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A blunted phasic autonomic response to errors indexes age-related deficits in error awareness

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ABSTRACT

Conscious error detection is impaired in older age, yet it is unclear which age-related changes in the nervous system contribute to this deficit. In younger adults, error commission is accompanied by phasic autonomic arousal, which purportedly contributes to conscious error detection. Because aging is associated with declining autonomic reactivity, reduced phasic arousal to errors may therefore contribute to age-related error detection deficits. To test this, we measured pupil dilation in younger (<30 years) and older (60–80 years) healthy adults during an eye movement task. The task required a subjective assessment of response accuracy, as well as a “meta-judgment” of the certainty underlying that accuracy-assessment. This allowed for a precise quantification of subjective error awareness. Behaviorally, we found reduced error awareness in older adults. Furthermore, while younger adults showed “residual” awareness of error commission on unreported errors (indicated by decreased rating certainty compared with correct responses), this effect was absent in older adults. Notably, pupil dilation correlated with both measures: between subjects, greater pupil dilation to reported errors was correlated with greater subjective certainty of error detection, and greater pupil dilation to unreported errors was correlated with greater “residual” awareness of unreported errors. In line with this association, older adults showed a reduced pupil response to both reported and unreported errors. Notably, older adults showed no pupil dilation to unreported errors, in line with their lack of “residual” error awareness on such trials. Taken together, our results suggest that reduced autonomic reactivity may contribute to age-related error awareness deficits.

1. Introduction

Performance monitoring is an important aspect of cognitive control that enables humans to monitor ongoing actions, correct mistakes, and maintain safe and efficient goal-directed behavior. Recent research has shown that older adults (>60 years) display a specific deficit regarding performance monitoring: Although older adults tend to successfully avoid increased error rates by trading off speed for accuracy (Starns and Ratcliff, 2010), their ability to consciously detect their own action errors is significantly impaired (Harty et al., 2013, 2014). The potential negative implications of such a deficit in conscious error detection are obvious, as impaired error detection will likely aggravate problems associated with the declining sensorimotor abilities of older adults. Although the age-related deficit in error detection has been reported in several recent studies, the age-related changes to the nervous system that underlie this age-related deficit are hitherto unclear.

Much research has focused on neural markers and mechanisms underlying conscious error detection. Younger adults show several reliable markers of conscious error detection in the central nervous system (CNS) and, of primary relevance to the present study, in the autonomic nervous system (ANS). In the ANS, pupil diameter (Wessel et al., 2011), heart rate (Wessel et al., 2011), and the skin-conductance response (O’Connell et al., 2007) are all increased on consciously reported errors compared with unreported errors. Based on this evidence, it has been proposed (Ullsperger et al., 2010; Wessel, 2012, 2018) that phasic changes in both ANS and CNS activity serve as input signals into the decision-making process underlying conscious error detection (Steinhauser and Yeung, 2010). In the context of such “evidence accumulation” models of error awareness, one factor that may contribute to age-related deficits in error awareness could be the non-specific age-related reduction of phasic ANS reactivity (Levenson et al., 1991; Uchino et al., 2010; Verdu et al., 2000). A reduced phasic ANS response to errors could limit that system’s input into the performance

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monitoring system that ultimately determines whether an error is consciously perceived or not. Therefore, if older adults show a reduced autonomic response to error commission, this may influence their ability to consciously detect their action errors.

The primary goal of our study was to test this hypothesis. To this end, we recruited 1 group of older (60–80 years) and 1 group of younger (<30 years) neurologically healthy adults to perform a novel version of the antisaccade task (Hallet, 1978). The antisaccade task is one of the most commonly used paradigms to test error awareness—largely, because it produces a significant proportion of unreported errors (Endrass et al., 2007; Klein et al., 2007; Nieuwenhuis et al., 2001). The newly developed component of the task used in the present study was the method for assessing conscious error detection: in addition to the usual post-response, binary assessment of error awareness ("did you make an error or not?"), we also quantified the exact subjective certainty of each assessment using a visual analogue scale. This allowed us to precisely quantify the degree of subjective certainty of the accuracy rating on each trial (reported errors, unreported errors, and hits [i.e., correct responses rated as correct]). We used this precise measurement of error awareness to investigate the relationship between the degree of subjective certainty of error commission and the phasic autonomic response to errors, measured by phasic changes in pupil dilation. Moreover, we tested whether older adults showed a blunted pupil dilation response to errors, and whether this ostensible reduction was related to their impaired error awareness.

A secondary goal of our study was to test the role of conscious error awareness in age-related changes of post-error slowing (PES). PES is thought to be an adaptive posterror behavior that may depend on conscious error detection (for a review, see Danielmeier and Ullsperger, 2011). PES is increased in older adults (Band and Kok, 2000; Ruitenberg et al., 2014), which may appear counterintuitive, given this group's deficit in conscious error detection. To allow an investigation of the relationship between PES, error awareness, and aging, we designed our task to allow for a trial-to-trial assessment of error awareness that does not impair the measurement of PES. This is a nontrivial problem (Navarro-Cebrian et al., 2013) because PES varies with changing intertrial intervals (ITIs) and is reduced—or even absent—when that interval becomes too long (Jentzsch and Dudschig, 2009; Laming, 1968). Because assessing error awareness after each response leads to longer ITIs, doing so results in the fact that many studies of error awareness find little or no PES on either type of error (Klein et al., 2007; Navarro-Cebrian et al., 2013; Wessel et al., 2011). We addressed this problem in our new experimental paradigm by assessing error awareness after the emission of the *next* response following the error, instead of immediately *after* the erroneous response. This allowed us to use ITIs that are more typical of error processing experiments that do not involve an error awareness probe, while still querying error awareness.

