Pupillometric evidence for the decoupling of attention from perceptual input during offline thought

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Accumulating evidence suggests that the mind is not only proficient at processing external events;[1,2] it is also adept at disengaging from the stream of sensory input to process internally generated thoughts and feelings.[3,4] This distinct "offline" cognitive mode requires not only spontaneously generated mental activity; it has also been hypothesized to require a decoupling of attention from perception in order to separate competing streams of internal and external information.[3,5,6] We use measurements of pupil diameter (PD)[7] to provide concrete evidence for the role of decoupling during spontaneous cognitive activity. First, during periods conducive to offline thought, but not during periods of task focus, PD exhibited spontaneous activity decoupled from task events. Second, during periods requiring task focus, the same spontaneous PD activity preceded episodes of encoding failure. Third, spontaneous PD activity occurred prior to only the slowest 20% of correct responses, suggesting it reflects a distinct mode of cognitive functioning. Together, these data suggest that the capacity to decouple attention from perceptual input allows spontaneous cognitive activity to flourish by minimizing disruptions from the external world. Moreover, the correlation between PD and neural activity in the brainstem locus coeruleus (LC)[8,9] implicate the brain's norepinephrine (NE) system in switching between states of offline and online cognition.

Taking a shower, queuing for coffee, or riding the bus are all everyday tasks with minimal cognitive demands that allow the mind to wander.[3,4] These common experiences of dual engagement or multi-tasking illustrate that the mind is not only efficient at the online processing of sensory information; it also has an offline mode in which cognition is initiated spontaneously.[10-12] The fact that the offline mode persists in the face of the distractions of the coffee queue or the bus ride raises a question: Why isn't spontaneous cognitive activity continually disrupted by the information available through perception?[1,2]

One hypothesis is that the internal train of thought is not interrupted by external events because the mind can reversibly decouple attention from sensory information.[3,6] This "decoupling" would reduce competition between internally generated representations (offline information) and those derived from perception (online information).[6] Critically, decoupling could explain our capacity for orderly, spontaneous thought because it would prevent external events from interfering with offline cognitive processes.[6]

Indirect support for such decoupling comes from evidence that offline thought impairs sensory processing,[13-15] although these studies have generally lacked evidence for simultaneous cognitive engagement. One exception is the observation of dorsolateral prefrontal cortex (DLPFC) activation during offline thought;[16] DLPFC is a brain area known to be involved in sustaining cognition in the face of distraction.[17] Recently, however, the role of DLPFC activity in decoupling has been challenged by the suggestion that it instead reflects attempts to reinstate task-focus.[18]

The present study tests whether the dynamics of pupil diameter (PD) – a recognized measure of cognitive activity - exhibits behavior consistent with the decoupling hypothesis. PD exhibits rapid stimulus-evoked increases following the encoding of external stimuli,[7] increases during long term memory retrieval,[19] and has been linked to DLPFC activity.[20] These data make PD an ideal covert measure of cognitive activity. In addition, single-cell recordings in primates suggest that PD is coupled to activity in the brainstem locus coeruleus (LC),[8,9] the primary source of brain norepinephrine (NE). This correlation allows our study to explore the potential role that NE plays in the decoupling of attention from perception; a role for NE in offline cognition seems plausible given the suggestion that it has a mode of operation which facilitates task disengagement. [8,9]

The decoupling hypothesis suggests PD should exhibit two modes of activity: (i) an "online" mode in which baseline PD activity is suppressed (reflecting the absence of spontaneous cognition) and transient responses to external events are observed and (ii) an "offline" mode in which PD exhibits minimal task evoked changes and instead exhibits high baseline activity indicative of spontaneous cognitive activity. To examine this hypothesis we formulated five predictions, labeled (P1)-(P5) and summarized in Table 1, on how the dynamics of the online/offline modes of PD should behave.

To test these five predictions we developed two tasks (Figure 1a) that differed primarily in the mode of cognition required for performance. In the Working Memory (WM) task, participants were presented with a sequence of digits and asked to retain the identity of the most recent number in memory. The participants responded to intermittent probes (a colored "?") by reporting the parity (odd/even) of the previous number shown.

The WM task requires continuous external attention and so satisfactory task performance requires that participants maintain an online external focus. In the Choice Reaction Time (CRT) task, a similar sequence of digits was observed but the intermittent probes only required participants to report the parity of a colored number currently displayed on the screen. Hence, no encoding of the non-colored digits was required for high levels of accuracy in the CRT, and in these periods participants should be able to engage the offline mode to a greater extent than in the WM task.

