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Compensatory processing during rule-based category learning in older adults

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ABSTRACT

Healthy older adults typically perform worse than younger adults at rule-based category learning, but better than patients with Alzheimer's or Parkinson's disease. To further investigate aging's effect on rule-based category learning, we monitored event-related potentials (ERPs) while younger and neuropsychologically typical older adults performed a visual category-learning task with a rule-based category structure and trial-by-trial feedback. Using these procedures, we previously identified ERPs sensitive to categorization strategy and accuracy in young participants. In addition, previous studies have demonstrated the importance of neural processing in the prefrontal cortex and the medial temporal lobe for this task. In this study, older adults showed lower accuracy and longer response times than younger adults, but there were two distinct subgroups of older adults. One subgroup showed near-chance performance throughout the procedure, never categorizing accurately. The other subgroup reached asymptotic accuracy that was equivalent to that in younger adults, although they categorized more slowly. These two subgroups were further distinguished via ERPs. Consistent with the compensation theory of cognitive aging, older adults who successfully learned showed larger frontal ERPs when compared with younger adults. Recruitment of prefrontal resources may have improved performance while slowing response times. Additionally, correlations of feedback-locked P300 amplitudes with category-learning accuracy differentiated successful younger and older adults. Overall, the results suggest that the ability to adapt one's behavior in response to feedback during learning varies across older individuals, and that the failure of some to adapt their behavior may reflect inadequate engagement of prefrontal cortex.

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Introduction

Categories are central to the mental lives of human beings and allow us to describe and order our mental and physical worlds (Rips, Smith, & Medin, 2012). Our ability to create and manage categories becomes increasingly important as we learn categories related to our social life (e.g., which friends can keep a secret or what is appropriate to post on Facebook), to our occupation (e.g., which emails should be sent through the company account), and to our health (e.g., which medications to take with food or at bedtime). Categories come in many different types, from simple featural categories (e.g., objects that are red) to much more complicated relational concepts (e.g., chases or conduit; see Ashby & Maddox, 2011; Kéri, 2003; Rips et al., 2012). Neuropsychological (e.g., Koenig, Smith, Moore, Glosser, & Grossman, 2007; Reber, Knowlton, & Squire, 1996; Smith et al., 2013; Smith & Grossman, 2008; Ullman et al., 1997), electrophysiological (e.g., Folstein & Van Petten, 2004; Morrison, Reber, Bharani, & Paller, 2015), and neuroimaging studies (e.g., Foerde, Knowlton, & Poldrack, 2006; Nomura, Maddox, & Reber, 2007; Nomura et al., 2007; Nomura & Reber, 2012; Reber, Martinez, & Weintraub, 2003) have suggested that there is an explicit, rule-based mechanism to learn categories which is distinct from an implicit, featural similarity-based mechanism.

Although deficits in rule-based category learning have already been related to cognitively pathological aging disorders such as Alzheimer's disease and Parkinson's disease (e.g., Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Ashby, Noble, Filoteo, Waldron, & Ell, 2003; Filoteo, Maddox, Ing, & Song, 2007; Kéri, 2003; Koenig et al., 2007; Maddox, Aparicio, Marchant, & Ivry, 2005; Reber et al., 2003; Reber & Squire, 1994, 1999), significant decreases in category-learning performance can still be seen when comparing performance between younger and neuropsychologically typical older adults (e.g., Ashby et al., 2003; Maddox, Pacheco, Reeves, Zhu, & Schnyer, 2010; Racine, Barch, Braver, & Noelle, 2006; Ridderinkhof, Span, & Van Der Molen, 2002). Understanding this diminished performance in older adults in relation to their cognitive profile may be useful in the future, diagnostically, in order to identify candidates for early interventions.

Category learning in older adults

Despite the abundance of studies involving category learning in children and college-aged adults, relatively few studies have focused on category learning in older adults. One common category-learning task used with older adults is the Wisconsin Card Sorting Task (WCST), a neuropsychological test requiring participants to learn and shift between explicit categorization rules based on trial-by-trial feedback (Berg, 1948). Successful performance in this task has been found to be dependent on the prefrontal cortex (Smith, Taylor, Brammer, & Rubia, 2004) and has been related to increased cortical thickness in frontal and parietal brain regions (Burzynska et al., 2012). Although the WCST requires both rule induction and rule shifting, rule induction is typically quite easy for participants, and declines in older adults' performance are typically explained by difficulties in rule shifting (Hartman, Bolton, & Fehnel, 2001; Ridderinkhof et al., 2002). Thus, a more challenging rule-induction task may add additional insight into how real-world category learning changes with age.

Using an explicit category-learning task with abstract shapes that varied on two dimensions (i.e., circle size and line angle), Racine et al. (2006) found that older adults could learn simple and complex rules as well as younger adults. However, when asked to apply the previously learned complex rule without receiving trial-by-trial feedback, older adults showed decreased performance compared with younger adults even though they could recall the rule at the end of the task. Thus, older adults are able to learn and recall rules like younger adults but have difficulty meeting the increased demands on cognitive resources that are required to apply complex rules. This result is consistent with relational reasoning results in older adults, where relational complexity also interacts with age (Viskontas, Morrison, Holyoak, Hummel, & Knowlton, 2004) and is likely attributable to age-related changes in prefrontal cortex or the way it interacts with more posterior brain areas (Cabeza & Dennis, 2012). Age-related deficits in rule-based categorization have additionally been related to deficits in working memory, episodic memory, inhibitory control, and verbal reasoning (Ashby et al., 1998; Maddox et al., 2010; Racine et al., 2006).

Although Racine et al. (2006) reported that younger and older adults were able to learn both simple and complex rules with equivalent accuracy, other studies have reported differences between younger and older adults' ability to learn explicit rules. For instance, Ashby et al. (2003) found that 14% of their older adult control group were unable to achieve at least 10 correct responses in a row within 200 trials. Likewise, Maddox et al. (2005) reported large individual differences in neuropsychologically typical older adults' performance in their rule-based category-learning task, with several participants failing to reach 55% accuracy. Similarly, older Parkinson's disease patients also show great variability in performance (Ashby et al., 2003; Maddox et al., 2005; Maddox & Filoteo, 2001). However, Filoteo et al. (2007) ultimately demonstrated that diminished performance in rule-based category learning in Parkinson's patients was likely due to deficits in selective attention that prevented them from ignoring irrelevant stimulus features.

Category learning event-related potentials

Results from the studies discussed so far have explored variability in older adult performance in rule-based category learning using behavioral measures; however, neuroimaging techniques may help us better understand the variability in older adult category-learning behavior. The sensitivity of neuroimaging has already established structural differences between two types of category learning. In particular, rule-based category learning has been found to be dependent on the prefrontal cortex and the medial temporal lobes (MTLs), areas associated with age-related structural and functional decline (for review see Dennis & Cabeza, 2008) and is distinguished from implicit, featural, category learning which is dependent on striatal-frontal circuitry (e.g., Foerde et al., 2006; Nomura, Maddox, & Reber, 2007; Nomura et al., 2007; Nomura & Reber, 2012; Reber et al., 2003). Additionally, although both younger and older adults activated the MTL during an explicit category-learning task, functional magnetic resonance imaging (fMRI) results showed that younger adults' MTL activity was significantly greater than older adults' (Dennis & Cabeza, 2011). These studies show that neuroimaging techniques are useful both for distinguishing between types of category learning and for investigating changes due to aging.

Maddox, Ashby, and Bohil (2003) developed a particularly useful paradigm for studying rule-based and implicit category learning. In their task, participants must discover how to divide Gabor patches varying in spatial frequency (i.e., number of stripes in the patch or mean width of stripes in a patch) and spatial orientation (i.e., the angle of stripes in a patch), into two groups, based on trial-by-trial feedback. Morrison, Reber, Bharani, and Paller (2015) used this task with scalp electroencephalography (EEG) to measure brain activity while people learned categories either explicitly or implicitly. From the EEG recorded during learning, they calculated event-related potentials (ERPs) elicited by categorical and feedback stimuli. Specifically, a stimulus-locked ERP known as the late positive complex (LPC) was found to differentiate correct and incorrect responses and be predictive of accuracy in the explicit condition, but not in the implicit condition, supporting the hypothesis of distinct neural systems engaged in explicit and implicit category learning (Nomura et al., 2007). Additionally, a feedback-locked P300 was found to be larger in incorrect trials in the explicit condition, but not the implicit condition, suggesting participants form a firm hypothesis about the categorization rule in the explicit condition and express "surprise" (Polich, 2007) when their expectations are violated by negative feedback.

