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Adult Age Differences in Learning and Generalization of Feedback-Based Associations

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Feedback-based associative learning (e.g., acquiring new associations from positive or negative outcomes) and generalization (e.g., applying past learning to new settings) are important cognitive skills that enable people to make economic decisions or social judgments. This ability to acquire new skills based on feedback and transfer those experiences to predict positive outcomes in novel situations is essential at all ages, but especially among older adults who must continually adapt to new people, environments, and technologies. Ample evidence from animal work, clinical research, and computational modeling has demonstrated that feedback-based associative learning is sensitive to basal ganglia dysfunction and generalization to medial temporal lobe dysfunction. This dissociation is relevant because of recent evidence that has suggested healthy aging compromises the basal ganglia system earlier than the medial temporal lobes. However, few studies have investigated how healthy aging influences these cognitive processes. Here, we examined both feedback-based associative learning and generalization in younger, middle-aged, and older adults using a computerized acquired equivalence task. Results revealed a significant effect of age group on feedback-based associative learning, consistent with evidence of persistent age-related declines in the basal ganglia. In contrast, generalization was spared in all but the oldest adult group, likely reflecting preserved medial temporal lobe function until advanced old age. Our findings add behavioral evidence to the emerging view that healthy aging affects the striatal system before the medial temporal lobes. Although further evidence is needed, this finding may shed light on the possible time course of neural system dysfunction in healthy aging.

Keywords: aging, associative learning, generalization, basal ganglia, hippocampus

Learning to predict positive outcomes is essential for successful functioning in our ever-changing world. This type of learning guides us when facing novel situations that can critically affect our lives or the lives of others, including economic decisions or social judgments. For example, people often select stocks based on wins and losses in the financial market, and the integration of such reinforcement outcomes over multiple experiences can help when navigating new investments, such as retirement planning. Whether deciding what to invest in, what to buy, or even whom to trust, how we learn from experience and transfer this knowledge to new situations is fundamental to our daily lives. Despite their relevance to adults of all ages, feedback-based learning and generalization have remained relatively understudied in healthy aging research compared to other cognitive processes, such as working and episodic memory (e.g., Luo & Craik, 2008; Rajah & D'Esposito, 2005). Thus, the present study sought to bridge this gap, by examining the effects of healthy aging on learning from feedback and applying those experiences to predict positive outcomes in novel situations.

In particular, we focused on *feedback-based associative learning* or the acquisition of reward contingencies over time (e.g., learning the stock market) and *generalization* or applying prior learning to new instances (e.g., choosing a retirement plan). These cognitive processes can be measured using a single "acquired equivalence" task that has two distinct phases (Myers et al., 2003). In the learning phase of this Rutgers Acquired Equivalence Task, participants incrementally learn the rewarded object in a series of stimulus presentations. Specifically, participants must learn to associate different faces with different colored fish. Each of the pairings is learned individually via trial and error, but sometimes associations overlap, such that different faces are associated with a common fish and vice versa (e.g., FaceA → FishX, FaceB → FishX, and FaceA → FishY). After learning, there is a test phase that requires transfer of what has been learned, without feedback, when familiar information is presented in novel recombinations. Here, participants must predict new fish−face pairings as related to their previous training; if they had learned that Faces A and B were equivalent based on overlapping associations, participants should generalize that FaceB → FishY. This type of transfer should occur even though participants had never encountered this particular pairing before.

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The ability of healthy older adults to perform these cognitive processes is not yet well characterized. Most previous research using the Rutgers Acquired Equivalence Task has evaluated the performance of patients with aging-related diseases. For example, patients with Parkinson's disease (PD) have shown impairments in feedback-based associative learning, but intact generalization, whereas patients with Alzheimer's disease (AD) have shown the reverse (Bódi, Csibri, Myers, Gluck, & Keri, 2009; Myers et al., 2003). Moreover, generalization is sensitive to hippocampal atrophy, as measured by neuroimaging, even in very mild cases among older adults with no other cognitive abnormalities (Myers et al., 2002). These findings provide some evidence that the basal ganglia are necessary for feedback-based associative learning and the medial temporal lobes (MTL) for generalization, because these neural substrates are damaged in PD and AD, respectively. This dissociation is relevant to healthy aging research—while neither the MTL or basal ganglia are completely spared, there is emerging evidence that healthy aging compromises the basal ganglia before the MTL (D. V. Howard & Howard, 2011).

