REVIEW

Implicit Learning in Aging: Extant Patterns and New Directions

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Abstract Research suggests that the striatum plays an important role in implicit learning (IL). The striatum exhibits marked age-related morphological and neurochemical losses. Yet, behavioral studies suggest that IL is generally well preserved in old age, and that age-related differences emerge only when highly complex IL tasks are used. In this review, we integrate behavioral and neuroimaging evidence on IL in aging. We suggest that relative stability of IL in old age may reflect neural reorganization that compensates for age-related losses in striatal functions. Specifically, there may be an age-related increase in reliance on extrastriatal regions (e.g., medial-temporal, frontal) during IL. This reorganization of function may be beneficial under less taxing performance conditions, but not when task demands become more challenging.

Keywords Aging · Compensation · Implicit learning · Neural underpinnings

Throughout the last decade, research on brain correlates of age-related changes in cognitive functioning has increased greatly. The advent of functional magnetic resonance imaging (fMRI) and other imaging modalities has contributed to our understanding of the neural underpinnings of age-related deficits in functions such as episodic memory, executive functions, and perceptual speed (e.g., Cabeza 2001; Langley and Madden 2000; Rajah and D'Esposito 2005).

By contrast, the neural basis of cognitive functions that remain relatively stable in old age has received considerably less empirical attention. There is no unequivocal

categorization of cognitive functions into whether these are preserved or impaired in old age. However, in relation to the degree of age-related impairment, cognitive functions are often broadly categorized as explicit or implicit (e.g., Bäckman et al. 2001; Prull et al. 2000). Intentional recall and acquisition of new facts and events are examples of explicit memory functions that decline in aging (e.g., Dixon et al. 2004; Nyberg et al. 2003; Verhaeghen et al. 1993). By contrast, the term "implicit" is often used as a catchall term to denote learning and memory that remain beyond the person's awareness, and are expressed only through performance.

Although comparatively little research has been directed at implicit cognition in old age, the available evidence is consistent in suggesting that age-related deficits are small in magnitude (e.g., Hoyer and Lincourt 1998; Meulemans et al. 1998; Schugens et al. 1997; Zacks et al. 2000), particularly when contrasted against the pattern for explicit cognition.

Of critical importance, hardly any research has addressed why implicit functions, as opposed to other cognitive functions, may remain stable in old age from a neurobiological perspective. The present review serves to highlight gaps in research on implicit learning (IL) and argues that future research to fill these gaps should be of great interest from both cognitive and neuroscientific perspectives on aging.

Implicit Learning

In experimental settings, IL is defined as the acquisition of, or memory for, co-occurrence and dependencies between stimuli or trials that are expressed through performance only (e.g., Cleeremans et al. 1998; Frensch 1998; Jimenez

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2008; Seger 1994). The participant remains unaware of between-stimuli relations, yet demonstrates performance increments, evidenced through a decrease in reaction time (RT) or an increase in accuracy for previously encountered stimuli.

Throughout the last 15 years, there has been much debate about the nature of IL (e.g., Cleeremans et al. 1998; Frensch and Rünger 2003; Gaillard et al. 2006; Perruchet and Pacton 2006; Seger 1994, Shanks and St. John 1994, Willingham and Preuss 1995). Much of this discussion concerns the fact that, although a wide range of tasks have been used to demonstrate the existence of IL, not much is known about the processes underlying performance.

Some researchers integrate IL with skill or procedural learning (e.g., Gabrieli 1998; Prull et al. 2000; Squire et al. 1993), although there are differences between these task categories. Skill or procedural learning denotes more generally the acquisition of new habits or abilities through practice. Classic examples of skill learning tasks include rotor pursuit, mirror tracing, and mirror reading, as well as problem solving tasks such as the Tower of Hanoi. In these tasks, participants gradually improve performance through practice even though they often cannot verbalize how they solved the task (e.g., Brooks and Baddeley 1976; Cohen et al. 1985). However, performance during skill learning is often superimposed by explicit learning (EL), particularly during puzzle solving, as participants are clearly aware of the task they are required to perform, of certain steps in performance (Reber and Kotovsky 1992; Seger 1994; Squire and Frambach 1990), and of improvements in performance. Most skill and procedural learning tasks therefore constitute poorly controlled measures of IL.