With regard to our primary goal of investigating the relationship between aging, error awareness, and ANS arousal, our hypotheses were as follows: Based on prior research (Harty et al., 2013, 2014), we expected to find a lower percentage of reported errors in the older age group (i.e., impaired error awareness). Based on prior pupil dilation work in younger adults (Critchley et al., 2005; Murphy et al., 2016), we expected to find increased pupil dilation on errors compared to correct responses and on reported errors compared with unreported errors (Wessel et al., 2011). Based on the evidence accumulation theories of error awareness (Ullsperger et al., 2010; Wessel, 2012), we predicted that error-related pupil dilation would be related to the certainty of subjective error awareness between subjects. Based on reports of decreased overall ANS reactivity in older age (Levenson et al., 1991; Uchino et al., 2010; Verdu et al., 2000), we predicted that older adults would show a decreased phasic ANS response to errors. Combined with the predictions of the evidence accumulation theories, we finally predicted that if such a reduction was present, it would be associated with the error detection deficit.

In regard to our secondary hypotheses about PES, we tentatively predicted that PES would be increased for consciously reported errors compared with unreported errors (for a review of preliminary evidence, see Danielmeier and Ullsperger, 2011). Based on existing work (Band and Kok, 2000; Ruitenberg et al., 2014), we also predicted that older adults would show increased PES. We then also aimed to test whether an age-related increase in PES was independent of error awareness or specific to consciously reported or unreported errors only.

2. Methods

2.1. Participants

Participants were recruited via a research-dedicated mass email list at the University of Iowa. We recruited 80 participants in total. Forty were younger adults (ages 19–30), and 40 were older adults (ages 60–80). Two younger participants' data were excluded because of technical problems with the eye tracker, and 1 older participant's data were excluded because the participant failed to follow task instructions. This left a remaining sample of $N = 38$ younger participants (mean age: 22.3 years, SD: 3; 14 males, 1 left-handed) and $N = 39$ older participants (mean age: 68.23 years, SD: 5.25; 18 males, 5 left-handed). Sensitivity calculations performed using G*Power (Faul et al., 2007) showed that we achieved 80% power to detect an effect size of $d = 0.57$ at a critical alpha level of $p = 0.05$.

The gender distribution did not differ between both groups ($\chi^2 = 0.68$, $p > 0.4$). All participants were screened to have normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The older group performed the Minimal Mental State Examination before participation (all participants had scores above 24; range: 27–30). Participants were paid at a prorated hourly rate of $10. All procedures were approved by the University of Iowa Institutional Review Board (IRB # 201510772).

2.2. Materials

Stimuli were presented using a PC running Windows and Psychtoolbox 3 (Brainard, 1997) under MATLAB 2015b. Stimuli were presented on a 100-Hz LCD monitor (BenQ; 53.5 cm horizontal width) at a viewing distance of 77 cm. Eye movements and pupil dilation were recorded using a video-based SR Research EyeLink 1000 eye tracker at a sampling rate of 1000 Hz. A chin and forehead rest was used to maintain a consistent viewing distance and to minimize head movement. Participants responded to the stimuli using their eye movements and the computer mouse (for the error detection assessment and confidence rating). The ambient light in the room was kept at a constant, low level between subjects. The eye tracker was calibrated at the beginning of the experiment and recalibrated after each block of the experiment.

2.3. Experimental paradigm

Participants were instructed to respond to visual stimuli using their eyes and then rate the accuracy of their responses using the computer mouse. A diagram of the experiment can be found in Fig. 1. An initial fixation cross in the center of the screen (black background) instructed the participants about whether they had to perform a prosaccade or an antisaccade on the upcoming trial

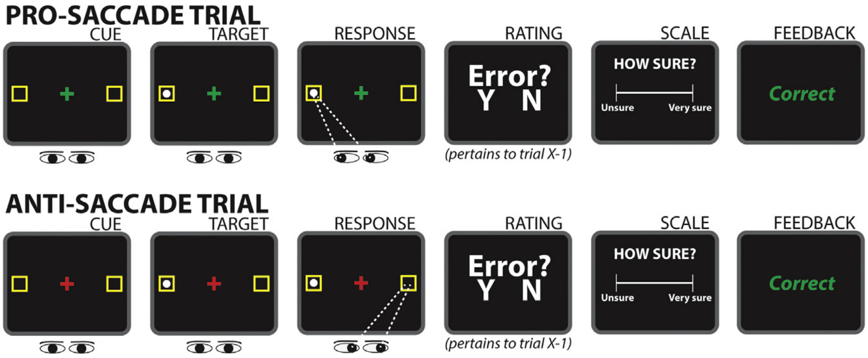

Fig. 1. Task diagram.