Specifically, there is cross-sectional and longitudinal evidence of robust age-related declines in the structure and function of the basal ganglia beginning in young adulthood (Raz et al., 2005). Studies have also reported age-related reductions in the striatal dopamine system (Reeves, Bench, & Howard, 2002), whereby healthy elders have shown similar pathology to patients with PD (Collier, Kanaan, & Kordower, 2011) and adults older than about seventy years have shown particularly dramatic damage to substantia nigra dopaminergic neurons (Kraytsberg et al., 2006). In contrast, the MTL do not show these same age-related declines. Many studies have suggested relatively little age-related volume loss within the MTL in healthy aging (Good et al., 2001; Grieve, Clark, Williams, Peduto, & Gordon, 2005; Head, Snyder, Girton, Morris, & Buckner, 2005; Kalpouzos et al., 2009; Laakso et al., 1998; Mueller et al., 1998; Sullivan, Marsh, Mathalon, Lim, & Pfefferbaum, 1995; Sullivan, Marsh, & Pfefferbaum, 2005), though this region can be affected early with hypertension (Shing et al., 2011) or pathological aging such as AD (Hedden & Gabrieli, 2004). Although some research has shown healthy age differences in MTL volume (e.g., Kennedy & Raz, 2005; Raz, Rodrigue, Head, Kennedy, & Acker, 2004), function (e.g., Ramsøy et al., 2012), and cognition (e.g., Craik, 2008; Geinisman, Detoledo-Morrell, Morrell, & Heller, 1995), one emerging view is that the MTL is relatively spared until advanced old age or greater than roughly seventy years (Jernigan et al., 2001; Lupien et al., 2007; Scahill et al., 2003; Zhang et al., 2010).

Such patterns of healthy brain aging are likely to produce differential behavioral deficits in feedback-based associative learning and generalization. To our knowledge, only two previous studies have addressed this possibility, but both yielded ambiguous results. The first study compared healthy young adults to older adults using a probabilistic variation of our acquired equivalence task, described above (Weiler, Bellebaum, & Daum, 2008). Results revealed age-related impairments in learning and mild deficits in generalization, whereby performance was numerically better in younger than older adults. But it is unclear whether these age-related differences merely reflect known age deficits in forming probabilistic associations (J. H. Howard, Howard, Dennis, & Kelly, 2008; Simon, Howard, & Howard, 2011). Recent findings have suggested that older adults exhibit impaired performance only when outcome information is probabilistic; when it is deterministic, older adults are able to learn as well as younger adults (Eppinger, Hammerer, & Li, 2011). Moreover, only a subset of their participants met learning criteria, and generalization accuracy was not significantly greater than chance level for either age group, making it challenging to detect age deficits, should any exist.

The second study used a different learning and generalization task (i.e., concurrent discrimination; see Myers et al., 2002), but in a sample of older adults only, including young-old (45–60 years), middle-old (61–75 years), and old-old (76–90 years) groups (Krishna, Moustafa, Eby, Skeen, & Myers, 2012). Results revealed age-related deficits in feedback-based associative learning, and only the oldest-old had impaired generalization. However, it remains unclear how the older adults' performance compares to a younger, college-aged population. More important, several notable issues make it difficult to interpret these findings. First, performance in this task required participants to ignore redundant or nonrelevant stimulus features, so age differences could be attributed to age deficits in suppression of nonrelevant information (Hasher, Stoltzfus, Zacks, & Rypma, 1991). Second, similar to Weiler et al. (2008), only half the adults over 60 (and only 74% of participants total) were able to reach learning criterion, and analyses of generalization led to different conclusions depending on whether those failing to reach criterion were included. That is, primary analysis of generalization with all subjects revealed a difference between the youngest and oldest groups, while a follow-up analysis of generalization with the smaller group of individuals who reached criterion revealed a significant difference between the middle and oldest groups. Because there were only 18 older-old subjects prior to data elimination, leaving what we assume is only about nine subjects in the final analysis, it is not clear how to interpret these mixed results. Moreover, generalization in their task showed a bimodal response pattern (i.e., either total failure or perfect performance), resulting in many subjects who were unable to solve this task phase (approximately 25% in the middle-old group and 65% in the oldest-old group). This means that the critical generalization data are based on a very small number of subjects, particularly for the oldest group. Third, participants in this study encountered a variable number of learning and generalization trials, depending on when criterion was met. But, only the sum number of errors was reported versus the proportion of errors to the total number of trials experienced. Unmeasured age differences in how long it took to learn may, in turn, have influenced learning and generalization performance; it may be that oldest-old group took longer to learn and/or generalize, despite equivalent overall accuracy to the younger groups. This explanation is quite possible when viewing the distribution of blocks needed to reach criterion in both task phases. The majority of young-old adults reached criterion in the first few blocks, whereas those in the middle and oldest groups took much longer.

Thus, the purpose of the current study was to more clearly characterize the effects of healthy aging on feedback-based associative learning and generalization, and to provide an adult lifespan perspective. To rule out alternative interpretations for previously observed age deficits, we administered our deterministic Rutgers Acquired Equivalence Task, which does not require suppression of nonrelevant information, to a sample of healthy college-aged, middle-aged, and older adults. Further, participants easily meet our learning criterion, and generalization in our task

avoids the bimodal distribution mentioned above, with performance varying in a more continuous fashion across individuals (typically ranging from about 38−100% performance; see Farkas et al., 2008; Keri, Nagy, Kelemen, Myers, & Gluck, 2005; Shohamy & Wagner, 2008). Based on evidence that feedback-based associative learning recruits the basal ganglia and that generalization recruits the MTL, we predicted that increasing age would be associated with increasing impairments in feedback-based associative learning, whereas generalization would be spared until advanced old age, reflecting regional patterns of healthy brain aging.

