Age-Related Deficits in Conjunctive Representation of Complex Objects

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Abstract: Although some evidence is consistent with the notion that distinct cortical systems support memory and perception, mounting evidence supports a representational-hierarchical view of cognition, which posits that distinctions lie in simple feature representations versus more complex conjunctive representations of many stimulus features simultaneously. Thus, typical memory tasks engage different regions from typical perception tasks because they inherently test information on opposing ends of this continuum. Memory deficits are reliably reported with age, but the tasks used to make these conclusions predominantly rely on conjunctive representations. To test the extent to which age-related deficits may be accounted for by perceptual processing, this study investigated discriminations involving conjunctive representations in older adults. Results show that adults aged 50 to 77 are impaired, relative to their younger counterparts, on discriminations requiring feature conjunctions, but not simple feature representations. These findings support recent data showing an age-related decline in the ability to form conjunctive representations. Furthermore, these data suggest that some 'mnemonic' deficits associated with age may in fact be the result of deficits in perception rather than memory.

Keywords: Memory, perirhinal cortex, hippocampus.

INTRODUCTION

Memory impairment is a commonly reported sign of cognitive aging. Although generally reliable, memory processes are susceptible to errors and distortions. Moreover, these false recollections become increasingly prevalent with age [1-5]. The search for the neural mechanisms behind these deficits has been underway for some time, and current debates about the functional specialization of the neural systems supporting mnemonic and perceptual processing have great relevance to this area of research.

Many researchers suggest that regions of the ventral visual stream are functionally distinct, with anterior portions mediating mnemonic processing, while posterior portions mediate perceptual processing [6-8]. Alternatively, a representational-hierarchical view of cognition has recently been proposed, positing that simple feature representations occur in posterior brain regions, while conjunctive representations of many features and their relationships occur in more anterior regions [9-12]. Since many perceptual tasks are adequately performed using simple feature representations, posterior portions of the ventral visual stream can often solely support perceptual processing. Conversely, mnemonic tasks frequently require the disambiguation of items with shared features, a process that requires the use of feature conjunctions [10, 13]. For this reason, adequate performance on mnemonic tasks often requires the use of feature conjunctions, representations that are supported by anterior portions

of the ventral visual stream [10]. Nevertheless, with careful manipulation of stimulus complexity and feature ambiguity, these anterior portions of the ventral visual stream have also been shown to mediate perceptual processing [14, 15]. Thus, regional dissociations in the ventral visual stream can be interpreted as dissociations in the degree to which conjunctive representations are required for the completion of a task, rather than dissociation between two cortical systems selectively supporting mnemonic or perceptual processes [9, 10].

Some of the most compelling evidence for hierarchical organization within the medial temporal lobe comes from studies of amnesic patients. Barense and colleagues [16, 17] found that amnesic patients with damage isolated to the hippocampus performed much like healthy control subjects on discrimination tasks that required the use of feature conjunctions. However, amnesic patients with damage that included the perirhinal cortex had difficulty discriminating between objects when the use of feature conjunctions was required, despite performing normally when discriminations only required the use of simple feature representations. These findings suggest that damage to the perirhinal cortex results in difficulty creating conjunctive representations [11, 14, 16-19]. Without feature conjunctions, stimuli can only be encoded at the simple feature level. As a result, representations of ambiguous stimuli in memory become highly susceptible to interference from external stimuli sharing similar features. Because of this interference, stimuli containing ambiguous features evoke a large number of false-positives on tests of recognition memory [11, 18, 19]. This interference effect is consistent with the ability to encode stimuli only at the simple feature level, as novel stimuli sharing features with the target stimulus become more likely to be perceived as familiar.

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Recently, Burke and colleagues [18] exploited the tendency of rodents to explore novel objects more than familiar objects, in order to investigate recognition memory in a group of aged rats. Using a spontaneous object recognition task, Burke and colleagues [18] found that young rats, but not aged rats, showed an exploratory preference for novel objects presented after a delay. In subsequent testing, it was shown that in many circumstances, aged rats consistently treated novel objects as familiar and spent less time exploring them. These results suggest that age-related impairments in object recognition in older rats result from false recognition of novel objects.

