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## Prediction errors bidirectionally bias time perception

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## **Prediction errors bidirectionally bias time perception**

Ido Toren, Kristoffer C. Aberg, Rony Paz

Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel

### **Abstract**

Time perception and prediction errors are essential for everyday life. We hypothesized that their putative shared circuitry in the striatum might enable these two functions to interact. We show that positive and negative prediction errors bias time perception by increasing and decreasing perceived time, respectively. Imaging and behavioral modelling identifies this interaction to occur in the putamen. Depending on context, this interaction may have beneficial or adverse effects.

Correspondence should be addressed to: R.P (rony.paz@weizmann.ac.il)

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27 Time perception in the sub-second range is essential for many animal behaviors<sup>1</sup>.  
28 Subjective perception is affected by motivational and emotional states, which usually increase  
29 perceived duration<sup>2,3</sup>. Learning is driven by efficient processing of reinforcement signals, and  
30 mainly by prediction error(PE)<sup>4,5</sup>: outcomes can be better than expected, a positive prediction  
31 error (PE+), or worse than expected, a negative prediction error (PE-). Although classically  
32 independent processes, recent studies suggest time perception and PE might be related<sup>6,7</sup>.  
33 Time perception engages striatal regions and their dopaminergic inputs<sup>8,9</sup>, and neural  
34 correlates of PEs have been found in the same circuits. Moreover, PE+/PE- have been  
35 associated with increased/decreased activation of dopaminergic neurons, respectively<sup>4,10</sup>, and  
36 perceived duration could be increased/decreased by activation/deactivation of dopaminergic  
37 neurons<sup>11</sup>. In addition, time perception is compromised in Parkinson disease and other basal-  
38 ganglia/dopamine related disorders<sup>12,13</sup>. We therefore hypothesized that signed prediction  
39 errors would differentially affect the perceived duration of a stimulus, and that such bias  
40 would be associated with differential striatal activity.

41 Participants determined which of two sequentially presented images is of longer  
42 duration in a 2-alternative-forced-choice paradigm (2AFC, Fig.1a). There were two types of  
43 trials: ‘Short-Long’ (SL) where the duration of the first image was shorter, and ‘Long-Short’  
44 (LS). The difference in time duration between the two images ( $\Delta t$ ) varied across trials. Each  
45 image was overlaid by a number indicating a monetary gain or loss.

46 Assuming a reference-dependent model of value where subjects learn to predict the  
47 relative outcome<sup>14,15</sup>, the value of the first image serves as a reference point for predicting the  
48 value of the second image. Therefore, a prediction error would be PE+ if the difference  
49 between the images’ values is larger than expected, and PE- if the difference is smaller than  
50 expected. A PE0 occurs when the difference was as expected. Importantly, a trial’s outcome  
51 was determined only by the numbers presented on the images and was completely  
52 independent of the time discrimination performance (correct/incorrect). A first study  
53 established the behavioral bias, and a consecutive fMRI study replicated the behavior and  
54 elucidated the neural correlates (n=18/35).

55

56 *An opposite bias of PE+ and PE- on perceived duration*

57

58 Because discrimination is easier for larger values of  $\Delta t$ , we indeed found a significant  
59 main effect of  $\Delta t$  (Fig.1b; no significant interaction between PE-type and  $\Delta t$ , or three-way  
60 interaction). In line with our hypothesis, we found a significant interaction between PE type  
61 and Trial type (SL/LS) (Fig.1c). This result was robust for each group separately (behavior-  
62 only and fMRI), and also when considering the different PE magnitudes (Extended Data  
63 Fig.1,2,3).

64

65 What drives this interaction between PE type and Trial type? In our design, the PE  
66 occurs only when the second stimulus appears. Therefore, in SL trials when the value induces  
67 a PE+/PE-, if the image is perceived as longer/shorter, it would lead to a perceived  
68 larger/smaller  $\Delta t$  between the two stimuli resulting in easier/harder discrimination and hence  
69 better/worse performance. For LS trials, PE+/PE- would induce the opposite change in  
70 perceived  $\Delta t$  resulting in an opposite effect on performance.

71

72 Accordingly, we observed better performance in SL trials for PE+ compared to PE-  
73 and to PE0, and trials with PE- showed worse performance compared to PE0. The opposite  
74 pattern occurred in LS trials: performance was worse in PE+ compared to PE- trials and to  
75 PE0 trials, and PE- showed better performance compared to PE0 (Fig.1c).

74 Together, the results demonstrate that PE+ and PE- induce an increase and decrease in the  
75 perceived stimulus duration, respectively.

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### 77 *The contribution of order, individual thresholds, value and expectation*

78

79 A second consecutive stimulus may bias the perceived duration of the first stimulus,  
80 termed Time-Order Error (TOE). Here, this would induce more errors in SL trials because the  
81 first image would be perceived as longer (Fig.1c; Extended Data Fig.4a,5). To account for  
82 this, we quantified the individual TOE and normalized performance accordingly (Fig.1c-  
83 Inset; Fig.1d; Extended data Fig.5). As expected, the main effect of Trial type was no longer  
84 significant, nor was the interaction between Trial type and  $\Delta t$ , whereas all other results, and  
85 importantly the significant interaction between PE type and Trial type, remained significant  
86 (Fig.1c-inset, Fig.1d).

87 We further accounted for individual differences by normalizing the objective  $\Delta t$  by  
88 each subject's just-noticeable-difference (JND). All findings were replicated using the  
89 individually-normalized psychometric curves (Fig.1e, Extended data Fig.1e,2e,3e). There was  
90 no overall change in perceptual thresholds (Extended Data Fig.6b), indicating that the bias is  
91 due to the instantaneous PE imposed in a trial.

92 We performed several control experiments to confirm that the bias is due to PE,  
93 rather than to valence or the outcome of the second image. First, we found that if the  
94 difference between the 1<sup>st</sup> and the 2<sup>nd</sup> image is predictable (even if it holds value), time  
95 perception is not altered (Extended Data Fig.6b; Supp. Information). Second, the results were  
96 replicated in a similar experiment but when all values were positive, i.e. where PE+/PE-  
97 include only gains. Finally, the results were replicated when the value in the second image  
98 was fixed, and PE+, PE0, or PE- were respectively induced by different values on the first  
99 image (Extended Data Fig.7). Therefore, time perception is biased by the processing of signed  
100 PEs, and not by the valence (gains/losses) or the magnitude.

101

### 102 *Modelling the PE-time bias and brain activations*

103

104 To provide a trial-by-trial and individual information, we adapted a reinforcement-  
105 learning (RL)-based approach that considers main factors affecting the perceived duration: the  
106 objective time difference ( $\Delta t$ ), the bias due to PE ( $\theta$ ), and the TOE ( $\epsilon$ ). According to the main  
107 findings, PE- decreases the perceived duration of the second image, which  
108 decreases/increases the perceived difference in SL/LS trials, respectively; and an opposite  
109 bias occurs in PE+ trials (Fig.1f). The Expected Value (EV) is the expected difference  
110 between the value in the second and the first images throughout the experiment, and is  
111 updated on a trial-by-trial basis (Extended Data Fig.4b). The probability of making a correct  
112 discrimination is then modeled by a logistic function and fitted individually for each subject.  
113 This model successfully captured individual behavior (Fig.2a,b; Extended Data Fig.2f, 3f),  
114 performance (Fig.2c), and TOE (Fig.2d). The bias magnitude ( $\theta$ ) was similar across PE+ and  
115 PE- (Fig.2e). To further validate the model accuracy, notice it estimates a continuous PE  
116 value, and we therefore replicated the main result (PE-type\*Trial-type interaction) with  
117 several different thresholds ( $|\text{PE0}| < 0.005/0.01/0.1/0.2/0.5$ ).

118 Using the model-derived trial-by-trial PEs as parametric modulators, we identified  
119 brain regions previously shown to be involved in PE encoding: the ventral striatum, midbrain,  
120 and dorsal ACC (Fig.2f, Extended Data Fig.8, Supplementary Table 1).

121 In addition, we used the estimated probability for a discrimination-error as reflecting  
122 fluctuations of uncertainty in the perceptual task, and found a negative correlation (higher  
123 activation with low error-probability) in Brodmann 47 (Fig.2g-right) and between the nucleus  
124 accumbens and ventral ACC (Fig.2f-left), previously implicated in perceptual confidence  
125 (Supplementary Table 2). These findings strengthen the model validity and show that it  
126 integrates prediction error and time estimations in our task to capture variability in perceptual  
127 judgements.

#### 128 129 *Putamen activity corresponds to the PE-time bias*

130  
131 Because both time perception and prediction error involve striatal activity, we  
132 hypothesized that interaction in the striatum could contribute to the PE-time bias. We  
133 therefore conducted a whole-brain analysis using two-way ANOVA with factors PE type and  
134 performance (incorrect/correct), designed to identify regions that underlie the effect of PE  
135 leading to differences in performance, namely the PE time perception bias.

136 We found a significant interaction between PE type and performance in the putamen  
137 (Fig.3a). During PE+ trials, activation in the putamen was increased for incorrect compared to  
138 correct discriminations, whereas during PE- trials the putamen was de-activated for incorrect  
139 compared to correct judgements. This was the case both when including PE0 trials and when  
140 omitting them. Moreover, the individual difference in putamen activity between PE+ and PE-  
141 was correlated across correct and incorrect trials (Fig.3b). A significant interaction was also  
142 found in the dorsal ACC (Fig.3c, Supplementary Tables 3,4) with individual relationship  
143 when considering separately PE+ vs. PE0 and PE0 vs. PE- (Fig.3d).

144 Finally, to further establish a link between regional activations and the behavioral PE-  
145 time bias, we quantified the interaction in putamen activity and correlated it with the  
146 behavioral bias at an individual level (Fig.3e,f: lower-insets). These results suggest a direct  
147 link between interaction of activity in the putamen for PE and time duration, and the  
148 behavioral bias that PE induces on time perception.

#### 149 *Conclusions*

150  
151 Our findings provide evidence that prediction errors bias time perception, and suggest  
152 that interaction between these two fundamental functions is driven by interaction in striatal  
153 activations. We found a bidirectional effect, where a positive prediction error results in over-  
154 estimation of duration, and negative prediction error results in under-estimation of duration.  
155 These findings calls for revisiting the notion that arousal alone, during either negative<sup>16</sup> or  
156 positive stimuli<sup>17</sup>, dictates longer perceived duration, and that predictability may induce  
157 shorter perceived duration<sup>18</sup>. The bidirectional bias that accompanies signed prediction error  
158 cannot be accounted for by absolute (attention-like) signals. A more integrative mechanism  
159 that combines differential patterns of attention due to valence, saliency<sup>19</sup>, information<sup>20</sup>, and  
160 unpredictability<sup>18</sup>, might account for our findings.

161 Because both these processes are essential for daily tasks, the impact of such biases  
162 on learning and memory formation that rely on computations of predictions errors on one  
163 hand and on estimating durations on the other, can be of major importance. Therefore, the  
164 overlap in striatal activity that underlies the behavioral bias can either be an evolutionary  
165 benefit or an unfortunate by-product, for example, by influencing temporal-difference  
166 learning<sup>6,7</sup>. Abnormal interactions in striatal circuits underlying time duration and PE driven  
167 learning can therefore underlie and contribute to psychopathologies.