Method

Participants

We tested 32 college-aged younger adults (M = 20.3 years, SD = 1.8, range: 18–25) and 64 healthy older adults between the ages of 50 and 89 years. Seniors were divided into two groups: 32 middle-aged adults (M = 62.2 years, SD = 5.6, range: 50–69) and 32 older adults (M = 79.1 years, SD = 4.5, range: 70–89). These groupings were based on (a) a median split and (b) literature indicating that age 70 may be a critical demarcation in healthy brain aging (e.g., Kraytsberg et al., 2006; Zhang et al., 2010). As shown in Table 1, these elderly groups differed significantly in age ($p < .001$) but not education ($p > .73$). Younger adults were all Rutgers University students, and healthy elderly adults were recruited from the community using local advertisements in retirement centers and community organizations and at brain health events. All participants were in good health: they were not colorblind, had normal or corrected-to-normal vision, had no existing neurological or psychological conditions or untreated hypertension (determined by general health questionnaires), and did not use drugs known to influence cognition. Furthermore, participants did not have abnormal cognitive status (i.e., scores outside the expected age range on neuropsychological measures of verbal memory) and did not meet criteria for dementia (i.e., score below 27 on the Mini-Mental Status Examination) (see Table 1 for results). The Rutgers University Institutional Review Board approved all experimental procedures, and all participants gave informed consent. Subjects received monetary compensation for participation.

Experimental Paradigm

Stimuli were programmed and presented using SuperCard on a Macintosh PowerBook laptop. As seen in Table 2, the Rutgers Acquired Equivalence Task consists of an acquisition phase (feedback-based associative learning) followed by a test phase (generalization) (Myers et al., 2003). On each trial, regardless of phase, participants see one face drawing and two colored fish. Faces consist of a brown-haired man, a blonde-haired woman, a blonde-haired boy, or a brown-haired girl. These drawings differ in three obvious, binary-features, including age (adult vs. child), gender (male vs. female), and hair color (blond vs. brunette), but each face shares exactly one feature with another face. The fish are colored red, green, blue, or purple. Throughout the task, participants are required to select the fish that belongs to each face using a corresponding button, and their response circles the selected fish drawing. For each participant, fish−face associations are assigned randomly, as is the left−right ordering of the fish drawings.

During the acquisition phase, participants receive feedback after choosing which fish belongs to which face (e.g., the circled fish and "Correct" or "Incorrect" displayed for 1 s). The participant initially makes the selection at random, but eventually participants learn the fish−face pairings via this trial-and-error feedback. Between trials, there is a 1-s pause during which the screen goes blank before the next trial is initiated. This phase is divided into three training stages: shaping, equivalence training, and new consequent learning. Stage 1 terminates after four consecutive correct responses, Stage 2 terminates after eight consecutive correct responses, and Stage 3 terminates after 12 consecutive correct responses, or a maximum of 112 trials. The start of a new training stage is not signaled to the participant.

Example screen shots are provided in Table 2. In this particular example, participants first learned, in Stage 1 (shaping), that the brown-haired girl belonged with the blue fish (FaceA → ×1). Then, in Stage 2 (equivalence training), participants learned that the blonde-haired woman also belonged with the blue fish (FaceC → ×1). In this way, pairs of faces (i.e., FaceA and FaceC) can be treated as "equivalent" because they mapped onto the same outcome. Finally, in Stage 3 (novel consequents), participants learned that the brown-haired girl was also associated with a novel red fish (FaceA → ×2). At each stage, participants continued to encounter previously learned fish−face associations (e.g., shaping continued through Stages 2 and 3).

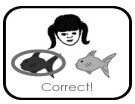
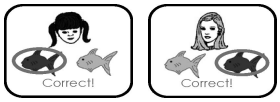
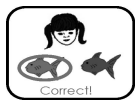
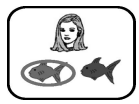
A test phase follows. Participants are told that, although the selected fish will still be circled, corrective feedback will no longer be provided. Here, participants are presented with novel fish−face trials to test whether participants show generalization, defined as predicting the same outcome (fish) for faces that were previously

Table 1
Demographics and Neuropsychological Performance

Variable	Younger adults	Middle-aged adults	Older adults	Comparisons for significance
Age	20.3 (1.8)	62.2 (5.6)	79.1 (4.5)	Y < M < O
Education	14.6 (1.7)	17.1 (3.2)	16.9 (2.3)	Y < M = O
Gender (female)	14	18	24	
MMSE screen for dementia	NA	29.3 (.8)	29.0 (1.1)	*ns*
WMS-III Logical Memory I, immediate[a]	22.9 (7.1)	21.6 (7.4)	22.8 (5.3)	*ns*
WMS-III Logical Memory II, delayed[a]	19.2 (8.1)	15.9 (7.9)	16.7 (6.2)	*ns*

Note. All scores are M (SD) or n. MMSE = Mini-Mental State Examination; WMS-III = Wechsler Memory Scale−Third Edition; Y = younger adults; M = middle-aged adults; O = older adults; NA = not applicable.
[a] Three younger, 18 middle-aged, and 10 older participants did not complete the WMS-III Logical Memory I and II.