IL tasks attempt to circumvent the superimposition of EL by deliberately not revealing the task at hand. For example, in the Serial Reaction Time task (SRTT), participants are typically instructed that they will perform a motor task when, unbeknown to the participant, the stimuli alternate between random and predictable sequences (Nissen and Bullemer 1987). Similarly, in artificial grammar (AG) learning, participants are instructed to memorize strings of letters. They are not informed that the strings are constructed according to certain rules, which they need to apply at a later stage (Reber 1989). In the weather prediction task, participants predict one of two outcomes (good or bad weather) from a set of arbitrary cues. The high complexity of the underlying relation between cues and outcomes is thought to circumvent EL, and participants are typically instructed to "guess" the outcome of the weather (Gluck and Bower 1988). A gradual performance improvement is seen over many trials without participants showing awareness of the dependencies between cues and outcomes, which is taken as evidence for IL. Additionally, in IL tasks awareness is usually assessed using self-reported awareness

and/or reproduction and recognition tests. That said, it should be noted that the influence of explicit processes upon IL has been widely debated (e.g., Gaillard et al. 2009; Shanks and St. John 1994), and IL and EL tasks are probably never fully dissociable. Pertaining to this point, there is little evidence for IL under anesthesia (Merikle and Daneman 1996; Shanks and St. John 1994).

It is important to differentiate IL tasks from implicit memory tasks (e.g., perceptual priming). Priming tasks assess whether previous exposure to a specific stimulus (e.g., a word) facilitates later processing of that word or a related item (Schacter 1987). Although the two types of implicit tasks are unarguably linked, they differ in a number of respects (Seger 1994). Priming studies address implicit memory for single stimuli, whereas IL tasks address learning of statistical covariations and dependencies between stimuli. Moreover, neuroimaging and patient studies have revealed quite distinct neural correlates of priming and IL. Priming is associated with a decrease of activation in posterior cortical regions (Bäckman et al. 1997, 2000; Squire et al. 1992), whereas IL comes with increased activation of a subcortical-cortical network, in which the striatum is a central component (e.g., Lieberman et al. 2004; Poldrack et al. 2001; Rauch et al. 1997).

Thus, in keeping with the definition of IL provided above, in the IL studies selected for review (a) the influence of explicit, declarative processes is minimized, typically by the experimenter concealing the true nature of the task (hence excluding skill and procedural learning); and (b) performance increments are dependent on co-occurrence and dependencies between stimuli (hence excluding priming).

IL research first sparked interest in the 1960s (Reber 1967) and flourished in the 1990s when different methods for assessing IL were widely debated (e.g., Berry 1997; Berry and Dienes 1993; Cleeremans et al. 1998; Frensch 1998; Seger 1994; Shanks and St. John 1994). Moreover, patient data contributed during that time to establish IL as a "striatal" memory system, as opposed to the medial temporal lobe (MTL) memory system critical to EL (e.g., Knowlton et al. 1996; Reber and Squire 1994; Squire and Zola 1996). More recently, however, neuroimaging studies directly comparing EL and IL have failed to find evidence that awareness or intention critically determines MTL recruitment during task performance (Fletcher et al. 2005; Schendan et al. 2003; Willingham et al. 2002). Rather, the MTL is more generally involved in the rapid formation of associations between previously unrelated events, which are stored as flexible representations (e.g., Cohen et al. 1997; Curran 1997; Eichenbaum 2000; Knowlton et al., 1996; Poldrack et al. 2001; Reber et al. 1996). By contrast, the striatum is recruited for incremental stimulus-response binding based on statistical likelihoods of stimulus occurrence

over time that leads to automatic behavior (see Packard and Knowlton 2002; Shohamy et al. 2008, for reviews).

Research on IL in aging also commenced during the 1990s (e.g., Howard and Howard 1989, 1992), resulting in a rich knowledge base, incorporating different tasks, stimuli, and modalities. However, a cognitive neuroscience perspective on IL in aging is still lacking. Very few studies have investigated the neural basis of IL in old age, and the findings are equivocal (Aizenstein et al. 2005; Daselaar et al. 2003; Fera et al. 2005; Rieckmann et al. 2009). Yet, new insights and hypotheses pertaining to this issue can be derived from patient studies and neuroimaging work in young adults. In the past few years, considerable research has been directed at the interaction of striatal and MTL systems during IL (e.g., Albouy et al. 2008; Fletcher et al. 2005; Poldrack et al. 2001; Poldrack and Rodriguez 2004; Schendan et al. 2003; Seger and Cincotta 2006). This has led to insights into cognitive impairments in patients with striatal lesions, particularly regarding possible compensatory mechanisms during IL (Beauchamp et al. 2008; Moody et al. 2004; Rauch et al. 2007; Voermans et al. 2004). These findings are important to consider when investigating the neural basis of IL in old age, as the striatal complex undergoes marked volumetric and neurochemical changes during the normal aging process (Bäckman et al. 2006, in press; Raz et al. 2003, 2005). To our knowledge, IL in aging has not yet been approached from this perspective, and hence, it is timely to review behavioral findings on IL in aging and integrate these with relevant neuroscientific evidence, in order to derive ideas about how and when aging does or does not affect IL, as well as the neural basis for these outcomes.