(green = prosaccade; red = antisaccade). The fixation cross was flanked by 2 yellow boxes ($3^\circ \times 3^\circ$ of visual angle), presented in the vertical center of the screen, with an offset of $\pm 10^\circ$ of visual angle. After 750 ms, the target stimulus, a white disc (diameter: 2°) was displayed in one of the 2 boxes, and the participants had to respond as quickly as possible by making either a prosaccade, toward the target, or an antisaccade, toward the opposite box. After the 1000-ms response window was over, a rating screen appeared on a select number of trials. The rating screen appeared on the first correct trial after error commission, after every action error (erroneous prosaccade in the antisaccade condition, and vice versa). After every error, a random number between 4 and 10 was generated, and the posterror trial that corresponded to that number (and its subsequent posttrial) was slated for an error awareness query. The automatic algorithm ensured that this trial, as well as the following trial, would be of the same type (antisaccade/prosaccade) as the trial on which the error was committed and the posterror trial. This achieved 2 things: first, it ensured an equal number of error detection queries after correct and erroneous responses and therefore prevented a bias toward error signaling on the part of the participants; and second, it automatically led to matched trial and posttrial types for posterror behavioral comparisons. If the trial that was slated for the error detection query was itself an error, the error detection query was then performed after the next pair of correct trials. The rating screen itself consisted of a simple query ("Error?") with 2 response options ("Y"/"N"), one of which the participants had to select by moving the mouse cursor to one of the alternatives and pressing the left mouse button. Participants were instructed that the error detection query pertained to the last-but-one trial (instead of the immediate last trial). That way, reaction times (RTs) on the posterror and postcorrect trials were unaffected by the error detection query. After the initial binary query, a visual analogue scale appeared, which prompted the participants to indicate the subjective certainty of the accuracy assessment by using the mouse to click on the appropriate point of the spectrum that ranged from "unsure" to "very sure". After the performance rating, participants received feedback about the accuracy of their assessment ("correct" in green or "incorrect" in red, displayed in the middle of the screen). Participants were incentivized to respond as accurately as possible on the error detection query by receiving a "time-out" on incorrectly rated trials: the feedback on correctly rated trials (hits and reported errors) was on the screen for 1 second, whereas the feedback for incorrectly rated trials (false alarms and unreported errors) was on the screen for 5 seconds. After an ITI of 1 second (during which only a white fixation cross and the yellow boxes were displayed), the next trial began with the next cue (red or green fixation cross). Participants performed 600 trials in total (300 antisaccade and 300 prosaccade trials), spread across 6 blocks.

2.4. *Behavioral data analysis*

Behavioral data were analyzed using custom scripts in MATLAB 2015b. The error-related analyses were restricted to responses made to antisaccade trials; as expected, prosaccade trials yielded an insufficient number of errors for analysis. Trials were excluded if there was an eyeblink before response emission, if saccadic RT was faster than 80 ms (reflecting an anticipatory saccade), and if no response was made within the 1000-ms response window (i.e., misses). Error rates and primary saccadic RTs were quantified based on all remaining trials. Error detection, error certainty, and PES were quantified based on all trials (correct and errors) that included an error detection query after the trial. Error rates, error detection rate, and false alarm rate were compared between groups using t-tests. For analyses that involved generating marginal means for unreported error trials within groups, 3 participants from the younger group were removed because of having only a single unreported error included in the analysis after applying the abovementioned exclusion criteria. Saccadic RTs were compared using a mixed-model 2 × 3 ANOVA including the factors GROUP (OLD vs. YOUNG) and TRIAL TYPE (HITS, REPORTED ERRORS, UNREPORTED ERRORS). To account for interindividual differences in overall RT, PES was quantified in percent change from correct RT as follows:

$$\text{PES} = 100 \times (\text{posterror RT} - \text{postcorrect RT})/\text{postcorrect RT}.$$

This was done separately for reported and unreported errors.

PES was then compared between groups using a mixed-model 2 × 2 ANOVA including the factors GROUP (OLD vs. YOUNG) and ERROR TYPE (REPORTED vs. UNREPORTED). Rating certainty was compared between groups using a mixed-model 2 × 3 ANOVA including the factors GROUP (OLD vs. YOUNG) and TRIAL TYPE (HITS, REPORTED ERRORS, UNREPORTED ERRORS). Follow-up t-tests were performed where indicated, using the degrees of freedom of the ANOVA, whereas correcting for multiple comparisons using the Bonferroni-Holm method. Effect sizes are reported in Cohen's d for t-tests, and partial eta^2 for ANOVAs.

2.5. *Pupil dilation data analysis*

Pupil data were analyzed using custom scripts in MATLAB 2015b. For inclusion into the pupil diameter analyses, participants had to have at least 5 trials of every type (hits, reported errors, and unreported errors) after the abovementioned rejection criteria were applied. Owing to a hardware error, pupil dilation data were not saved in the disc for 6 participants from the older group. This, combined with a relatively low number of unreported errors in the younger group (leading to their exclusion based on the 5-trials-per-condition criterion), left a total sample of 42 participants for which appropriate pupil dilation analyses could be performed (N = 19 in the younger group, N = 23 in the older group). Overall, these participants averaged 21.3 valid reported error trials (SEM: 2.1) and 12.5 valid unreported error trials (SEM: 1.4). Sensitivity calculations performed using G*Power (Faul et al., 2007) showed that we achieved 80% power to detect an effect size of d = 0.78 at a critical alpha level of $p = 0.05$.

After conversions into ASCI format using the SR Research's EDF2ASC tool, raw pupil tracking data were imported into MATLAB and processed in event-related fashion as follows. As a first step, blinks were interpolated in the continuous data trace (unless they occurred between stimulus and response, in which case the trial was excluded). Epochs were then extracted using time windows ranging from 0 to 3500 ms relative to primary response emission on each trial. The average activity within a 500-ms baseline period preceding the onset of the target stimulus was subtracted from each epoch.