Interestingly, a similar increase in false-positives is reported in healthy older adults performing recognition memory tasks [1-4]. For example, Norman and Schacter [3] asked groups of young and elderly participants perform a remember/know recognition task. After studying lists of words, participants were given a recognition test that included studied words, non-studied words that were semantically related to the studied words, and non-studied words that were unrelated to the studied words. In addition to recalling significantly fewer studied words, older participants also falsely recalled significantly more non-studied words that were semantically related to the studied words. It has been suggested that failure to access source information, a process reliant on conjunctive level encoding and retrieval, plays an important role in the age-related increase in false positives on these types of memory tests [4]. If the memory deficits observed in the older population are in fact a result of an inability to encode and retrieve conjunctive level representations, older adults may show deficits on perceptual discrimination tasks involving stimuli possessing a high degree of feature ambiguity. Although an earlier study reported no significant differences between individuals in their early fifth and late sixth decade [16], a subsequent study [20] found that adults in their sixth and seventh decade were impaired relative to those in their second decade at matching blob objects when these objects shared a large number of similar features. Thus, there remains only a single demonstration of deficits in a population of older adults that do not have diagnosed, or do not self-report, memory deficits.

The current study aims to further this finding by confirming an age-related decline in perceptual discrimination ability. During this study, young and older adults performed a four-pair concurrent discrimination task, utilizing stimuli that varied in their degree of feature ambiguity. As the level of feature ambiguity increased, or the stimuli possessed increasingly similar features, conjunctive level encoding was required in order to successfully complete the discrimination task. Furthermore, the discrimination task was designed in a manner to minimize memory demands. On each trial, the participant was presented with a target and a non-target stimulus simultaneously, and these stimuli remained onscreen until a response was recorded. Previous research suggests that presenting stimuli with zero-delay between the appearance of the stimuli and the response creates little or no memory load, and allows for the assessment of perceptual functioning [14]. In addition, the number of items to be discriminated was held constant across the different levels of ambiguity, ensuring that the key change across conditions

was perceptual difficulty, not memory demand. It was expected that as the level of ambiguity increased, participants' performance would decline, and this decline would also be magnified in the older adult population, as the formation of feature conjunctions is hypothesized to be more difficult for this population.

MATERIALS AND METHODS

Subjects

Forty-four participants were divided into two groups: young [n = 20, age = 18.6 ± 0.8 (mean ± SD), 12 females] and older [n = 24, age = 61.2 ± 8.6 (mean ± SD), 16 females] adults. All participants had normal or corrected-to-normal vision. Participants reported no mood or thought disorders, cardiovascular conditions, breathing conditions, concussions, loss of consciousness for extended periods of time, or vision problems beyond what can be resolved with corrective lenses. Informed consent was obtained from each participant in accordance with the ethical policies at Wilfrid Laurier University. All participants received financial compensation or course credit for their participation in this study.