Implicit Learning and Aging

In the following section, we review behavioral findings on IL and aging, separately for findings from implicit sequence learning and covariation learning (e.g., weather prediction and AG). In sequence learning, participants learn to predict the onset of a stimulus location based on the locations of one or more preceding stimuli. In covariation learning, participants learn to predict an outcome (e.g. weather or group membership) by a preceding stimuli set (e.g. a grammar string/a set of cards). Both types of task converge on assessing learning co-occurrences between stimuli (spatial or temporal) and dependencies between stimuli and an outcome, independently of awareness of the to-be-learned relationships. However, sequence learning, but not covariation learning, typically has a motor component, and thus perceptual-motor associations rather than purely perceptual associations are made. There is mixed support for sequence learning without the motor component (e.g.,

Kelly and Burton 2001; Lungu et al. 2004; Willingham et al. 1989; Willingham 1999; but see Dennis et al. 2006; Heyes and Foster 2002; Song et al. 2008).

We will therefore review the available literature separately for sequence learning and covariation learning, but occasionally compare and contrast findings across types of tasks. It should also be noted that, although the review attempts to cover IL more generally, the literature on IL and aging is far more abundant in relation to sequence learning, so that many of our conclusions will be largely based on this type of learning.

Sequence Learning

Following introduction of the SRTT (Nissen and Bullemer 1987) and AG (Reber 1989) tasks, experimental research on IL increased greatly during the 1990s. The advent of the SRTT also marked the onset of research into potential age-related differences in IL. Howard and Howard (1989, 1992) first used the SRTT to demonstrate that both younger and older adults increased typing speed for repeating sequences compared to random sequences, although overall RT was longer in the older group. These initial findings have recently been extended to show that practice length (15 vs 30 blocks) also did not differentially affect IL in younger and older adults (Gaillard et al. 2009). Both age groups showed comparable RT decreases with extended practice. IL in older adults was also demonstrated when the classical SRTT was modified to assess sequences of whole hand and arm movements (Harrington and Haaland 1992; Shea et al. 2006; Seidler 2006). However, in two studies the size of the IL effect was slightly smaller for older compared to younger adults (Harrington and Haaland 1992; Shea et al. 2006). Notably, questionnaire data (Shea et al. 2006) as well as free recall tests and generation of sequences (Harrington and Haaland 1992) revealed almost complete awareness of the repeating sequence in both these studies, and awareness contributed to the diminished IL effect in aging (Harrington and Haaland 1992).

In younger adults, most studies have shown that EL of the sequence in the SRTT does not interfere with IL (Curran and Keele 1993; Song et al. 2007; Willingham and Goedert-Eschman 1999; Willingham et al. 2002; but see Fletcher et al. 2005), and may even facilitate IL (Howard and Howard 2001), suggesting separate explicit and implicit systems. In older adults, the relationship between EL and IL appears less straightforward. In a version of the SRTT, half of the participants were informed of the existence of a repeating sequence, whereas the other half was not (Howard and Howard 2001). All participants showed IL on measures of RT and accuracy. However, the informed elderly group showed the lowest degree of IL and also needed the most training before exhibiting an effect

(four sessions as compared to one session for the corresponding young group). Thus, awareness of the existence of the repeating sequence facilitated IL for younger adults, but impaired performance of older adults when compared to the uninformed condition. These findings may reflect a processing capacity limit, which is exceeded by simultaneous explicit and implicit processing demands in older adults. However, when EL of the repeating sequence was aided by color-cuing sequence trials in comparison to random trials, both younger and older showed similar levels of IL, which suggests that IL and EL can proceed in parallel in older adults when the EL demands are sufficiently low (Song et al. 2008, 2009).

Relatedly, IL in younger and older adults has been compared in the SRTT under both single- and dual-task conditions, which involved a concurrent tone-counting task (Frensch and Miner 1994; Nejati et al. 2008). During dual-task performance, which added demands on explicit memory through keeping count of tones, only older adults showed IL impairments. Frensch and Miner (1994) concluded that, "capacity affects implicit learning only when the capacity limit is reached" (p. 108).