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175

176 **Author contribution**

177 I. T. and R. P. designed the study. I. T. performed the experiments and analyzed the data.

178 K.C.A. contributed ideas for analysis. I. T., K.C.A. and R. P. wrote the manuscript.

179

180 **Declaration of interests**

181 The authors declare no competing interests.

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## Figure legends

### Figure 1. Prediction errors bidirectionally bias time perception.

- a. The 2AFC time-discrimination task. Example of Short-Long (SL) trial with PE0 (left) or with PE+ / PE- (right).
- b. Proportion of discrimination errors as a function of objective time difference between the two images ( $\Delta t$ ), averaged across all trials separately for each PE-type. Shown is the main effect of  $\Delta t$  (3-way ANOVA,  $F_{4,208} = 98.7$ ,  $p < 10^{-46}$ ,  $\eta^2 = 0.65$ ). Upper two insets show two individual subjects (all trials). Lower inset shows the proportion of discrimination errors in the first and second half of the experiment, indicating no change in perception throughout the experiment.
- c. Proportion of discrimination errors as a function of PE type and Trial type. An interaction between PE type and Trial type ( $F_{2,104} = 19.04$ ,  $p < 10^{-7}$ ,  $\eta^2 = 0.268$ ). SL trials: mean PE+ = 0.32, mean PE- = 0.49, mean PE0 = 0.43. Better performance in PE+ vs. PE- ( $p < 10^{-5}$ , Cohen's  $d = 0.79$ ) and PE0 ( $p = 0.0001$ , Cohen's  $d = 0.61$ ), worse performance in PE- compared to PE0 ( $p = 0.02$ , Cohen's  $d = 0.36$ ). LS trials: mean PE+ = 0.33, mean PE- = 0.22, mean PE0 = 0.275. Worse performance in PE+ vs. PE- ( $p = 0.0004$ , Cohen's  $d = 0.56$ ), and better performance in PE- compared to PE0 ( $p = 0.02$ , Cohen's  $d = 0.39$ ). Main effect of Trial type due to Time-Order Error (TOE) ( $F_{1,52} = 26.19$ ,  $p < 10^{-5}$ ,  $\eta^2 = 0.33$ ). Inset: after correction for individual TOE, no main effect for Trial type, whereas the main interaction remains (PE type x Trial type:  $F_{2,104} = 19.04$ ,  $p < 10^{-7}$ ,  $\eta^2 = 0.268$ ).
- d. Proportion of discrimination errors as a function of ( $\Delta t$ ), separately for LS and SL trials and corrected for TOE. PE+ and PE- bias performance in opposite directions relative to PE0, for all values of  $\Delta t$ .
- e. Proportion of discrimination errors as a function of subjective Just-Noticeable-Difference (JND), corrected for TOE, fitted to a logistic function after JND normalization, and replicating the main finding (PE type \* Trial-type,  $F_{2,96} = 17.26$ ,  $p < 10^{-6}$ ,  $\eta^2 = 0.264$ ).
- f. Schematic representation of the PE-time bias and the model. Right and left sides of the scheme represent LS and SL trials, respectively. Rectangles represent perceived duration of the images, with colors indicating different factors affecting the perceived duration: Gray represent the objective reference duration ( $t$ ); Yellow denotes the time difference  $\Delta t$  added to the first or second image; Blue represent the change in the first image due to the TOE; and Pink represent the bias due to PE ( $\theta$ ), added or subtracted for PE+ or PE- (the main finding). Last row shows the prediction for the perceived duration, denoted by a dashed rectangle. Inset shows real data, same as (c).

Error bars and error bands represent SEM (n=53).



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**Figure 2. Modelling the PE-time bias**

- a. Model fit to individual behavioral data, averaged over all subjects (n=53). Data points represent mean  $\pm$ SEM, lines represent average over model fits  $\pm$  SEM.
- b. Two subjects' (rows) behavior and model fit. Left: model-derived probability of error, with blue/red circles indicating actual correct/incorrect discrimination, respectively. Right: actual outcome overlaid on model-derived expected value.
- c. Difference between model-derived PE values is correlated between correct and incorrect trials, validating individual model-derived values (Pearson,  $r = 0.95$ ,  $p < 10^{-28}$ ).
- d. The correlation between model-estimated TOE and that computed directly from behavior (Pearson, behavior-only group:  $r = 0.73$ ,  $p < 10^{-3}$ ; fMRI group:  $r = 0.83$ ,  $p < 10^{-5}$ ).
- e. The correlation between the bias computed separately for PE+ and for PE- trials (Pearson correlation; behavior-only group:  $r = 0.73$ ,  $p < 10^{-3}$ ; fMRI group:  $r = 0.83$ ,  $p < 10^{-5}$ ). The bias magnitude was also similar (two-samples t-test;  $t_{51} = -1.1$ ,  $p = 0.26$ ). We therefore used a single bias in the model.
- f. Brain ROIs where activation correlates with trial-by-trial model-derived PE+ signals (n=35). Time courses represent mean % signal change extracted from the ROIs  $\pm$  SEM. Black vertical lines represent trial onset, offset and average onset of next trial, respectively. Activation was set to statistical threshold of  $q = 0.055$  for visualization.
- g. Activations in ventrolateral PFC/OFC (right) and NAc/vACC (left) correlate with model-derived probability for correct discrimination (n=35). Average activation  $\pm$  SEM for correct and incorrect choices is plotted below, showing higher activation for correct discriminations. Inset shows the mean probability for discrimination error.

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**Figure 3. Putamen activity underlies PE-time interaction and behavioral bias**

- a. Activation in the anterior right putamen is associated with an interaction between PE-type (PE+, PE-) and time discrimination accuracy (correct or incorrect responses). Mean parameter estimates (beta) for PE-type and performance extracted from ROI. Also shown are the corresponding time-course activations. Inset shows individual data points. Error bars represent SEM (n=35).
- b. Individual-subject putamen activations (extracted from the above ROI) for PE+/PE- in incorrect vs. correct discrimination trials, showing an interaction between PE type and performance at an individual level (Pearson;  $r = 0.45$ ,  $p = 0.005$ ).
- c. Same as (a) for the dorsal anterior cingulate cortex (dACC; n=35). Inset shows individual data points.
- d. Individual subject dACC activations (extracted from the above ROI) for PE+/PE0 (left) and PE0/PE- (right) in incorrect vs. correct discrimination, showing an interaction between PE-type and performance at an individual level (Pearson; PE+/PE0:  $r = 0.37$ ,  $p=0.03$ ; PE-/PE0:  $r = 0.6$ ,  $p<0.0001$ ).
- e. Individual interaction score for putamen activity is correlated with the individual behavioral bias ( $\theta$ ). Shown is the distribution of p-values using bootstrap (two-sided test, 20% with  $p<0.05$ , dashed red line and red bars, significantly different than expected,  $p<0.001$ , Fisher's test). Upper inset show the significantly right-skewed distribution of the correlation coefficients. Lower inset shows the correlation for the original data.
- f. Same as in (d) when the model includes a separate bias for PE+ and for PE- ( $\theta+$  and  $\theta-$ ), revealing an even closer match between behavioral bias and activation patterns in the Putamen (42% with  $p<0.05$ ,  $p<0.001$ , Fisher's test).

355

## 356 **Methods**

357

### 358 **Experimental design**

#### 359 *Participants*

360 Eighteen (18) healthy participants (5 males) participated in the behavior-only group  
361 and 35 healthy right-handed participants (15 males) participated in the imaging group (fMRI).  
362 Additionally, 19 participants (8 males) participated in a gain-only control group. Subjects'  
363 age varied between 22-40. In the imaging group, mean age was 26 and median age was 25.  
364 No statistical methods were used to pre-determine sample sizes but our sample sizes are  
365 similar to those reported in previous publications. All studies were approved by the Helsinki  
366 committee of the Sourasky medical center, protocol number 0287-09-TLV (Ministry of health  
367 protocol #HT5271), and further approved by the IRB of the Weizmann Institute. All  
368 participants had normal or corrected-to normal vision and reported no attention deficit  
369 hyperactivity disorder (ADHD). Informed consent was obtained from all participants prior to  
370 the experiment. Participants were compensated for their time, and according to the  
371 accumulation of gains and losses in the experiment (but no less than the minimum payment as  
372 determined in the protocol). Compensation was independent of the performance in the time  
373 discrimination task. All investigators were blind to any group, subject or sequence allocation  
374 during data collection and analyses. One participant in the imaging group was unable to  
375 complete the fMRI scan due to unexpected stress inside the magnetic field and another  
376 participant could not complete the scan due to extensive movements, and both had been  
377 excluded.

378

#### 379 *Visual stimuli*

380 White images with black numbers displayed in the center of the image were presented  
381 on a gray background. The images were identical in size, presented in the center of a 21''  
382 screen with refresh rate of 60 Hz (lag smaller than 1ms), and spanning a visual angle of  
383 approximately 5.1° x 3.8°, with a red fixation cross displayed before the image appears. In all  
384 tests stimulus presentation was implemented by MATLAB (R2014b, MathWorks) using the  
385 Psychophysics Toolbox<sup>21,22</sup>.

386

#### 387 *Time duration discrimination paradigm*

388 Two images were presented sequentially with 0.5sec delay between them. After the  
389 presentation of the second image, participants had to determine which image had been  
390 presented for a longer duration (Fig. 1a). One image was always displayed for a duration of  
391 500 ms – the 'reference' duration, whereas the other image was presented for 500ms plus an  
392 additional duration ( $\Delta t$ ). Because the Just Noticeable time Difference (JND) in time duration  
393 discrimination tasks have been reported to range around 15-20% of the standard duration<sup>23,24</sup>,  
394 we set  $\Delta t$  in the present experiment to range from 0 ms (equal presentation time for both  
395 images) to 133 ms, corresponding to  $\Delta t$  of 0-26.6% of the 500 ms reference duration.

396 To generate prediction errors, numbers representing monetary gains and/or losses  
397 were overlaid on each image. The first image was always presented with the number zero,  
398 while the number of the second image could be negative - generating (PE-); zero - generating  
399 no PE (PE0), or positive - generating (PE+). To create a baseline expectation of the difference  
400 between values overlaid on the images (2<sup>nd</sup> image – 1<sup>st</sup> image), a large proportion of trials  
401 were PE0 trials (60% in the behavior-only group and 80% in the imaging group), with an

402 equally smaller proportion of trials being PE+ and PE- trials. For the behavior-only group,  
403 PEs were generated by presenting numbers ranging from -5 to +5, in steps of 0.5. For the  
404 imaging group, to avoid loss-aversion effects<sup>25</sup> in brain activity, we used twice the magnitude  
405 of PE+ compared to PE-<sup>26</sup>, and PEs were generated by presenting either -2 (PE-), 0 (PE0), or  
406 +4 (PE+). There was a uniform distribution of presentations across PE values (i.e. all values  
407 were presented in a similar number of trials; with the exception of PE0 trials). Moreover, the  
408 number of trials for each  $\Delta t$  was equal across PE values, with a counterbalanced and fully  
409 random order of presentation. Randomization of trials was used for all participants. For the  
410 imaging group, we used OPTSEQ2 software to determine sequence of trials and inter-trial-  
411 intervals prior to the experiment, and every subject was randomly assigned to a one of the  
412 generated sequences. The accumulation of monetary gains and losses corresponded to an  
413 actual monetary compensation provided at the end of the experiment. Importantly, the  
414 monetary compensation was independent of the performance on the duration discrimination  
415 task.