Table 2
Rutgers Acquired Equivalence Task and Sample Screen Displays

Feedback-based associative learning			Generalization* (no feedback)
Stage 1: Shaping	Stage 2: Equivalence training	Stage 3: New consequents	Equivalence testing
			
FaceA → ×1	FaceA → ×1 FaceC → ×1	FaceA → ×1 FaceC → ×1 FaceA → ×2	FaceC → ×2
FaceB → Y1	FaceB → Y1 FaceD → Y1	FaceB → Y1 FaceD → Y1 FaceB → Y2	FaceD → Y2

* The generalization phase interleaved novel pairs with previously learned information or "retention" pairs (shaping (FaceA → ×1), equivalence training (FaceC → ×1), and new consequents trials (FaceA → ×2).

trained to be equivalent. Using the above example, participants should associate the blonde-haired woman with the red fish (e.g., FaceC → ×2), even though this pairing had never been trained. This response indicates that a functional equivalence had been formed between the blonde-haired woman and brown-haired girl during acquisition. In contrast, association of the blonde-haired woman with the purple fish is viewed as an error, or a failure to generalize. No feedback was provided to ensure that participants could not acquire theses new associations via feedback-guided learning. During this phase, participants were also tested on their recall of shaping (e.g., FaceA → ×1), equivalence training (e.g., FaceC → ×1), and new consequent (e.g., FaceA → ×2) associations, by viewing and responding to 12 trials of each type. These trials were included to evaluate retention of the learned pairs; in order to show successful generalization, participants had to accurately learn and retain each of the critical pairings, or else what appears to be a generalization deficit may merely reflect an encoding deficit or forgetting. Trial order was random for each participant.

Results

Acquisition Phase

All participants reached criterion, by completing the training in fewer than the maximum allowed trials. A one-way analysis of variance (ANOVA) with age group (younger, middle-aged, older) as the independent variable and number of training trials as the dependent variable revealed a main effect, $F(2, 96) = 16.54$, $p < .001$, $r_{effect} = .51$. Younger adults required almost half the training to reach criterion ($M = 35$ trials, $SD = 9$) than middle-aged ($M = 59$ trials, $SD = 28$) and older adults ($M = 66$ trials, $SD = 26$) ($ps < .001$). The latter two groups did not differ ($p > .34$).

To examine feedback-based associative learning, we conducted a one-way ANOVA with age group as the independent variable and overall mean learning accuracy as the dependent variable. As predicted and shown in Figure 1a, this produced a significant main effect, $F(2, 93) = 28.98$, $p < .001$, $r_{effect} = .53$. Post hoc tests using the Bonferroni procedure to control for Type I error showed that younger adults performed significantly better than both middle-aged and older adults ($ps < .05$), and middle-aged adults performed significantly better than older adults ($p < .001$). To ensure this effect was not driven by age deficits in learning any one critical pairing (i.e., shaping, equivalence training, and new consequents), we also compared mean accuracy for these pairs separately across the three age groups in an Age Group × Pairing ANOVA using Bonferroni post hoc corrections. As above, and as seen in Figure 1b, a main effect of age group, $F(2, 93) = 16.56$, $p < .001$, $r_{effect} = .51$, showed that younger adults outperformed both middle-aged and older adults ($ps < .03$), and middle-aged adults outperformed the older adults ($p < .001$). A main effect of pairing, $F(2, 186) = 6.71$, $p < .005$, $r_{effect} = .26$, revealed greater overall accuracy on new consequent pairs than either shaping or equivalence training pairs ($ps < .005$). This pattern is likely due to increased familiarity with the task by the time the new consequent pairing was introduced (i.e., Stage 3 of training). Of import, the lack of an Age Group × Pairing interaction ($p > .05$) indicates age constancy in learning the three face−fish pairings; hence, observed differences in learning between younger, middle-aged, and older adults did not result from age deficits in acquiring any single type of association. Similarly, one-sample t tests verified that each age group performed significantly better than chance level on all pairs ($ps < .001$), further ensuring no age-related failures in encoding the different critical pairings.

Test Phase

We conducted a mixed ANOVA on test performance with age group and trial type (generalization, retention) as the independent variables and mean accuracy as the dependent variable (see Figure 2a). A main effect of age group, $F(2, 93) = 27.42$, $p < .001$, $r_{effect} = .61$, revealed that younger adults had higher overall accuracy than middle-aged ($p = .09$) and older adults ($p < .001$), and that middle-aged adults had higher overall accuracy than older adults ($p < .001$). Further, as is typical, overall accuracy was higher for retention (old pairs) than generalization (new pairs), as shown by a main effect of trial type, $F(1, 93) = 33.73$, $p < .001$, $r_{effect} = .52$. The Age Group × Trial Type interaction was also significant, $F(2, 93) = 3.12$, $p < .05$, $r_{effect} = .25$. We follow-up with separate analyses below to more fully examine this interaction.