Finally, working memory capacity and general cognitive ability have been related to degree of IL in older, but less so in younger, adults (Cherry and Stadler 1995). Cognitively advantaged older adults showed IL effects comparable to those of younger adults, whereas less advantaged older adults showed smaller IL effects (Cherry and Stadler 1995). In a recent study, Howard et al. (2007) artificially slowed down younger adults' stimulus-response times in an SRTT to be equivalent to those of older adults. This manipulation affected performance only marginally, suggesting that age-related IL differences are not merely a result of different stimulus and response timings. Overall, these results suggest that explicit memory demands may affect IL in older adults more than in younger adults, which indicates that IL may draw on different processes (and possibly neural circuitries) in early and late adulthood.

The constraints on IL in old age have also been investigated by varying the complexity of sequence structures. More complex, higher-order IL typically involves sequences in which one stimulus can only be predicted by more information than what is available in the immediately preceding stimulus. These are higher-order probabilistic sequences such as 1r4r3r2r1r4r3r2... in which the spatial positions 1432 alternate with random positions (e.g., Howard and Howard 1997), and higher-order deter-ministic sequences, in which each pair of stimuli occurs equally often (e.g., 121423413243). The structure of the sequence requires participants to extract more than pairwise information in order to show improved performance. By contrast, lower-order sequences only require acquisition of information about frequencies (in the sequence

4213423423, position 3 occurs more often than position 1) or pairwise information (in the sequence 4231324321, the transition from 3 to 2 occurs more often than the transition from 3 to 1).

When sequence-structure characteristics were varied, younger adults learned both pairwise and higher-order sequences equally well, but older adults showed better learning of the pairwise sequences (Curran 1997). A subsequent test of explicit knowledge showed that awareness had no impact on the results. These findings suggest that, when acquiring the repeating sequence requires learning more than pairwise co-occurences of trials, age differences in IL appear. Curran (1997) concluded that "young subjects may be capable of learning larger sequence chunks than elderly subjects" (p. 37), which reflects an age-specific capacity limit in the formation of higher-order associations. It has subsequently been shown that young, old, and old-old adults could successfully learn higher-order information in the SRTT; however, the magnitude of the effect was generally smaller for the older groups (Feeney et al. 2002; Howard and Howard 1997). IL was selectively abolished in older adults when complexity of the sequence information was increased even further by interleaving two random positions between fixed positions (1rr2rr3rr4rr), although younger adults too showed reduced IL with this sequence complexity (Howard et al. 2004b). Still, even for this third-order sequence, IL was demonstrated in older adults when the number of different stimuli was reduced from four to three, although the effect again was smaller than for younger adults (Bennett et al. 2007).

The effect of complexity by EL and varying sequence structure is illustrated in Fig. 1: Older adults are generally at an IL disadvantage when sequence learning requires
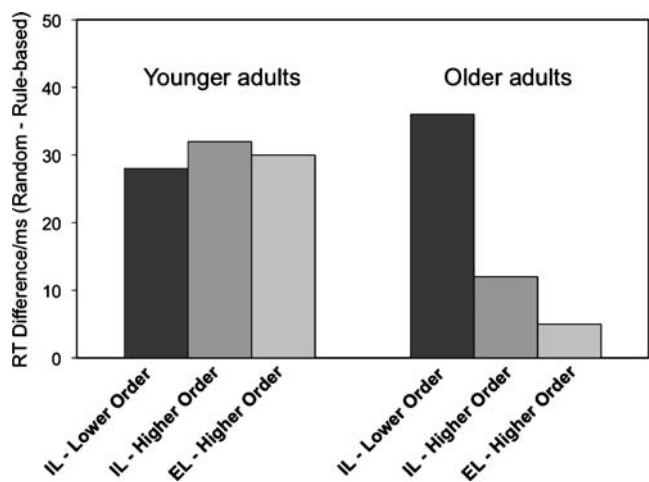
Fig. 1 Effects of sequence complexity (higher order versus lower order) and instructions (IL versus EL) on performance in an SRTT in younger and older adults. Adapted from Howard and Howard (1989) for illustration of lower-order sequence learning and from Howard and Howard (2001) for illustration of higher-order sequence learning

formation of associations across several sequence items, whether induced by instructions (i.e., in the case of EL) or sequence complexity. For younger adults, the relationship between information complexity and IL is weaker, as learning is often present under intentional learning conditions, and varying the structure complexity independently of awareness shows only a very small effect on the degree of IL (Howard and Howard 1989, 2001).

IL in the classical SRTT depends on several sources of information. Relations between stimuli are expressed through visuospatial information, but also through motor sequencing. Several researchers have argued that motor sequencing is essential for IL in the SRT, as there is little evidence for transfer across different stimulus-response mappings (e.g., Kelly and Burton 2001; Willingham 1999). However, other studies have shown that perceptual information alone is sufficient for IL in both younger (Heyes and Foster 2002) and older (Howard et al. 2008; Song et al. 2008) adults.