We then identified the time range to identify the period during which the expected modulation of the pupil dilation by error awareness took place (Wessel et al., 2011). To this end, we ran a 2 × 3 mixed-model ANOVA (factors GROUP and TRIAL TYPE) on every sample point following the response until the end of the epoch. This resulted in 3 vectors of p-values with a length of 3500 (number of sample points in the epoch); 1 vector each for both main effects and the interaction terms at each sample point. To identify the critical period, we then used the vector for the main effect of TRIAL TYPE and corrected the p-values to a threshold of $p = 0.01$ using the false-discovery rate procedure (Benjamini et al., 2006).

For further analyses, we then averaged the signal across that time period for each trial type and each subject and tested these values using a 2 × 3 mixed-model ANOVA (TRIAL TYPE, GROUP, INTERACTION), along with the appropriate planned comparisons using follow-up t-tests.

Finally, we tested the association between error awareness rating certainty and pupil dilation across the group. To this end, we correlated the certainty of error awareness (mean rating certainty on reported errors) to pupil dilation on reported errors (extracted as described in the previous paragraph). Furthermore, we correlated the degree of "residual" error awareness on unreported errors (i.e., the decrease in rating certainty on unreported errors compared with hits) to pupil dilation on unreported errors.

3. Results

3.1. Reaction time

RT data largely adhered to the typical results found in studies of error processing and studies of age-related changes in RT. Errors in antisaccade trials tended to result from trials with faster RT [factor TRIAL TYPE: F (2/138) = 6.1, $p = 0.0029$], and younger adults responded faster than older adults [factor GROUP: F (1/69) = 13.1, $p = 0.0005$]. The interaction was not significant [F (2/138) = 2.75, $p = 0.07$].

3.2. Antisaccade response accuracy, error reporting, and rating certainty

Performance-monitoring behavioral metrics are displayed in Fig. 2A. As expected, older adults showed a significantly impaired error detection rate [t (75) = 2.86, $p = 0.005$, d = 0.66]. Furthermore, this impairment was specific to error awareness, as false alarm rate [t (75) = 0.41, $p = 0.68$, d = 0.095] did not differ significantly between groups. Notably, the numerical false alarm rate was 13.1% for the younger adults and 11.9% for the older adults. Therefore, despite the delayed rating in our current procedure, the false alarm rate was comparable to our prior study that used binary error awareness probes immediately after each response (~10% in Wessel et al., 2011). Unlike previous reports, we also found a numerical difference in error rates between groups, which, however, did not reach significance [t (75) = 1.8, $p = 0.072$, d = 0.4].

In addition to the impaired error detection in older adults, the visual analogue scale confidence rating revealed significant differences in rating certainty (Fig. 2B), with a significant factor TRIAL TYPE [F (2/138) = 16.6, $p < 0.000001$] and a significant INTERACTION [F (2/138) = 4.05, $p = 0.019$]. The factor GROUP revealed no significant differences [F (1/69) = 0.008, $p = 0.93$]. Follow-up t-tests revealed the following significant effects that survived correction for multiple comparisons: Within the younger group, unreported errors were associated with a significantly lower rating certainty compared with both reported errors [t (138) = 4.9, $p < 0.00001$, d = 0.82] and hits [t (138) = 2.3, $p = 0.02$, d = 0.413]. Although the old group also showed a difference in rating certainty between reported and unreported errors [t (138) = 2.4, $p = 0.02$, d = 0.31], there was no difference between unreported errors and hits [t (138) = 1.24, $p = 0.22$, d = 0.12].

Taken together, our data show a clear impairment in error detection in the older age group. Moreover, the results reflect a high degree of specificity of this impairment to error detection, as other measures of performance monitoring (false alarm rate) were unaffected by age. Moreover, our data show a significant group effect with respect to unreported errors: although the younger group showed clear signs of residual (implicit, below reporting-threshold) error awareness, this effect was absent in the older group. Hence, both the explicit and implicit measures of error detection indicated a reduced sensitivity to error commission in older participants.

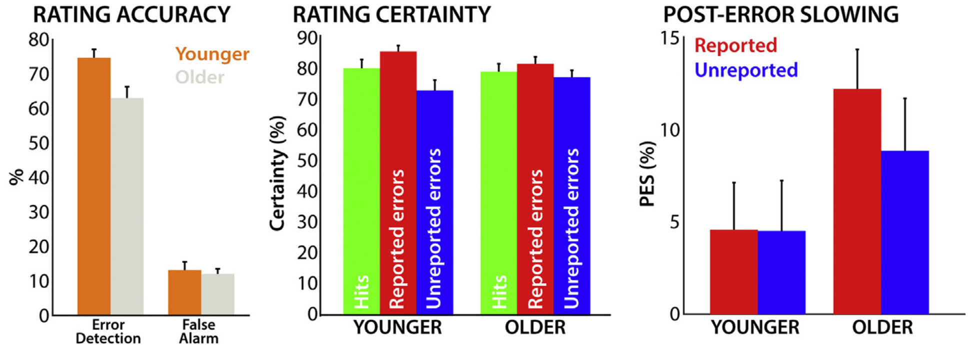

Fig. 2. Behavioral results. Error bars represent 1 SEM.

3.3. *Post-error slowing*

PES data are depicted in Fig. 2C. One outlier was removed from the PES analysis. This participant was in the younger group and showed a PES of 95% in the reported errors condition, 4.26 standard deviations above the mean. The ANOVA revealed that PES was significantly increased for older versus younger adults [factor GROUP: F (1/68) = 4.14, p = 0.046]. There were no significant differences between error types [factor TRIAL TYPE: F (1/68) = 0.6, p = 0.44] and no significant interaction [F (1/68) = 0.56, p = 0.45]. Although the interaction was not significant, the older adults did show an increase in PES on reported errors, relative to the younger group [t (68) = 2.3, p = 0.024, d = 0.56].