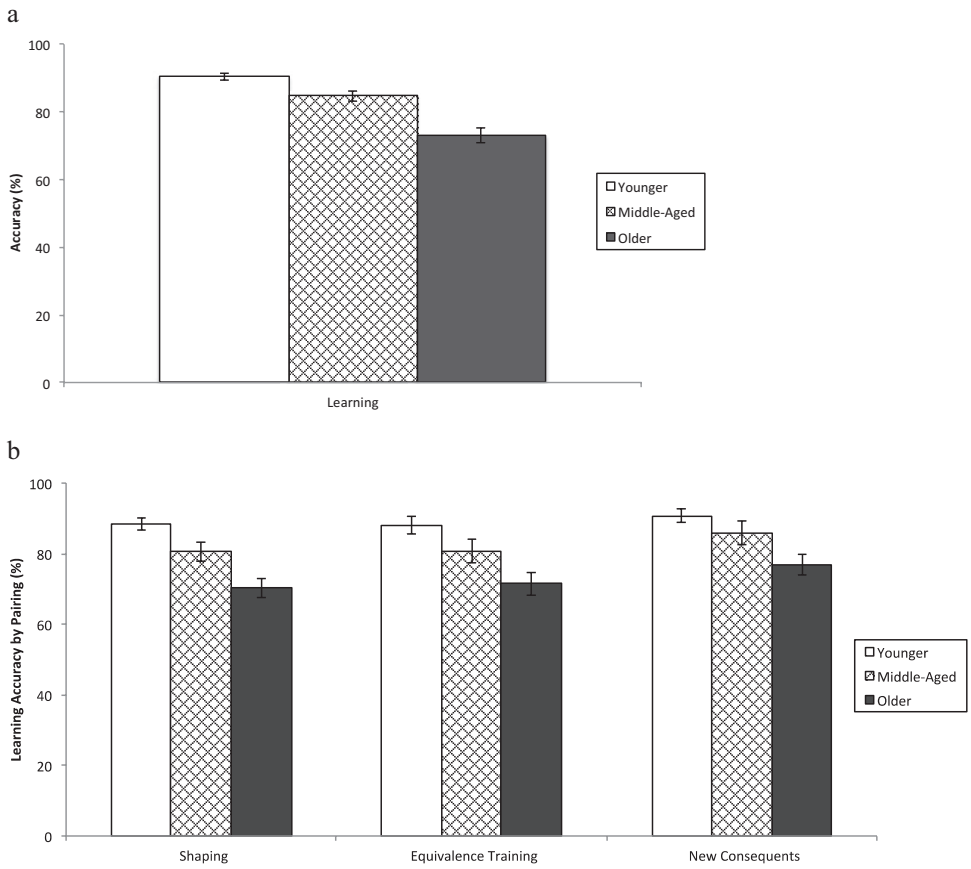


Figure 1. The acquisition phase: feedback-based associative learning. Overall mean accuracy scores (a). Mean accuracy scores for shaping, equivalence training, and new consequent pairings (b). Error bars represent the standard error of the mean.

For mean retention accuracy, a one-way ANOVA testing for age-group differences produced a significant main effect in a manner consistent with learning performance, $F(2, 93) = 17.84$, $p < .001$, $r_{effect} = .47$. Post hoc tests using the Bonferroni procedure confirmed that younger adults performed significantly better than both middle-aged and older adults ($ps < .02$), and middle-aged adults performed significantly better than older adults ($p < .005$). To establish that there were no age-related differences in retention across the three critical pairings, we also conducted a mixed ANOVA of Age Group × Retention Pairing (i.e., shaping retention, equivalence training retention, and new consequents retention) using Bonferroni post hoc corrections. The interaction did not produce significance, $F(4, 186) = 1.76$, $p > .14$, $r_{effect} = .26$, establishing that the observed age-group differences in retention were not due to age-related forgetting of one particular type of association. Of note, each age group performed significantly better than chance level on all retention pairs ($ps < .001$), further confirming that younger, middle-aged, and older adults, on average, retained each of the learned pairs. Moreover, as indicated above and shown in Figure 2b, there was a significant main effect of age group, $F(2, 93) = 16.56$, $p < .001$, $r_{effect} = .51$. That is, younger adults had higher retention accuracy than both middle-aged and older adults ($ps < .02$), and middle-aged adults had higher retention accuracy than the older adults ($p < .01$). The main effect of pairing was also significant, $F(2, 186) = 8.71$, $p < .001$, $r_{effect} = .29$. Retention accuracy was higher for shaping pairs than both equivalence training and new consequent pairs ($ps < .05$), presumably because participants encountered more shaping pairs than any other during training. Retention for equivalence training and new consequent pairs did not differ statistically ($p > .05$).

For generalization, we compared age groups with a one-way analysis of covariance using training performance (i.e., overall learning accuracy and number of training trials) and overall retention accuracy as covariates. We controlled for learning and retention performance to be certain that age differences in generalization did not result from encoding failures or forgetting. Of import, this analysis was significant, $F(2, 90) = 3.24$, $p < .05$, $r_{effect} = .25$. Post hoc tests using the Bonferroni procedure were conducted to evaluate pairwise differences among the adjusted means for generalization. As predicted, and as shown in Figure 2c, results showed significant differences in generalization accuracy between younger and older adults as well as middle-aged and older adult ($ps < .05$), but not between the younger and middle-aged adults ($p > .9$). Additionally, one-sample t tests revealed that generalization accuracy was clearly above chance level for younger and middle-aged adults ($ps < .001$), but not for older subjects, $t(31) = .63$, $p > .05$, $r_{effect} = .11$.