416

#### 417 *Gain only group*

418 The paradigm for this group is largely similar to the main paradigm described above,  
419 with the following modifications: First, values on the images were positive only (+1,+2,+4),  
420 meaning that participants could only gain money in each trial. In addition, whereas for the  
421 other groups we fixed the value in the first image, here we allowed different values also in the  
422 first image. Specifically, in SL trials the first image was always overlaid with the number  
423 (+2), while the number of the second image could be either (+1) - generating (PE-); (+2) -  
424 generating no PE (PE0), or (+4) - generating (PE+). In LS trials, in contrast, the second image  
425 was always overlaid with the number (+2), while the number of the first image could be either  
426 (+1) - generating (PE+); (+2) - generating no PE (PE0), or (+4) - generating (PE-). Finally, as  
427 in the main group, 80% of the trials were PE0 trials, with an equally smaller proportion of  
428 trials being PE+ and PE- trials, and the  $\Delta t$  was varied in the same range and distribution, with  
429 one additional value of 83ms, corresponding to 16.6% of reference duration (500ms).

430

#### 431 *Just Noticeable Difference (JND) paradigm*

432 JND estimates for each participant represent the minimal difference in time duration  
433 between two stimuli that can still be detected with high probability. Two psychophysical  
434 methods were used to estimate the JND in the present study. First, we used a one-up-two-  
435 down staircase procedure<sup>27</sup>. Specifically, in each trial two images were presented sequentially  
436 (one for 500 ms, the other for 500ms+ $\Delta t$ ). If participants correctly discriminated which image  
437 was presented for the longer duration, the order of presentation was reversed, and if  
438 participants again made a correct discrimination,  $\Delta t$  was decreased by an adaptive amount of  
439 time. Whenever an incorrect discrimination was made,  $\Delta t$  was increased by the same amount  
440 (up to a maximum of 250 ms). Initial  $\Delta t$  was determined on 125 ms, with a 10% decrease of  
441 the step size after every trial (regardless of participants' discrimination accuracy). This  
442 process repeats itself until a stopping criterion of correct discrimination after cumulative 6  
443 previous errors have been reached (number of trials was not limited), at which point a  
444 threshold has been determined which yields an expected value of 0.707 probability of making  
445 a correct discrimination. Of note, while numbers were presented on the images at all times,  
446 monetary gains and losses were only associated with the numbers at the test conducted at the  
447 end of the experiment (see *Procedure* below). The second procedure used the method-of-  
448 constant-stimuli (MCS) in which a fixed set of pre-determined  $\Delta t$ 's (identical to main

449 paradigm) were used. Otherwise, the presentation of images was similar as before. The  
450 resulting data was then used to generate a psychometric curve for each participant, by fitting a  
451 generalized linear regression of the responses to a binomial distribution, and the threshold  
452 was defined as the  $\Delta t$  in which participants had a 0.707 probability of making a correct  
453 discrimination.

454

#### 455 *Constant-loss (no surprise) condition*

456 Following the main task, all participants in the imaging group performed 40  
457 additional trials using the same paradigm as in the main task, except that the second image  
458 value was always -2 while the first image value was always 0. This condition was designed to  
459 generate a ‘constant loss’ condition, where the trials are identical to PE- trials except of the  
460 predicted nature of outcomes. We therefore hypothesized that performance in ‘constant loss’  
461 trials would resemble performance during main task PE0 trials, but would be different than  
462 performance during main task PE- trials, even though the images and outcomes are identical.

463

#### 464 **General procedure**

##### 465 *Behavior-only group*

466 Following general instructions, a JND time duration discrimination threshold was  
467 first estimated for each participant. JND estimate using the staircase procedure was conducted  
468 with a zero number overlaid on both images, and two additional JNDs were estimated using  
469 two MCS procedures of 40 trials each. In one of the MCS procedures, both the first and the  
470 second image had the number zero, while in the other MCS procedure the first image was  
471 presented with the number zero, while a random number was presented on the second image.  
472 This allowed us to control for threshold, visual confounds and value (Extended Data Fig.6a).  
473 Next, participants performed the time duration discrimination paradigm.

474

##### 475 *Imaging group*

476 The procedure of the imaging group is largely similar to behavior-only group, with  
477 the following modification: JNDs were estimated outside the MRI scanner, before and after  
478 the main paradigm, and for all images and pairs. In the second estimation of JND (but not the  
479 first), after the scan, participants gained and lost money based on the numbers presented on  
480 the image, thus allowing us to control for reward value confounds. The time duration  
481 discrimination task and the ‘constant loss’ task was performed while undergoing fMRI  
482 scanning. Minimum of three training trials were provided inside the scanner to allow  
483 participants to become accustomed to the scanner.

484

##### 485 *Gain-only group*

486 The procedure of the gain-only group was similar to the procedures described above:  
487 following instructions, a JND threshold was estimated using a staircase method followed by a  
488 time-duration discrimination paradigm. At the end of the experiment, the JND was re-  
489 evaluated.

490

#### 491 **TOE measures from behavior**

492 A well-established perceptual phenomena is the Time Order Error (TOE), which  
493 predicts that the duration of the first stimulus in a sequence of stimuli with equal durations, is  
494 perceived as longer as compared to succeeding stimuli durations<sup>28,29</sup>.

495 TOE can be defined as the difference in probability of successful discrimination as a function  
 496 of Trial-type (i.e., Short-Long or Long-Short):  
 497

$$[1] \quad TOE = \frac{p(R_{10}|S_{10}) - p(R_{01}|S_{01})}{2}$$

498  
 499 Where  $R_{10}$  represent a response that the first stimulus is longer, and  $S_{10}$  represent LS trial, i.e.  
 500 first stimulus is longer.  $R_{01}$ ,  $S_{10}$  represent the opposite response (i.e. the second stimulus is  
 501 longer) given a SL trial.

502 To compute the above we extracted individual performance during PE0 trials separately for  
 503 every  $\Delta t$ , and used the resulted TOEs to correct the probability of discrimination error in all  
 504 PE-type trials (Fig. 1c-inset, 1d, Extended Data Fig. 1b-inset, 1d, 2b-inset, 2d, 3b-inset, 3d):  
 505

$$[2] \quad \begin{aligned} corrected\_p(dt)_{SL} &= observed\_p(dt)_{SL} - TOE(dt) \\ corrected\_p(dt)_{LS} &= observed\_p(dt)_{LS} + TOE(dt) \end{aligned}$$

506  
 507 Consequently, positive and negative TOE in time duration discrimination occurs if the first  
 508 stimulus is perceived as having a longer and shorter duration, respectively. In our experiment,  
 509 we found positive TOE across all  $\Delta t$ 's (Extended Data Fig. 4a), thus offering an explanation as  
 510 to why the probability of making a mistake when  $\Delta t=0$  (i.e. the duration of both images is  
 511 identical) is different than chance level and opposite between LS and SL trials (Extended  
 512 Data Fig. 1c, 2c, 3c). Specifically, when the duration of the first image was longer (LS trials),  
 513 TOE causes an even longer perceived duration, generating easier trials (larger perceived  $\Delta t$ ).  
 514 By contrast, when the duration of the first image is shorter (SL trials), TOE causes a shorter  
 515 perceived duration, leading to more difficult trials (smaller perceived  $\Delta t$ ).  
 516 To compute unbiased behavioral TOE (and compare it to the model-derived estimate), we  
 517 took the intersection between performance in PE0 trials and 0.5 proportion of discrimination  
 518 errors at  $\Delta t = 0$ .  
 519

## 520 **Computational Modeling**

521 Performance (the probability of making an incorrect discrimination) was modeled as  
 522 a logistic function<sup>24,30,31</sup>:  
 523

$$[3] \quad p(\Delta t) = \frac{1}{1 + e^{-f(\Delta t)}}$$

524  
 525 We assume that performance depends linearly on  $\Delta t$ , i.e. larger  $\Delta t$  leads to better  
 526 performance:  
 527

$$[4] \quad f(\Delta t) = b_1(\Delta t) + b_2$$

528  
 529 Next, we address other parameters that could influence the perceived  $\Delta t$ .  
 530 First, we included the Time Order Error (TOE). We found positive TOE across all  $\Delta t$ 's  
 531 (Extended Data Fig. 4a), which predicts that the duration of the first stimulus is perceived as  
 532 of longer duration. TOE was here modeled by the parameter  $\varepsilon$ .  
 533 Second, the bias in time duration discrimination due to PE, here denoted by the parameter  $\theta$ ,  
 534 is caused by the mismatch between the difference in outcomes presented in first and the

535 second image ( $2^{\text{nd}} - 1^{\text{st}}$ ), and the expected outcome difference. Namely, the value of the  
 536 prediction error on trial  $i$  was computed as the difference between the actual presented values  
 537 and current estimation of expected value (EV):  
 538

$$[5] \quad PE_i = (R_i - EV_{i-1})$$

539 Where  
 540

$$[6] \quad R_i = R_{i,2^{\text{nd}} \text{ image}} - R_{i,1^{\text{st}} \text{ image}}$$

541 EV was initialized to 0 and was updated on every trial using a learning-rate parameter  $\alpha$ :  
 542  
 543

$$[7] \quad EV_i = EV_{i-1} + \alpha * (R_i - EV_{i-1})$$

544 Our results indicate that PE+ and PE- cause the duration of a stimulus to be perceived as  
 545 longer and shorter, respectively. Accordingly, PE+ decreases performance in LS trials  
 546 (causing the perceived duration of the second stimulus to be more similar to that of the first  
 547 stimulus), and vice versa in SL trials. Incorporating  $\varepsilon$  and  $\theta$  into the model gives the  
 548 following expression:  
 549  
 550

$$[8] \quad f(dt) = b_1(\Delta t_i + k_1(\varepsilon + \theta * PE_i)) + b_2$$

551 Where  
 552

$$k_1 = \begin{cases} -1, & SL \text{ trials} \\ 1, & LS \text{ trials} \end{cases}$$

553 Finally, one additional parameter  $\gamma$  was added to the model to account for a ceiling effect  
 554 observed in LS trials (in these trials performance is initially much closer to the perceptual  
 555 threshold (JND) due to TOE, thus might be bounded). The final model looks as follows:  
 556  
 557

$$[9] \quad f(dt) = (b_1 - \gamma) * (\Delta t_i + k_1(\varepsilon + \theta * PE_i)) + b_2$$

558 Where  
 559

$$\gamma = \begin{cases} \gamma, & SL \text{ trials} \\ 0, & LS \text{ trials} \end{cases}$$

560 The model is then plugged into the logistic probability function and estimated  
 561 separately for every subject.  
 562

563 Model parameters were estimated by computing the maximum a-posteriori (MAP)  
 564 probability using MATLAB's function *fmincon* (MathWorks). We assumed uniform prior on  
 565 the parameters and used bounds as follows:  
 566

$$\begin{aligned} b1 &\in [-20,20] \\ b2 &\in [-20,20] \\ \gamma &\in [-10,10] \\ \theta &\in [-2,2] \\ \varepsilon &\in [-2,2] \end{aligned}$$

$$\alpha \in [0,1]$$

567

568 To make sure that results are not biased due to outliers, we repeated the estimation process  
569 with a Gaussian distribution over each parameter with a mean 0 and variance X, where X  
570 equals to the bound described above for every parameter (e.g.,  $\theta$  was modeled as  $N(0,2)$ ).  
571 Finally, we also computed unconstrained maximum likelihood of the parameters with no  
572 priors and no bounds (except from the learning rate which remained bounded) using  
573 MATLAB's function *fminunc*. All results are highly similar with respect to model fit and  
574 parameters values.