Experiment One used experience sampling[4] to confirm that attention was less task-constrained during performance of the CRT than the WM task (Figure 1b). As hypothesized from previous work,[21-23] the WM task required that participants maintain focus on the current task environment. In the CRT task participants were comparatively less likely to focus on the present and instead tended to anticipate future events.

Experiment Two measured PD for participants performing both tasks to examine whether the non-colored stimuli in the WM task would evoke a transient increase in PD (P1) and that no such task-synchronized increase in PD would be observed in response to these same events in the CRT task (P2). Figure 2a presents the dynamics of PD in a 2.5 second epoch after presentation of non-colored stimuli in both tasks. Baseline levels of PD were normalized using the 500ms interval prior to the non-probe stimulus. A clear evoked response was present in the WM task and absent from the CRT task. Experiment Two therefore confirmed our first two predictions; in the online mode PD exhibits increased activity which is coupled to task events (P1) and in the offline mode it does not (P2).

Given that PD activity was uncoupled to the task during the CRT, we next explored if the same context was accompanied by greater spontaneous cognitive activity (P3). If this were the case, PD should be generally larger during performance of the CRT than during the WM task (as shown with Experiment One). Figure 2b demonstrates that in the 1.5 s period prior to a non-probe stimulus, average PD in the CRT task was larger than in the WM task.

Next, if poor external encoding is necessary for spontaneous cognitive activity to persist (P4), high baseline PD levels should be apparent prior to encoding failure during WM responses. PD dynamics in the CRT task were indistinguishable prior to correct and incorrect probes (Figure 3a). However, higher baseline PD prior to incorrect probes was apparent in the WM task. To investigate this pre-probe difference with greater power we performed Experiment Three in which an additional group of participants completed a twenty minute version of the WM task. The data from these subjects were combined with the WM data from the subjects in Experiment Two. Figure 3b shows PD during the 1.5 second window prior to probes binned on subsequent accuracy. Higher baseline PD preceded incorrectly responded WM probes than the correctly responded probes. Together, Experiments Two and Three show that spontaneous PD activity is accompanied by a reduction in external attention (P4).

Finally, we investigated the relationship between baseline PD and degree of task focus. We capitalized on the fact that response time (RT) provides a continuously varying index of the efficiency of external attention. Assuming that offline cognition is associated with decoupling, then large PD should be associated with slower RT (P4). Moreover, based on brain imaging studies[24] suggesting that online and offline thought are discrete modes of cognition, we hypothesized (P5) that baseline PD should vary in a stepwise manner, rather than linearly, with RT. Individual subject RTs for correct WM responses in Experiments Two and Three were z-transformed, pooled (Figure 4a, main panel), and divided into five equal bins, the bin boundaries established using the cumulative RT distribution (Figure 4a, inset). We then computed the mean PD for each bin in the 1.5 second interval prior to the correctly responded probe. Only the very slowest RTs were associated with higher pre-probe baseline PD values; no other RT bins showed significant PD differences. This stepwise or binary relationship suggests that PD activity exhibits distinct modes of online and offline activity (P5).

Using PD as a neurocognitive marker, we tested five predictions derived from the decoupling hypothesis of offline thought. During online cognition, PD showed phasic increases to stimuli (P1). In contrast, during periods characterized by offline thought, PD did not change in response to external stimuli (P2) but instead showed high baseline levels of activity decoupled from task events (P3). The same high baseline activity in situations requiring task focus was associated with subsequent task errors and slower RT, indicating reduced attention to perceptual stimuli (P4). Finally, the stepwise relation between RT and PD suggested that online/offline thought represent distinct cognitive modes (P5). Our analysis provides clear evidence that PD exhibits a mode of spontaneous activity which is decoupled from task events and associated with reduced external attention.[3,6]

While other studies have indicated that offline thought leads to a disengagement from the external world [13-15, 25-27] our data are the first to document that both perceptual coupling and decoupling are apparent in the same neurocognitive measure. Importantly, the observation of cognitive engagement in the "non-demanding" CRT task indicates that this activity is likely to be involved in the initiation of spontaneous thought rather than reflecting an attempt to return attention to the task. Whether this decoupling represents a specific mechanism which keeps reality separate from mental simulations,[6] or arises because of the architecture necessary for conscious thought,[28] our data cannot address. However, regardless of the mechanism, the process of decoupling[3,6] provides an explanation for why the internal train of thought is not continually disrupted; the capacity to disengage cognition from physical reality prevents spontaneously generated mental content from being overshadowed by the continuing stream of sensory information.