The LPC is frequently implicated in studies of declarative memory where it has been linked to explicit memory encoding and retrieval processes (Finnigan, Humphreys, Dennis, & Geffen, 2002; Paller, Voss, & Westerberg, 2009). In an incidental memory paradigm, abnormal LPCs have been seen in amnestic mild cognitive impairment and probable Alzheimer's disease patients, and LPC abnormalities have been used to successfully predict conversion from amnestic mild cognitive impairment to probable Alzheimer's disease (Chapman et al., 2011; Olichney et al., 2006; Taylor & Olichney, 2007). In the category-learning task, we expect participants to have a more positive LPC when correctly categorizing a stimulus, reflecting the process of retrieval of the categorization rule and mental representation of the boundary condition. Furthermore, anterior shifts in LPC topography are expected in older adults to the extent that they are engaging prefrontal cortex (Joyce, Paller, McIsaac, & Kutas, 1998). Relating this frontal shift to performance in the task will provide insight on whether or not this frontal shift reflects a compensatory mechanism to counteract age-related neurocognitive deficits (Cabeza, Anderson, Locantore, & McIntosh, 2002) or inefficient recruitment (Li & Lindenberger, 1999).

The P300 has been shown to arise when working memory is updated after feedback (Kok, 2001; Polich, 2007) and is sensitive enough to discriminate among older adults, those with amnestic mild cognitive impairment, and patients with dementia (Bennys, Portet, Touchon, & Rondouin, 2007). When a participant who is confident in his or her categorization hypothesis receives negative feedback, a feedback-locked P300 is expected, reflecting a violation of expectation (Hajcak, Holroyd, Moser, & Simons, 2005; Morrison et al., 2015). A lower magnitude feedback-locked P300 is expected in response to positive feedback, reflecting confidence in the hypothesized categorization criteria. Previous studies have suggested that younger adults have an increased tendency to attend to negative information relative to positive information (Rozin & Royzman, 2001). Interestingly, this negative bias is attenuated by age, and older adults have been shown to exhibit decreased reactivity to negative information and emphasize wins rather than losses (Wood, Busemeyer, Koling, Cox, & Davis, 2005; Wood & Kisley,

2006). Thus, we expect the P300 to be modulated by this age-related difference in feedback processing.

In this study, we used a well-established rule-based category-learning paradigm (Maddox et al., 2003; Nomura et al., 2007) to examine individual differences in behavior and brain waves in healthy older adults. We included a group of younger adults for comparison.

Materials and methods

Participants

Nineteen younger adults (9 female; $M = 20.7$ years old, $SD = 2.0$) were recruited from Loyola University Chicago, and 23 cognitively healthy older adults (15 female; $M = 71.0$ years old, $SD = 3.3$) were recruited from the Clinical Core Registry of the Cognitive Neurology and Alzheimer's Disease Center (CNADC) at Northwestern University's Feinberg School of Medicine. Older adult participants had at least 20/30 corrected vision and completed regular neuropsychological testing at the CNADC using the Uniform Data Set of the Alzheimer's Disease program of the National Institute on Aging and additional tests (Morris et al., 2006; Weintraub et al., 2009), and had neuropsychological test scores of attention, executive function, memory, and language within normal range. None of the older adults had neuropsychological test scores below 2 SD of age-based norms, and all had no features of amnestic mild cognitive impairment or probable Alzheimer's disease. All participants in the study had normal or corrected-to-normal vision. Participants gave informed consent as approved by the Loyola University Chicago's Institutional Review Board and received $15 per hour to compensate them for participation in the study.

Task description

Morrison et al. (2015) previously adapted Maddox, Ashby, and Bohil's (2003) category-learning task for use with EEG. In this paradigm, participants learn to categorize circular sine-wave gratings (Gabor patches) that vary in spatial frequency and spatial orientation into two categories via auditory feedback following each response. In the rule-based (RB) version of the task used in the present study, the two categories are defined by a boundary based only on spatial frequency, such that variations in spatial orientation are irrelevant (see Figure 1).

Procedure

Participants were seated in a dimly lit, acoustically shielded room 100 cm away from a cathode ray tube monitor. Directions for the tasks were presented visually and were read aloud by the experimenter.

Category-learning task (see Figure 2)

Participants categorized 320 gratings presented in four blocks of trials. Criteria defining categories "A" and "B" were based solely on the spatial frequency of the sine-wave
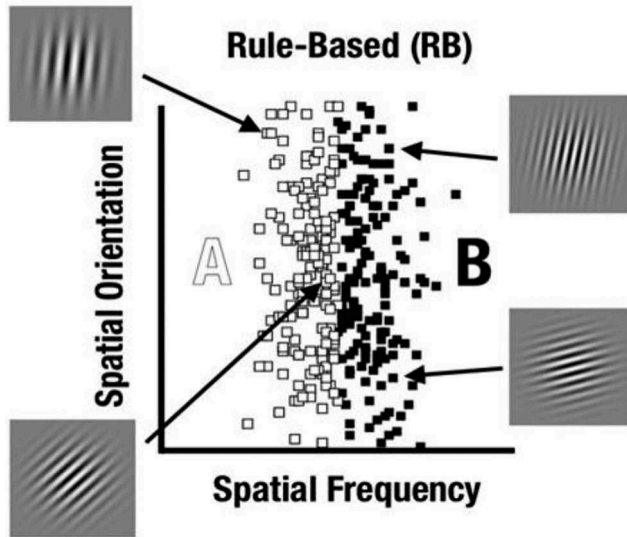
Figure 1. An example of a rule-based category distribution where categories were determined by spatial frequency regardless of spatial orientation.
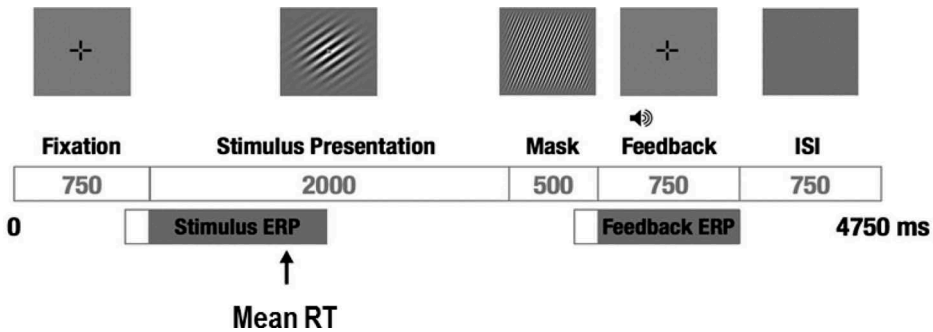
Figure 2. Participants saw a stimulus to be categorized after a fixation cross and were asked to press buttons labeled "A" or "B" indicating their categorization decision while the stimulus was on the screen. Feedback on the categorization decision was given in the form of a tone after 500 ms of stimulus offset. EEG was recorded continuously; stimulus- and feedback-locked ERPs were calculated for each trial.

grating, where category "A" consisted of stimuli with lower frequency (i.e., wider stripes) and category "B" consisted of stimuli with higher frequency (i.e., thinner stripes). Prior to testing, participants were familiarized with the procedures, including trial timing, button pressing, and feedback. Participants did not receive instructions about the nature of the categories. Instead, they were asked to discover them with the aid of auditory feedback. Participants were instructed to make a categorization decision before the stimulus disappeared (2 s after stimulus onset) and before a visual mask appeared. A bell then sounded for correct feedback, or a short buzzer sounded for incorrect feedback. For responses not made within the allotted time, participants heard a long buzzer. Trials on which participants did not respond within 2 s were not considered in the EEG analysis.

Participants were debriefed about their categorization strategies after the testing session. Compared with the distribution of sine-wave gratings used in the rule-based learning task in Morrison et al. (2015), the distribution of sine-wave gratings in the task used in the current study included more stimuli far from the boundary condition in order to reduce task difficulty for older adults.

Spatial frequency discrimination task

In order to ensure that participants were capable of discerning the difference in spatial frequency between category A and B stimuli, we administered a spatial frequency discrimination task after category learning. Participants viewed two sine-wave gratings side by side and were asked if the right sine-wave grating had wider or thinner stripes than the left sine-wave grating. The left sine-wave grating had spatial frequency representative of the boundary condition and remained on the screen throughout. The right sine-wave grating changed in every trial and was representative of the range of spatial frequency and orientation used during the category-learning task. All participants achieved at least 75% accuracy on this task ($M = 83.40\%$, $SD = 10.50\%$).

EEG recording and analysis

EEG was recorded from each participant using a Biosemi Active-Two EEG system. Elastic caps with 32 active electrodes (Ag-AgCl) arranged in a 10/20 pattern were used for data collection. Biosemi CMS/DRL electrodes were placed near the vertex. Four additional electrodes surrounding the eyes were used to monitor horizontal and vertical eye movements, and two additional electrodes were placed over the left and right mastoid bones for re-referencing after data collection. Data were recorded with a band pass of 0–104 Hz, and sampled at a rate of 512 Hz. EEG data were processed using EMSE (Source Signal Imaging, San Diego CA). EEG data were re-referenced to an average of the two mastoid electrodes and then digitally filtered with a 0.01 Hz high-pass filter and 59 to 61 Hz band-stop filter to remove AC electrical noise. All filters had a cutoff attenuation of 12 dB/octave. A spatial principal components analysis (PCA) filter was applied to remove ocular artifacts (Liu & Yao, 2006). Muscle and other artifacts were removed via visual inspection of the raw EEG signal and a $\pm$ 125µV trial-by-trial rejection criterion during averaging. A polynomial detrend was applied to the data to implement a 200-ms prestimulus baseline adjustment for stimulus-locked ERP averaging. Participants who were included in ERP analyses had fewer than 25% rejected trials in every condition (correct trials: $M = 219$, $SD = 40$; incorrect trials: $M = 69$, $SD = 36$).