Taken together, our novel task clearly produces reliable PES, which has been a problem for previous studies of error awareness. Furthermore, our data reveal that PES did not differ between unreported and reported errors. In addition, in line with prior research, there was some (limited) evidence for the fact that PES was increased in the older age group. However, it appeared that this effect was limited to reported errors, which would underlie the importance of conscious error detection and the associated deficit in older age.

3.4. *Pupil dilation*

Pupil dilation results are displayed in Fig. 3. The sample-to-sample ANOVA revealed significant effects of TRIAL TYPE beginning at 948 ms after the response and lasting until the end of the epoch (critical p-value < 0.01, FDR corrected; resulting mean p-value across the time range = 0.0015). In addition to the significant main effect of TRIAL TYPE, the ANOVA performed on the average pupil dilation in this time range and then revealed significant effects of GROUP [F (1/40) = 9.03, p = 0.005] and INTERACTION [F (2/80) = 5.22, p = 0.007]. Planned individual comparisons revealed significant group differences in pupil response to both reported [t (80) = 3.46, p = 0.0008, d = 1.1] and unreported errors [t (80) = 2.56, p = 0.012, d = 0.82], both with large effect sizes. No group differences were observed after hits [t (80) = 0.51, p = 0.61, d = 0.16].

Taken together, our data show a significantly blunted pupil response to errors in older adults. This was true for both unreported and reported errors.

3.5. *Relationship between pupil dilation and behavior*

As predicted by the evidence accumulation theories, error-related pupil dilation and subjectively perceived rating certainty were significantly positively related. There was a clear positive relationship between pupil dilation on reported errors and the certainty ratings on these trials—participants with increased pupil dilation showed greater subjective rating certainty (r = 0.39, p = 0.0098). Furthermore, there was a positive relationship between the degree of residual error awareness on unreported errors (i.e., the difference between subjective rating certainty on hits compared with unreported errors) and the pupil dilation response on unreported errors, which, however, was only significant in 1-sided testing (r = 0.28, p = 0.039, 1-sided). In both cases, the correlations indicated that greater pupil diameter was associated with greater subjectively reported error detection certainty (Fig. 4). Neither correlation was affected by outliers, as evident by maximal Cook's distance values of 0.288 and 0.698 for the reported and unreported error correlations, respectively. Both are well below the critical threshold of 1.

Although the correlation between pupil dilation and rating certainty for reported errors is unlikely to be attributable to age group differences (as the 2 groups do not differ with regard to rating certainty after reported errors), this factor could indeed be potentially problematic for the unreported errors (as older adults both show blunted pupil dilation and reduced residual error awareness on those trials). Therefore, we repeated both analyses with the variable AGE as an additional predictor. These analyses show that AGE is not a significant predictor to either model—neither in the unreported (r = −0.05, p = 0.75) nor in the reported (r = 0.014, p = 0.93) model. Furthermore, they show that both the magnitude and the significance of the correlation between rating certainty and pupil diameter remain intact when age is included (reported errors: r = 0.37, p = 0.029; unreported errors: r = 0.28, p = 0.049, 1-sided). Finally, the individual correlations within each age group retain their directionality when quantified independently (reported errors: r = 0.44 for the younger group; r = 0.23 for the older group; unreported errors: r = 0.38 for the younger group; r = 0.14 for the older group).

Therefore, our analyses show that pupil dilation is directly related to subjective error certainty, regardless of age, both for reported and unreported errors (with the caveat that the correlation for unreported errors is only significant when tested 1-sided and generally weaker overall).

3.6. *Exploratory data analysis: relationship between error rates and error awareness*

Following the suggestion of a reviewer, we also conducted an exploratory analysis of the relationship between error detection rate and overall error rate in the older participant group. This analysis (N = 39) revealed a significantly negative correlation (r = −0.397, p = 0.012)—participants with greater error detection

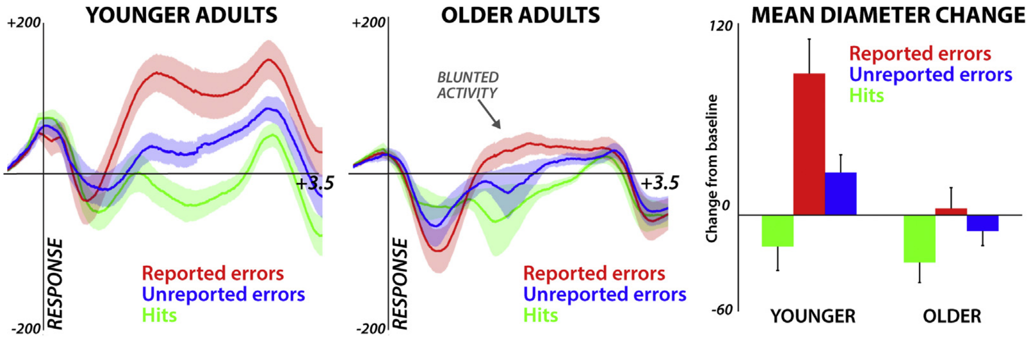

Fig. 3. Pupil dilation by groups. Left panel: younger adults; middle panel: older adults; and right panel: mean diameter change in time period modulated by error awareness (948 ms–3500 ms after the response). Error bars/shaded areas represent 1 SEM.

