results of Choi et al., it is expected that the color-salient

training will enhance performance at the short lag, such that the AB will be eliminated. Furthermore, if performance at the long lag is decreased after the color-salient training (Tang et al., 2013), this will reinforce the theory that temporal expectations underlie the training effect. Because the salient target is seen as a crucial factor in the training effect, no effects are expected in the Lag-2 condition and the Lag-2&6 condition.

Given that we do not expect an eliminated AB after both control conditions, the expectations with regard to training-induced changes in pupil dilation will focus on the color-salient condition. Here, we expect that, if less cognitive effort is needed as a result of general enhanced processing posttraining, this may be reflected in decreased amplitudes of the peaks that are associated with attentional target processing posttraining compared with pretraining. In addition, if the training either induces an attentional strategy change (Choi et al., 2012) or strengthens temporal expectations (Tang et al., 2013), this could result in temporal changes in attentional allocation to the targets, as reflected in shifts of peak latencies. Finally, if training induces temporal expectations, we expect to observe increased expectation effects, that is, increased pulses associated with attentional allocation to the expected, but not presented, second target, during single-target trials at the time points when a second target is expected to occur.

METHODS

Eighty-one students of the University of Groningen participated in the experiment in return for a € 15 payment or course credits. All participants had normal or corrected-to-normal visual acuity and no history of neurological problems. All participants performed a similar pretraining and posttraining task, but three different types of training were provided: the color-salient training (26 participants, 15 women, mean age = 21.7 [range = 19–26] years), the Lag-2 training (29 participants, 21 women, mean age = 21.4 [range = 18–29] years), and the Lag-2&6 training (26 participants, 16 women, mean age = 20.1 [range = 18–25] years). After preprocessing the eye data, four participants were excluded from the pupil dilation analyses because of too many artifacts. After exclusion, 25 participants remained in the color-salient condition, 27 remained in the Lag-2 condition, and 25 remained in the Lag-2&6 condition. The psychology ethical committee of the University of Groningen approved the experimental protocol, and written informed consent was obtained from each participant before the experiment.

Behavioral

AB Task

The experiment was generated using E-prime 2.0 and presented on a 19-in. computer screen with a 100-Hz

refresh rate. Participants performed an AB task in the practice block, the pretraining block, and the posttraining block. The practice block contained three trials, and the pretraining and posttraining blocks contained 90 trials. In these blocks, each trial contained a rapid serial visual presentation (RSVP) of 32 items, which was presented in the middle of the screen at a rate of ~10 Hz with no ISI. Target stimuli consisted of uppercase consonants, excluding "Q," "V," and "Y," whereas distractor stimuli consisted of digits ranging from 2 to 9. All stimuli were presented in black, 18-point Courier New on a white background. On a third of the trials, one target was presented, whereas on the remainder of the trials, two targets were presented. The first target (T1) was always presented as the sixth stimulus of the RSVP. On dual-target trials, the second target (T2) was presented as either the eighth stimulus (Lag 2) or the 12th stimulus (Lag 6). All types of trials (single target, Lag 2, and Lag 6) were presented randomly and equally often. In addition, stimuli were selected pseudorandomly, with the constraints that target letters were not repeated within a single trial and that distractor digits were not presented twice in succession. Preceding the stream, a fixation cross was presented for 850 msec. To ensure that participants would stay fixated on the middle of the screen until the end of the trial, a comma or a dot was shown for 100 msec after the last distractor. This comma or dot had to be identified in addition to the target letters and allowed for recording the pupil response to the second target. After each trial, participants were prompted to type in the letters on the keyboard in the order they had seen them or to press spacebar when no target was observed. Hereafter, participants had to indicate whether the last character was a comma or a dot.

Training Task

The training block in each condition contained 450 trials. The trials were similar to the ones in the pretraining and posttraining blocks with the following exceptions. The RSVP consisted of 10 items, and T1 was always presented as the second item of the stream. The color-salient training consisted of Lag-2 trials only, and T2 was always presented in red. The Lag-2 training also consisted of Lag-2 trials only; however, all stimuli were presented in black. In addition, the Lag-2&6 training contained both Lag-2 and Lag-6 trials, presented randomly and equally often. Here, all stimuli were also presented in black.

Participants could take a short break in between blocks and halfway through the training block. They completed the experiment in approximately 70 min.

Statistical Methods

Statistical analyses were performed using the *lmerTest* package (Kuznetsova, Brockhoff, & Christenen, 2013) in R (version 2.14.2; R Development Core team, 2012). The behavioral data were analyzed using generalized linear mixed models (GLMMs), and Tukey's HSD tests were performed as post hoc comparison tests. In all models, "participants" was entered as random intercept, and fixed factors were included based on theoretical grounds. Trials in which T1 and T2 were identified correctly but reported in reversed order were also considered correct. Furthermore, tests for overdispersion did not reveal any problems.

Pupil Dilation

Pupil dilation was measured using the EyeLink 1000 eye tracker (www.sr-research.com). Before the experiment, the eye tracker camera was configured to track the left eye, and the eye tracker was then calibrated. Viewing distance was ~50 cm. Pupil dilation was measured during the pretraining and posttraining blocks. However, participants kept their head in a chin rest during all blocks to keep task conditions comparable.