Given the close correlation between PD and the dynamics of the brain NE system,[8,9] we suspect that the NE system plays a role in the decoupling process. During waking cognition the NE system has two distinct modes of function. In the *phasic* mode, LC activity is low except in response to task-relevant events and functions to reinforce goal focus. In contrast, in the *tonic* mode (which involves a high baseline firing rate), task disengagement occurs, allowing the agent the chance to search for alternative environmental goals.[6,7] Based on our data, the tonic mode of the NE system may aid the process that "tunes out" the present, thereby enhancing the capacity for the mind to wander.

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Methods

Pupil size and gaze direction were acquired using a Tobii 120 eye tracker (Tobii, Stockholm, Sweden) with a sampling rate of 125 Hz. Participants were seated on a comfortable chair, approximately half a meter from the eye tracker and did not use a chin rest or other immobilization device. Prior to data collection the eye tracker was calibrated to each individual using Tobii Studio. PD was computed for each sample as follows: if measurements from both eyes were recorded as "good" the two pupil diameters were averaged. If only one eye was "good" that measurement was used for PD at that time point. Any remaining times in which both eyes were flagged as "bad" were linearly interpolated. These gaps were generally short (due to either blinks or the hooding of the eye by eyelashes), and we employed a quality control process that rejected subjects with excessive amounts of interpolated data. The data was then median filtered (order 5) in order to remove spikes, and then low-pass filtered with a cutoff frequency of 10 Hz. Finally, data were z-transformed within participants; for participants performing both CRT and WM tasks (Experiment Two), both tasks were transformed together to retain task differences.

Experiment One. Forty-one participants (27 females, Mean Age 18.5(2)) completed and experience sampling study.

Experiment Two. Twenty-seven healthy (17 females, Mean Age 18.6(3)) participants completed the same versions of both the CRT and WM tasks while being eye tracked.

Experiment Three. Nineteen participants (Mean Age 19.5(3)) completed a twenty minute version of the WM task while being eye tracked.

No participants in any Experiment had neurological or psychiatric problems, all had normal or corrected to normal vision, and none were color blind. They were tested alone in a dim room with stable artificial lighting. Eye tracking participants (Experiments Two and Three) with more than 40% interpolated data were excluded, as were all participants whose accuracy was less than 50%, representing chance in both tasks.

Task

A schematic of the task is shown in Figure 1a. Stimuli were presented against a white background in 40 point Arial font. Non-probe stimuli were presented for 1000 ms followed by a fixation cross which varied in duration from 900-2300 milliseconds (mean duration 1500ms). Probes (either a "?" during WM or a colored number during CRT) followed between 2 and 5 black non-probe stimuli, and were presented in color (red or green, counterbalanced across tasks and participants) to reduce perceptual demands of probe detection. Probes were equally likely to follow an even or an odd digit in both tasks. Participants were instructed to respond only to the colored events, and to use the mouse to indicate if the number was odd (press the left button) or even (press the right button) and indeed no responses were made to the non-probes in either task. Task duration for all experiments was twenty minutes; each ten minute section contained 48 probes. Task order was counterbalanced in Experiments One and Two.

In the experience sampling study (Experiment One) all features of the task were identical with the exception that 18 odd/even probes were replaced with experience sampling probes. These probes asked participants to indicate whether, in the period immediately prior to the probe, they were thinking about (i) the task / here and now, (ii) task unrelated personal events in the past, (iii) task unrelated personal events in the future or (iv) abstract task unrelated thoughts with no temporal focus. Responses were recorded using the computer keyboard.