Apparatus and Stimuli

Participants completed a four-pair concurrent discrimination task programmed using Superlab 4.5 (Cedrus Corporation, San Pedro, CA, USA) and presented on a desktop with a 17" monitor (Dell Inc., Round Rock, TX, USA). The experiment utilized two types of stimuli, barcodes and bugs, used in previous publications (see [16] for the complete stimulus set) and generously provided by Morgan Barense (Fig. **1**). Each stimulus was composed of two features (*e.g.* legs and body), which allowed for systematic manipulation of feature ambiguity. All stimuli were presented in pairs with one item arbitrarily designated the target item. These stimulus pairs were fixed, resulting in four different stimulus pairs in each block. For each pair of stimuli, three levels of feature ambiguity were possible. In the minimum ambiguity condition, all features comprising the target and non-target items were unique. The four stimulus pairs utilized in the minimum ambiguity condition can be depicted as follows: (1) AB+ EF- (2) AB+ GH- (3) CD+ EF- (4) CD+ GH-, with each feature represented by a unique letter, and the target stimulus indicated by a '+'. In the medium ambiguity condition, one feature was shared, while the other feature was unique to each item. The four stimulus pairs utilized in the medium ambiguity condition can be depicted as follows: (1) AB+ AF- (2) AB+ CE- (3) CD+ AF- (4) CD+ CE-, with each feature represented by a unique letter, and the target stimulus indicated by a '+'. Lastly, in the maximum ambiguity condition all features were ambiguous, as both target features appeared separately as part of the non-target items. As a result, successful discrimination in the maximum ambiguity condition required the use of feature conjunctions, as no single feature was unique to the target items. The four stimulus pairs utilized in the maximum ambiguity condition can be depicted as follows: (1) AB+ AD- (2) AB+ CB- (3) CD+ AD- (4) CD+ CB-, with each feature represented by a unique letter, and the target stimulus indicated by a '+'.
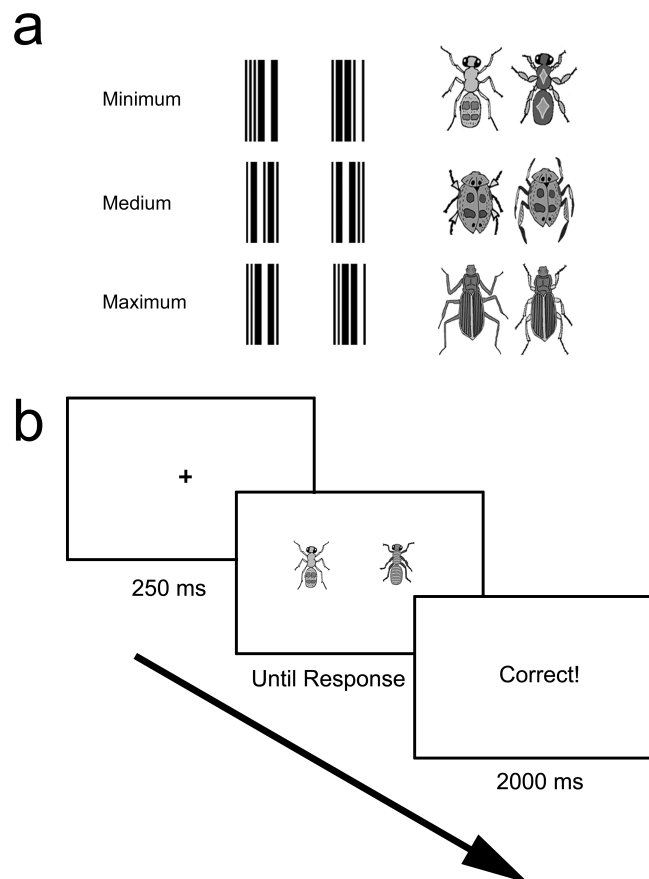
Fig. (1). (**a**) Examples of barcode (left) and bug (right) stimuli used in the minimum, medium, and maximum ambiguity conditions are shown. (**b**) The experimental paradigm is shown. A fixation cross was presented for 250 ms followed by the stimulus display, which remained on screen until the participant's response was recorded. Following each response, a feedback screen was provided, displaying either "correct" in green text or "incorrect" in red text, for 2000 ms.

Behavioural Procedure

The behavioral task was adapted from the procedures of Barense and colleagues [16]. The experiment was divided into six blocks based on stimulus type (barcodes or bugs) and level of feature ambiguity (minimum, medium, or maximum). On each trial participants were presented with a fixation cross for 250 ms, followed by a stimulus display (Fig. **1**). Each stimulus display was comprised of a target item and a non-target item presented side by side in the center of the screen ~8 cm apart. Target and non-target items appeared an equal number of times in both the right and left position, but the position was varied randomly throughout the block. In addition, the order in which the stimulus pairs were presented was varied randomly throughout the block. During each trial, the stimulus display remained on screen until a response was recorded from the participant.