575

576 fMRI data acquisition

577 Images were acquired on a 3T Siemens MAGNETOM Tim-Trio scanner. Functional  
578 T2\* weighted images were acquired using a gradient-echo EPI sequence (TR = 2000 ms, TE  
579 = 30 ms, flip angle = 75°, 32 slices with 10% gap scanned in a descending order with phase  
580 encoding direction anterior-to-posterior at 30° toward coronal from anterior commissure–  
581 posterior commissure (ACPC) plane<sup>32</sup>, slice thickness 3 mm, voxel size 3x3x3 mm, FOV 216)  
582 in 5 separate scanning sessions (up to two minutes between sessions). Anatomical T1-  
583 weighted images were acquired after the functional scans (TR = 2300 ms, TE = 2.98 ms, flip  
584 angle = 9°, voxel size 1x1x1 mm, FOV 256). The anatomical scan covered the whole brain  
585 while functional scan covered the whole brain except a small area in the dorsal part of the  
586 parietal lobe. To improve signal-to noise ratio of the event-related design, order of trials and  
587 Inter-Trial-Interval (ITI) in the scanner was determined using OPTSEQ2<sup>33</sup>.

588 All imaging data were preprocessed and analyzed using Brain Voyager QX 3.4 (Brain  
589 Innovation Maastricht, The Netherlands<sup>34</sup> and MATLAB R2014a (MathWorks) with  
590 BVQX/Neuroelf toolbox v1.0 (Jochen Weber, <http://neuroelf.net/>). Preprocessing included  
591 slice scan time correction, motion correction and high-pass filtering. Images were then co-  
592 registered and normalized into Talairach space<sup>35</sup> and spatially smoothed with an isotropic 6  
593 mm FWHM Gaussian kernel.

594

## 595 **Statistical analysis**

### 596 *Data analysis*

597 Performance on the time duration discrimination task was estimated as the proportion  
598 of incorrect discriminations for each combination of PE-type (PE+, PE-, PE0), Trial-type  
599 (SL/LS), and  $\Delta t$ . These results were then analyzed via repeated measures ANOVAs with  
600 these factors and performance as the dependent variable. Post-hoc tests were done using  
601 Tukey-Kramer test, effect sizes were estimated by Cohen's d or  $\eta^2$ , and null results were  
602 estimated by Bayes Factor. Data distribution was assumed to be normal but this was not  
603 formally tested. Trials in which no response was made were discarded from analysis.

604

### 605 *Normalization to JND*

606 The objective  $\Delta t$  was normalized by each subject's staircase Just-Noticeable-  
607 Different (JND) measured at the beginning of the experiment. Normalization for every  
608 individual was done as follows:  $\Delta t$  values in ms were transformed to individual JND units,  
609 interpolated for a range of [0-1.5] JND and then fit to a logit function. Four (4) participants  
610 with no valid Just-Noticeable-Difference (JND) measure were pre-excluded from this  
611 analysis.

612



613

614 *fMRI data analysis*

615 Analyses consist of random effects Analysis of variance (ANOVA) based on general  
616 linear models (GLM), with event regressors defined from the onset of the first image until the  
617 offset of the second image, models as box-car functions and convolved with a canonical  
618 hemodynamic response function (HRF). All models included 6 regressors to account for head  
619 movements and a regressor to account for the motor response, modeled from the onset of the  
620 cue until the subject's response.

621 Multiple comparison correction on cluster size was done using non-parametric permutation  
622 test<sup>36,37</sup>. Null distribution of maximal cluster size was built separately using 1000 iterations  
623 for every analysis (PE x Correctness interaction, all trials with probability weights as  
624 parametric modulators). On every iteration, all labels of all trials were randomly shuffled for  
625 every subject, and a GLM for every voxel was computed using the same definitions as in  
626 main analysis. Finally, ANOVA model was created and maximum cluster size was extracted  
627 (direct or diagonal proximity in one dimension was sufficient to include voxels in same  
628 cluster) using the MATLAB function *bwlabeln*. Cluster Defining Threshold (CDT) level was  
629 set on  $p < 0.005$ .

630 Analysis using trial-to-trial PE estimates as parametric modulations consist of separate  
631 contrasts for PE-types and was corrected for multiple comparisons using false discovery rate  
632 of  $q < 0.05$ . Three (3) participants were pre-excluded from the trial-by-trial fMRI analysis  
633 because their modelled learning rate was zero, generating a regressor of zeros which cannot  
634 be included in this analysis.

635

636 *Computational model selection*

637 Our computational models were built to track trial-to-trial probability of  
638 discrimination error, corresponds to the behavioral measure used in analyses.

639 We tested 5 variations of the model:

640 Model 1 – The selected model (6 parameters;  $b_1, b_2, \alpha, \varepsilon, \theta, \gamma$ ).

641 Model 2 – no free parameter  $b_2$  (5 parameters).

642 Model 3 – no  $\gamma$  (5 parameters).

643 Model 4 – no  $b_2$ , no  $\gamma$  (4 parameters).

644 Model 5 – Separate parameters for the bias due to PE+ ( $\theta^+$ ) and PE ( $\theta^-$ ) (7 parameters).

645

646 For each model, AIC (Akaike Information Criterion) was estimated using the computed  
647 likelihood of the model for each subject regulated by the number of parameters. AICs were  
648 used as model evidence in a Bayesian Model Selection for group studies<sup>38</sup>, in which the  
649 exceedance probabilities of all models (i.e., the probability that each model is more frequent  
650 in the population than other models) is estimated. Results indicated a 0.98 probability for  
651 model 1 to be the model best explaining the evidence, therefore it is the selected model.

652

653 *Assigning PE-type to trials according to the computational model*

654 In order to generate different trial types according to the modeled PE, trials were  
655 categorized based on the sign and the magnitude of the estimated PE. Since almost no trials  
656 estimated precisely PE=0, and in order to assign enough trials for all PE types to generate a  
657 valid statistic, we selected a threshold for which a trial with absolute value of PE smaller than  
658 that threshold would be assigned as a PE0 trial, and PE larger or smaller would be assigned as  
659 PE+ and PE- trials, respectively:

660

$$\begin{aligned} |PE_i| < \text{threshold} &: \text{trial } i \text{ is PE0} \\ PE_i \leq -\text{threshold} &: \text{trial } i \text{ is PE-} \\ PE_i \geq \text{threshold} &: \text{trial } i \text{ is PE+} \end{aligned}$$

661

662 A threshold of 0.1 was chosen since it produced a similar proportion of PE0 trials as in the  
663 actual design. To make sure that this selection did not bias the results, we also tested  
664 thresholds of 0.2, 0.5, 0.01, and 0.005. All tests resulted in the same main effects and  
665 interactions except the three-way interaction which wasn't significant for low (below 0.05)  
666 thresholds. This indicates a robust PE type statistic across different levels of classification.  
667

#### 668 *Correlation between individual interaction activations and behavioral bias*

669 We calculated an interaction-score for each subject's Putamen activity and correlated  
670 it with the individual behavioral bias ( $\theta$ ) derived from the model:  
671

$$\begin{aligned} [10] \quad & \text{Interaction\_activity\_score} \\ & = (\beta(\text{PE+}, \text{Correct}) - \beta(\text{PE-}, \text{Correct})) - (\beta(\text{PE+}, \text{InCorr}) \\ & \quad - \beta(\text{PE-}, \text{InCorr})) \end{aligned}$$

672

673 Where  $\beta(\text{PE+}, \text{Correct})$  is the average regional activity in trials of PE+ with correct  
674 response, and so forth. The Interaction\_activity\_score provides an approximate individual  
675 quantification of the interaction found in the imaging analysis (PE\_TYPE \* performance). To  
676 establish robustness of this measure we performed a bootstrap by resampling a different set of  
677 subjects every time and re-calculating the correlation between the Putamen interaction-factor  
678 and the behavioral bias for each subset of subjects. The distribution of the correlation  
679 coefficients and their respective p-values was estimated using Fisher's test.  
680

#### 681 *Reporting Summary*

682 Further information on research design is available in the Nature Research Reporting  
683 Summary linked to this article.  
684

#### 685 *Code availability*

686

687 Custom code for behavioral and imaging tests is available from the corresponding author  
688 upon reasonable request.  
689