Results

Behavioral results

Criteria for learning subgroups

Although older adults were within their age-based norms on neuropsychological tests, many of the older adults performed near chance in the category-learning task, unlike younger adults who all learned the category rule. To distinguish high and low performers, participants who achieved over 60% accuracy (chance was 50%) were considered
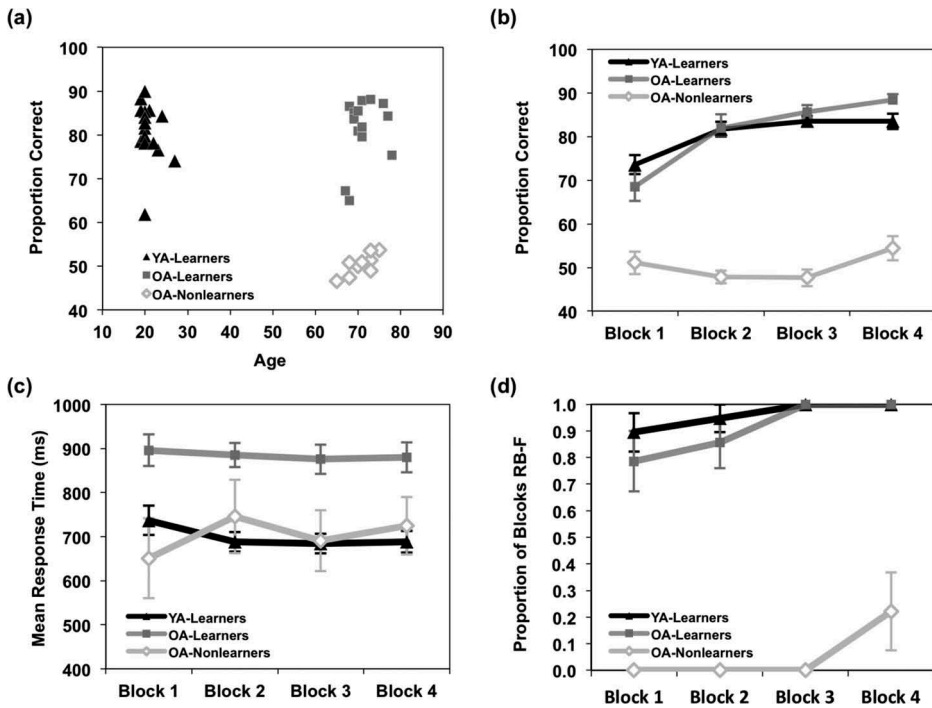
Figure 3. (a) A plot of overall task accuracy and age showing the accuracy-age distribution of YA-Learners, OA-Learners, and OA-Nonlearners. Older adults that achieved 60% or higher categorization accuracy were considered OA-Learners. Accuracy (b) and correct response time (c) from YA-Learners, OA-Learners, and OA-Nonlearners in each of four 80-trial blocks. (d) Proportion of 80-trial blocks best fit by an RB-F DBT model for each participant. Error bars represent ±1SEM.

to be learners, and those who did not achieve over 60% accuracy were considered to be nonlearners. As shown in Figure 3a, 14 older adults (9 female; $M = 71.3$ years old, $SD = 3.5$) were high performers (hereto referred to as *OA-Learners*) while 9 older adults (6 female; $M = 70.7$ years old, $SD = 3.2$) were low performers (hereto referred to as *OA-Nonlearners*). From this point forth, the term *YA-Learners* refers to the entire group of younger adults and the term *Older Adults* refers to the entire group of older adults including both OA-Learners and OA-Nonlearners.

Neuropsychological results
Older adults completed the Unified Data Set (UDS) neuropsychological battery (Morris et al., 2006; Weintraub et al., 2009) within 1 year prior to EEG testing. These testing results as well as results from the spatial frequency discrimination task are presented for the OA-Learners and OA-Nonlearners groups in Tables 1 and 2.

Categorization accuracy
As shown in Figure 3a, accuracy was found to differ across the participant groups (YA-Learners, OA-Learners, and OA-Nonlearners), as confirmed via a one-way Analysis of Variance (ANOVA; $F(2, 39) = 90$, $p < 0.001$, $\eta_p^2 = 0.82$). A Tukey's post-hoc comparison of the three groups showed that YA-Learners ($M = 0.81$, $SD = 0.06$) and OA-Learners

Table 1. Characterization of analysis groups.

	YA- Learners		OA- Learners		OA-Nonlearners		
	M	SD	M	SD	M	SD	p
Demographics							
Age	20.68	2.03	71.29	3.47	70.67	3.20	0.90
Education	14.52	1.58	16.54	2.39	16.75	2.12	0.82
Rule-based category-learning task							
Accuracy (proportion correct)	**0.81**	**0.06**	**0.81**	**0.07**	**0.50**	**0.02**	**<0.001**
RT (ms)	**697**	**100**	**883**	**114**	**703**	**223**	**0.02**
Global functioning							
MMSE (total = 30)			29.79	0.58	28.67	1.00	0.03
Vision							
Spatial frequency discrimination task	0.84	0.08	0.81	0.15	0.83	0.10	0.52
Harder trials near to category boundary	0.81	0.11	0.83	0.13	0.83	0.14	0.59
Easier trials far from category boundary	0.88	0.14	0.80	0.19	0.85	0.13	0.58
Processing speed							
Digit Symbol (WAIS-R) (total = 99)			52.36	8.38	50.67	12.54	0.17
Attention							
Digit Span Forward (WMS-R)			6.86	1.17	7.22	0.97	0.41
Trail Making Test (Part A) (seconds to complete)			25.57	6.37	23.67	6.44	0.71
Language							
Boston Naming Task (Short, Total = 30)			29.07	1.14	27.44	3.17	0.09
Executive function							
Digit Span Backwards (WMS-R)			5.57	1.02	4.56	0.88	0.88
Trail Making Test (Part B) (secs)			62.86	24.30	68.11	29.32	0.90
Category List (animals in 60 secs)			23.71	4.39	21.56	4.82	0.61
Category List (vegetables in 60 secs)			17.14	5.11	16.11	3.89	0.39
Memory							
Logical Memory I (WMS-R)			16.43	2.50	15.67	3.16	0.76
Logical Memory II (WMS-R)		#	16.00	2.89	14.00	2.91	0.76
RAVLT Immediate Recall Trial 5 (Total = 15)			12.14	2.93	11.78	1.86	0.39
RAVLT Delayed Recall (total = 15)			12.14	2.93	10.89	2.15	0.37

Note: Mean and standard deviations for three analysis groups. p-Values are for independent t-tests between OA groups. MMSE, mini mental status exam score.

($M = 0.81$, $SD = 0.07$) performed equivalently ($p = 0.98$) while OA-Nonlearners ($M = 0.50$, $SD = 0.02$) performed reliably lower than OA-Learners and YA-Learners ($p < 0.001$). We also report the relationship of category-learning accuracy and a variety of neuropsychological measures in Table 2. Most notably, accuracy was significantly correlated with both MMSE and a composite of executive function measures even though all participants in the study were well within the normal range for their age.

To further explore learning differences, mean accuracy was calculated separately for every block of 80 trials, as shown in Figure 3b. These data were subjected to a 2 group (YA-Learners, OA-Learners) × 4 block Mixed ANOVA. There was a main effect of block ($F(3, 93) = 39$, $p < 0.001$, $\eta_p^2 = 0.56$), and category learning linearly increased over the four blocks ($F(1, 31) = 67$, $p < 0.001$, $\eta_p^2 = 0.68$). The group × block interaction was also statistically significant ($F(3, 93) = 3.7$, $p < 0.01$, $\eta_p^2 = 0.11$), suggesting that OA-Learners continued to improve with experience while YA-Learners reached asymptotic accuracy during the second half of learning.