One study investigated IL in younger adults under three different conditions (Robertson and Pascual-Leone 2001). Sequence learning was guided by spatial location across four positions, by the color of the target in the center of the screen, or by both color and spatial position. There was evidence of IL when sequence information was guided by only color or position and there were no differences in degree of IL between these two conditions. When both position and color were combined, however, IL was facilitated, suggesting that both spatial and perceptual information are sufficient for IL, and that there is an additive effect when both are provided.

Several studies have investigated whether the largely preserved IL in older adults in the SRTT is specific to visuo-spatial information or can be generalized to different modalities, much like in younger adults. Negash et al. (2003) examined learning of non-spatial sequences in younger and older adults. Higher-order probabilistic sequences were used, but items were letters (abcd) presented in the center of the screen. Each letter was matched with one of four response buttons. In line with previous results using sequences of similar structures (Howard and Howard 1997, 2001), groups of younger and older adults showed significant effects of learning the repeating stimuli as compared to random control trials, although the onset of learning occurred later in the older group. In another study in which stimuli were presented as higher-order sequences of spoken words (Dennis et al. 2003), similar results were obtained: Both younger and older adults showed IL, although the older group showed a smaller effect. The results from both these studies suggest that older adults' reduced IL of complex dependencies between stimuli does not reflect domain-specific deficits (e.g., impaired visuospatial abilities), but rather reflects a general deficit in IL when contingencies between stimuli are complex.

These findings were recently extended in a study from the same group (Dennis et al. 2006). In this study, the stimulus-response mapping changed on every trial, so that sequences of spoken words and sequences of button presses were unrelated. Removing the spatio-motor component of sequence learning eliminated IL for higher-order sequences in older adults. However, when less complex sequences were used, IL in older adults was comparable to that of younger adults, again suggesting no domain-specific patterns of IL in old age. Removing stimulus-response mappings likely increased the complexity of the to-be-learned material, and thus, the results support previous findings that age differences in IL are observed when the to-be-learned material is complex.

However, domain-specific age differences in IL were reported in a Hebbian supraspan learning (HSL) task. In this task, participants are typically presented with span-exceeding sequences for immediate recall. Unbeknown to the participant, every third list contains the same order of stimuli. It is assumed that participants improve performance in recalling the repeated lists compared to other lists during the course of the experiment. Age-related deficits were found in visuospatial HSL, whereas verbal HSL was intact in older adults (Gagnon et al. 2005; Turcotte et al. 2005). The authors suggested that the selective impairment might reflect domain-specific differences in working memory capacity (e.g., Myerson et al. 1999), such that visuospatial working memory is affected more in older age than verbal working memory. However, other research indicates that visuospatial and verbal working memory are not differentially affected in aging (e.g., Kemps and Newson 2006; Park 2000; Salthouse 1995). One reason for the different results in the HSL and SRTT tasks may be that they tap into different systems, as the two types of tasks differ in a number of ways. Most importantly, the likelihood of participants becoming aware of the repeating lists is much greater in HSL. Repeated lists are presented in isolation rather than in blocks and participants are instructed to memorize the items. Indeed, both HSL studies reviewed above showed that age-related differences in learning coincided with 70–80% of the participants reporting awareness of the repeated sequence. Moreover, functional imaging studies have shown that different IL paradigms such as the SRTT, the weather prediction task, and the AG task activate a similar cortico-striatal network. To our knowledge, HSL has not been examined in imaging research and the neural correlates are largely unknown, but patient studies suggest involvement of the left medial-temporal cortex in verbal supraspan learning, and the right medial temporal cortex in visuospatial supraspan learning (Rausch and Ary 1990). Thus, the results of HSL tasks do not generalize to IL, as performance in the HSL appears to depend on the explicit memory system, as judged from behavioral data on both healthy persons and patients.

Covariation Learning

Covariation learning tasks encompass a range of procedures, in which an outcome is determined by co-occurences of features within, typically visual, stimuli. For example, in contextual cuing tasks, such as target detection, the location of the target (e.g., the letter L) correlates with the arrangement of distracters (e.g., the letter T). In conceptual fluency tasks, such as the weather prediction task (Gluck and Bower 1988), the outcome (the weather) is probabilistically related to the covariation of features (e.g., shapes), and in AG research the classification of letter strings as grammatical or not depends on the rule-based covariation between letters. Importantly, participants perform these tasks without being informed about feature co-occurences, and normally remain unaware of any stimulus-response relations.