#### 690 *Data availability*

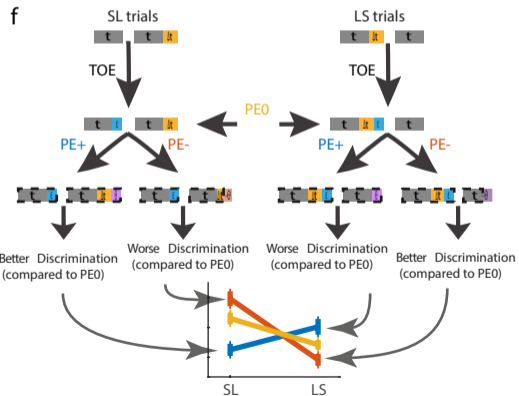
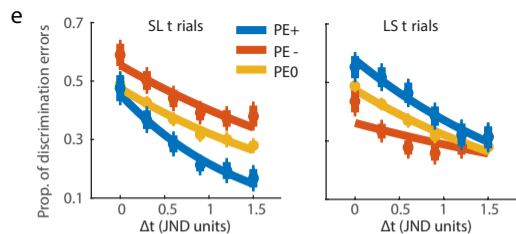
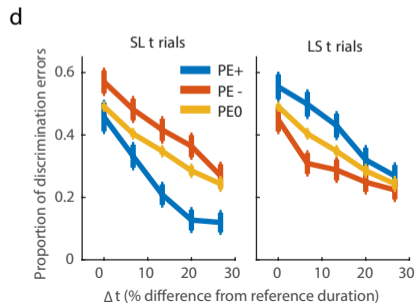
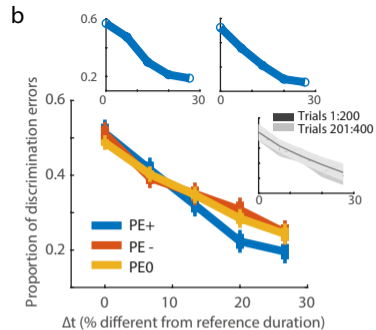
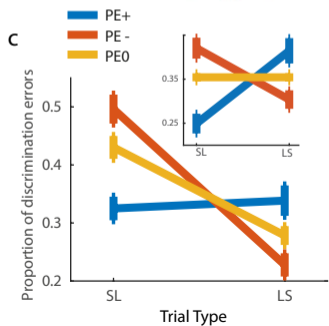
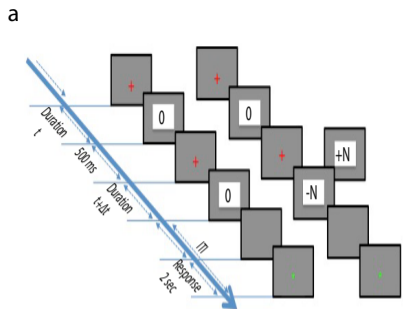
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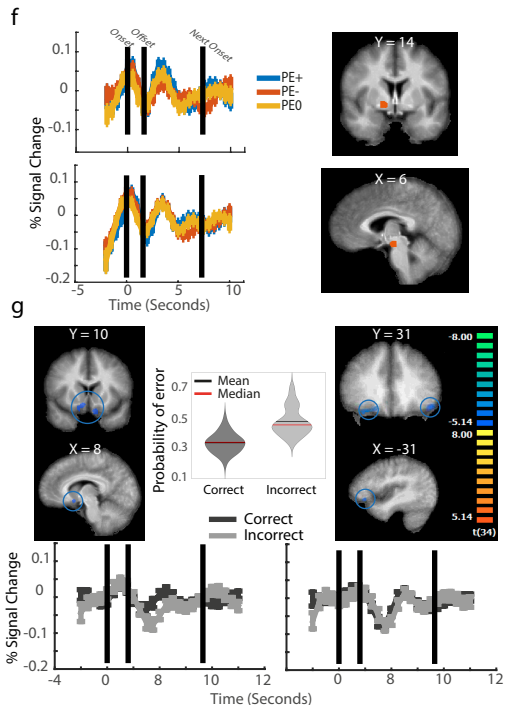
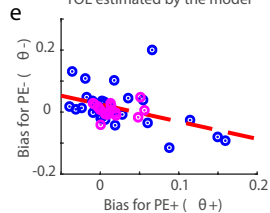
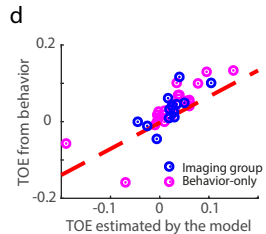
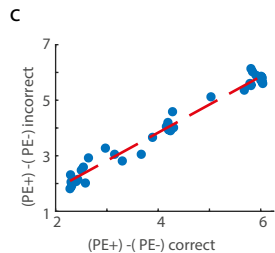
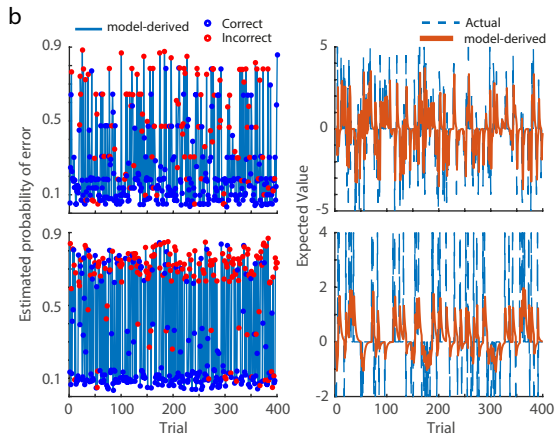
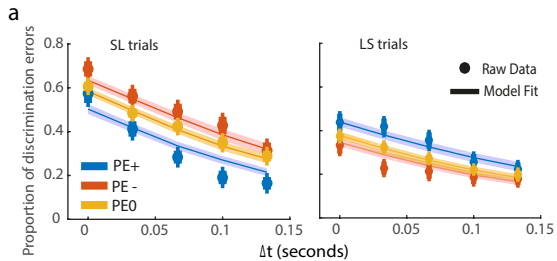
692 All data supporting the findings of this study are available from the corresponding author  
693 upon reasonable request.  
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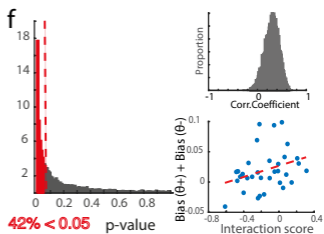
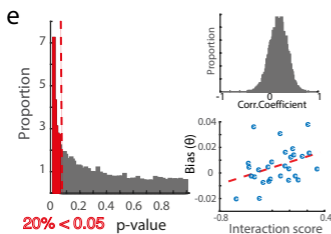
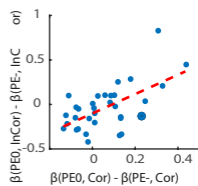
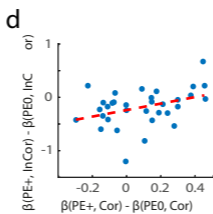
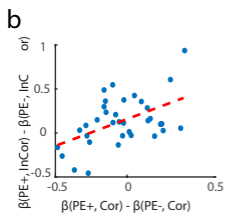
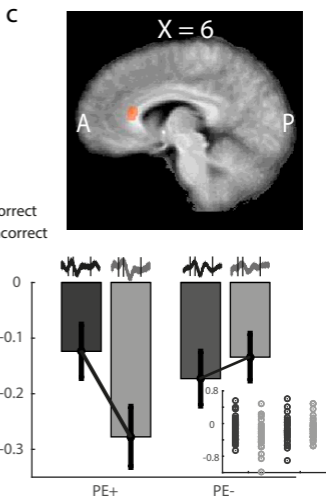
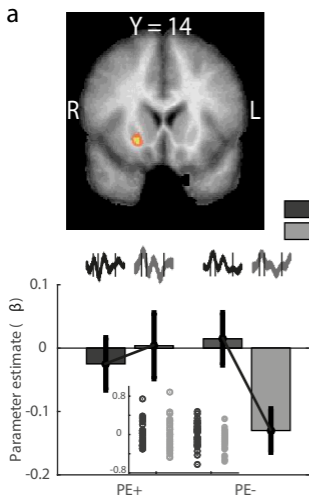
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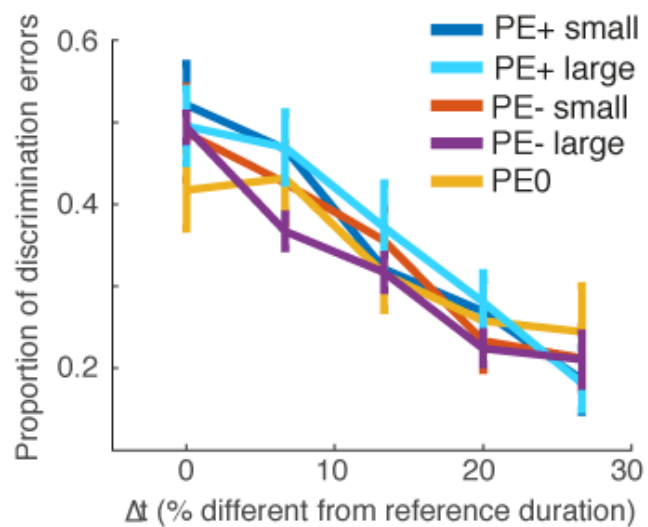
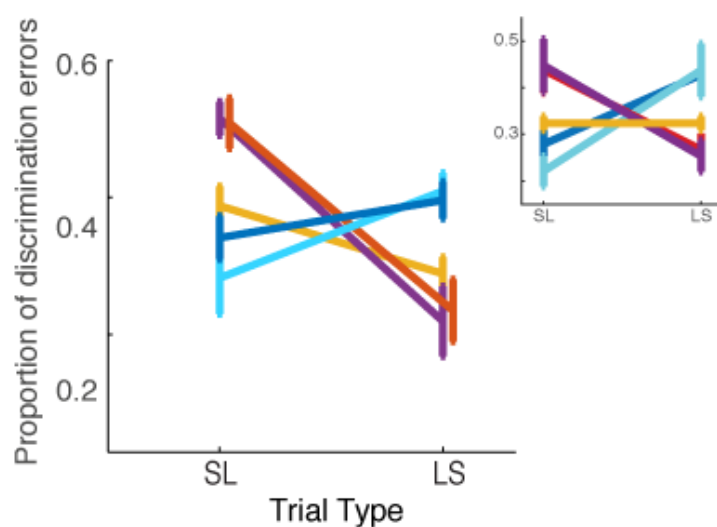
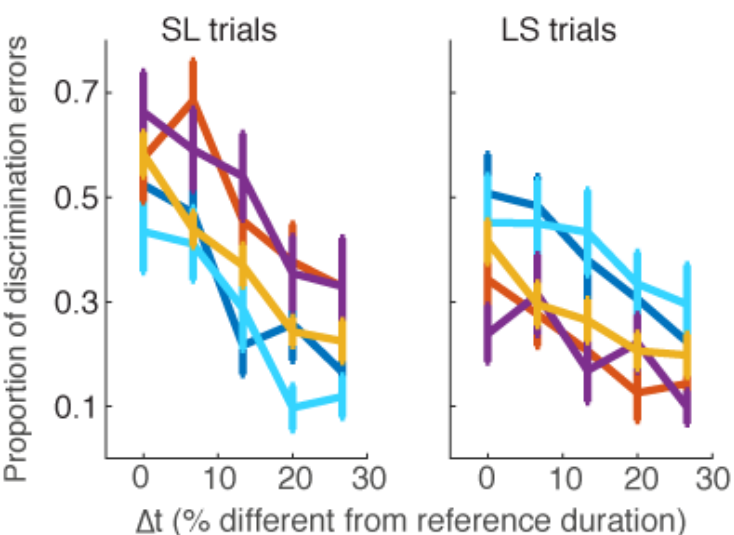
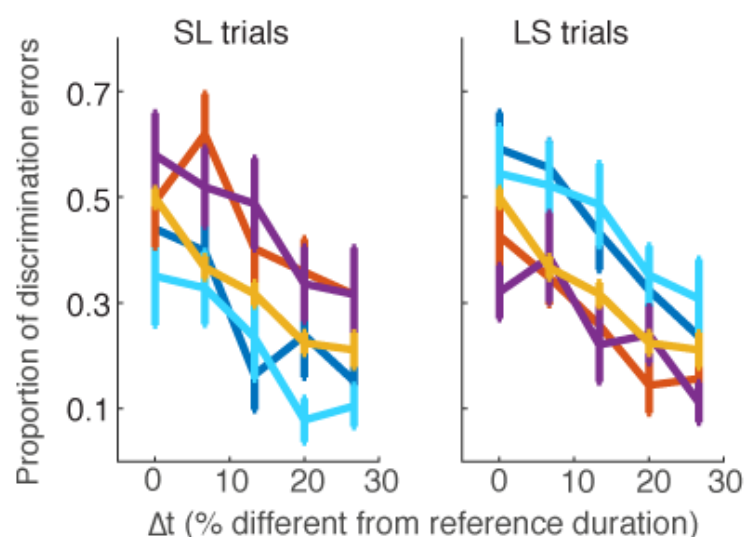
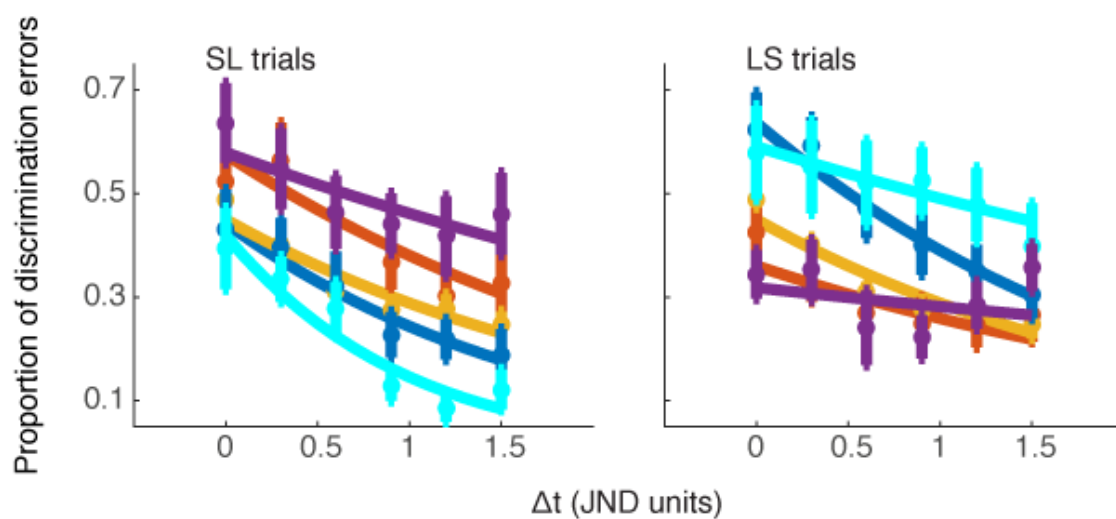
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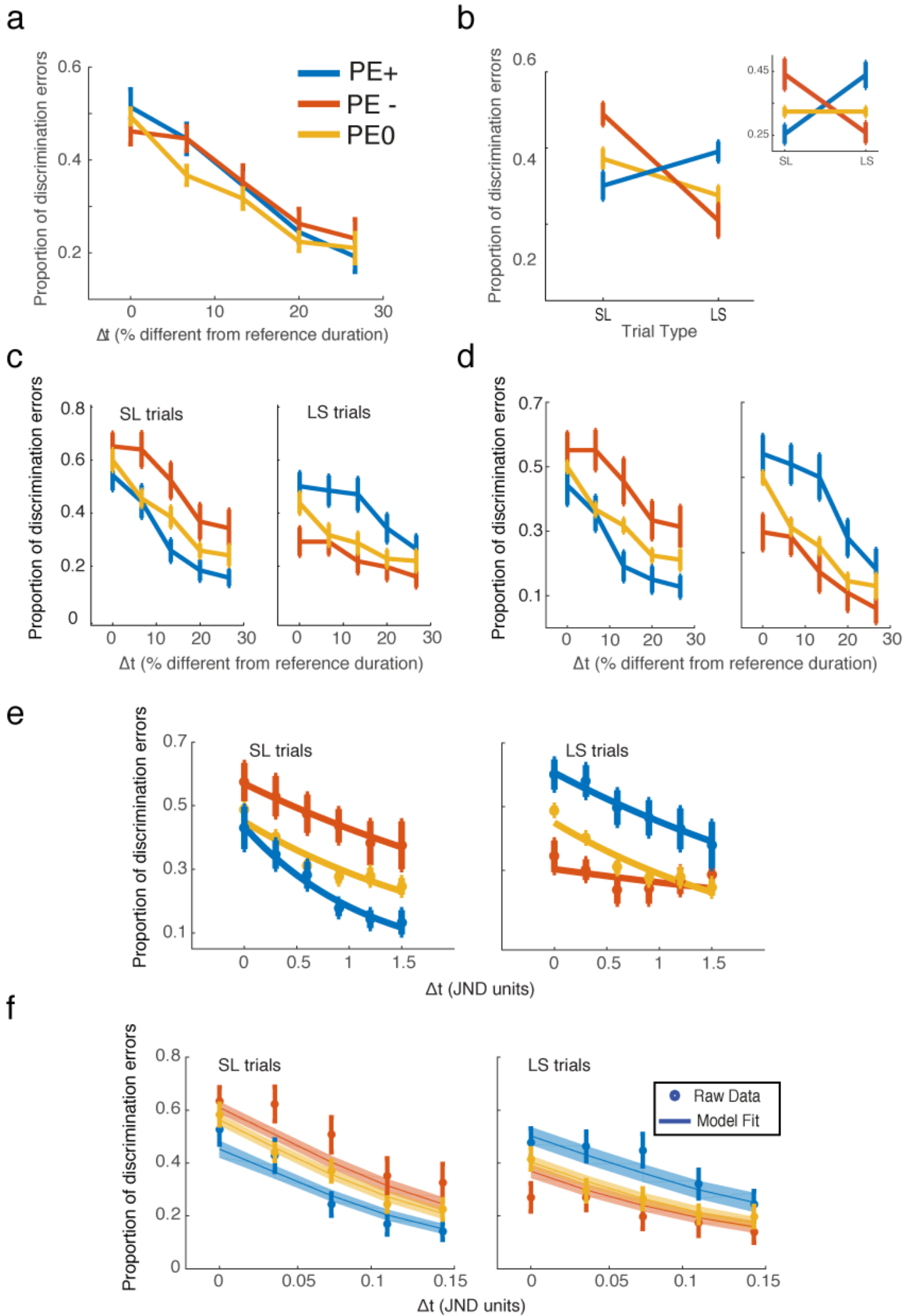
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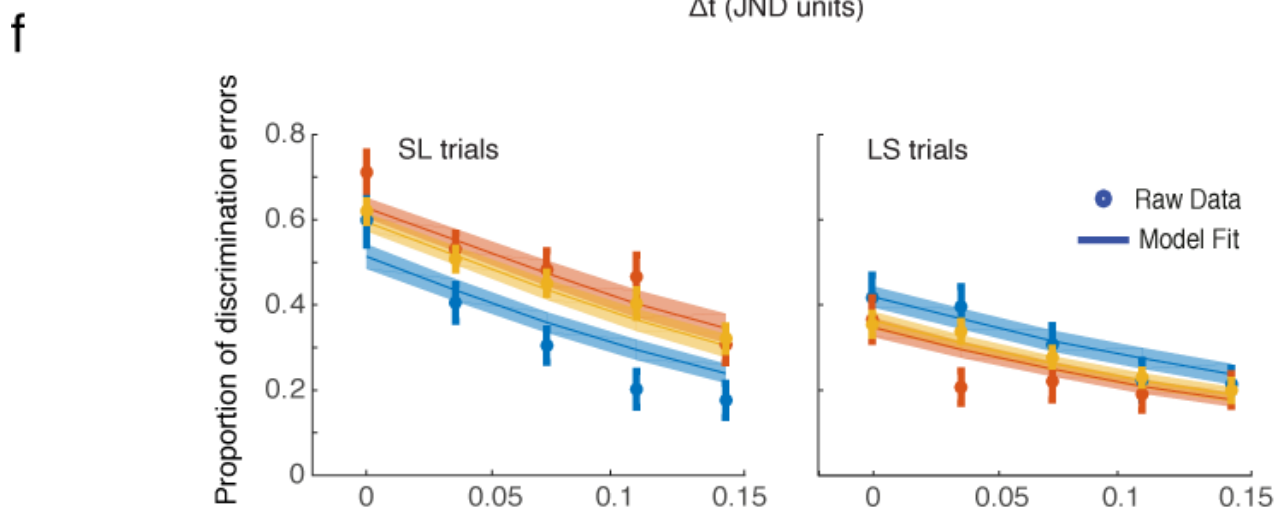
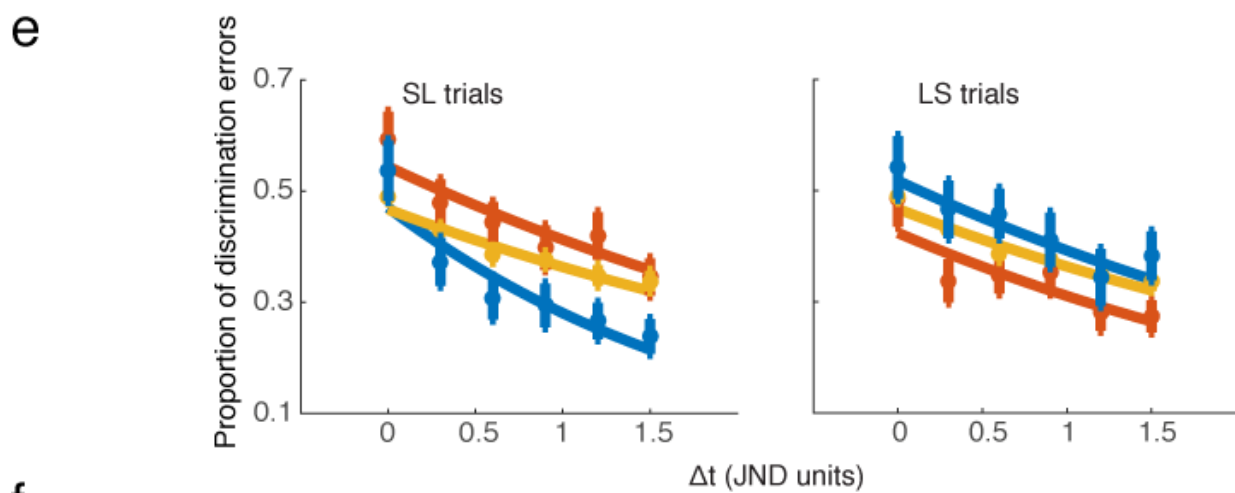
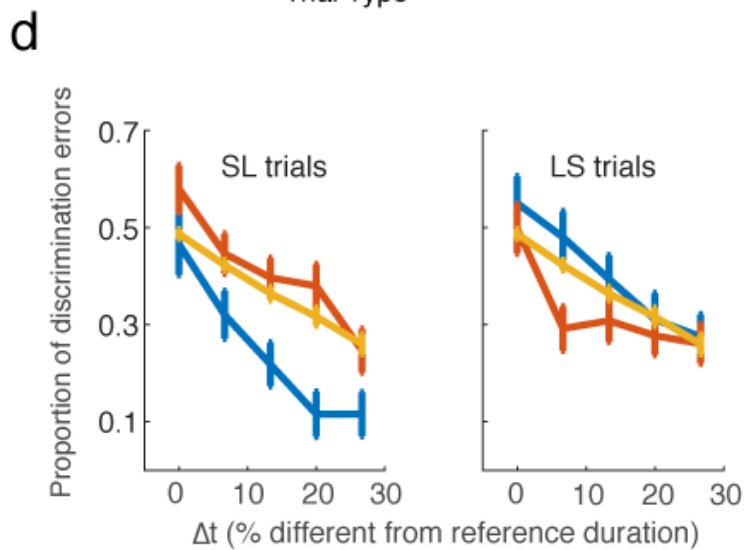
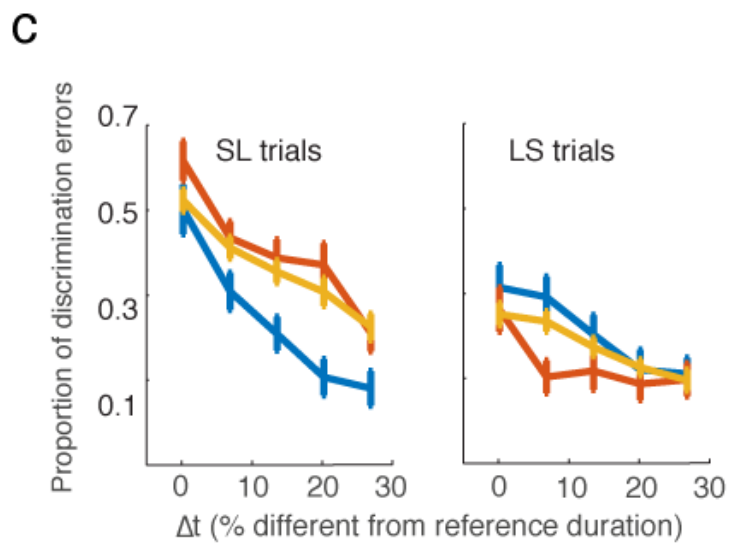
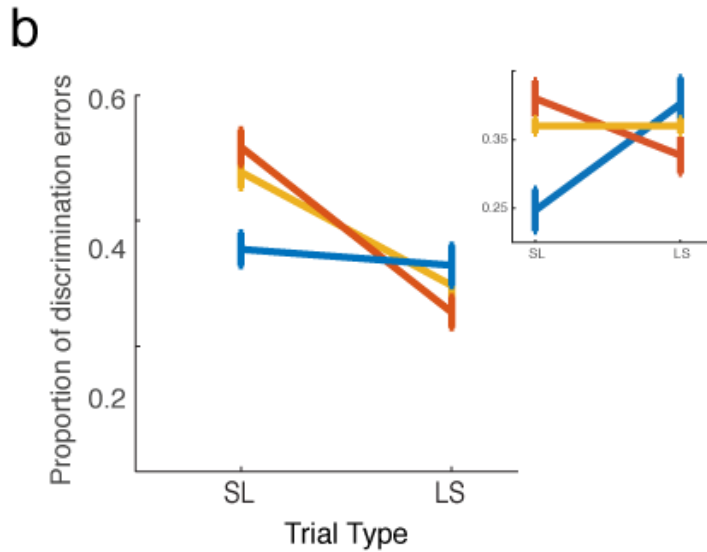
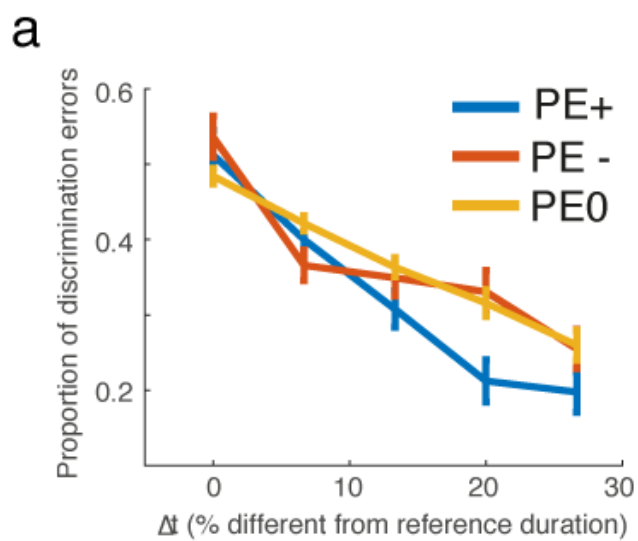