Categorization response time (Figure 3c)

Response time (RT) on correct trials was evaluated across the three participant subgroups (YA-Learners, OA-Learners, and OA-Nonlearners) using a one-way ANOVA, revealing statistically significant differences among subgroups ($F(2, 39) = 8.4$, $p = 0.001$,

Table 2. Correlations of sample characterization measures with categorization task accuracy for older adult participants and OA-Learners.

| | Task accuracy | | | |
| | All Older Adults | | OA-Learners | |
	r	p	r	p
Demographics				
Age	0.21	0.34	0.28	0.33
Education	0.21	0.37	**0.83**	**< 0.01**
Task performance				
RB-F Model Fit	−0.36	0.09	**−0.96**	**<0.01**
Global functioning				
MMSE	**0.53**	**0.01**	0.01	0.98
Vision				
Spatial frequency discrimination task	−0.05	0.87	0.21	0.79
Harder trials near to category boundary	−0.05	0.87	−0.01	0.97
Easier trials far from category boundary	−0.04	0.89	0.19	0.66
Processing speed				
Digit Symbol (WAIS-R)	0.13	0.54	0.27	0.35
Attention				
Digit Span Forward (WMS-R)	−0.15	0.51	0.07	0.82
Trail Making Test (Part A)	0.00	0.99	−0.50	0.07
Language				
Boston Naming Task	0.36	0.09	0.22	0.45
Executive Function				
Digit Span Backwards (WMS-R)	**0.49**	**0.02**	0.25	0.38
Trail Making Test (Part B-Reversed)	0.26	0.23	**0.60**	**0.03**
Generation (animals)	0.35	0.09	**0.53**	**0.05**
Generation (vegetables)	0.26	0.23	**0.53**	**0.05**
EF Composite (all tasks)	**0.46**	**0.03**	0.48	0.09
Memory				
Logical Memory I (WMS-R)	0.22	0.30	0.35	0.23
Logical Memory II (WMS-R)	0.36	0.10	0.24	0.42
RAVLT Immediate Recall	0.07	0.76	−0.06	0.84
RAVLT Delayed Recall	0.19	0.38	−0.03	0.92
LTM Composite (LM II, RAVLT Delay)	0.29	0.18	−0.01	0.97

Correlation between indicated measure and categorization task accuracy.

$\eta_p^2 = 0.30$). A Tukey's post-hoc comparison indicated that YA-Learners ($M = 697$ ms, $SD = 99$ ms) and OA-Nonlearners ($M = 703$ ms, $SD = 223$ ms) had similar RTs ($p = 0.99$) while OA-Learners ($M = 884$ ms, $SD = 114$ ms) took significantly more time to respond than YA-Learners ($p = 0.001$) and OA-Nonlearners ($p = 0.01$), suggesting OA-Learners required increased processing time to perform as well as YA-Learners.

Decision-bound theory modeling

In addition to the accuracy-based analysis above, we also employed Decision-Bound Theory (DBT) models based on General Recognition Theory (Ashby & Gott, 1988; Ashby & Maddox, 1993) to classify behavior in relation to particular categorization strategies. We previously used this approach to dissociate neural correlates of explicit (RB) and implicit (information integration) versions of this task (Morrison et al., 2015). Using Matsuki's (2014) implementation of General Recognition Theory in R, we fit the pattern of categorization responses for each participant using maximum likelihood procedures (Maddox & Ashby, 1993; Wickens, 1982) to three different models. The RB-F model is based on spatial frequency (a vertical boundary in stimulus space). The RB-O model is based on spatial orientation (a horizontal boundary in stimulus space). The random responder (RR) model assumes a participant guessed or applied different strategies

across trials. For the category distributions used in this experiment, the RB-F strategy would yield the highest accuracy. The quality of the fit was contrasted across models using Akaike's (1974) information criterion (AIC). We compared the AIC for the various models and tabulated whether the RB-F fit significantly better (Burnham & Anderson, 2002) than both the RB-O and RR models for a given block of trials (see Figure 3d). We conducted a 3 group (YA-Learners, OA-Learners, OA-Nonlearners) × 4 block Mixed ANOVA for RB-F model fit. There was a main effect of group (F(2, 39) = 88, $p < 0.001$, $\eta_p^2 = 0.82$), and block (F(3, 117) = 7.0, $p < 0.001$, $\eta_p^2 = 0.15$) but no significant group x block interaction (F(6, 117) = 1.4, $p = .24$, $\eta_p^2 = 0.07$). A Tukey's post-hoc comparison of the three groups confirmed that that YA-Learner and OA-Learners were not significantly different in RB-F model fit ($p = 0.85$) while OA-Nonlearners were less likely to be fit by the RB-F model than either OA-Learners ($p < 0.001$) or YA-Learners ($p < 0.001$). Lastly, we examined the two learner groups using a 2 group (YA-Learners, OA-Learners) × 4 block Mixed ANOVA. There was no main effect of group (F(1, 31) = .24, $p = .63$, $\eta_p^2 = 0.008$), a significant effect of block (F(3, 93) = 9.8, $p < 0.001$, $\eta_p^2 = 0.24$) but once again no group × block interaction (F(3, 93) = .64, $p = .59$, $\eta_p^2 = 0.02$).

Overall, the OA-Nonlearners showed considerable random responding, perhaps as a result of frequent strategy shifts. One of the nine OA-Nonlearners was best fit by the RB-O model in the first two blocks and then by the RR model in the final two blocks. This participant may have been fixated on spatial orientation, as seen in children who fail to learn with this task (Huang-Pollock, Maddox, & Karalunas, 2011). Another of the OA-Learners appears to have learned the RB-F rule late during learning and was best fit by the RB-F only in block 4.

EEG results

Comparisons between older and younger adult ERPs are complicated by differences in topography (Mueller, Brehmer, Von Oertzen, Li, & Lindenberger, 2008) and latency (Gazzaley et al., 2008). To address these complications, we used a data-driven approach to identify time windows and locations of interest. The same large time windows of interest were used to compare components between younger and older adults in order to account for any possible latency differences between the two age groups. Regions of interest were determined from the topography of each age-grouped component, and clusters of electrodes within the regions of interest were used to incorporate possible individual differences in topography.

Stimulus-locked categorization ERPs (Figure 4)

Agreeing with the ERP results reported by Morrison et al. (2015), a stimulus-locked LPC was found to be largest in parietal-occipital recordings at 400–700 ms after stimulus onset, as shown in Figure 4. Mean amplitudes from the same electrodes (Pz and Oz) and time ranges (400–700 ms) were used in a 3 participant group (YA-Learners, OA-Learners, OA-Nonlearners) by 2 accuracy (Correct, Incorrect) mixed ANOVA which yielded a significant main effect of accuracy (F(1, 39) = 25.60, $p < 0.001$, $\eta^2 = 0.40$) and an interaction between group and accuracy (F(1, 39) = 6.93, $p = 0.003$, $\eta_p^2 = 0.26$), suggesting that the LPC was larger for correct trials than incorrect trials and that the LPC correct/incorrect difference was different between groups. Additionally, in both the YA-Learners and the
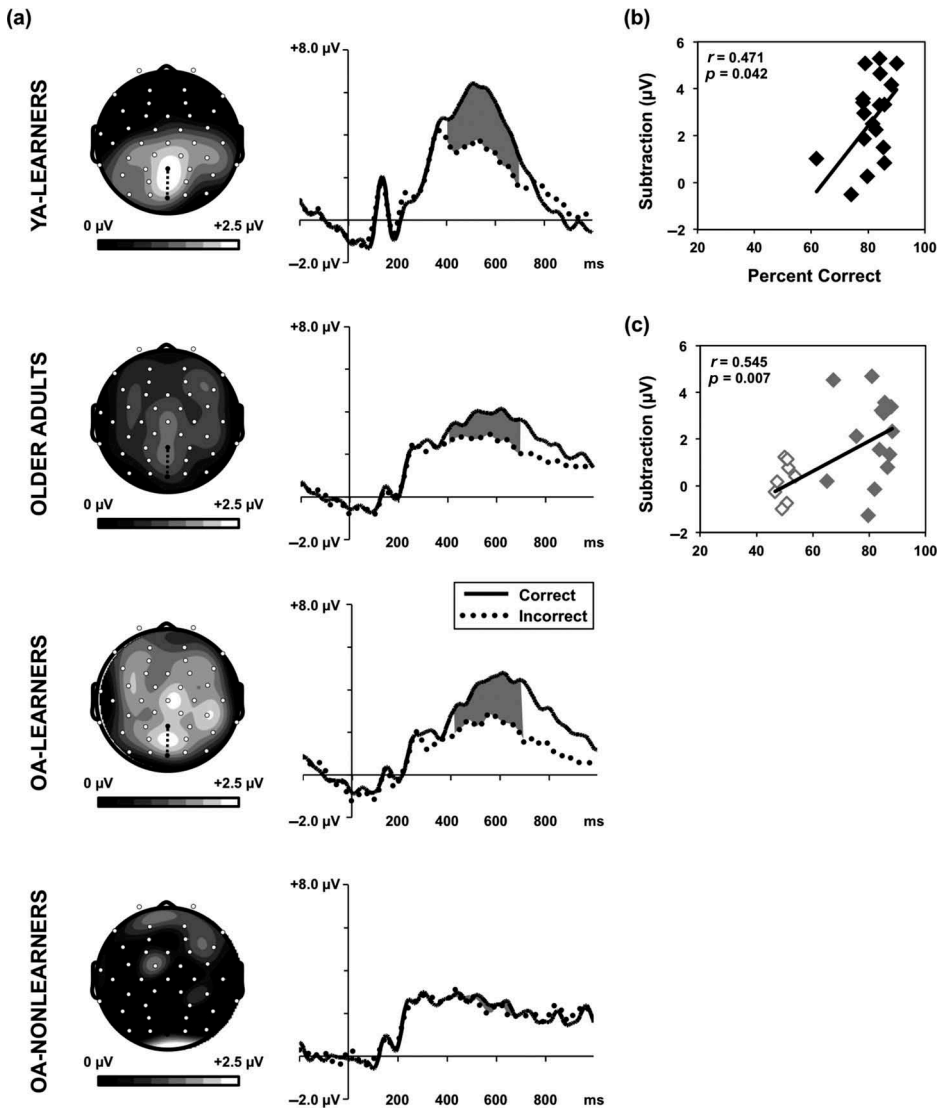
Figure 4. (a) Grand average stimulus-locked ERPs and corresponding topographic maps for YA-Learners, Older Adults, OA-Learners, and OA-Nonlearners. The LPC was measured from 400–700 ms (gray shading) from a parietal electrode cluster marked in the topographic maps with black dots. Scatterplots showing the relationship of accuracy to correct minus incorrect mean amplitude ERP subtractions from 400–700 ms for YA-Learners (b) and Older Adults (c) with OA-Learners depicted in solid gray diamonds and OA-Nonlearners depicted in open gray diamonds.