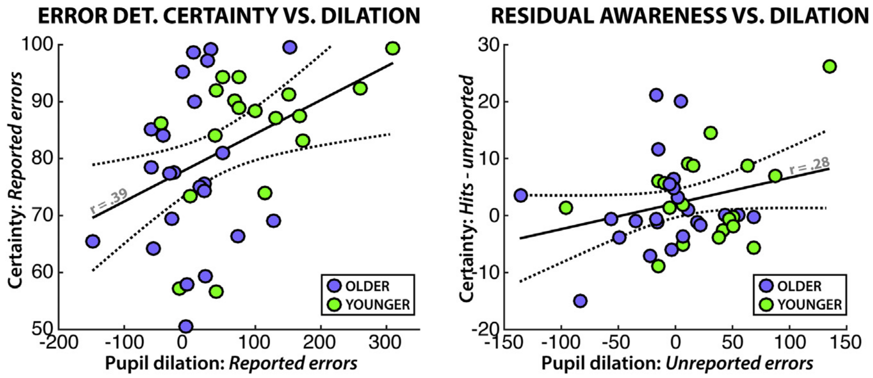

Fig. 4. Relationship between error-related pupil dilation response (x-axis) and rating certainty. Left: y-axis = rating certainty on reported errors. Right: y-axis = Difference between certainty on hits and certainty on unreported errors. Green dots = younger participants, purple dots: older participants. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

deficits also showed higher error rates overall. There was no such correlation in the younger group (r = −0.15, $p > 0.36$, N = 38).

4. Discussion

In the present study, we investigated the potential role of an age-related reduction of ANS reactivity in declining error awareness in older adults. In line with prior research (Harty et al., 2013, 2014), we found that older adults showed impaired error awareness. Our novel experimental paradigm allowed us to also quantify the certainty of each error assessment. We found that the previously demonstrated error awareness impairment extends beyond conscious error awareness and even affects unreported errors: while younger adults exhibited a residual degree of implicit awareness of the inaccuracy of their response—indicated by a reduced rating certainty on unreported errors compared with correct hits—this effect was absent in older adults. This finding suggests that the error awareness impairment in older adults is more severe than previously thought: not only do older adults report a lower percentage of their errors overall, but unreported errors appear to be missed completely, with no residual accumulated awareness that could provide a subthreshold signal that something went awry. Importantly, our data suggest that a blunted ANS response to errors indeed contributes to these error awareness deficits: although the younger group showed a graded pupil response depending on error awareness (with reported errors producing the largest pupil response, and unreported errors producing an intermediate response between reported errors and hits, the same pattern as in Wessel et al., 2011), the older group showed a reduced pupil response to both types of errors. The interpretation that the pupil response is related to error awareness was further supported by the individual differences analyses, which showed that the degree of pupil dilation after reported errors was related to the subsequently reported subjective certainty of error detection. Furthermore, a similar effect could be observed for unreported errors: participants who showed a greater pupil response to unreported errors indicated greater uncertainty on their error awareness rating.

We interpret our results in line with evidence accumulation theories of error awareness (Ullsperger et al., 2010; Wessel, 2012, 2018). Specifically, we propose that the CNS and ANS contribute independently to error awareness, and that both provide feed-forward signals into central performance monitoring systems, where they become integrated and contribute to the decision process underlying error awareness (Harty et al., 2017; Steinhauser and Yeung, 2010). It is known from prior studies that the phasic reactivity of the ANS is reduced in older adults (Levenson et al., 1991; Uchino et al., 2010). Therefore, an interpretation using evidence accumulation theories would propose that this reduced reactivity is expressed in a reduction of the preconscious autonomic response to errors (here measured by pupil dilation) and causes a lack of ANS-input into the central error detection system, thereby contributing to impaired error awareness in older age.

However, it is also possible to interpret the causal relationship as the reverse: instead of reduced autonomic activity contributing to diminished error awareness, it is also possible that error awareness itself causes the ANS response. According to this interpretation, the reduced ANS response in the older age would be merely an expression of the reduction of error awareness in that group. In this scenario, age-related malfunctions in earlier performance monitoring processes (likely in the CNS) would be the likely cause of the error awareness deficit, whereas the ANS response would be a mere epiphenomenon of error awareness. Using the current data, we cannot directly test whether error awareness is solely determined by these (or other) CNS processes, or whether the ANS response is a contributing cause, or a mere consequence of the degree of awareness. However, the graded relationship between the degree of error awareness measured in our present study and the amplitude of the error-related pupil dilation leads us to prefer the former interpretation. If the ANS activity is a mere expression of error awareness, one would likely expect it to be an all-or-none phenomenon, whereas our current findings suggest that the degree of pupil dilation is directly related to the subjective "evidence" for error commission. This interpretation is also in line with findings from the wider literature that associate pupil dilation with different measures of decision certainty (Lavin et al., 2013; Urai et al., 2017).

A definitive test of these interpretations could be provided by causal studies aiming at changing the phasic reactivity of the ANS. For example, pharmacological blockades of the transmitter systems underlying individual components of the phasic autonomic response to errors could inform whether the ANS contributes to error awareness, or whether it is a mere epiphenomenon. Under the evidence accumulation theories, one would predict that artificially decreasing the phasic reactivity of the ANS should lead to impaired error awareness. However, if the ANS response is a mere epiphenomenon, transmitter blockades that lead to a decreased phasic autonomic response should not affect error detection. A second potential approach could be to investigate time-on-task effects (Beatty, 1982; Nuechterlein et al., 1983): if older participants who show a stronger decrease of the phasic ANS response over the course of the experiment also show a greater decrease in error detection performance, this could provide further indications for the proposed causal chain. Our new experimental paradigm could be used to study these hypotheses.