Preprocessing

The pupil data were sampled at 250 Hz and down-sampled to 50 Hz. The data of each trial were time-locked to the onset of T1. Segments containing eye blinks were recovered using linear interpolation or excluded based on semi-automatic inspection. The average pupil size during the 200 msec before stream onset was used as a baseline, and the data were normalized by applying the following formula:

$$Xnorm = \frac{X - Baseline}{Baseline}.$$

Attentional pulses were estimated by using the pupil dilation deconvolution method (Wierda et al., 2012). Per combination of participant and condition, 80 pulses were modeled, starting 400 msec before stream onset. The set of pulse strengths $i = \{w1, w2, w3,\ldots, w78, w79, w80\}$ was convolved with the Erlang gamma function $h = s * t(n) * e^{\left(\frac{-n * t}{t_{max}}\right)}$. In this function, s is a scaling factor, n is the number of layers, and t_{max} is the position of the maximum response. Following Wierda et al. (2012), these parameters were set to $n = 10.1$, $t_{max} = 930$, and $s = 1/1027$. The pulse strengths were obtained by optimizing the fit between the estimated signal $x = l * b + i * h$ and the measured pupil dilation signal, where l is the position of each pulse in vector i and b controls for linear drifts in the data. In contrast to Wierda et al., an interpulse interval of 50 msec was used to increase temporal resolution of the pulses. Furthermore, instead of the Nelder–Mead method, we used the Levenberg–Marquardt algorithm (i.e., a nonlinear least-squares algorithm) for optimizing the strengths of the attentional pulses. The advantage of the latter is that it is computationally cheap and converges toward the same unique solution every run, whereas the Nelder–Mead method yields slightly different outcomes because of randomization, such that it should be repeated multiple times to get a reliable solution.

Local peaks were calculated to determine the latency of the attentional pulses per target. Because there were substantial individual differences in the timing of the pulses, it was difficult to specify a general time window for all individuals that captured the T1 pulse but did not include the T2 pulse. Therefore, based on the assumption that the first pulse after T1 presentation represents attentional allocation to this target, T1 latency was determined by selecting the first local peak within a time window of −100 to 500 msec. T2 latency was determined as the local peak within a window ranging from 400 to 1000 msec for Lag 2 and 800 to 1400 msec for Lag 6. The amplitude of the pulses was calculated by averaging amplitudes of the local peak with that of the point preceding it and of the point after it.

Statistical Methods

The latencies and amplitudes of the deconvolved attentional pulses were analyzed using LMMs. Using the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core team, 2012), we fitted various covariance structures, which were compared using the Akaike information criterion (Akaike, 1974). In all cases, either the initial model, which assumes that there are no within-group correlations, fitted best or the results of the best fitting model did not differ from the initial model. We therefore used the initial model in all subsequent analyses. Expectancy effects in the single-target trials were analyzed by comparing the pulse strength in the pretraining and posttraining blocks within the same time windows as those that were used to determine T2-related pulses for Lag-2 trials and Lag-6 trials. A permutation test was performed per time point within these windows. Further statistical methods were similar to those for the behavioral data.

RESULTS

Behavioral

The mean accuracy for T1 and for T2 given correct report of T1 (T2|T1) in the pretraining and posttraining blocks in all three training conditions is shown in Figure 1. For T2|T1 accuracy, we performed three behavioral omnibus GLMM with lag (2 and 6), session (pretraining session and posttraining session), condition (color-salient, Lag-2, and Lag-2&6), and its two-way and three-way interaction terms as fixed factors. For each model, a different training condition served as reference category. A summary of the most important results of these models is presented in Table 1. The results of the full models can be found in the SI. We found that the Lag × Session interaction was different both in the color-salient condition compared with the Lag-2&6 condition and in the Lag-2 condition compared with the Lag-2&6 condition. However, there was no evidence that the Lag × Session effect differed between the color-salient condition and the Lag-2 condition. As can be seen in Figure 1, there was a Lag × Session interaction in the color-salient condition and in the Lag-2 condition. However, this was not the case in the Lag-2&6 condition. For T1 accuracy, we performed a similar omnibus GLMM, and here, we only found an unconditional main effect of lag ($\beta = -0.47$, $SE = 0.09$, $z = -5.12$, $p < .001$). There was neither an overall effect of session ($p = .96$) nor any interactions between the factors ($p > .1$).