Older Adults, the LPC difference between correct and incorrect trials was correlated with task accuracy (YA-Learners: $r = 0.47$, $p = 0.04$; Older Adults: $r = 0.54$, $p = 0.007$).

Next a one-way ANOVA was used to compare the LPC correct/incorrect difference among the three participant groups (YA-Learners, OA-Learners, and OA-Learners) and was found to be significant ($F(2, 39) = 6.93$, $p = 0.003$, $\eta_p^2 = 0.26$). Post-hoc comparisons confirmed that the LPC difference in YA-Learners ($M = 2.55$, $SD = 2.03$) and OA-Learners

($M = 2.10$, $SD = 1.78$) was not significantly different ($p = 0.77$), whereas OA-NonLearners' LPC difference ($M = -0.16$, $SD = 1.37$) was significantly smaller (YA-Learners, $p = 0.002$; OA-Learners, $p = 0.02$). This result suggests that the reduced LPC effect in Older Adults was driven by the negligible LPC correct/incorrect difference in OA-Nonlearners.

Topographic results during categorization

To examine whether greater engagement of the frontal lobe may have been partly responsible for OA-Learners' successful performance, we examined whether there were differences in ERP topography between the younger and older learners. Because topographical comparisons could be influenced by differential amplitudes, LPC mean amplitudes were normalized by dividing by the root mean squared activity across all electrodes (McCarthy & Wood, 1985; Picton et al., 2000). A 2 group (YA-Learners, OA-Learners) by accuracy (correct, incorrect), by electrode (32) ANOVA with Greenhouse–Geisser correction on the normalized data yielded a significant group by accuracy by electrode interaction ($F(8.4, 261.4) = 3.5$, $p = 0.001$, $\eta_p^2 = 0.1$). Next, we compared electrodes over the front and back half of the scalp to look for a specific frontal shift in the neural correlate of successful categorization in the older adults. A 2 group (YA-Learners, OA-Learners) by 2 (Front, Back) by 2 (Correct, Incorrect) ANOVA on the normalized data yielded a significant three-way interaction ($F(1,31) = 15.6$, $p < 0.001$, $\eta_p^2 = 0.34$). Specifically, YA-learners showed a greater difference effect in posterior electrodes ($F(1,18) = 23.2$, $p < 0.001$, $\eta_p^2 = 0.56$) while OA-Learners showed no difference between frontal compared to posterior electrodes ($F(1,13) = 0.16$, $p = .69$, $\eta_p^2 = 0.012$).

Feedback-locked ERPs

The difference between correct and incorrect feedback P300 was measured from 250–450 ms after feedback tone onset for each group and subgroup (see Figure 5). Electrode clusters for analysis were selected to capture the separate maximum activity in YA-Learners and in Older Adults. A 3 participant group (YA-Learners, OA-Learners, OA-Nonlearners) by 2 accuracy (Correct, Incorrect) mixed ANOVA yielded a significant main effect of accuracy ($F(1,39) = 43.59$, $p < 0.001$, $\eta_p^2 = 0.53$) and a significant group by accuracy interaction ($F(2,39) = 20.00$, $p < 0.001$, $\eta_p^2 = 0.51$), suggesting that the P300 was larger for incorrect than correct trials and that the P300 correct-incorrect mean amplitude difference was different between groups. Additionally, YA-Learners' P300 correct/incorrect difference was correlated with accuracy in YA-Learners ($r = -0.62$, $p = 0.005$) and in Older Adults ($r = -0.74$, $p < 0.001$).

A one-way ANOVA of the P300 correct/incorrect difference was used to compare the three participant groups (YA-Learners, OA-Learners, OA-Nonlearners) and was found to be significant ($F(2, 39) = 20.00$, $p < 0.001$, $\eta_p^2 = 0.51$), confirming that the P300 correct/incorrect effect differs between groups. A post-hoc comparison of the three groups further revealed that the YA-Learners' ($M = -12.86$, $SD = 7.19$) P300 correct/incorrect difference was significantly greater than that of OA-Learners' ($M = -4.75$, $SD = 3.97$; $p < 0.001$) and OA-NonLearners' ($M = 0.20$, $SD = 1.45$; $p < 0.001$), but that OA-Learners' and OA-Nonlearners' P300 correct/incorrect difference did not significantly differ ($p = 0.097$). This suggests that YA-Learners and Older Adults processed feedback differently. In addition, Older Adults' P300 from positive feedback was negatively
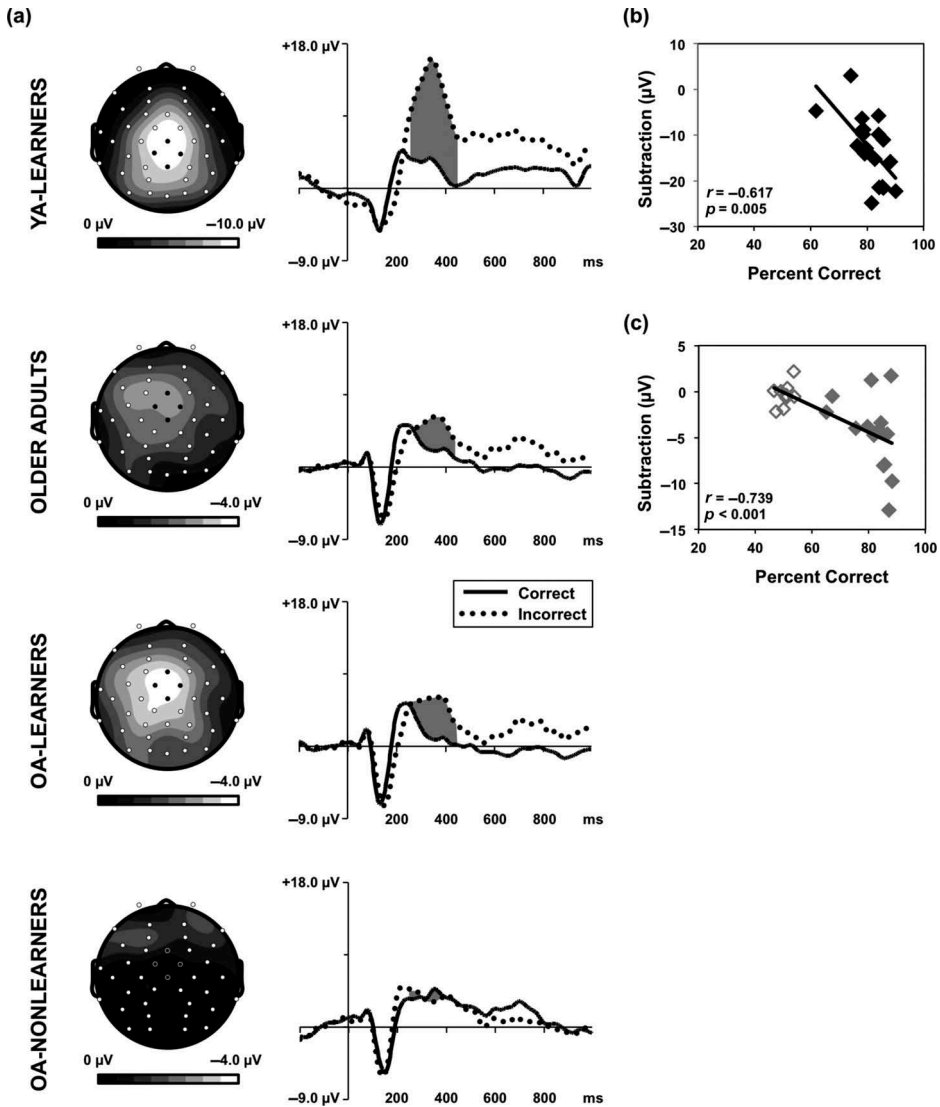
Figure 5. (a) Grand average feedback-locked ERPs and corresponding topographic maps for YA-Learners, Older adults, OA-Learners, and OA-Nonlearners. The P300 was measured from 250–450 ms (gray shading) from an electrode cluster marked in the topographic maps with black dots. Scatterplots showing the relationship of accuracy to correct minus incorrect mean amplitude ERP subtractions from 250–450 ms for YA-Learners (b) and Older Adults (c) with OA-Learners depicted in solid gray diamonds and OA-Nonlearners depicted in open gray diamonds.

correlated with the frontal LPC during categorization ($r = -0.44$, $p = 0.04$), suggesting an Older Adult specific interaction between stimulus processing and feedback processing.