Table 1: Five predictions derived from the decoupling hypothesis of offline thought

Claim	Prediction	Experiment(s)	Figure(s)
During online cognition attention is coupled to task events	(P1) PD will increase as events in the task are encoded	One, Two	1b, 2a
During offline cognition attention is decoupled from task events	(P2) PD will not increase when events in the task are presented	One, Two	1b, 2a
	(P3) PD will show high baseline activity which is uncoupled from task events	One, Two	1a, 2b
Processing of spontaneously generated mental content requires decoupling of attention from external information	(P4) High baseline PD prior to probes will be indicative of slow correct responses and / or a failure to encode task events	Two, Three	3
States of on/offline cognition are distinct modes of thought	(P5) Baseline PD will show a nonlinear or stepwise relationship to continuous measures of external attention	Two, Three	4

Figure 1. Task description, experience sampling and motor response. (a) A schematic illustrating the choice reaction time (CRT, blue) and working memory (WM, red) tasks. In the CRT task, correct responses can be made without attention to the non-colored stimuli; this is not true in the WM task. **(b)** Results of Experiment One. Thirty participants who performed above chance for both the WM and CRT tasks were included in the analysis. Participants were asked on 18 occasions whether attention was focused on the here and now (the task), the future, or the past. A 2×3 analysis of variance (ANOVA) was conducted on the experience sampling data with two factors of task [WM / CRT] and three factors of experience [“Future”/ “Here and Now”/ “Past”]. This analysis indicated a Task × Experience interaction ($F(1, 29) = 8.51$, $p<.001$, $\eta^2 = .23$) in which thoughts of the “Here and Now” were more frequent in the WM task ($p<0.001$) and “Future” thoughts more prevalent in the CRT ($p<0.025$). “Past” thoughts did not vary across tasks ($p=.11$). **(c)** Scaled pupil diameter time locked to all responses in the WM and CRT tasks. Thirteen subjects from Experiment Two passed quality control cutoffs. Shaded regions indicate one standard error of the mean, and the response instant at t = 0 is indicated with a dashed line and arrow. In both the WM and CRT tasks the expected robust motor component[29] to pupil size is observed.

Figure 2. Task differences in baseline and evoked PD in the Working Memory and Choice Reaction Time tasks. (a) Thirteen participants from Experiment One passed the quality control cut-offs and are included in this analysis. Time courses locked to non-probe stimulus presentation were created for each trial for each individual and each task. Values were averaged into ten 250 ms bins and compared using a 2×10 ANOVA with factors of Task [2 levels] and Epoch [10 levels]. A significant Task×Time interaction (F (9, 108) = 4.05, p<.001, η^2 = .25) indicated differences in the pupil response to non-colored stimuli across the tasks. No other main effects or interactions were statistically significant (all p-values >.05). Contrast analysis examining the difference between conditions indicated the larger evoked response in the WM task accounted for 71% of the variance (F (1, 11) = 28.1, p<.001, η^2 =.71). (**b**) To examine tonic pupil size we compared the mean non-baselined PD in the 1.5 seconds prior to the presentation of non-colored stimuli. An ANOVA including the task order as a comparison revealed that PD was substantially higher in the CRT than the WM task (F (1, 11) = 6.78, p<.05, η^2 =.38). Neither the main effect of task order nor the interaction between task order and task was significant (all p-values >.05).

Figure 3. Baseline differences in PD are larger prior to incorrect responses to WM probes. Scaled pupil diameter prior to correct and incorrect responses in the CRT (**a**) and WM **(b)** tasks. Twenty-nine participants from Experiments Two and Three passed the quality control cut-offs and were included here. Time courses for each trial for each subject, locked to probes, were calculated for correct and incorrect responses during the WM task. The 1.5 s interval prior to the probe was divided into ten 150 ms bins, as in Figure 2A. Experiment number (Two / Three) was included as a between participants variable in the ANOVA. A main effect of accuracy ($F(1, 25) = 11.0$, $p<.005$, $\eta^2 = .31$) indicated that baseline PD was higher prior to incorrect responses and there was no effect of time, experiment, or their interaction.

Figure 4. Extremely slow response times to correct WM probes are associated with high baseline PD. (a) Reaction times (RTs) to all 2103 correct working memory responses (Experiments Two and Three) were within-subject z-transformed and then pooled. These RTs were divided into five equal mass bins, whose boundaries were determined using the cumulative RT distribution (inset) are denoted by the colored areas in the main panel. **(b)** Binned, mean scaled PD for the 1.5 second window before correct WM probes, plotted against median bin RT. ANOVA including Experiment (Two / Three) as a between-participants variable and participant as a random effect indicated a significant effect of pupil size on subsequent RT ($F(4, 108) = 7.02$, $p<.001$, $\eta^2 = .19$). No main effects or interactions (experiment number, participant, etc.) were significant (all p-values>.05). Post-hoc comparisons (Bonferroni corrected) among the ANOVA results indicated that the slowest bin differed significantly from all other bins except the fourth bin (all corrected p-values <.05). No other inter-bin differences were significant (all p-values > .05).