Participants were instructed that on each trial they would be presented with two items, one item was designated the target item, while the other item was designated the non-target item. Participants were instructed to indicate by keypress which item they believed to be the target item. Following each response, "correct" appeared in green text if the target item was selected, or "incorrect" appeared in red text if the non-target item was selected. Participants were instructed to use this feedback in order to determine which

items were target items. When participants were able to identify eight consecutive target items, they progressed to the next block. A break was provided after each block. Participants were instructed that they were not being timed, thus accuracy was stressed over speed. The order of barcode and bug presentation was counterbalanced, but within each category, participants were always presented with the minimum ambiguity stimuli first, followed by the medium, and then the maximum ambiguity stimuli.

In order to ensure progression from block to block, a time-out function was implemented. If participants were unable to correctly identify eight consecutive target items in the minimum ambiguity conditions within five minutes, the blocks were terminated. Similarly, blocks were terminated if the medium and maximum ambiguity conditions could not be completed within 20 minutes. Participant unable to complete the minimum ambiguity condition were omitted from statistical analyses. This resulted in 13 rejected participants (3 young, 10 older), and a total of 31 valid participants.

Data Analysis

Errors committed before reaching the criterion of successfully identifying eight consecutive target items were calculated for each participant in each block. Two groups (young, older) by three levels of ambiguity (minimum, me-

dium, maximum), repeated-measures analysis of variances (RM-ANOVAs) were conducted on the errors to criterion for barcode and bug stimuli using SPSS. Significant interactions were investigated using t-tests where appropriate. Where Mauchley's sphericity assumption was violated, the Greenhouse Geisser correction was applied [21]. However, for ease of interpretation, original degrees of freedom were reported. Correlation analyses were also conducted to investigate potential relationships between errors to criterion and age.

RESULTS

Barcodes

The RM-ANOVA revealed a main effect of feature ambiguity [$F(2, 58) = 9.486$, $MSE = 206.92$, $p < 0.001$]. This effect was driven by fewer incorrect responses in the mini-

mum feature ambiguity condition relative to the maximum ambiguity ($p < 0.001$) condition. Although the main effect of group was not significant [$F(1, 29) = 3.510$, $MSE = 368.14$, $p = 0.071$], young adults committed fewer errors (29.53) relative to older adults (49.00). As expected, the interaction between group and ambiguity was significant [$F(2, 58) = 4.026$, $MSE = 206.92$, $p = 0.023$], indicating that changes in performance across the three levels of ambiguity were different for young and older adult groups (Fig. **2**). Follow-up independent samples t-tests confirmed that the older adults committed significantly more errors before reaching the criterion in the maximum ambiguity condition [$t(15.626) = 2.430$, $p = 0.028$], but not in the medium [$t(24.819) = 0.337$, $p = 0.739$] or minimum [$t(27.106) = 0.339$, $p = 0.693$] ambiguity conditions.