Post hoc tests revealed that, after the color-salient training, T2|T1 accuracy improved at the short lag but decreased at the long lag ($ps < .004$). Furthermore, T2|T1 accuracy was lower at Lag 2 than at Lag 6 pretraining ($p < .001$), but this difference was not found posttraining ($p = .061$). After the Lag-2 training, there also was an increase in T2|T1 performance and a decrease in Lag 6 performance ($ps < .003$). Thus, accuracy changed in a similar fashion after the Lag-2 training as after the color-salient
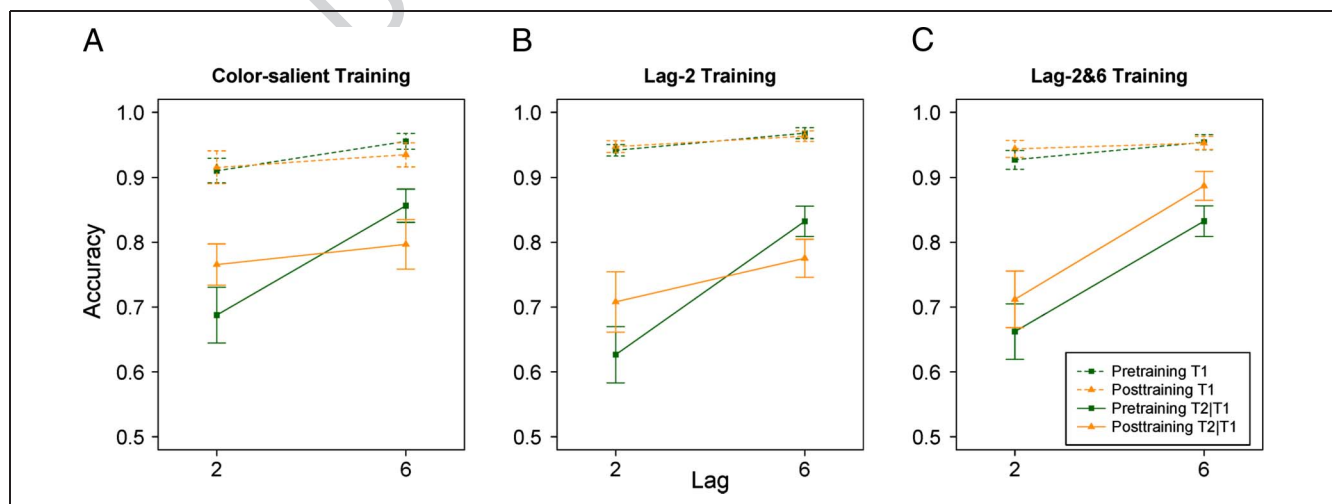
Figure 1. The mean percentage of correct reports of T1 (dotted lines) and T2 given correct report of T1 (solid lines) as a function of lag for the pretraining (green squares) and posttraining (orange triangles) blocks in (A) the color-salient condition, (B) the Lag-2 condition, and (C) the Lag-2&6 condition. The error bars reflect the standard errors of the mean.

Table 1. Summary of Omnibus GLMM Results with Different Reference Categories

Factor	β	SE	z	p
Lag[a] × Session[b,c]	0.86	0.19	4.46	<.001***
Lag × Session × Lag-2 condition[c]	−0.05	0.26	−.18	.856
Lag × Session[d]	0.82	0.17	4.71	<.001***
Lag × Session × Lag-2&6 condition[d]	−1.05	0.26	−3.99	<.001***
Lag × Session[e]	−0.23	0.20	−1.17	.241
Lag × Session × Color-salient condition[e]	1.10	0.28	3.95	<.001***

Significance codes: *$p < .05$, **$p < .01$, ***$p < .001$.

[a]Reference category is "Lag 6."

[b]Reference category is "pretraining session."

[c]Reference category is "color-salient condition."

[d]Reference category is "Lag-2 condition."

[e]Reference category is "Lag-2&6 condition."

training. However, after the Lag-2 training, a difference in accuracy between Lag 2 and Lag 6 remained ($p < .001$). These results suggest that the AB was attenuated after both the color-salient training and the Lag-2 training but not after the Lag-2&6 training (MacLean & Arnell, 2012).

In the training block, mean T1 accuracy was 91.1% ($SE = 1.6$), 96.3% ($SE = 0.6$), and 95.0% ($SE = 0.8$) in the color-salient condition, the Lag-2 condition, and the Lag-2&6 condition, respectively. At Lag 2, mean T2|T1 accuracy in the training block was 83.9% ($SE = 3.1$), 65.9% ($SE = 3.9$), and 64.7% ($SE = 3.4$) in the color-salient condition, the Lag-2 condition, and the Lag-2&6 condition, respectively. At Lag 6, in the Lag-2&6 condition, mean T2|T1 accuracy was 90.4% ($SE = 1.0$) in the training block.

Pupil Dilation

To study the attentional deployment during the pretraining and posttraining sessions, the normalized pupil dilation signal was deconvolved to attentional pulses that can be associated with the processing of the targets. For the T1 analyses concerning all lags, we only took trials into account in which T2 was correctly identified, that is, no-blink trials. This was motivated by the lack or absence of blink trials, that is, correct T1 and incorrect T2, during Lag-6 trials and single-target trials. Differences between no-blink trials and blink trials were investigated for Lag 2 in separate analyses. Furthermore, all LMMs were modeled with the constraint that T1 was reported correctly, and in the analyses concerning T2 pulses, only trials in which T2 was reported correctly were taken into account.

T1 Latency

For T1 latency, that is, the first local peak within the −100- to 500-msec time window, we analyzed whether

session (pretraining session and posttraining session), condition (color-salient, Lag-2, and Lag-2&6), and Session × Condition were predictive factors over all lags (single target, Lag 2, and Lag 6). We found no evidence that the effect of session differed between the color-salient training, the Lag-2 training, and the Lag-2&6 training (ps > .8). However, as depicted per lag and per condition in Figures 2–5, there was an unconditional main effect of session ($\beta = −56.04$, $SE = 12.11$, $t = −4.63$, $p < .001$), which indicates that, over all conditions, attention was allocated earlier in time to the first target after the training compared with before the training. In addition, as tested in a separate LMM, T1 latency over all lags could not be predicted by individual mean T1 accuracy ($p = .80$).