Figure 1

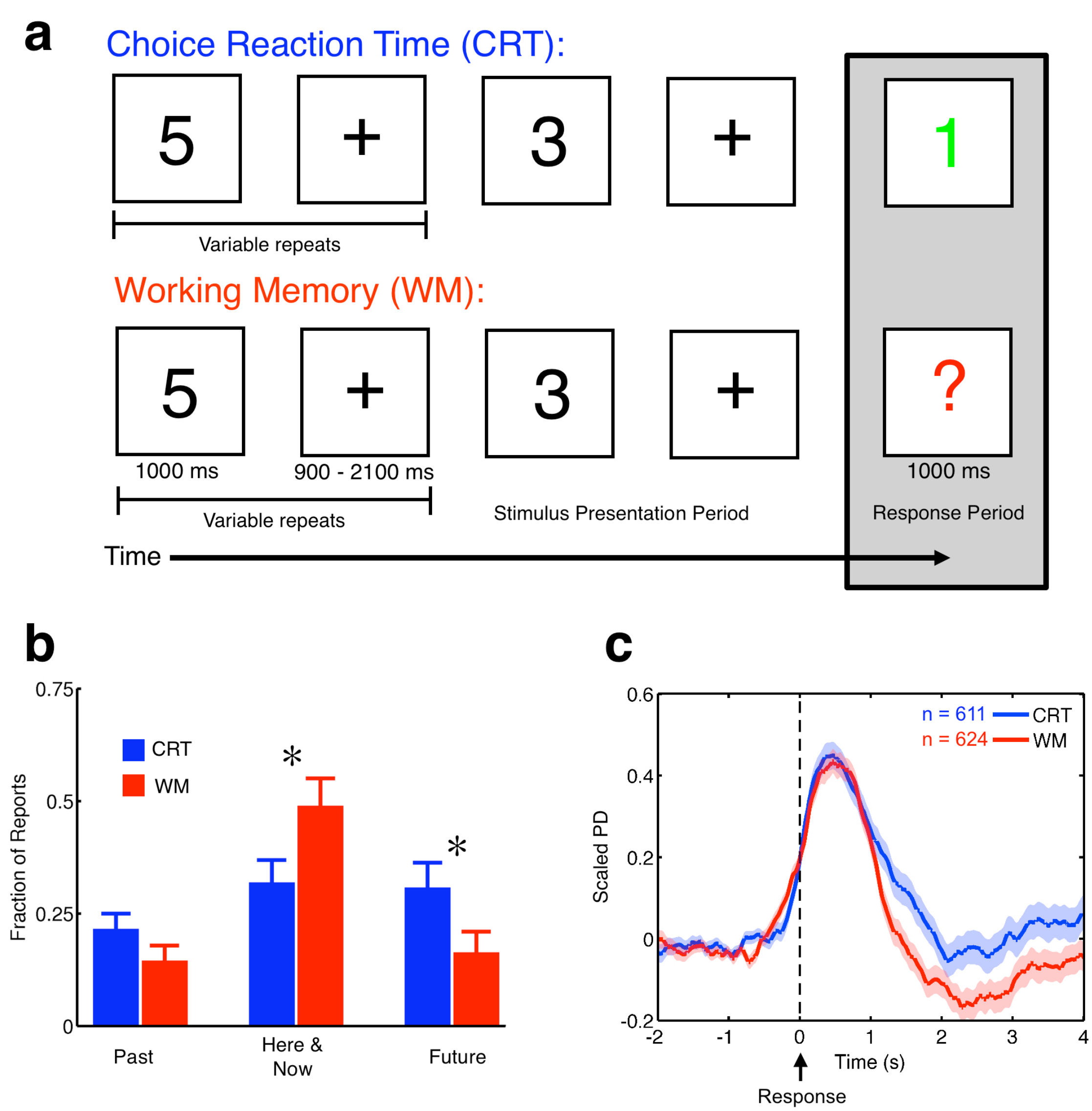

a
Choice Reaction Time (CRT):
5
+
3
+
1
Variable repeats
Working Memory (WM):
5
+
3
+
?
1000 ms
900 - 2100 ms
1000 ms
Variable repeats
Stimulus Presentation Period
Response Period
Time
b
Fraction of Reports
0.75
0.5
0.25
0
CRT
WM
*
*
Past
Here & Now
Future
c
Scaled PD
0.6
0.4
0.2
0
-0.2
n = 611 CRT
n = 624 WM
-2
-1
0
1
2
3
4
Time (s)
Response