Beyond the insights into performance monitoring, the data provide an interesting link between the specific impairment of error awareness in older adults and, more generally, age-related neuronal decline in the locus-coeruleus-norepinephrine (LC-NE) system. The integrity of the LC-NE system is broadly predictive of intact or impaired cognitive ability in the aging brain, and age-related reductions in the functioning of this system correlate with the progression of age-related diseases such as Alzheimer's (Mather and Harley, 2016). Importantly, pupil dilation is theorized to be an indirect index of the activity of the LC-NE system (Aston-Jones and Cohen, 2005; Gilzenrat et al., 2010; Jepma and Nieuwenhuis, 2011). Hence, the reduced pupil dilation observed in the older age group in our study could be an indication of the overall reduction in LC-NE system functionality in older age. Instead of a general cognitive decline, however, our study demonstrates an association between a highly specific age-related behavioral deficit, thereby providing a more precise characterization of the relationship between performance monitoring and neurotransmitter systems in older age. In turn, our exploratory data analysis of the relationship between error detection rates and error commission rates (which was suggested post hoc by a reviewer) revealed that older participants with greater error detection deficits also commit more errors overall. There are 2 potential explanations for this. First, in participants who commit fewer errors overall, errors may elicit a stronger orienting response and could therefore be more easily consciously detected. However, the absence of the same correlation in the younger participant group speaks against this interpretation. A second explanation could be that error awareness is a more sensitive marker of declining performance monitoring in older age compared with overall error rate: although older participants do not make significantly more errors (though this comparison almost reached significance in our well-powered present study), there are clear differences in error awareness between younger and older adults (see also Harty et al., 2013, 2014).

Beyond these insights into cognitive decline in older age, our study also establishes a novel way to assess error awareness. From a methodological perspective, the experimental paradigm has 2 additional beneficial features that go beyond the increased sensitivity of the novel error awareness probe. First, because of the delayed error awareness probe, our paradigm allowed us to use a short ITI, which was comparable to studies of error detection that do not use an awareness probe. Hence, post-error adaptive behaviors (in this case, PES) were unaffected by the presence of the error awareness probe in our study, allowing us to measure PES without interference. Prior studies, including our own, have struggled to find significant PES in error awareness studies (Klein et al., 2007; Navarro-Cebrian et al., 2013; Wessel et al., 2011). Our new paradigm produced reliable PES following both reported and unreported errors. The second key new feature of our experimental paradigm is that it involves an unbiased measurement of error awareness that is independent of overall RT deficits. Most prior studies of age-related error awareness impairments required the participants to make a speeded second motor response to signal error awareness. After the expiration of a given deadline for this "error awareness signal," a trial was classified as "participants did not notice any error" if no error was signaled before the deadline. However, since older adults showed overall slower reaction times, this could have skewed between-group comparisons: the reaction time distribution of the error signal response in older adults to was closer to the deadline (which was the same across both groups). This could lead to a greater percentage of late-signaled errors (errors that were correctly signaled, but after the deadline for the error signal response), which were then mistakenly classified as unreported errors. Because it uses no deadline, our current paradigm does not suffer from this issue.

Finally, we found that the increase in PES commonly found in older adults (Band and Kok, 2000; Ruitenberg et al., 2014) appears to be limited to reported errors. This illustrates the potential impact of age-related error awareness impairments: if older adults strategically increase adaptive behaviors such as PES (perhaps to countermand other sensorimotor deficits), but these adaptive behaviors are partially contingent on error awareness, the age-related impairment in error awareness poses a severe safety issue for seniors. Furthermore, our data can potentially speak to the theoretical discussion regarding the role of PES in error processing. Theories about PES can be roughly divided into 2 groups (for a review, see: Wessel, 2018): adaptive theories, which suppose that PES is an adaptive behavior designed to improve post-error behavior, and maladaptive theories, which suppose that PES is part of an orienting response after errors, pulling attention away from the primary task, and resulting in lower post-error accuracy. In our study, we found that the participant group that showed an impaired orienting response (viz., the blunted pupil dilation in older adults) also showed increased PES. However, because our study was not designed to explicitly distinguish maladaptive from adaptive explanations for PES, this evidence must be interpreted with caution.

In summary, we used a novel task design to test whether the error awareness deficit in older adults is related to potential age-related changes in the phasic autonomic response to errors. Older participants showed decreased pupil dilation after both reported and unreported errors, consistent with their deficit in conscious (and residual subconscious) error detection. The direct association between behavioral and nervous system changes is supported by positive correlations between the subjective certainty of error judgments and the amplitude of the phasic pupil response. We therefore conclude that the diminished ANS response in older adults is a useful index of their error awareness deficit. Future studies should be aimed at elucidating whether this relationship is of a causal nature.

Disclosure statement

The authors have no actual or potential conflicts of interest.

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References

Aston-Jones, G., Cohen, J.D., 2005. An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. Annu. Rev. Neurosci. 28, 403–450.

Band, G.P., Kok, A., 2000. Age effects on response monitoring in a mental-rotation task. Biol. Psychol. 51, 201–221.

Beatty, J., 1982. Phasic not tonic pupillary responses vary with auditory vigilance performance. Psychophysiology 19, 167–172.

Benjamini, Y., Krieger, A.M., Yekutieli, D., 2006. Adaptive linear step-up procedures that control the false discovery rate. Biometrika 93, 491–507.

Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vis. 10, 433–436.

Critchley, H.D., Tang, J., Glaser, D., Butterworth, B., Dolan, R.J., 2005. Anterior cingulate activity during error and autonomic response. Neuroimage 27, 885–895.