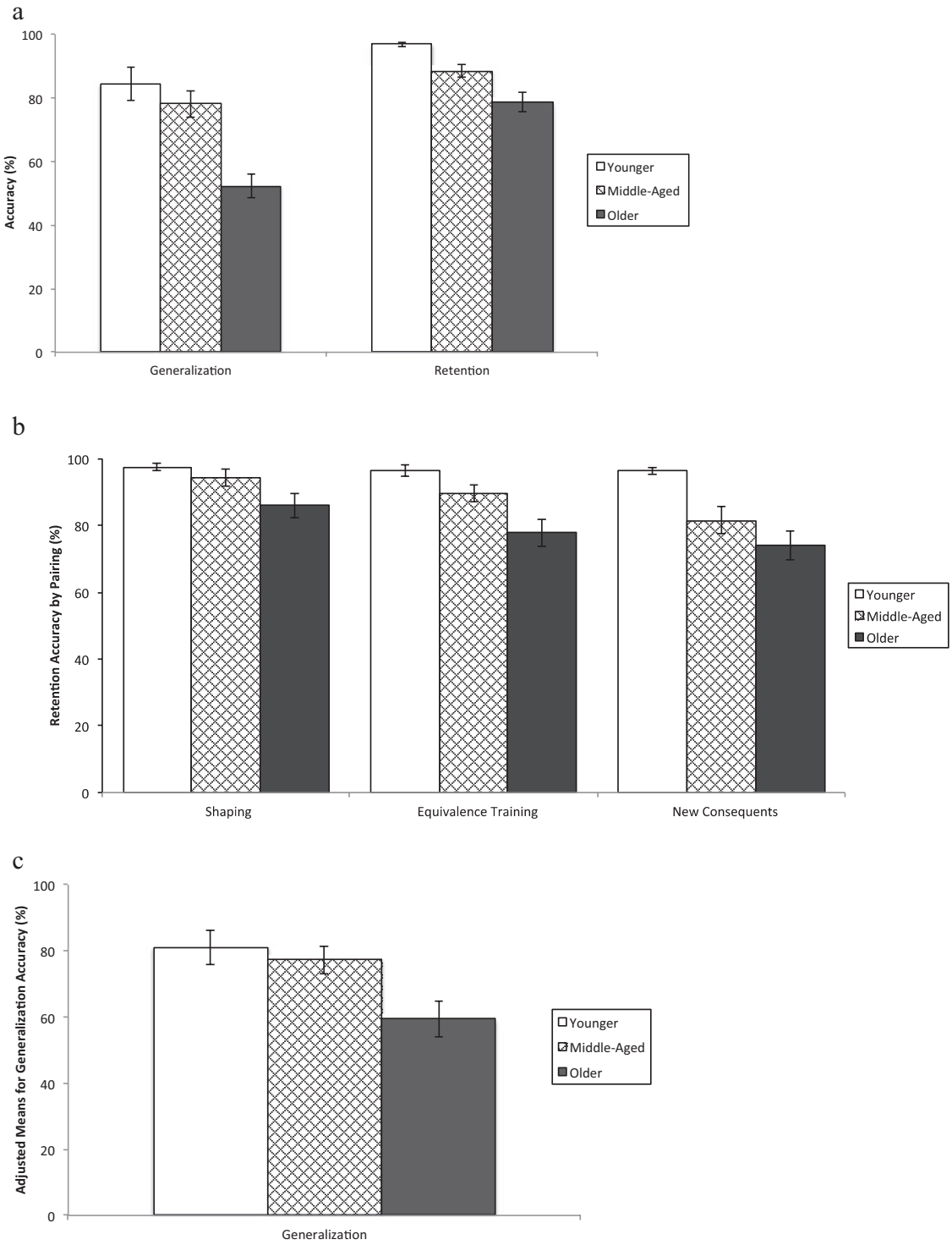


Figure 2. The test phase: retention (old-pairs) and generalization (new-pairs). Overall mean accuracy scores (a). Mean retention accuracy scores for shaping, equivalence training, and new consequents pairings (b). Adjusted mean accuracy scores for generalization (c). Covariates include learning performance (i.e., accuracy and number of training trials) and retention accuracy. Error bars represent the standard error of the mean.

To examine age differences in generalization more fully, we classified any subject with accuracy greater than 66.67% (8 of 12 trials correct) as showing successful generalization, whereas any other subject was impaired. Of the successful individuals, 28 were young, 23 were middle-aged, and eight were older adults; and of the impaired, six were young, nine were middle-aged, and 24 were older adults, $\chi^2(2) = 21.1$, $p < .001$. Thus, at the individual level, most younger and middle-aged adults were successful and most older adults were impaired at generalization.

Discussion

This study examined age differences in feedback-based associative learning and generalization in younger (18–25 years), middle-aged (50–69 years), and older adults (70–89 years). Results showed healthy age-related deficits in learning associations from feedback, revealed as reduced accuracy in learning in older adults relative to middle-aged adults, and in middle-aged adults relative to younger adults. In contrast, generalization was impaired only in the older group, whereas younger and middle-aged adults performed equivalently. Thus, only the oldest group showed a deficit in applying previous knowledge to new situations. Such evidence of cognitive differences between elderly groups (i.e., middle-aged vs. older adults) is consistent with past work (e.g., Frank & Kong, 2008; Krishna et al., 2012) and underscores the importance of asking when age-related declines begin (Salthouse, 2009).