For Lag-2 trials only, we tested whether T2 accuracy (no-blink trials and blink trials), session, condition, and their two-way interaction terms were predictive for T1 latency. These results are shown for blink trials and no-blink trials in Figures 2 and 3, respectively. There were no significant interactions ($p > .1$), but again, there was an unconditional main effect of session ($\beta = −60.06$, $SE = 16.59$, $t = −3.62$, $p < .001$). This indicates that, at Lag-2 trials, T1 latency shifted to an earlier time point after the training in all conditions. The results did not indicate any differences between no-blink and blink trials ($p = .25$). Furthermore, neither AB magnitude ($p = .35$), defined as T2|T1 Lag-2 accuracy normalized by T2|T1 Lag-6 accuracy, nor mean T1 accuracy ($p = .13$) was predictive for T1 latency at Lag-2 trials. Together, these results suggest that, regardless of lag or condition, attention to T1 was allocated earlier in the posttraining session compared with the pretraining session.

T1 Amplitude

The amplitude of the T1 pulse over all lags was analyzed with an LMM with session, condition, and its interaction
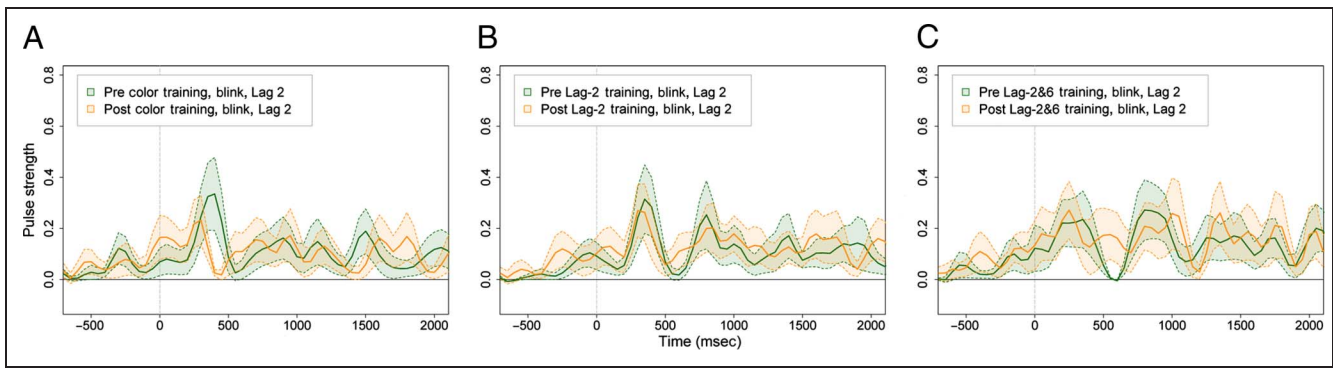
Figure 2. The mean strength of the deconvolved attentional pulses pretraining and posttraining for Lag-2 blink trials, that is, T1 reported correctly and T2 reported incorrectly, in the (A) color-salient condition, (B) Lag-2 condition, and (C) Lag-2&6 condition. The x axis is time-locked to the onset of T1, and the depicted signal was smoothed with a Butterworth filter. The error bars reflect the standard errors of the mean.

term as fixed factors. This model revealed that the session effect of the color-salient training condition was different from the session effect in the Lag-2&6 training condition ($\beta = 0.09$, $SE = 0.04$, $t = 2.44$, $p = .015$). That is, T1 amplitude increased significantly after the Lag-2&6 training ($\beta = 0.07$, $SE = 0.03$, $t = 2.71$, $p = .007$) but was not affected by the color-salient training ($p = .46$). However, T1 amplitude did not differ as a result of session between the color-salient condition and the Lag-2 condition or between the Lag-2 condition and the Lag-2&6 condition ($ps > .09$). Individual mean T1 accuracy was not related to the strength of the T1 pulse ($p = .95$).

For Lag-2 trials, as graphed in Figures 2 and 3, we performed an LMM on T1 amplitude with T2 accuracy, session, condition, and their two-way interactions as fixed factors. None of the factors interacted significantly with one another ($p > .1$), but overall, whether a trial was a blink trial or a no-blink trial was predictive for T1 amplitude ($\beta = -0.07$, $SE = 0.02$, $t = -3.18$, $p = .002$): The strength of the T1 pulse was lower in trials where T2 was identified correctly than in trials where T2 was perceived incorrectly. Finally, we did not find an effect of AB magnitude ($p = .28$) or of mean T1 accuracy ($p = .51$) on T1 amplitude at Lag 2. Taken together, these results implicate that allocating less

attention to the first target increases the chance for T2 to be correctly identified.

T2 Latency

For T2 Lag-2 latency, we tested whether session, condition, and Session × Condition were predictive factors with regard to no-blink trials. These results are depicted per training condition in Figure 3A–C. Except for an overall group difference between the color-salient condition and the Lag-2&6 condition ($\beta = -73.97$, $SE = 30.11$, $t = -2.46$, $p = .016$), which indicates possibly an initial group difference, no effects were found ($p > .4$). However, the timing of the T2 pulse was related to the mean T2|T1 accuracy at Lag 2 ($\beta = -122.42$, $SE = 54.19$, $t = -2.26$, $p = .026$). Given that we only took trials into account where T2|T1 was identified correctly, this means that, even for trials where performance is equal for all participants at trial level, there is a difference in the timing of attentional allocation that is related to individual mean T2|T1 performance. That is, an earlier T2 peak was related to better T2|T1 performance.