To control for the impact of task difficulty, an additional RM-ANOVA tested the influence of feature ambiguity on
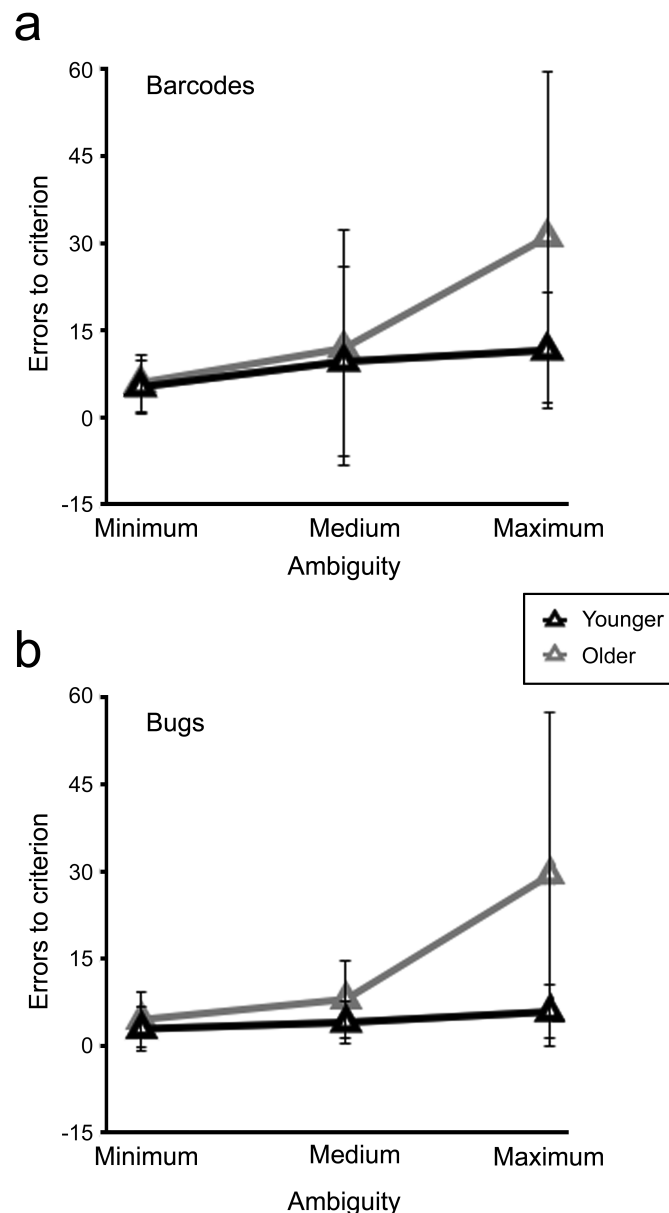

Fig. (2). Mean errors committed to reach the criterion of 8 consecutive correct responses is plotted for the younger (age = 18.6 ± 0.8; black) and older (mean age = 61.2 ± 8.6; grey) adults for barcodes (**a**) and bugs (**b**). All data displayed as mean ± SEM.

the performance of the young adult population. The main effect of feature ambiguity was not significant [F (2, 32) = 1.498, *MSE* = 117.90, *p* = 0.239], indicating that increased ambiguity did not result in increased difficulty for young adults.

Correlation analyses demonstrated a significant positive correlation between age and errors to criterion in the maximum ambiguity condition (r = 0.476, *p* = 0.007), but not in the medium (r = 0.165, *p* = 0.374) or minimum (r = 0.072, *p* = 0.699) ambiguity conditions. These results suggest that the ability to discriminate simple features is not modulated by age, while progressive age significantly impacts discrimination of more ambiguous stimuli.

Bugs

A RM-ANOVA revealed a significant main effect of feature ambiguity [F (2, 58) = 11.878, *MSE* = 144.21, *p* = 0.001]. This effect was driven by more errors in the maximum feature ambiguity condition relative to the medium (*p* = 0.007) or minimum (*p* = 0.003) ambiguity conditions. The main effect of group was also significant [F (1, 29) = 10.512, *MSE* = 206.82, *p* = 0.003], as younger participants committed fewer errors (12.35) than older adults (41.51). Moreover, a significant interaction between group and ambiguity was observed [F (2, 58) = 7.750, *MSE* = 144.21, *p* = 0.007], showing that of the impact of ambiguity was different for the young and older adults (Fig. **2**). Follow-up independent samples t-tests indicate that the older adults made significantly more errors before reaching the criterion in the maximum ambiguity condition [t (13.494) = -2.811, *p* = 0.014], but not the medium [t (19.235) = -1.930, *p* = 0.069] or minimum [t (24.955) = -0.956, *p* = 0.348] ambiguity conditions.

To rule out the effect of task difficulty, an additional RM-ANOVA was conducted in order to analyse the influence of feature ambiguity on errors to criterion in young adults. The main effect of feature ambiguity was not significant [F (2, 32) = 2.287, *MSE* = 16.39, *p* = 0.118], indicating that increasing the level of ambiguity did not result in increased difficulty for the young adult population.