Considering the large accuracy difference between OA-Learners and OA-Nonlearners, additional analysis on feedback processing was limited to YA-Learners and OA-Learners whose accuracy were similar. YA-Learners' P300 from *negative* feedback was found to be positively correlated with accuracy ($r = 0.64$, $p = 0.003$) while OA-Learners' feedback
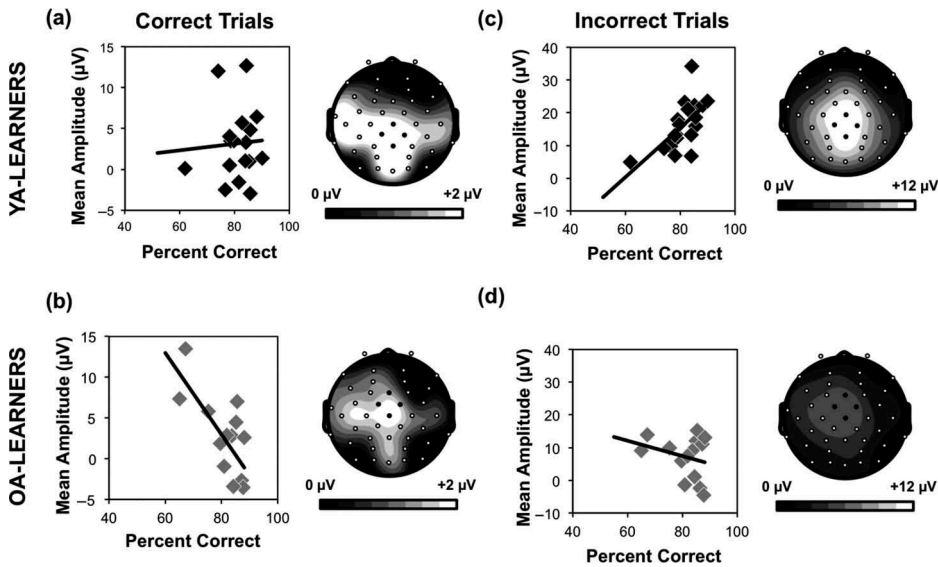
Figure 6. Scatterplots showing the relationship of accuracy to correct feedback-locked 250–450 ms mean amplitude ERP and corresponding mean amplitude topographic maps for YA-Learners (a) and OA-Learners (b). Scatterplots showing the relationship of accuracy to incorrect feedback-locked 250–450 ms mean amplitude ERP and corresponding mean amplitude topographic maps for YA-Learners (c) and OA-Learners (d).

P300 to *positive* feedback was found to be negatively correlated with accuracy ($r = -0.71$, $p = 0.004$; see Figure 6. This suggests an age-related shift in feedback processing or feedback preference where younger adults' attention to negative feedback, rather than positive feedback, is related to their successful categorization while older adults attention to positive feedback, rather than negative feedback is related to their successful categorization.

Discussion

The current study examined rule-based category learning in younger and older adults utilizing EEG to monitor neural signals of categorization-related processing. Similar to previous reports (Ashby et al., 2003; Maddox et al., 2010; Racine et al., 2006; Ridderinkhof et al., 2002), learning in older adults was generally less successful than that in younger adults. However, large individual differences in performance led us to classify a subgroup of high-performing older adults who learned the category rule and were able to use it to successfully categorize stimuli (OA-Learners). These high-performing older adults exhibited rule-based category-learning accuracy equivalent to that in younger adults, but took longer to make correct categorization responses. In contrast, low-performing older adults (OA-Nonlearners) failed to learn the category rule and categorized at near-chance levels. RTs in this subgroup were equivalent to those in younger adults, and were much faster than those of OA-Learners.

Racine et al. (2006) suggested that older adults had slower RTs and lower accuracy when categorizing complex rules with high interference. Considering that the category-learning

task in the present study did not reproduce the accuracy difference but did reproduce slower RTs in successful older adults, our results suggest that older adults need to take more time to properly apply an explicit categorization rule. This finding is consistent with a large body of literature, suggesting that older adults show age-related response slowing in cognitive tasks (Salthouse, 1996). ERP results can help clarify whether or not this slowing in older adults is simply a hallmark of inefficient processing or instead reflects a compensatory mechanism to counteract age-related cognitive decline.

Compensation in aging

Replicating the brain potential findings reported by Morrison et al. (2015), we found a posterior LPC difference between correct and incorrect trials related to categorization accuracy (Figure 4). Interesting, older adults who learned showed a frontal shift in their correct/incorrect LPC subtraction compared to younger adult learners. Likewise, categorization accuracy in older adults was correlated with a variety of measures of executive function (Table 2). Although it is tempting to entertain the possibility that these enhanced frontal ERPs reflect prefrontal cortical activity engaged to improve task performance, we cannot infer the neural sources based on merely scalp EEG data. Nevertheless, this possibility is consistent with results from a previous study with concurrent EEG and fMRI where a similar posterior–anterior shift in P300 topography was suggestive of increased frontal lobe engagement in a visual oddball task (O'Connell et al., 2012).

The significance of the posterior–anterior shift in older adults is highly debated (for review, see Cabeza et al., 2002; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Friedman, 2003; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005). O'Connell et al. (2012) interpreted their concurrent EEG and fMRI results as suggesting that increased frontal engagement may help overcome inefficient perceptual processing of task stimuli in posterior cortical regions. This idea is in agreement with the posterior–anterior shift in aging (PASA) model proposed by Davis et al. (2008), where the frontal shift in activity was specifically attributed to aging and not to task difficulty or confidence levels. In this study, however, we did not find significantly diminished posterior activity in high-performing older adults as the PASA theory would predict. Instead, we found that high-performing older adults and younger adults had similar posterior magnitudes. This may suggest that a frontal-posterior network of activity, instead of just a frontal shift of activity, was necessary for our older adults to succeed.

In further support of the compensation hypothesis of aging, in this study, we found frontal LPC activity in high-performing older adults was significantly larger than in younger adults, while low-performing older adults' frontal activity was not significantly different than younger adults'. This parallels the results described by Cabeza et al. (2002), where high-performing older adults who performed as well as younger adults in a source memory task had increased neural activity in the left prefrontal cortex and low-performing older adults had similar frontal activity as younger adults. This increase in frontal activity in successful older adults may be related to scaffolding theory of aging and cognition (STAC), where recruitment of additional circuitry is required to maintain high cognitive function despite neural deterioration (Park & Reuter-Lorenz, 2009).

Feedback learning and aging

According to the context-updating theory of P300 (for review, see Polich, 2007), P300 amplitude is related to updating a mental representation or schema in working memory after receiving meaningful information. Previous literature has shown that younger and older adults respond to feedback differently (Eppinger & Kray, 2011; Frank & Kong, 2008; Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2008; Wood & Kisley, 2006). In this study, younger adults' P300 to negative feedback were correlated with task accuracy, suggesting that their success in refining the categorization rule was related to their attention to negative feedback and not positive feedback. In our previous study with a more difficult rule-based category distribution (Morrison et al., 2015), we found that younger adults' P300 to positive feedback, instead of negative feedback, was related to rule-based categorization performance. The easier distribution of stimuli and the consequently higher performance of younger adults in this study may explain this discrepancy. Indeed, in the previous study, a similar negative feedback/P300 correlation was found when low-performing younger adults were excluded (unpublished results). In the present study, task accuracy for high-performing older adults was correlated with the P300 for positive feedback, instead of negative feedback, suggesting that success was related to preserving their mental representation of the rule instead of updating or changing their mental representation of the rule. Differences in the negative feedback P300 ERP magnitude between younger and older adult rule learners may be partially due to older adults' reduced reactivity to negative feedback (Wood & Kisley, 2006), related to their bias to learn from positive outcomes (Eppinger & Kray, 2011).

Older adult subgroups and future studies

The low-performing older adults identified in this study have neuropsychologically normal profiles (well within 2 SD of the UDS norms) but were distinguished by their poor performance in this task (see Table 1). Further analysis of their neuropsychological scores, in comparison with those of the high performing older adults, revealed that they had lower working-memory scores (i.e., Digit Span Backwards) and lower MMSE scores (Table 1). Indeed a composite of executive function measures in the UDS significantly correlated with categorization accuracy (Table 2). Considering that executive dysfunction at the time of a diagnosis of amnestic mild cognitive impairment has been shown to be an effective predictor of conversion to probable Alzheimer's disease (Albert, Moss, Blacker, Tanzi, & McArdle, 2007), longitudinal study is ongoing to check for risk of cognitive decline in older adults who exhibit difficulties in rule-based category learning of the sort studied here.

Additionally, electrophysiological analyses from the current study may further highlight the nature of individual differences in older adults. Specifically, in this study, high-performing older adults showed similar posterior activity but increased frontal activity during stimulus processing when compared to younger adults. This suggests that higher-performing older adults engaged additional processes to perform as well as younger adults. The degree to which they engage these additional resources may be related to the decline of their long-term memory capabilities.