For T2 Lag-6 latency, shown in Figure 4, we performed similar LMMs as for T2 Lag-2 latency. No effect of session, condition, or its interaction term was found ($p > .1$).
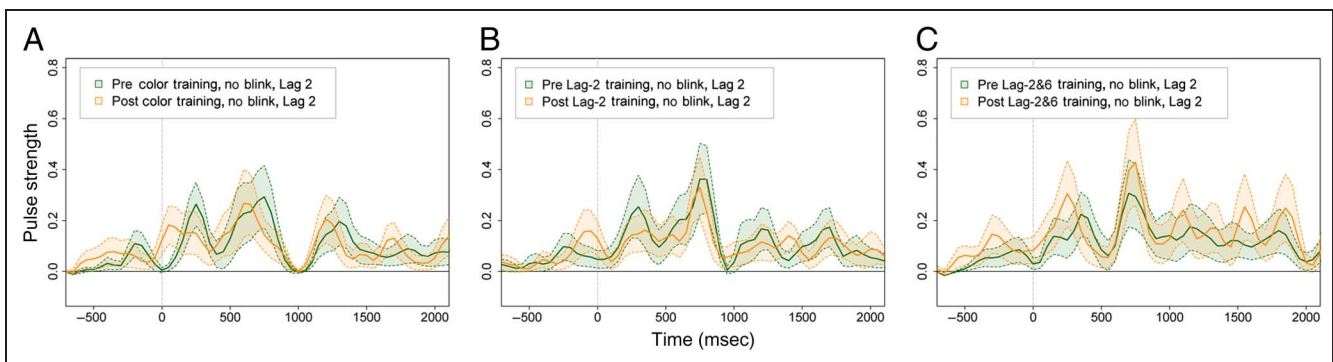
Figure 3. The mean strength of the deconvolved attentional pulses pretraining and posttraining for Lag-2 no-blink trials, that is, both targets reported correctly, in the (A) color-salient condition, (B) Lag-2 condition, and (C) Lag-2&6 condition. The x axis is time-locked to the onset of T1, and the depicted signal was smoothed with a Butterworth filter. The error bars reflect the standard errors of the mean.
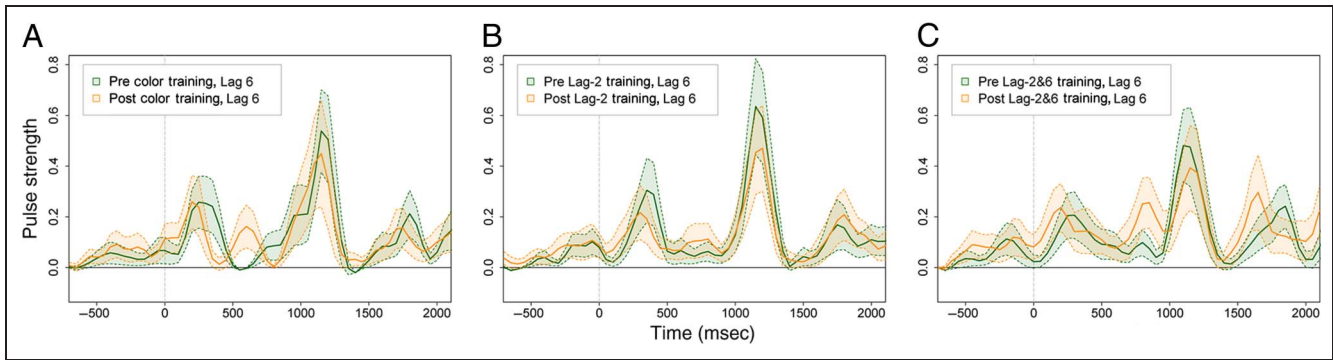
Figure 4. The mean strength of the deconvolved attentional pulses pretraining and posttraining for Lag-6 no-blink trials, that is, both targets reported correctly, in the (A) color-salient condition, (B) Lag-2 condition, and (C) Lag-2&6 condition. The *x* axis is time-locked to the onset of T1, and the depicted signal was smoothed with a Butterworth filter. The error bars reflect the standard errors of the mean.

However, again, the timing of the T2 pulse at Lag 6 was related to T2|T1 performance at that particular lag (β = −144.34, *SE* = 67.48, *t* = −2.14, *p* = .034). Thus, at Lag 6, at trials where T2|T1 performance was correct, an earlier T2 peak was associated with higher T2|T1 accuracy. These results concerning T2 latency show that earlier allocation of attention to the second target was associated with higher individual T2|T1 accuracy.

T2 Amplitude

With regard to T2 amplitude at Lag-2 trials, there were no effects of session, condition, or Session × Condition (*p*s > .07). In addition, T2 Lag-2 amplitude was not predicted by mean T2|T1 accuracy at that lag (*p* = .57). There were also no effects of session, condition, or Session × Condition for T2 Lag-6 amplitude (*p*s > .3). However, T2|T1 accuracy at Lag 6 was a marginally significant predictor of T2 Lag-6 amplitude (β = 0.44, *SE* = 0.23, *t* = 1.95, *p* = .053), such that better performance was related to a higher amplitude.