Our results complement and augment earlier work using other feedback-based learning tasks. Age deficits have previously been reported in various forms of *probabilistic* reward learning (Eppinger, Kray, Mock, & Mecklinger, 2008; Frank & Kong, 2008; Marschner et al., 2005; Mell et al., 2005; Pietschmann, Endrass, Czerwon, & Kathmann, 2011), but our results extend this finding to show an age-related deficit in *deterministic* feedback-based associative learning. This finding confronts the emerging hypothesis that age deficits are likely to emerge only when associations to be learned are probabilistic versus deterministic (Eppinger et al., 2011; D. V. Howard & Howard, 2011). Instead, it may be that older adults experience challenges in acquiring representations of expectation-outcome contingencies, whether or not the outcome information is inconsistent or completely predictable. In other words, the presence of feedback cues, and not the probabilistic nature of a task per se, may determine whether age deficits are observed (Schmitt-Eliassen, Ferstl, Wiesner, Deuschl, & Witt, 2007).

Further, our results agree with (a) a study of senior adults that reported age-related deficits in feedback-based learning, but a generalization deficit in only the very oldest adults (Krishna et al., 2012), as well as (b) a study of younger adults and middle-aged adults (between ages 50 and 71 years) that found age-group differences in feedback learning but not in generalization (Weiler et al., 2008). However, our findings go beyond theirs in overcoming several notable limitations. First, we provide evidence for different age-related trajectories for learning and generalization across the adult life span, using a task that requires neither ignoring irrelevant distractors nor learning probabilistic associations. Accordingly, we can now confidently attribute age differences to deficits in feedback learning and flexible transfer of learned associations versus known impairments in the suppression of nonrelevant information (Hasher et al., 1991) or forming probabilistic representations (J. H. Howard et al., 2008; Simon et al., 2011). Second, all of our 96 adult participants reached our learning criteria, and no subject completely failed generalization (the majority performed above 50% accuracy); thus, our findings are not hindered by small sample sizes or differential elimination of subjects across age groups that occurred in past work because subjects did not meet criterion. Finally, our data account for age-group differences in learning rate, by factoring in both the number of correct responses and the variable number of trials needed to reach criterion during training. Nonetheless, when taken together, these studies reveal a consistent pattern of aging-related impairments in acquiring new associations from feedback, but spared generalization to novel situations until later adulthood (i.e., $\geq$ 70 years of age) across a wide range of tasks, training methods, and category structures.

The learning and generalization phases of our acquired equivalence task were designed to be maximally sensitive to the neural processes of interest. Our task was inspired by analogous paradigms in animals (e.g., Coutureau et al., 2002), is informed by neurocomputational models of interactions between basal ganglia and MTL learning systems (e.g., Moustafa, Keri, Herzallah, Myers, & Gluck, 2010), and has been validated by both clinical patient work (e.g., patients with posttraumatic stress disorder, mild cognitive impairment, depression, schizophrenia, PD, AD; Bódi et al., 2009; Collie, Myers, Schnirman, Wood, & Maruff, 2002; Farkas et al., 2008; Herzallah et al., 2010; Keri et al., 2005; Levy-Gigi et al., 2012; Myers et al., 2003) and functional imaging in young adults (Shohamy & Wagner, 2008). The basal ganglia are thought to code for stimulus-specific feedback signals during learning (Shohamy, Myers, Kalanithi, & Gluck, 2008), whereas the hippocampus and MTL are important for flexible application of prior learning to novel recombinations at generalization (Cohen & Eichenbaum, 1995; Kumaran, 2012). Thus, one possible explanation for our observed patterns of behavioral age differences, especially between middle-aged and older adults, is that the basal ganglia are more sensitive to healthy aging than the MTL. Specifically, the basal ganglia show substantial healthy age-related declines in structure and function throughout adulthood (Raz et al., 2005) that may account for some of the age-related feedback-based associative learning deficits during the acquisition phase of our task. In fact, the increased learning deficit in adults older than 70 years is in agreement with a study that has showed this age demarcation is associated with substantial damage to midbrain dopaminergic cells (Kraytsberg et al., 2006). In contrast, studies have reported relatively spared MTL volume (Good et al., 2001; Grieve et al., 2005; Head et al., 2005; Kalpouzos et al., 2009; Laakso et al., 1998; Morrison & Baxter, 2012; Mueller et al., 1998; Sullivan et al., 1995; Sullivan et al., 2005) and white matter integrity (Bennett, Madden, Vaidya, Howard, & Howard, 2011) in the early stages of aging, and these data correspond to research has shown age constancy in behavior (J. H. Howard, Howard, Dennis, Yankovich, & Vaidya, 2004b; Van Petten, 2004) and functional activity in MTL-based tasks (Johnson, Schmitz, Asthana, Gluck, & Myers, 2008; Persson, Kalpouzos, Nilsson, Ryberg, & Nyberg, 2011; Rand-Giovannetti et al., 2006). Though age deficits have been reported in MTL-based pattern separation (Yassa, Lacy, et al., 2011; Yassa, Mattfeld, Stark, & Stark, 2011), other work has shown no age-group differences in a sample aged 59–80 years (Stark, Yassa, & Stark, 2010). Rather, there was individual variability in perfor-