On the other hand, the low-performing older adults showed significantly lower posterior activity than younger adults and failed to show increases in frontal activity compared to younger adults during stimulus processing. This suggests that low-performing older adults failed to recruit additional processing, which may be necessary for successful cognitive aging (Cabeza et al., 2002). This lack of recruitment of additional processing and possible lack of compensation for deficient systems in low-performing older adults is also complemented by our findings that low-performing older adults responded as fast as younger adults and failed to adjust their RT to succeed in this task. Moreover, differences in the parietal LPC in non-rule learning older adults is similar to LPC abnormalities in mild cognitive impairment patients who subsequently converted to Alzheimer's disease (Olichney et al., 2008) and may indicate that the non-rule learning older adults have deficiencies in integration of the MTL with working memory functions critical for effective category rule learning. Additionally, aberrations in the feedback P300, as seen in non-rule learning older adults, has been related to poor resource allocation and working memory (Kok, 2001) as well as pathologic aging (Bennys et al., 2007; Mathewson et al., 2008).

In summary, our results suggest that the ability to adapt one's behavior in response to feedback during learning is a source of marked individual differences in older adults. The failure of some individuals to adapt their behavior may be the result of a failure to adequately engage a network including prefrontal cortex. An important follow-up question that should be addressed in future studies is whether such individuals can be trained to engage this network so as to improve cognitive performance in such tasks. We also believe that our results suggest that a feed-back-based learning task such as this one may be a useful addition to efforts designed to predict subsequent cognitive change in both older adults already experiencing memory changes, as well as in older adults currently exhibiting neuropsychological profiles within normal range.

Disclosure statement

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References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. doi:10.1109/TAC.1974.1100705,MR 0423716

Albert, M., Moss, M. B., Blacker, D., Tanzi, R., & McArdle, J. J. (2007). Longitudinal change in cognitive performance among individuals with mild cognitive impairment. *Neuropsychology*, *21*, 158–169. doi:10.1037/0894-4105.21.2.158

Ashby, F. G., Alfonso-Reese, L. A., Turken, A. U., & Waldron, E. M. (1998). A neuropsychological theory of multiple systems in category learning. *Psychological Review*, *105*, 442–481. doi:10.1037/0033-295X.105.3.442

Ashby, F. G., & Gott, R. E. (1988). Decision rules in the perception and categorization of multidimensional stimuli. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *14*, 33–53.

Ashby, F. G., & Maddox, W. T. (1993). Relations between prototype, exemplar, and decision bound models of categorization. *Journal of Mathematical Psychology*, *37*, 372–400. doi:10.1006/jmps.1993.1023

Ashby, F. G., & Maddox, W. T. (2011). Human category learning 2.0. *Annals of the New York Academy of Sciences*, *1224*, 147–161. doi:10.1111/j.1749-6632.2010.05874.x

Ashby, F. G., Noble, S., Filoteo, J. V., Waldron, E. M., & Ell, S. W. (2003). Category learning deficits in Parkinson's disease. *Neuropsychology*, *17*, 115–124. doi:10.1037/0894-4105.17.1.115

Bennys, K., Portet, F., Touchon, J., & Rondouin, G. (2007). Diagnostic value of event-related evoked potentials N200 and P300 subcomponents in early diagnosis of Alzheimer's disease and mild cognitive impairment. *Journal of Clinical Neurophysiology*, *24*, 405–412. doi:10.1097/WNP.0b013e31815068d5

Berg, E. A. (1948). A simple objective technique for measuring flexibility in thinking. *The Journal of General Psychology*, *39*, 15–22. doi:10.1080/00221309.1948.9918159

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer-Verlag.

Burzynska, A. Z., Nagel, I. E., Preuschhof, C., Gluth, S., Bäckman, L., Li, S., & Heekeren, H. R. (2012). Cortical thickness is linked to executive functioning in adulthood and aging. *Human Brain Mapping*, *33*, 1607–1620. doi:10.1002/hbm.21311

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*, 1394–1402. doi:10.1006/nimg.2002.1280

Cabeza, R., & Dennis, N. A. (2012). Frontal lobes and aging: Deterioration and compensation. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (2nd ed., pp. 628–652). New York, NY: Oxford University Press.

Chapman, R. M., McCrary, J. W., Gardner, M. N., Sandoval, T. C., Guillily, M. D., Reilly, L. A., & DeGrush, E. (2011). Brain ERP components predict which individuals progress to Alzheimer's disease and which do not. *Neurobiology of Aging*, *32*, 1742–1755. doi:10.1016/j.neurobiolaging.2009.11.010

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior–anterior shift in aging. *Cerebral Cortex*, *18*, 1201–1209. doi:10.1093/cercor/bhm155. New York, N. Y.:1991.

Dennis, N. A., & Cabeza, R. (2008). Neuroimaging of healthy cognitive aging. *The Handbook of Aging and Cognition*, *3*, 1–54.

Dennis, N. A., & Cabeza, R. (2011). Age-related dedifferentiation of learning systems: An fMRI study of implicit and explicit learning. *Neurobiology of Aging*, *32*, 2318.e17–2318.e30. doi:10.1016/j.neurobiolaging.2010.04.004

Eppinger, B., & Kray, J. (2011). To choose or to avoid: Age differences in learning from positive and negative feedback. *Journal of Cognitive Neuroscience*, *23*, 41–52. doi:10.1162/jocn.2009.21364

Filoteo, J. V., Maddox, W. T., Ing, A. D., & Song, D. D. (2007). Characterizing rule-based category learning deficits in patients with Parkinson's disease. *Neuropsychologia*, *45*, 305–320. doi:S0028-3932(06)00297-1

Finnigan, S., Humphreys, M. S., Dennis, S., & Geffen, G. (2002). ERP "old/new" effects: Memory strength and decisional factor(s). *Neuropsychologia*, *40*, 2288–2304. doi:10.1016/S0028-3932(02)00113-6

Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 11778–11783. doi:10.1073/pnas.0602659103

Folstein, J. R., & Van Petten, C. (2004). Multidimensional rule, unidimensional rule, and similarity strategies in categorization: Event-related brain potential correlates. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *30*, 1026.

Frank, M. J., & Kong, L. (2008). Learning to avoid in older age. *Psychology and Aging*, *23*, 392–398. doi:10.1037/0882-7974.23.2.392

Friedman, D. (2003). Cognition and aging: A highly selective overview of event-related potential (ERP) data. *Journal of Clinical and Experimental Neuropsychology*, *25*, 702–720. doi:10.1076/jcen.25.5.702.14578

Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., & D'Esposito, M. (2008). Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 13122–13126. doi:10.1073/pnas.0806074105

Hajcak, G., Holroyd, C. B., Moser, J. S., & Simons, R. F. (2005). Brain potentials associated with expected and unexpected good and bad outcomes. *Psychophysiology*, *42*, 161–170. doi:10.1111/j.1469-8986.2005.00278.x

Hartman, M., Bolton, E., & Fehnel, S. E. (2001). Accounting for age differences on the Wisconsin card sorting test: Decreased working memory, not inflexibility. *Psychology and Aging*, *16*, 385–399. doi:10.1037/0882-7974.16.3.385

Huang-Pollock, C. L., Maddox, W. T., & Karalunas, S. L. (2011). Development of implicit and explicit category learning. *Journal of Experimental Child Psychology*, *109*, 321–335. doi:10.1016/j.jecp.2011.02.002

Joyce, C. A., Paller, K. A., McIsaac, H. K., & Kutas, M. (1998). Memory changes with normal aging: Behavioral and electrophysiological measures. *Psychophysiology*, *35*, 669–678. doi:10.1111/psyp.1998.35.issue-6

Kéri, S. (2003). The cognitive neuroscience of category learning. *Brain Research Reviews*, *43*, 85–109. doi:10.1016/S0165-0173(03)00204-2

Koenig, P., Smith, E. E., Moore, P., Glosser, G., & Grossman, M. (2007). Categorization of novel animals by patients with Alzheimer's disease and corticobasal degeneration. *Neuropsychology*, *21*, 193–206. doi:10.1037/0894-4105.21.2.193

Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577. doi:10.1017/S0048577201990559

Li, S., & Lindenberger, U. (1999). Cross-level unification: A computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. JOURNAL etc.

Liu, T., & Yao, D. (2006). Removal of ocular artifacts from EEG data using a cascaded spatio-temporal processing. *Computer Methods and Programs in Biomedicine*, *83*, 95–103. doi:10.1016/j.cmpb.2006.03.009

Maddox, W., & Filoteo, J. V. (2001). Striatal contributions to category learning: Quantitative modeling of simple linear and complex nonlinear rule learning in patients with Parkinson's disease. *Journal of the International Neuropsychological Society*, *7*, 710–727. doi:10.1017/S1355617701766076

Maddox, W. T., Aparicio, P., Marchant, N. L., & Ivry, R. B. (2005). Rule-based category learning is impaired in patients with Parkinson's disease but not in patients with cerebellar disorders. *Journal of Cognitive Neuroscience*, *17*, 707–723. doi:10.1162/0898929053747630

Maddox, W. T., & Ashby, F. G. (1993). Comparing decision bound and exemplar models of categorization. *Perception and Psychophysics*, *53*, 49–70.