Expectancy Effects

In line with previous findings by Wierda et al. (2012), expectancy effects for a second target can be seen in the single-target trials as shown per condition in Figure 5A–C. To determine whether these expectancy effects for T2 had increased after the training conditions, single-target trials were analyzed, but there was no evidence for enhanced expectancies of the second target after any of the training conditions (*p*s > .08). However, when inspecting Figure 5A–C visually, posttraining enhanced activity around 1300 msec can be seen in the Lag-2&6 condition compared with the color-salient condition and the Lag-2 condition. This point lies within the time frame we used to analyze T2 peaks at Lag 6. In addition, after further visual inspection of the pupil data, we analyzed the period 400–1000 msec in Lag-6 trials, as shown in Figure 4A–C. This is the time window in which, in case of Lag-2 trials, the second target was presented. In the color-salient condition, the posttraining activity was higher than the pretraining session at time point 500 (*t* = −2.14, *p* = .017). However, in the Lag-2 condition and the Lag-2&6 condition, there were no significant differences (*p* > .10).

Normalized Pupil Dilation

Finally, prompted after visual inspection of the data, we analyzed the normalized dilation data at the onset of the first target, at which target processing does not yet influence the dilation of the pupil. The results are graphed in
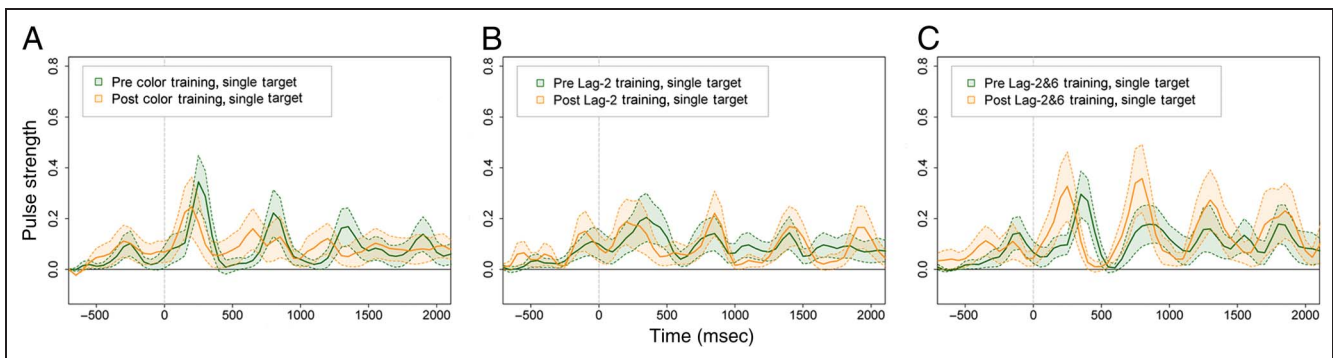
Figure 5. The mean strength of the deconvolved attentional pulses pretraining and posttraining for single-target no-blink trials, that is, both targets reported correctly, in the (A) color-salient condition, (B) Lag-2 condition, and (C) Lag-2&6 condition. The *x* axis is time-locked to the onset of T1, and the depicted signal was smoothed with a Butterworth filter. The error bars reflect the standard errors of the mean.
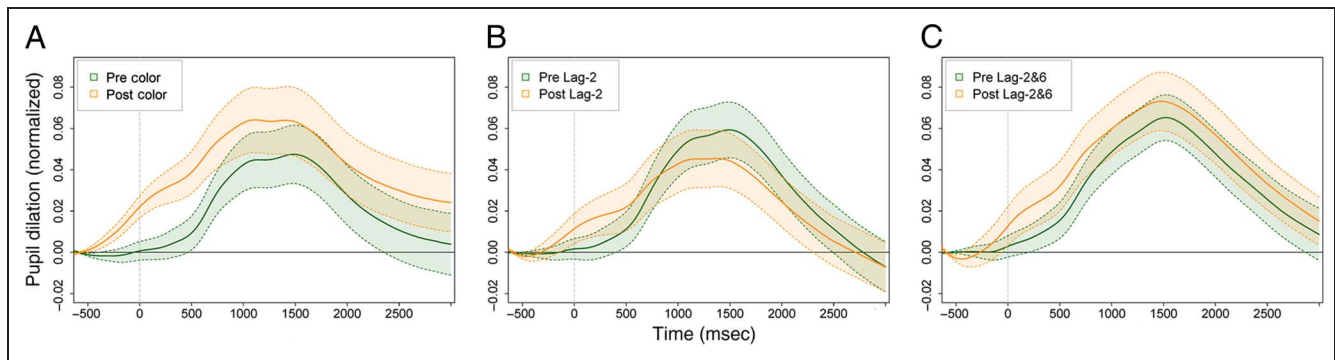
Figure 6. The averaged normalized pupil dilation for the pretraining and posttraining blocks in (A) the color-salient condition, (B) the Lag-2 condition, and (C) the Lag-2&6 condition. The *x* axis is time-locked to the onset of T1, and the error bars reflect the standard errors of the mean.