mance whereby only some older adults were impaired, and age accounted for some of the pattern separation deficits. Similarly, our data showed individual variability on MTL-based generalization, but, on average, performance was spared in younger and middle-aged adults and only those 70 and older had deficits. This finding adds interesting behavioral evidence to the emerging view that MTL reductions are relatively minor before approximately seventy years of age, after which there are accelerated declines (Jernigan et al., 2001; Lupien et al., 2007; Salami, Eriksson, & Nyberg, 2012; Scahill et al., 2003; Zhang et al., 2010). Certainly, debate remains on whether MTL structures and functions are affected in healthy, nonpathological aging (Buckner, 2004; Hedden & Gabrieli, 2004), but our study contributes to research that has shown that differences in age ranges across studies must be considered as an explanation for inconsistent findings concerning age-related MTL cognition and function (Eyler, Sherzai, Kaup, & Jeste, 2011).

It must be noted that the selective impairment in older adults' generalization cannot simply be attributed to poor learning or retention of the associative pairs. Even when controlling for learning and retention performance as confounding factors, we still observe impaired generalization in only the oldest group. This suggests that the cognitive processes supporting generalization are at least partially independent of those supporting learning and retention of the trained associations. Further, age-group differences in learning and retention accuracy were not specific to any one critical pairing, and performance was above chance for each pair and age group. This indicates that older adults' poor generalization deficit did not merely reflect an encoding deficit or forgetting of the critical associations that support flexible transfer. Poor generalization also cannot be due to the fact that older adults required more training, because neurocomputational models of our task suggest that more training ought to lead to a stronger generalization effect (Moustafa et al., 2010). Moreover, there was no difference in the amount of training required for middle-aged adults who had successful transfer versus older adults who had impaired transfer. And, even though both middle-aged and older adults required more training, they eventually met criterion similar to the younger adults (cf., Krishna et al., 2012; Weiler et al., 2008).

Age differences in retention are consistent with data showing marked age-related deficits in episodic memory or declarative recall (Craik, 2008). This type of memory is thought to rely on prefrontal regions (see Fletcher & Henson, 2001, for a review), which have greater age-related declines in both white (Davis et al., 2009) and gray matter (Raz et al., 2005) than any other brain region (Raz, Rodrigue, & Haacke, 2007). Thus, age differences in retention may reflect prefrontal declines, but further work is needed to address this possibility. Of note, previous work has ruled out the possibility that learning or generalization deficits in the Rutgers Acquired Equivalence Task are a consequence of prefrontal dysfunction. Farkas et al. (2008) revealed no correlations between learning and generalization performance and frontal lobe tests of executive function (e.g., Wisconsin Card Sorting Test, Trail-Making Test, Controlled Oral Word Association Test). Additionally, in a study of schizophrenic patients with severe prefrontal deficits, generalization correlated only with verbal memory (i.e., California Verbal Learning Test), but not with performance on an *n*-back working memory test that assesses prefrontal function (Keri et al., 2005). Finally, patients with frontal damage have shown intact generalization in related tasks (Chase et al., 2008; but see Iordanova, Killcross, & Honey, 2007).

Study Limitations

Future research will be needed to overcome some limitations in the current study. First, no direct conclusions about age-related neural changes can be drawn from our purely behavioral results. In addition to the MTL and basal ganglia, other brain structures are likely critical during learning and generalization. In fact, MTL activation during acquisition may predict subsequent generalization in humans and animals, although its involvement is not essential for learning (Shohamy & Wagner, 2008; Zeithamova, Schlichting, & Preston, 2012). Moreover, older brains can show different patterns of brain activity than younger brains, even when performance is equivalent across groups (e.g., Reuter-Lorenz & Cappell, 2008). For example, the MTL, prefrontal cortices, or other brain regions can compensate for basal ganglia losses in healthy older adults (Fera et al., 2005; Simon, Vaidya, Howard, & Howard, 2012). Yet, given that knowledge of behavioral age differences on well-developed tasks is critical for designing and interpreting neuroimaging experiments, we believe our present study offers interesting and specific questions for future neuroimaging work to address and a behavioral task for doing so.

Second, despite our screening for cognitive health, there may be concern about the inclusion of incipient AD in our sample of "healthy" older adults, because poor generalization can predict risk for cognitive impairment at least 2 years before symptom onset (Myers, Kluger, Golomb, Gluck, & Ferris, 2008). Follow-up study with these individuals will determine whether our behavioral measures can forecast future cognitive status. If impairment does represent warning signs of disease, our task may have utility as an inexpensive and rapid screening tool to diagnose disease in its preclinical stages.

Conclusion

The ability to acquire new associations and apply that knowledge to predict positive outcomes in novel situations is essential for daily living, especially later in life when adults face complex social, financial, and medical choices. Specifically, our past experiences can guide our future actions, by providing flexible and generalizable representations of our environments. We found that both middle-aged and older adults are impaired at learning feedback-based associations, but only older adults show a deficit in abstracting previously learned information to novel situations. How this extends to real-world decision-making is still unknown. Though the exact mechanisms underlying these behavioral patterns are yet to be determined, our results relate to evidence showing that the basal ganglia and MTL are differentially sensitive to aging.

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