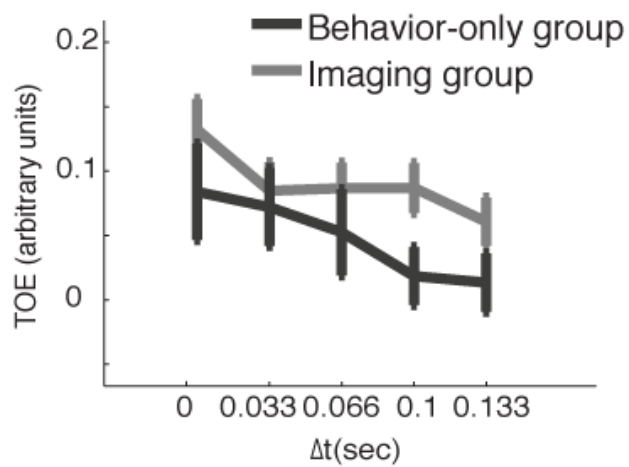
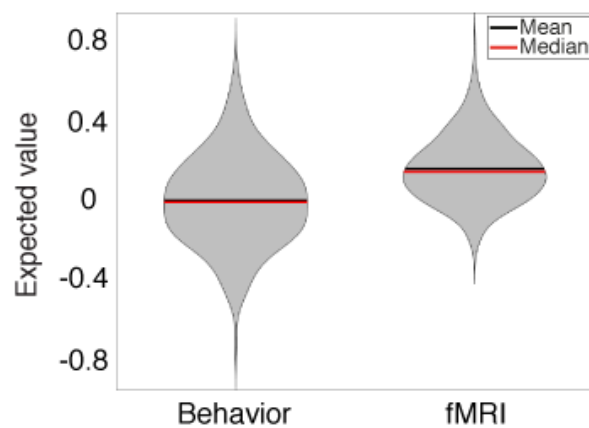
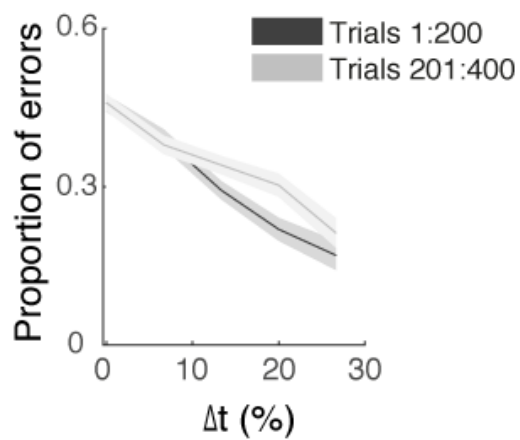
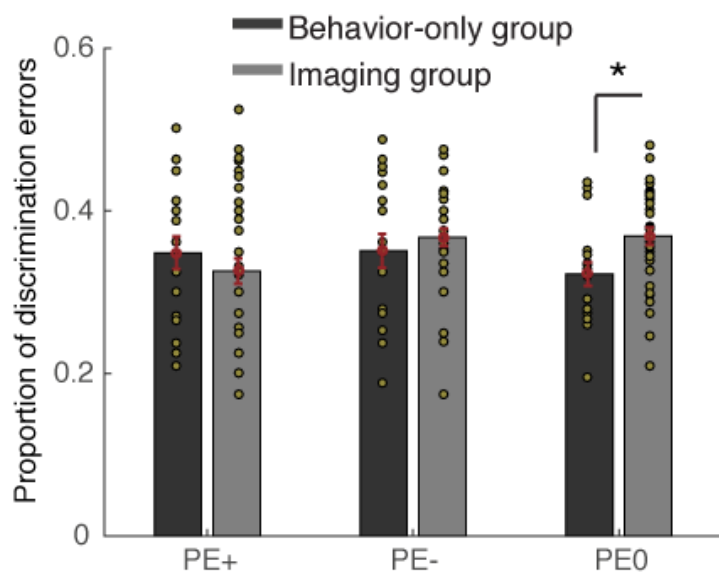