Correlation analyses also highlighted a significant positive correlation between age and errors to criterion in the maximum (r = 0.510, *p* = 0.003) and medium (r = 0.371, *p* = 0.039) ambiguity conditions, but not the minimum ambiguity condition (r = 0.193, *p* = 0.299). These results suggest once again that errors to criterion are modulated by age when the task involves discriminating between highly ambiguous stimuli, but not relatively unambiguous stimuli.

DISCUSSION

The results of this study reveal that in both the barcode and bug conditions, errors to criterion increased as the level of feature ambiguity increased. This pattern is consistent with the idea that as stimuli become more ambiguous, participants are forced to rely on conjunctive level representations in order to successfully discriminate between target and non-target stimuli. Furthermore, significant interactions between the degree of feature ambiguity and age in both conditions reveal striking differences in young and older adults' abilities to discriminate between stimuli as the degree of

feature ambiguity increases. Young adults showed consistent performance on the experimental task as the level of ambiguity increased, while the performance of older adults rapidly deteriorated at the highest level of feature ambiguity. This observation is supported by significant correlations between age and errors to criterion in both sets of maximum ambiguity stimuli, but not with either minimum ambiguity sets of stimuli. These results are consistent with previous findings [20] and suggest that the ability to discriminate between objects with a high degree of feature ambiguity declines progressively with age.

Although robust performance differences between young and older adults were found in the maximum ambiguity conditions, both groups of participants performed similarly on the minimum and medium feature ambiguity conditions. The lack of significant group differences in the minimum and medium feature ambiguity conditions highlights the fact that this deficit does not reflect a purely mnemonic impairment, as the older group was capable of remembering the target cue when it consisted of unambiguous features. Performance declined only when discrimination of the target required a conjunction of features. Furthermore, consistent performance across the three levels of ambiguity by the young adult group verifies that perceptual difficulty, rather than memory demand, changed across the increasingly ambiguous conditions.

The response patterns observed here show striking parallels to those generated by the subjects with brain damage to the medial temporal lobe [16]. Using a very similar experimental paradigm, it was shown that patients with damage that was relatively isolated to the hippocampus were able to successfully discriminate between objects with a high degree of feature ambiguity, much like the young adults in this study. Amnesic patients with more generalized damage to the medial temporal lobe that included the perirhinal cortex, however, were unable to successfully discriminate between items when the level of feature ambiguity increased. The performance similarities between the amnesic patients with damage to the perirhinal cortex and the older adults in the current study suggest that portions of the medial temporal cortex (including the perirhinal cortex) may become less functionally efficient with age, even in the absence of pathology. These findings are also consistent with those of Ryan and colleagues [20] who reported that older adults who showed impaired performance on an object matching task that utilized stimuli with a number of overlapping features, also showed less recruitment of the bilateral anterior perirhinal cortical region during the task. The results of these studies collectively support a hierarchical organization of the medial temporal lobe. Furthermore, this pattern of results suggests that anterior portions of the medial temporal lobe thought to be responsible for complex conjunctive representations [9, 11, 12] may be particularly susceptible to the effects of cognitive aging.

The deficit displayed by older adults when attempting to discriminate between perceptually ambiguous stimuli provides evidence that some 'age-related memory deficits' may be the result of underlying perceptual deficits, rather than solely the product of mnemonic failures. However, a great deal of variability was observed in the performance of

these older adults. It remains to be seen why some older adults are more capable than others of maintaining conjunctive representations of complex objects. Understanding the factors that give rise to differential rates of aging are critical for the development of initiatives to promote healthy aging [22].

Although the current results demonstrate that a deficit in the ability to form conjunctive representations emerges progressively with age, future research is required to clearly elucidate the contribution of perceptual deficits and memory impairments to changes in cognition over the lifespan. Nevertheless, these results provide support for the notion that age-related changes in perception and memory cannot be considered in compartmental terms.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

ACKNOWLEDGEMENTS

PATIENT'S CONSENT

Declared none.

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