Danielmeier, C., Ullsperger, M., 2011. Post-error adjustments. Front. Psychol. 2, 233.

Endrass, T., Reuter, B., Kathmann, N., 2007. ERP correlates of conscious error recognition: aware and unaware errors in an antisaccade task. Eur. J. Neurosci. 26, 1714–1720.

Faul, F., Erdfelder, E., Lang, A.G., Buchner, A., 2007. G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav. Res. Methods 39, 175–191.

Gilzenrat, M.S., Nieuwenhuis, S., Jepma, M., Cohen, J.D., 2010. Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. Cogn. Affect Behav. Neurosci. 10, 252–269.

Hallett, P.E., 1978. Primary and secondary saccades to goals defined by instructions. Vision Res. 18 (10), 1279–1296.

Harty, S., Murphy, P.R., Robertson, I.H., O'Connell, R.G., 2017. Parsing the neural signatures of reduced error detection in older age. Neuroimage 161, 43–55.

Harty, S., O'Connell, R.G., Hester, R., Robertson, I.H., 2013. Older adults have diminished awareness of errors in the laboratory and daily life. Psychol. Aging 28, 1032–1041.

Harty, S., Robertson, I.H., Miniussi, C., Sheehy, O.C., Devine, C.A., McCreery, S., O'Connell, R.G., 2014. Transcranial direct current stimulation over right dorsolateral prefrontal cortex enhances error awareness in older age. J. Neurosci. 34, 3646–3652.

Jentzsch, I., Dudschig, C., 2009. Why do we slow down after an error? Mechanisms underlying the effects of posterror slowing. Q. J. Exp. Psychol. (Hove) 62, 209–218.

Jepma, M., Nieuwenhuis, S., 2011. Pupil diameter predicts changes in the exploration-exploitation trade-off: evidence for the adaptive gain theory. J. Cogn. Neurosci. 23, 1587–1596.

Klein, T.A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D.Y., Ullsperger, M., 2007. Neural correlates of error awareness. Neuroimage 34, 1774–1781.

Laming, D.R.J., 1968. Information Theory of Choice-reaction Times. Academic P, London.

Lavin, C., San Martin, R., Rosales Jubal, E., 2013. Pupil dilation signals uncertainty and surprise in a learning gambling task. Front. Behav. Neurosci. 7, 218.

Levenson, R.W., Carstensen, L.L., Friesen, W.V., Ekman, P., 1991. Emotion, physiology, and expression in old age. Psychol. Aging 6, 28–35.

Mather, M., Harley, C.W., 2016. The locus coeruleus: essential for maintaining cognitive function and the aging brain. Trends Cogn. Sci. 20, 214–226.

Murphy, P.R., van Moort, M.L., Nieuwenhuis, S., 2016. The pupillary orienting response predicts adaptive behavioral adjustment after errors. PLoS One 11, e0151763.

Navarro-Cebrian, A., Knight, R.T., Kayser, A.S., 2013. Error-monitoring and post-error compensations: dissociation between perceptual failures and motor errors with and without awareness. J. Neurosci. 33, 12375–12383.

Nieuwenhuis, S., Ridderinkhof, K.R., Blom, J., Band, G.P., Kok, A., 2001. Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. Psychophysiology 38, 752–760.

Nuechterlein, K.H., Parasuraman, R., Jiang, Q., 1983. Visual sustained attention: image degradation produces rapid sensitivity decrement over time. Science 220, 327–329.

O'Connell, R.G., Dockree, P.M., Bellgrove, M.A., Kelly, S.P., Hester, R., Garavan, H., Robertson, I.H., Foxe, J.J., 2007. The role of cingulate cortex in the detection of errors with and without awareness: a high-density electrical mapping study. Eur. J. Neurosci. 25, 2571–2579.

Ruitenberg, M.F., Abrahamse, E.L., De Kleine, E., Verwey, W.B., 2014. Post-error slowing in sequential action: an aging study. Front. Psychol. 5, 119.

Starns, J.J., Ratcliff, R., 2010. The effects of aging on the speed-accuracy compromise: boundary optimality in the diffusion model. Psychol. Aging 25, 377–390.

Steinhauser, M., Yeung, N., 2010. Decision processes in human performance monitoring. J. Neurosci. 30, 15643–15653.

Uchino, B.N., Birmingham, W., Berg, C.A., 2010. Are older adults less or more physiologically reactive? A meta-analysis of age-related differences in cardiovascular reactivity to laboratory tasks. J. Gerontol. B Psychol. Sci. Soc. Sci. 65B, 154–162.

Ullsperger, M., Harsay, H.A., Wessel, J.R., Ridderinkhof, K.R., 2010. Conscious perception of errors and its relation to the anterior insula. Brain Struct. Funct. 214, 629–643.

Urai, A.E., Braun, A., Donner, T.H., 2017. Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. Nat. Commun. 8, 14637.

Verdu, E., Ceballos, D., Vilches, J.J., Navarro, X., 2000. Influence of aging on peripheral nerve function and regeneration. J. Peripher. Nerv Syst. 5, 191–208.

Wessel, J.R., 2012. Error awareness and the error-related negativity: evaluating the first decade of evidence. Front Hum. Neurosci. 6, 88.

Wessel, J.R., 2018. An adaptive orienting theory of error processing. Psychophysiology 55, e13041.

Wessel, J.R., Danielmeier, C., Ullsperger, M., 2011. Error awareness revisited: accumulation of multimodal evidence from central and autonomic nervous systems. J. Cogn. Neurosci. 23, 3021–3036.