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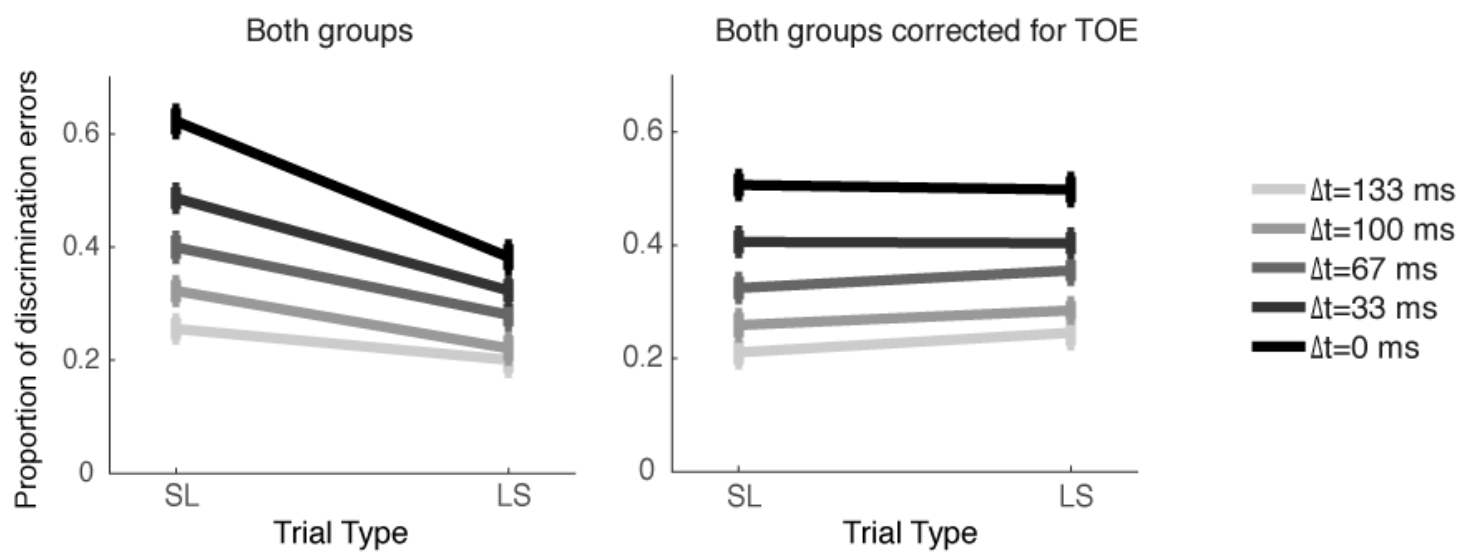