Maddox, W. T., Ashby, F. G., & Bohil, C. J. (2003). Delayed feedback effects on rule-based and information-integration category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 650–662.

Maddox, W. T., Pacheco, J., Reeves, M., Zhu, B., & Schnyer, D. M. (2010). Rule-based and information-integration category learning in normal aging. *Neuropsychologia*, *48*, 2998–3008. doi:10.1016/j.neuropsychologia.2010.06.008

Mathewson, K. J., Dywan, J., Snyder, P. J., Tays, W. J., & Segalowitz, S. J. (2008). Aging and electrocortical response to error feedback during a spatial learning task. *Psychophysiology*, *45*, 936–948. doi:10.1111/psyp.2008.45.issue-6

Matsuki, K. (2014). General Recognition Theory [Computer software]. Retrieved from http://cran.r-project.org/web/packages/grt/index.html

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, *62*, 203–208.

Morris, J. C., Weintraub, S., Chui, H. C., Cummings, J., Decarli, C., Ferris, S., & Kukull, W. A. (2006). The Uniform Data Set (UDS): Clinical and cognitive variables and descriptive data from Alzheimer's disease centers. *Alzheimer Disease and Associated Disorders*, *20*, 210–216. doi:10.1097/01.wad.0000213865.09806.92

Morrison, R. G., Reber, P. J., Bharani, K. L., & Paller, K. A. (2015). Dissociation of category-learning systems via brain potentials. *Frontiers in Human Neuroscience*, *9*, 389. doi:10.3389/fnhum.2015.00389

Mueller, V., Brehmer, Y., Von Oertzen, T., Li, S. C., & Lindenberger, U. (2008). Electrophysiological correlates of selective attention: A lifespan comparison. *BMC Neuroscience*, *9*, 18-2202-9-18. doi:10.1186/1471-2202-9-18

Nomura, E. M., Maddox, W. T., Filoteo, J. V., Ing, A. D., Gitelman, D. R., Parrish, T. B., & Reber, P. J. (2007). Neural correlates of rule-based and information-integration visual category learning. *Cerebral Cortex*, *17*, 37–43. doi:10.1093/cercor/bhj122. New York, N. Y.: 1991.

Nomura, E. M., Maddox, W. T., & Reber, P. J. (2007). Mathematical models of visual category learning enhance fMRI data analysis. In D. McNamara & G. Trafton (Eds.), *Proceedings of the 29th annual meeting of the cognitive science society* (pp. 539–544).

Nomura, E. M., & Reber, P. J. (2012). Combining computational modeling and neuroimaging to examine multiple category learning systems in the brain. *Brain Sciences*, *2*, 176–202. doi:10.3390/brainsci2020176

O'Connell, R. G., Balsters, J. H., Kilcullen, S. M., Campbell, W., Bokde, A. W., Lai, R., & Robertson, I. H. (2012). A simultaneous ERP/fMRI investigation of the P300 aging effect. *Neurobiology of Aging*, *33*, 2448–2461. doi:10.1016/j.neurobiolaging.2011.12.021

Olichney, J. M., Iragui, V. J., Salmon, D. P., Riggins, B. R., Morris, S. K., & Kutas, M. (2006). Absent event-related potential (ERP) word repetition effects in mild Alzheimer's disease. *Clinical Neurophysiology*, *117*, 1319–1330. doi:10.1016/j.clinph.2006.02.022

Olichney, J. M., Taylor, J. R., Gatherwright, J., Salmon, D. P., Bressler, A. J., Kutas, M., & Iragui-Madoz, V. J. (2008). Patients with MCI and N400 or P600 abnormalities are at very high risk for conversion to dementia. *Neurology*, *70*, 1763–1770. doi:10.1212/01.wnl.0000281689.28759.ab

Paller, K. A., Voss, J. L., & Westerberg, C. E. (2009). Investigating the awareness of remembering. *Perspectives on Psychological Science}*, *4*, 185–199. doi:10.1111/j.1745-6924.2009.01118.x

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196. doi:10.1146/annurev.psych.59.103006.093656

Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson Jr., R., . . . Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, *37*, 127–152. doi:10.1111/psyp.2000.37.issue-2

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148. doi:10.1016/j.clinph.2007.04.019

Racine, C. A., Barch, D. M., Braver, T. S., & Noelle, D. C. (2006). The effect of age on rule-based category learning. *Aging, Neuropsychology, and Cognition*, *13*, 411–434. doi:10.1080/13825580600574377

Reber, P. J., Knowlton, B. J., & Squire, L. R. (1996). Dissociable properties of memory systems: Differences in the flexibility of declarative and nondeclarative knowledge. *Behavioral Neuroscience*, *110*, 861–871. doi:10.1037/0735-7044.110.5.861

Reber, P. J., Martinez, L. A., & Weintraub, S. (2003). Artificial grammar learning in Alzheimer's disease. *Cognitive, Affective, & Behavioral Neuroscience*, *3*, 145–153. doi:10.3758/CABN.3.2.145

Reber, P. J., & Squire, L. R. (1994). Parallel brain systems for learning with and without awareness Cold Spring Harbor, NY. *Learning & Memory*, *1*, 217–229.

Reber, P. J., & Squire, L. R. (1999). Intact learning of artificial grammars and intact category learning by patients with Parkinson's disease. *Behavioral Neuroscience*, *113*, 235–242. doi:10.1037/0735-7044.113.2.235

Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*, 177–182. doi:10.1111/j.1467-8721.2008.00570.x

Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: Reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, *15*, 245–251. doi:10.1016/j.conb.2005.03.016

Ridderinkhof, K. R., Span, M. M., & Van Der Molen, M. W. (2002). Perseverative behavior and adaptive control in older adults: Performance monitoring, rule induction, and set shifting. *Brain and Cognition*, *49*, 382–401. doi:10.1006/brcg.2001.1506

Rips, L. J., Smith, E. E., & Medin, D. L. (2012). Concepts and categories: Memory, meaning, and metaphysics. In K. J. Holyoak, & R. G. Morrison (Eds.), *Oxford handbook of thinking and reasoning* (pp. 177–209). New York, NY: Oxford University Press.

Rozin, P., & Royzman, E. B. (2001). Negativity bias, negativity dominance, and contagion. *Personality and Social Psychology Review*, *5*, 296–320. doi:10.1207/pspr.2001.5.issue-4

Salthouse, T. A. (1996). The processing speed theory of adult age differences in cognition. *Psychological Review*, *103*, 403–428.

Smith, A. B., Taylor, E., Brammer, M., & Rubia, K. (2004). Neural correlates of switching set as measured in fast, event-related functional magnetic resonance imaging. *Human Brain Mapping*, *21*, 247–256. doi:10.1002/(ISSN)1097-0193

Smith, E. E., & Grossman, M. (2008). Multiple systems of category learning. *Neuroscience & Biobehavioral Reviews*, *32*, 249–264. doi:10.1016/j.neubiorev.2007.07.009

Smith, J. D., Boomer, J., Zakrzewski, A. C., Roeder, J. L., Church, B. A., & Ashby, F. G. (2013). Deferred feedback sharply dissociates implicit and explicit category learning. *Psychological Science*, *25*(2), 447–457. doi:10.1177/0956797613509112

Taylor, J. R., & Olichney, J. M. (2007). From amnesia to dementia: ERP studies of memory and language. *Clinical EEG and Neuroscience*, *38*, 8–17. doi:10.1177/155005940703800106

Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., & Pinker, S. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *Journal of Cognitive Neuroscience*, *9*, 266–276. doi:10.1162/jocn.1997.9.2.266

Viskontas, I. V., Morrison, R. G., Holyoak, K. J., Hummel, J. E., & Knowlton, B. J. (2004). Relational integration, inhibition, and analogical reasoning in older adults. *Psychology and Aging*, *19*, 581–591. doi:10.1037/0882-7974.19.4.581

Weintraub, S., Salmon, D., Mercaldo, N., Ferris, S., Graff-Radford, N. R., Chui, H., & Morris, J. C. (2009). The Alzheimer's disease centers' uniform data set (UDS): The neuropsychologic test battery. *Alzheimer Disease and Associated Disorders*, *23*, 91–101. doi:10.1097/WAD.0b013e318191c7dd

Wickens, T. D. (1982). *Models for behaviour: Stochastic processes in psychology*. San Francisco, CA: Freeman.

Wood, S., Busemeyer, J., Koling, A., Cox, C. R., & Davis, H. (2005). Older adults as adaptive decision makers: Evidence from the Iowa gambling task. *Psychology and Aging*, *20*, 220–225. doi:10.1037/0882-7974.20.2.220

Wood, S., & Kisley, M. A. (2006). The negativity bias is eliminated in older adults: Age-related reduction in event-related brain potentials associated with evaluative categorization. *Psychology and Aging*, *21*, 815–820. doi:10.1037/0882-7974.21.4.815