Figure 6. We tested whether session, condition, and Session × Condition had an effect on the normalized size of the pupil. This model revealed that, in every training condition, the normalized pupil dilation increased significantly as a result of session (color-salient: β = 0.02, *SE* = 0.002, *t* = 14.44, *p* < .001; Lag-2: β = 0.001, *SE* = 0.002, *t* = 7.69, *p* < .001; Lag-2&6: β = 0.001, *SE* = 0.002, *t* = 7.42, *p* < .001). This increase was higher after the color-salient training than after both the Lag-2 training (β = −0.01, *SE* = 0.002, *t* = −4.97, *p* < .001) and the Lag-2&6 training (β = −0.01, *SE* = 0.002, *t* = −4.91, *p* < .001). The effect of session did not differ between the Lag-2 and Lag-2&6 conditions (*p* = .98). Furthermore, as tested in a model with AB magnitude, condition, and AB magnitude × Condition as fixed factors, AB magnitude was a predictive factor for normalized pupil size in the color-salient condition (β = −0.03, *SE* = 0.004, *t* = −8.97, *p* < .001) and in the Lag-2 condition (β = −0.03, *SE* = 0.004, *t* = −7.08, *p* < .001) but not in the Lag-2&6 (*p* = .37). The difference between groups was also expressed in the interactions: The effect of AB magnitude differed between the color-salient condition and the Lag-2&6 condition (β = 0.04, *SE* = 0.01, *t* = 4.17, *p* < .001) and between the Lag-2 condition and the Lag-2&6 condition (β = 0.04, *SE* = 0.01, *t* = 3.56, *p* < .001). However, no evidence was found for a different effect of AB magnitude between the color-salient condition and the Lag-2 condition (*p* = .27). Thus, we found an increased pupil size in the posttraining session, irrespective of training condition. In the color-salient and Lag-2 conditions, this increase could be associated with the decrease of AB magnitude, but this was not the case in the Lag-2&6 condition.

DISCUSSION

In this study, we aimed to reveal training-induced changes in attentional allocation by measuring pupil dilation during a pretraining and posttraining AB task to elucidate the underlying mechanism of the color-salient training effect as found by Choi et al. (2012). On the one hand, it has

been argued that the color-salient training may induce a fundamental improvement in target processing, which may be because of changes in top–down attention or to more efficient processing (Choi et al., 2012). On the other hand, it has been suggested that this training may strengthen temporal expectations of the targets, which enhances target perception (Tang et al., 2013). In the current study, in addition to the color-salient training condition, we also included two control conditions: the Lag-2 training and the Lag-2&6 training.

In the behavioral data, we found that the AB was eliminated after the color-salient training, thus replicating previous findings reported by Tang et al. (2013) and Choi et al. (2012). Surprisingly, however, we showed that training without a salient target, but with a consistent, short target interval, is already sufficient to produce a similar effect. Only when the target interval in the training block was variable, no attenuation of the AB occurred after the training. The deconvolved pupil dilation data showed a shift in the timing of attention allocated to T1 rather than T2. However, this posttraining shift was present in all three training conditions. Although expectancies for T2 were visible during single-target trials, they were not modulated by any type of training. In addition, whereas in all three conditions, the normalized posttraining pupil dilation was enhanced before target onset compared with pretraining dilation, the increase was largest after the color-salient training. Finally, AB magnitude was found to be negatively related to the size of pretarget dilation in the color-salient condition and in the Lag-2 condition but not in the Lag-2&6 condition.

Target Expectancy

An important difference between the current behavioral findings and those by Choi et al. (2012) is that we found comparable reductions in AB magnitude in both the color-salient training and the Lag-2 training conditions. Choi et al. reported no such improvement in a similar control condition without color saliency (Exp. 3) and concluded that the salient T2 is crucial for the training effect. In addition,

although compared between participants, it was found that a constant time interval between the lags per block did not attenuate the AB compared with variable time intervals per block (Martens & Johnson, 2005). However, compared with Choi et al. and Martens and Johnson, in the current study, we tested a larger group of participants and analyzed the results more thoroughly by using mixed models instead of single *t* tests, providing strong evidence that the presence of a salient target is not crucial to induce increased performance after training.

The behavioral results further suggest that temporal expectations play an important role in the improved accuracy. That is, in accordance with Tang et al. (2013), in both the color-salient condition and the Lag-2 condition, performance increased at Lag 2 but decreased at Lag 6. However, after the Lag-2&6 training, performance was enhanced equally at both lags. In other words, accuracy improved at the trained lags and decreased at the untrained lags, suggesting that training a specific time interval was likely to be an important aspect of the learning process.

This view seems to contradict the finding that the training effect was generalizable to multiple lags (Exp. 5; Choi et al., 2012). However, the results of Choi et al. actually show the largest improvement at Lags 2 and 3, which are in close temporal proximity of each other and resemble the trained interval. Furthermore, at first sight, it seems as if Choi and colleagues did not find the decrease in performance at the long lag, as was found by Tang et al. (2013) and observed in the current study. However, the slightly different presentation of the results by Choi et al. may play a crucial role here. In Choi et al.'s study, participants performed a pretraining task, the color-salient training, and a posttraining task for 3 consecutive days. The results presented as posttraining results in Choi et al.'s article are actually the results from the pretraining sessions on Days 2 and 3 compared with the pretraining session on Day 1. In terms of the current experiment, this means that, in Choi et al.'s study, the participants performed not only the color-salient training but also a Lag-2&6 training before the block that was reported as posttraining block. This can explain the combination of an eliminated AB and the lack of decreased Lag 6 performance. Furthermore, in line with our results, the supporting information of Choi et al.'s study shows that, in the posttraining block of the first day, there was also a decrease in Lag-6 T2|T1 performance. All of this taken together, our behavioral results indicate strongly that training strengthens temporal expectations, even without an explicit cue or a salient target.