Figure 2

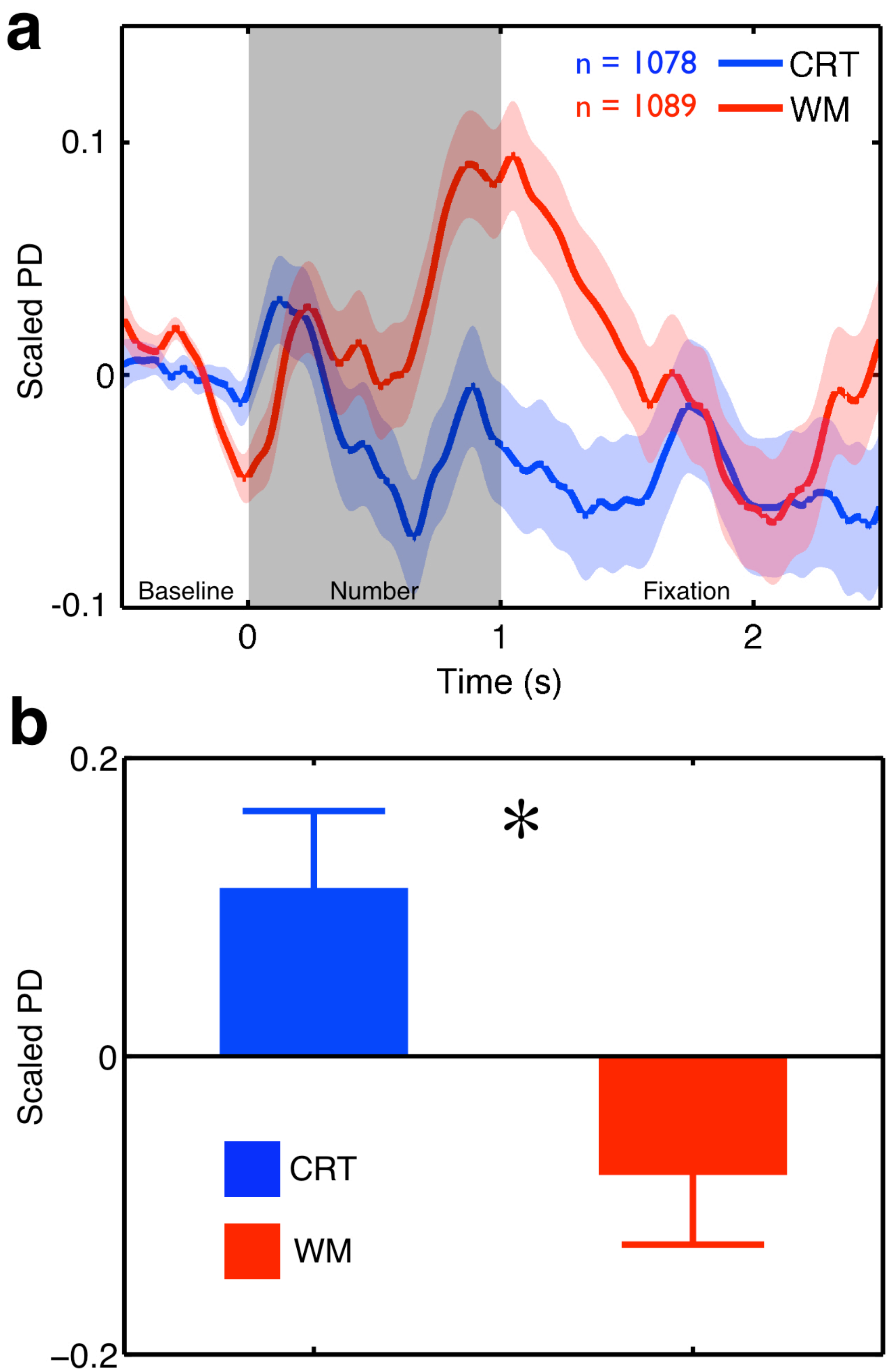

a
n = 1078
CRT
n = 1089
WM
0.1
0
-0.1
Scaled PD
Baseline
Number
Fixation
0
1
2
Time (s)
b
0.2
0
−0.2
Scaled PD
*
CRT
WM