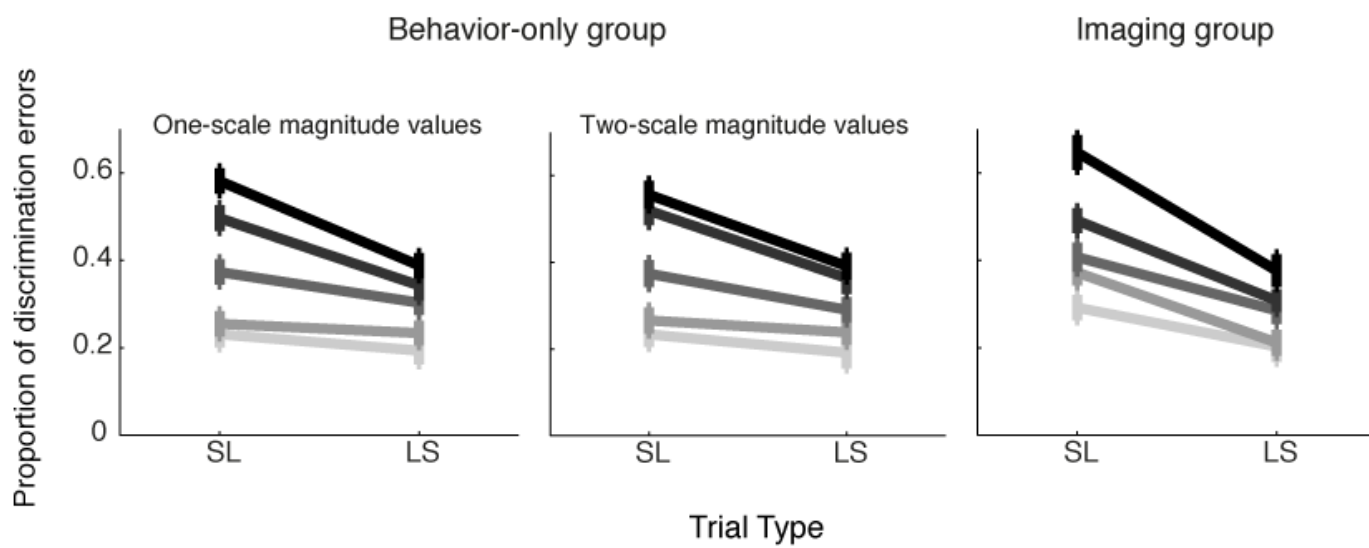


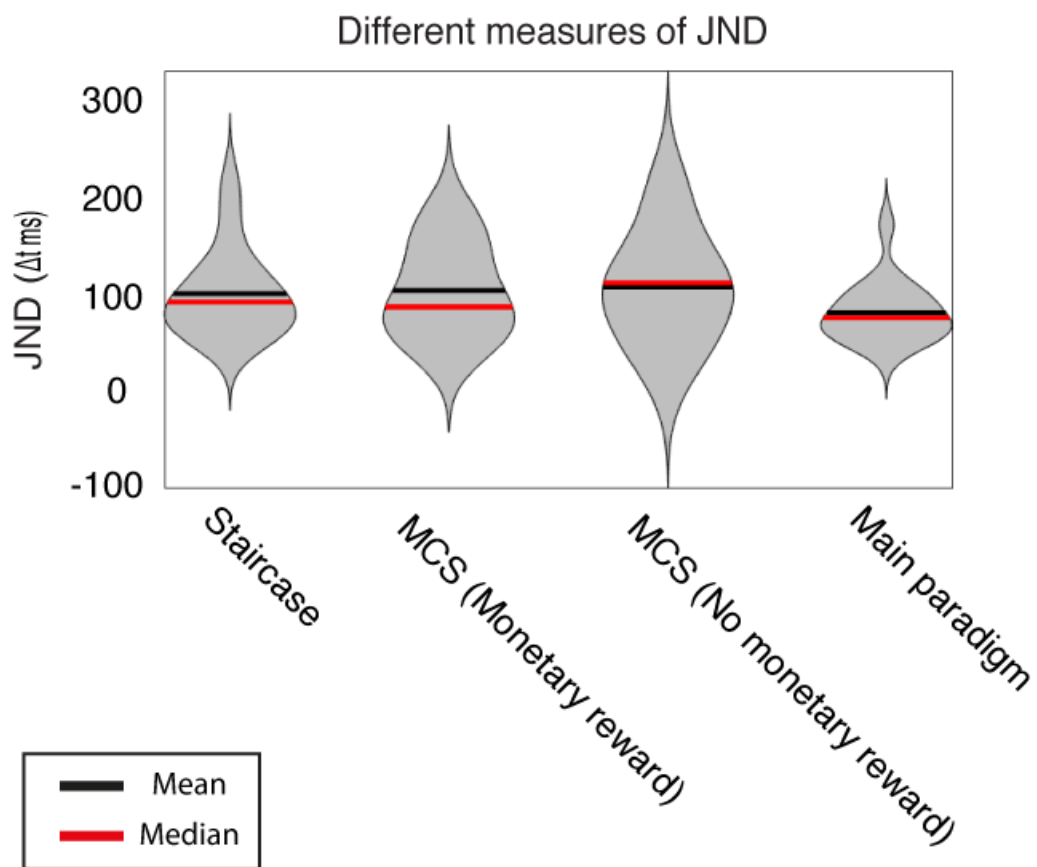
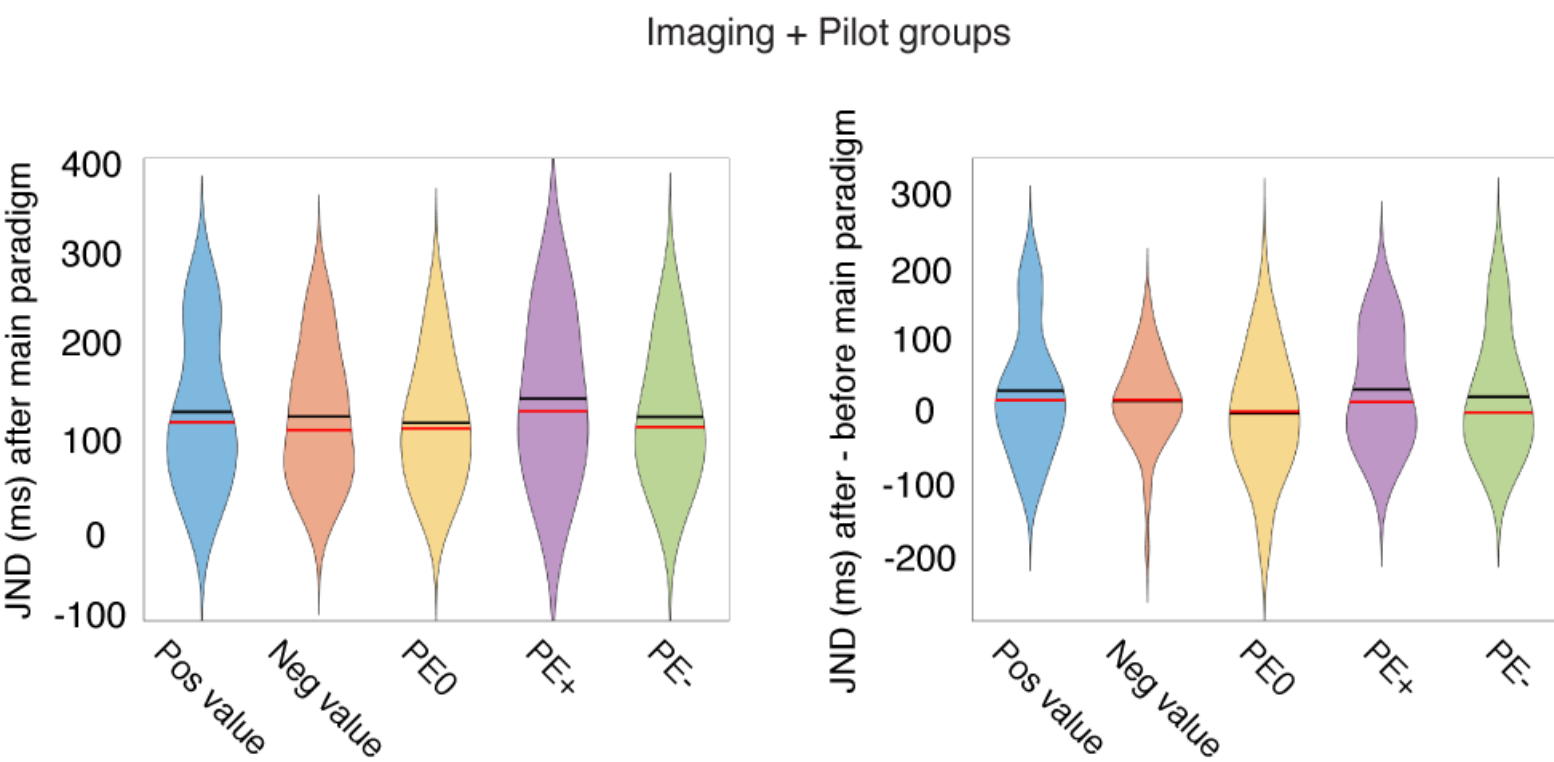
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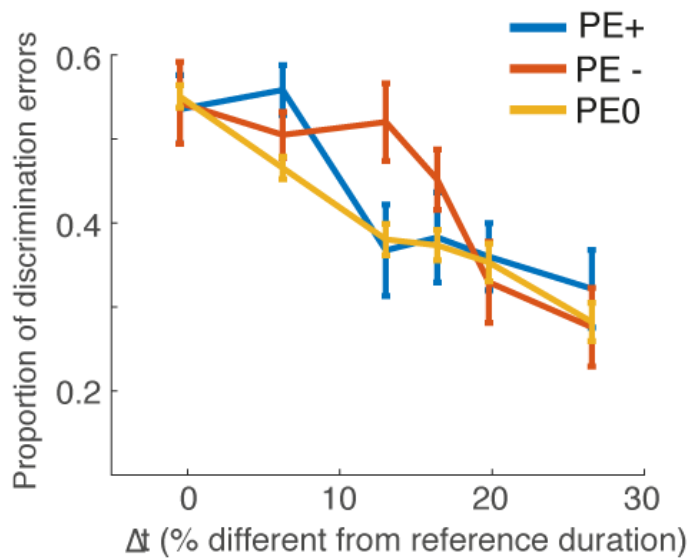
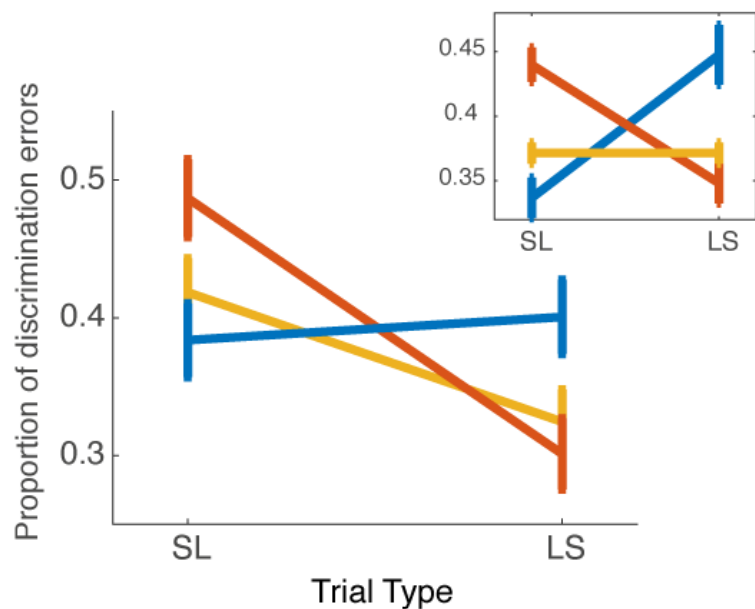
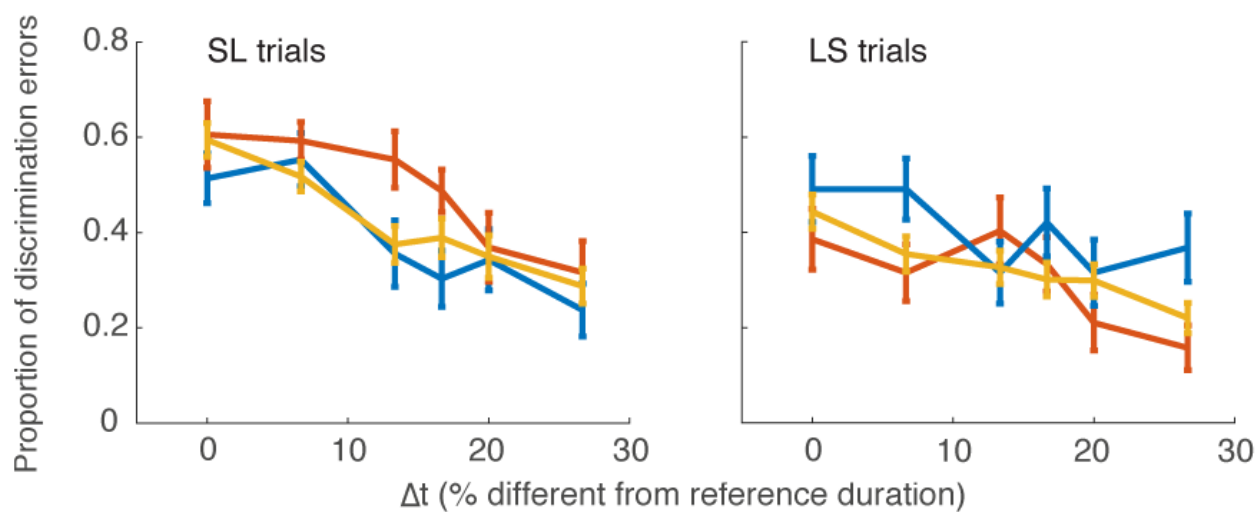
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