Performance-driven Pupil Changes, Independent of Training Condition

The pupil dilation data, however, are less straightforward than the behavioral data. We neither found any condition-related effects regarding the attentional allocation to the first and second targets nor any evidence for enhanced expectancies of the second target in the single-target trials. With regard to our hypotheses, we did not find any evidence for reduced peak amplitudes as a result of training, which indicates that the cognitive workload was not decreased posttraining compared with pretraining. Therefore, it seems unlikely that general, more efficient target processing lies at the root of the training effect. However, overall, we did find decreased T1 amplitudes for no-blink trials compared with blink trials. This finding is in line with Wierda et al. (2012) and supports the theory that overinvestment of attention in T1 processing lies at the root of the AB effect (Wierda, van Rijn, Taatgen, & Martens, 2010; Taatgen et al., 2009; Olivers & Nieuwenhuis, 2005, 2006). Thus, the amount of invested attention in processing T1 seems important at trial level, where it can predict whether the second target will be perceived correctly, but this was not influenced by any of the training conditions.

Irrespective of condition, posttraining, we found a temporal shift of T1-allocated attention and a higher level of normalized pupil dilation before any target processing. With regard to the normalized pupil dilation, we revealed that AB magnitude was negatively related to the size of the pupil at the onset of T1 processing in both the color-salient condition and the Lag-2 condition, but no such relationship was found in the Lag-2&6 condition. Ergo, in each training condition, normalized pupil size was increased in the posttraining session, and in the color-salient condition and the Lag-2 condition, this increase could be linked to AB magnitude but not in the Lag-2&6 condition. Thus, although we found a link between posttraining attention-based changes and performance differences, there was no indication that the color-salient training or the Lag-2 training, with similar behavioral results, induced different changes in pupil dilation than the Lag-2&6 training did. Because the behavioral patterns were not reflected in the pupil dilation associated with the targets in any of the training conditions, it seems unlikely that the attenuation of the AB is because of fundamental changes in attentional processing of the targets (Choi et al., 2012).

With regard to the temporal expectation theory (Tang et al., 2013), we did not find any training-induced differences in the expectation of the second target in the single-target trials. However, the earlier attentional allocation to T1 may be the result of enhanced temporal expectations of the first target posttraining. That is, a more precise attentional timing to T1 may result in less interference between the two targets at the short lag. In addition, the focus on the first target would also explain why the effect was generalizable to another task with a single target (Choi et al., 2012). Although a more precise attentional timing to T1 was not substantiated behaviorally by a training-induced increase in T1 performance, this may be explained by the fact that T1 performance was already at ceiling pretraining.

It remains unclear, however, why a more precise timing to T1 would result in decreased accuracy at a longer lag. A clue might be found in the Lag-6 trials, which can be seen in Figure 4A–C. Here, a posttraining increase in activity can be seen in the period in which the short-lag T2 is expected but not presented. However, this increase was only significant in the color-salient condition. A similar expectancy effect can be observed in single-target trials after the Lag-2&6 training. Here, in the timeframe 800–1400 msec, the level of activity seems strongest in the Lag-2&6 posttraining condition (Figure 5C), when compared with the color-salient condition and the Lag-2 condition (Figure 5A and B). This might be an indication for increased temporal expectancies at the time point of the second target at Lag 6 in the Lag-2&6 condition. However, within the Lag-2&6 condition, there was no significant increase in activity within this period. Thus, inspection of the graphs does reveal some speculative clues that point toward strengthened temporal expectancies during the training tasks. However, clearly, future research is needed to establish the role of temporal expectations more thoroughly.

Finally, somewhat beyond the primary focus of our study, we observed a number of interesting relations between pupil dilation and performance on the AB task. First, the finding that the size of normalized pupil dilation before any target processing could be predicted by AB magnitude suggests a role of attentional preparation or strategy in individual AB task performance. Second, we found that the T1 amplitude was lower at trials where the second target was reported correctly than at trials where T2 identification failed. This strengthens the idea that the AB is because of an overinvestment of attention to T1 (Wierda et al., 2010; Taatgen et al., 2009; Olivers & Nieuwenhuis, 2005, 2006; Shapiro, Schmitz, Martens, Hommel, & Schnitzler, 2006). Third, we found that, overall, the latency of T2-induced pupil dilation is related to individual mean T2|T1 accuracy at that particular lag, despite identical behavioral performance at trial level. Apparently, there are overall individual differences in the timing of attentional allocation that result in different levels of AB task performance, but which are not predictive at trial level. Future research is needed to further disentangle the relationship between individual differences in pupil dilation and individual differences in the AB.

In summary, the behavioral results suggest that the trained interval is an important part of the training effect, even without the presence of an explicit cue. The pupil dilation data showed a more complex picture. We found evidence for enhanced expectancies of the Lag-2 second target in Lag-6 trials after the color-salient training but not for the seemingly enhanced expectancies in the other conditions. In addition, we found changes in attentional allocation to T1 and enhanced normalized pupil dilation after training. Given that these changes generally occurred irrespective of the type of training, we concluded

that the color-salient training does not induce a fundamental change in target processing (Choi et al., 2012). It seems plausible that the shift in timing of allocated attention to T1 was because of enhanced temporal preparation for the first target, which is in line with the temporal expectation theory (Tang et al., 2013).

Conclusion

In the current study, we have demonstrated that a training task without a salient target, but with a consistent inter-target interval, can reduce the AB. Furthermore, our results point to the existence of temporal expectations at the time points of the trained targets posttraining. At least a major source of the training effect as originally reported by Choi et al. must therefore lie in the strengthening of temporal expectations.

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