Figure 3

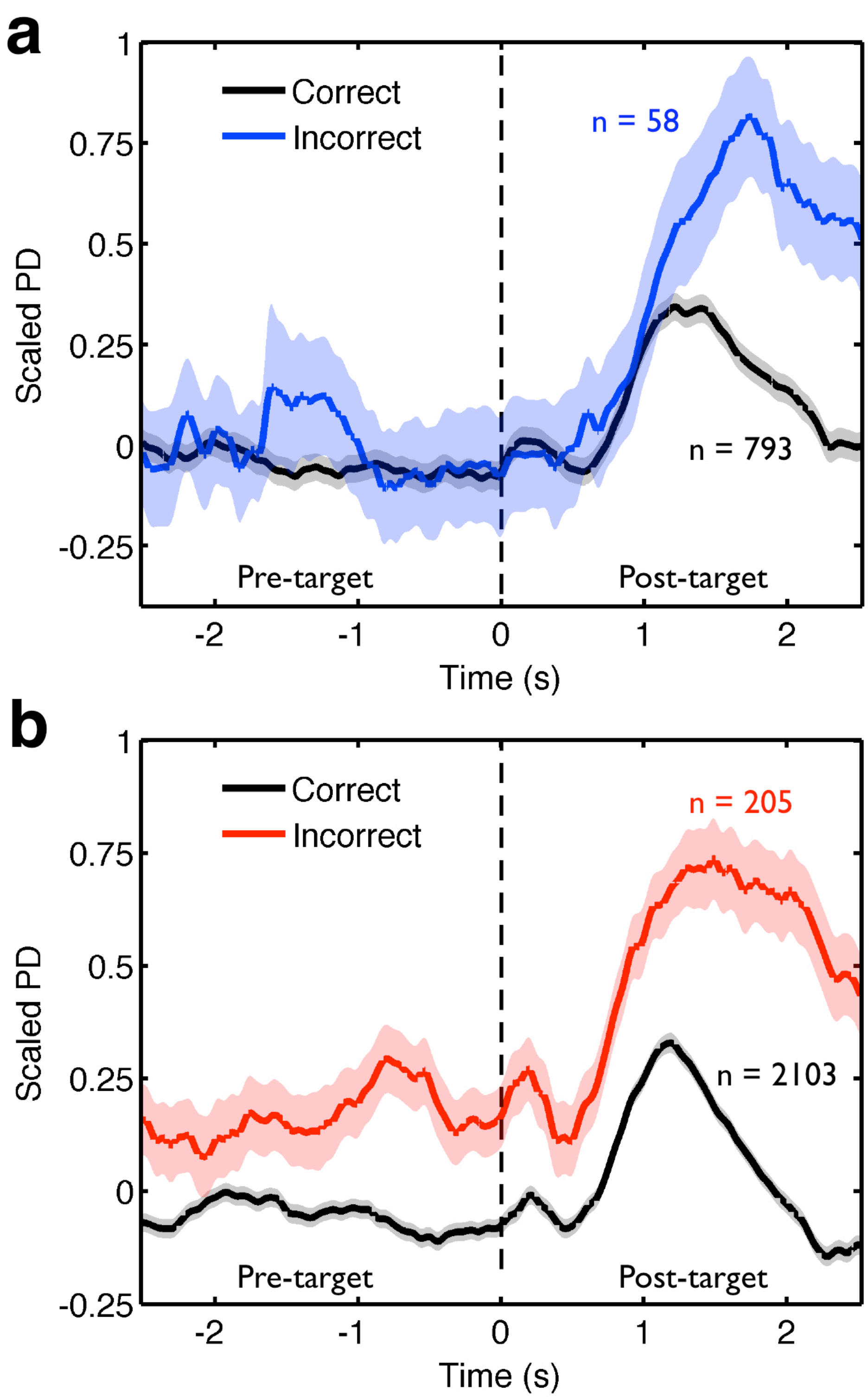
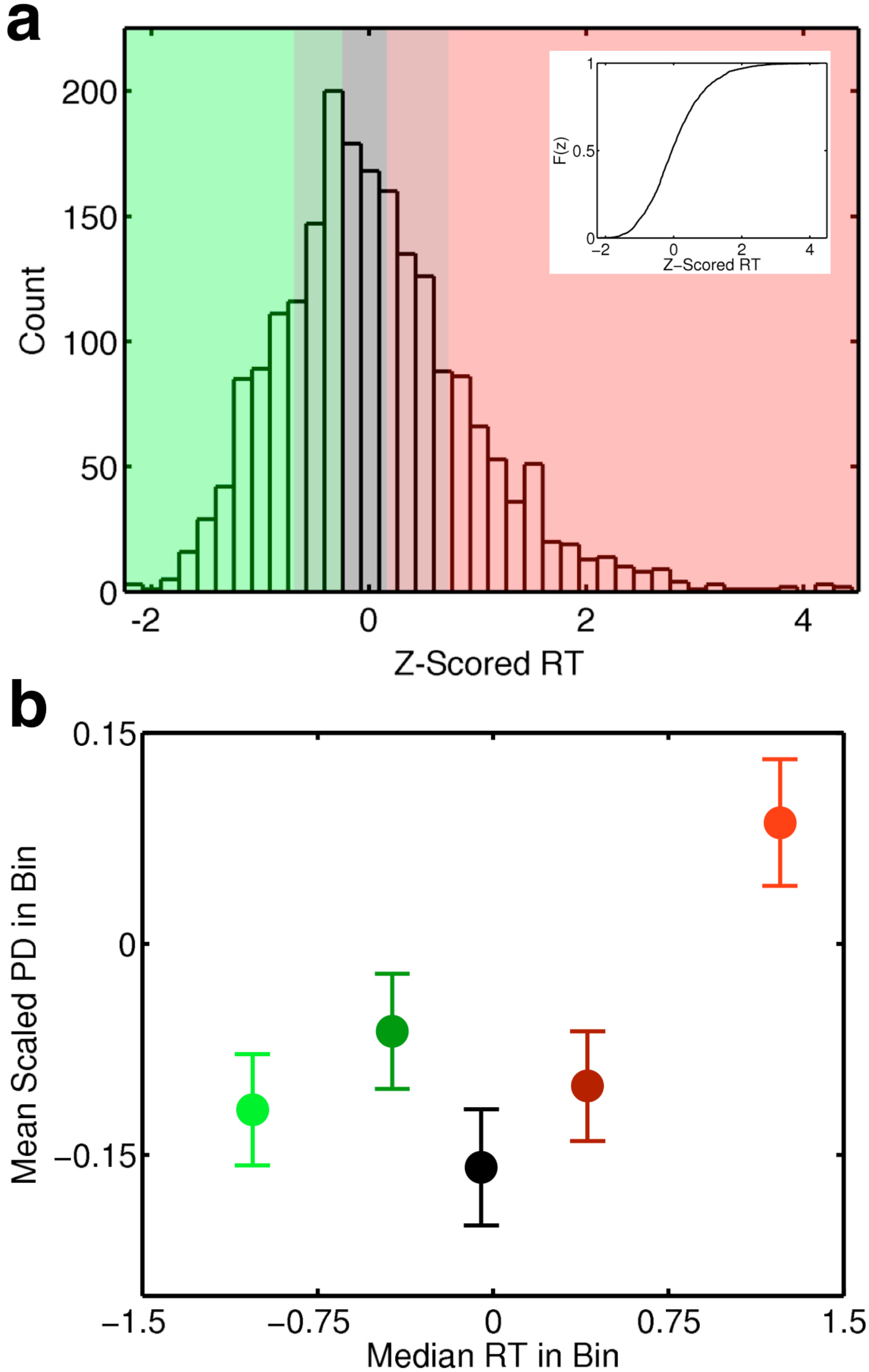

a
1
0.75
0.5
0.25
0
-0.25
Scaled PD
Correct
Incorrect
n = 58
n = 793
Pre-target
Post-target
-2
-1
0
1
2
Time (s)
b
1
0.75
0.5
0.25
0
-0.25
Scaled PD
Correct
Incorrect
n = 205
n = 2103
Pre-target
Post-target
-2
-1
0
1
2
Time (s)

Figure 4


a
200
150
100
50
0
Count
-2
0
2
4
Z-Scored RT
1
F(z)
0.5
0
−2
0
2
4
Z−Scored RT
b
0.15
0
−0.15
Mean Scaled PD in Bin
−1.5
−0.75
0
0.75
1.5
Median RT in Bin