Two studies have compared older and younger age groups on visual feature-detection tasks, in which participants were required to identify a letter or digit among distracters (Howard et al. 2004a; Schmitter-Edgecombe and Nissley 2002). In both studies, participants were not informed that the distracter arrangement cued the location of the target in the majority of trials and IL was demonstrated through prolonged RTs when distracter arrangement and target location violated the learned co-occurrence of location and distracters. However, there were age-related differences when participants were classified as aware or unaware of the distracter-target relations (Howard et al. 2004b). Among unaware participants, younger and older adults showed comparable IL. By contrast, for aware participants, IL was selectively eliminated in the older group. It also appeared that learning among aware younger adults occurred faster than among unaware younger adults. In this way, these results extend previous SRTT findings that EL can co-occur and facilitate performance in IL tasks for younger adults, but impair IL in older adults (Howard and Howard 2001).

Similar results were reported using a category learning task (Price 2005). This study assessed younger and older age groups on two tasks, which required participants to predict an outcome from a combination of cues (Gluck and Bower 1988). In the first task, participants were told that there was a complex relationship between cues, and that they should start by guessing, but would increase performance throughout the experiment. In the second task, they were told to rely on their "gut instincts" to make the decisions and that the task was designed to assess passive learning. Results showed no difference in performance between age groups in the latter condition, although younger adults performed better than the older in the former condition. Thus, triggering an explicit strategy by informing participants of a rule had no effect on IL in younger adults, but interfered with IL in the older adults.

These patterns of results are further supported by studies using classification tasks, such as the AG task. Younger and older adults were equally successful at classifying letter strings as familiar based on an invariant feature (same letter in second position; Howard et al. 2008b), and at classifying letter strings based on a "grammatical rule" under implicit conditions (Davis et al. 1998; Meulemans and van der Linden 1997). However, when participants were told about the relation between items in figural-grammar sequences, younger adults outperformed older adults (D´Eridita and Hoyer 1999). In one study, the instructions (rule provision or not) as well as the complexity of the grammar varied across four conditions (Midford and Kirsner 2005). The results showed that triggering of EL through rule provision impaired IL performance equally much in both age groups when complex grammar was used. However, when simple grammar was used, younger adults showed performance benefits from rule provision, whereas older adults did not. This pattern reinforces the point that EL and IL are more likely to coincide in a positive manner in younger than in older adults, although EL can interfere with IL also in younger adults when the to-be-learned information is very complex (see also Reber 1989).

Conclusions from Behavioral Research

In summary, although IL appears to remain largely intact in old age, awareness and conscious reflection differentially interfere with IL in older adults. Moreover, age differences that occur when awareness is high or EL is deliberately triggered are expressed in two directions: Younger adults often show preserved or better IL performance when EL can be utilized, whereas EL impairs performance in older adults, as if the two types of learning interfere with each other. This pattern applies to a range of IL tasks such as the SRTT, target detection, weather prediction, and AG learning. Hence, the available evidence suggests that age-related differences in IL reflect deficits in more general IL processes, such as extraction of statistical co-occurences or dependencies between stimuli or features, rather than task-specific deficits. That said, it is important to note that implicit covariation learning has been investigated less extensively than the SRTT. More research is needed to examine potential age differences across different IL tasks, with particular focus on the relative sparing in aging. This is especially so in light of reports that covariation learning tasks may be less reliable than the SRTT (Salthouse et al. 1999; Shanks and St. John 1994).

Research using the SRTT has also contributed to our understanding of how task complexity may interfere with IL in older adults. The SRTT assesses learning of co-occurences of temporally separated stimuli, which allows easy manipulation of the complexity of the to-be

learned material, and it has been shown that increasing the complexity of sequences has similar interfering effects on IL in older adults as does high awareness. Both sequence complexity and EL may increase the demands on higher-order association formation, because larger chunks of information are held in mind simultaneously, and age-related differences in IL may appear once capacity limits have been reached (Curran 1997; Frensch and Miner 1994). Behavioral research has not explored this hypothesis further and contributions from neuroscience may need to be considered in order to explain the observed patterns of IL in old age. Of special interest here is how the underlying neural activity during IL may change as a function of age and whether this potential change confirms the hypothesis that IL and EL can work in parallel in younger adults, but interfere with each other in old age.

Neuroscientific Perspectives on Implicit Learning

Neuroimaging Studies

Neuroimaging studies in healthy persons have shown that IL draws on a widespread network of striatal and extrastriatal brain regions. Specifically, fMRI studies have implicated a striatal-parietal-prefrontal network with the caudate nucleus as the central component in sequence learning (e.g., Grafton et al. 1998; Rauch et al. 1997), artificial grammar learning (e.g., Lieberman et al. 2004), and the weather prediction task (e.g., Poldrack et al. 1999).

In healthy younger adults the striatum and the MTL might work competitively as striatal activation during a weather prediction task was negatively correlated with activation of the MTL (Foerde et al. 2006; Poldrack et al. 2001). Importantly, it has been shown that early MTL activation that decreases across training runs in younger adults was unrelated to awareness, but that the MTL is involved in the rapid formation of higher-order associations in early stages of IL, with the striatum gradually "taking over" across time (Albouy et al. 2008; Schendan et al. 2003). It has further been suggested that the relationship between MTL and striatum, especially the caudate, is mediated by prefrontal areas, which is supported by findings that activation of prefrontal areas and deactivation of the MTL during IL lag behind activation of the caudate (Poldrack and Rodriguez 2004; Seger and Cincotta 2006).

Animal Studies

The striatum has also been implicated in gradual learning of stimulus-response associations in non-human animals (see Packard and Knowlton 2002; Packard 2009, for reviews).

This is best exemplified in the T maze task: Rodents can learn to find the reward location independent of starting location (place learning) or by gradual associations between turns relative to starting location and reward (response learning). It has been suggested that the animal demonstrates initial place learning, which then shifts to response learning after repeated exposures (Chang and Gold 2003; Hicks 1964; Packard 1999; Packard and McGaugh 1996). This pattern reflects a shift from an early hippocampal-dependent form of learning that leads to rapid acquisition of a flexible "cognitive map" to incremental learning of dependencies between stimuli and responses that leads to striatal-dependent automatic behavior (e.g. Packard 1999). Blocking the striatum pharmacologically leads to increased place learning (e.g., Lee et al. 2008; Packard and McGaugh 1996), which indicates that, much like in humans, the striatal and hippocampal memory systems in rodents do not operate independently.

Moreover, animal work on instrumental learning recently showed that the dorsal striatum is implicated in performance, whereas the ventral striatum is critical to acquisition (Atallah et al. 2007). When the ventral striatum (analogous to caudate in humans) was blocked pharmacologically, rats were impaired on a learning task. However, blocking of the dorsal striatum (analogous to putamen in humans) only affected learning when the compound was injected prior, but not after, the acquisition phase. Thus, the ventral striatum may have "directed" learning to medial-temporal and frontal areas when the dorsal striatum was impaired.

Patient Studies

Impaired striatal functioning (e.g., loss of dopaminergic input) is a hallmark of Parkinson's disease (PD; e.g., Kreitzer and Malenka 2007). When performance of patients with PD and healthy controls was compared on the SRTT, healthy participants showed a decrease in RT for the repeating sequence blocks, but not for the random sequence blocks. The patient group, however, did not show any differences in RT throughout the experiment (e.g. Willingham et al. 1996). Thus, striatal impairments in PD appeared to impair IL of sequential information and these results have since been replicated in other studies using similar designs (e.g., Smith and McDowall 2004). Importantly, impaired sequence learning in PD is not confined to the motor modality, as performance deficits were also reported on a verbal version of the SRTT as well as in AG learning (Smith and McDowall 2006). Research on patients with Huntington's disease (HD) indicates that impairments on the SRTT are not restricted to PD, but apply to other patient groups with basal ganglia lesions (e.g., Knopman and Nissen 1991; Willingham and Koroshetz 1993). However, results from patient studies are inconsistent, as IL has been

reported in many patients with striatal impairments (e.g., Beauchamp et al. 2008; Exner et al. 2002; Moody et al. 2004; Rauch et al. 2007; Smith et al. 2001; Werheid et al. 2003). Relatedly, Jackson et al. (1995) demonstrated that only PD patients with additional impairments of the frontal lobes showed deficits in IL, and a relationship between frontal lobe damage and PD severity has been observed (e.g., Locascio et al. 2003).

Taken together, evidence from neuroimaging research, animal work, and patient studies clearly shows that IL depends on a subcortical-cortical network with particularly strong involvement of the striatum, which is in line with the theory of multiple parallel striatal-cortical connections (Alexander et al. 1990). Nevertheless, neuroimaging and animal studies suggest that the MTL is involved in learning, at least in the early stages of IL. Further, there is evidence that the striatal and MTL systems work in competition, so that MTL activation peaks early on in learning but then decreases gradually as striatal involvement increases. Neuroimaging and patient studies both suggest that the prefrontal cortex also plays an important role in IL, possibly mediating the relation between striatum and MTL. The fact that patients with impaired striatal function can show preserved IL could reflect reorganization within the striatal-cortical network, a point that will be elaborated in a subsequent section.

Age-Related Brain Changes

Old age is accompanied by structural brain changes that have been extensively investigated in both humans and animals. Overall, aging is associated with a steady decrease in size and weight of the brain by about 2% per decade from early to late adulthood (e.g., Kemper 1994; Miller et al. 1980), but brain aging is not uniform. Shrinkage of the prefrontal cortices is more substantial than in other cortical areas, with a steady volume decrease between 5 and 10 % per decade, starting from early adulthood (e.g., Allen et al. 2005; Grieve et al. 2005; Raz et al. 2005). In contrast, hippocampal volume remains relatively stable until about 60 years of age, after which volume loss is observed (Allen et al. 2005; Raz et al. 2005). Subcortically, the striatum has been shown to decrease markedly with advancing age. Studies have reported age-related volumetric decreases between 5 and 10% for putamen and caudate (e.g., Raz et al. 2003) and these structural changes in the striatum are accompanied by biochemical changes, with dopamine biomarkers exhibiting decreases of up to 10% per decade from early to late adulthood (see Bäckman et al. 2006, in press).

A considerable amount of research has investigated the relation between age-related brain and cognitive changes. For example, several studies have shown a relationship between hippocampal volume and episodic memory performance (e.g., Hackert et al. 2002; Head et al. 2008; Persson et al. 2006). Similarly, volumetric decreases in the prefrontal cortex with increasing age show a relationship to performance on tasks assessing executive functions and problem solving (e.g., Head et al. 2002).

The question, then, is how one should reconcile the facts that (a) IL is highly dependent on the integrity of the striatal network; (b) age-related structural and biochemical losses are pronounced in the striatal complex and connected prefrontal areas; and (c) IL is relatively well preserved in aging. A similar paradox is evident in patients with striatal impairments, where striatal alterations are even more marked than in aging, yet IL is spared under some conditions (e.g., Moody et al. 2004; Rauch et al. 2007; Werheid et al. 2003).

Compensatory Mechanisms

Before much was known about neural correlates of IL, Reber noted that, "implicit cognitive processes are the functional components of the evolutionarily older, primitive system [which] predicts that they should show greater resistance [to neurological insult] than should explicit processes" (Reber 1989, p. 232). In light of today's knowledge about widespread age-related brain changes, neural reorganization and compensation may explain preserved cognitive abilities such as in the case of IL. Compensation is no new concept among psychologists (Bäckman and Dixon 1992), but the mechanisms behind neural compensation are not well explored. We will use the term compensation in the context of this review as neural reorganization that occurs in response to structural or biochemical losses in the brain in order to preserve cognitive functioning. Related age-comparative imaging research has mainly focused on episodic memory functions (e.g., Bäckman et al. 1997; Cabeza et al. 2002), and very few studies have targeted neural correlates of IL in old age.

The first comparison of older and younger adults in the SRTT using neuroimaging found no significant difference in neural activation between age groups: Both younger and older adults showed comparable levels of performance and recruited bilateral frontal, motor, parietal, and striatal areas during IL (Daselaar et al. 2003). A subsequent investigation of age-related neural differences in the SRTT reported greater activation of the ACC, but decreased striatal recruitment, in older compared to younger adults during IL (Aizenstein et al. 2005). These data are interesting to view in light of findings that decreased striatal dopaminergic functions were associated with increases in dopamine uptake in the ACC among early PD patients, which may be compensatory (Rakshi et al. 1999). In a recent study, we

investigated activation differences in IL and aging more closely and showed that IL in the SRTT was related to increases in striatal activation, but decreases in MTL activation across time for younger adults (Rieckmann et al. 2009). For older adults, however, IL was related to increases in both the striatum and the MTL, as well as in prefrontal areas. Most importantly, this pattern was related to degree of IL in aging, which provides initial evidence for a compensatory mechanism at play.

Increased reliance on the MTL in the presence of striatal losses has also been shown during covariation learning (Moody et al. 2004). Prefrontal and medial-temporal activation was associated with successful IL in a weather prediction task in PD patients, whereas controls relied more heavily on the striatum (Fig. 2).

The observed recruitment of the MTL during IL in patients with striatal impairment that is illustrated in Fig. 2 has also been demonstrated with other IL tasks and patient groups (Beauchamp et al. 2008; Rauch et al. 2007; Voermans et al. 2004). For example, Voermans et al. (2004) showed that when striatal capacity was compromised in HD patients, disease severity correlated positively with activation of the hippocampus during a navigation task, although the HD group showed no performance deficit.

It should be noted, however, that extrastriatal activation during IL in sequence learning and covariation learning has also been reported in more posterior cortical areas. During a probabilistic category classification task both younger and older adults showed similar levels of performance and activation of a prefrontal-parietal-striatal network (Fera et al. 2005), but correlations between BOLD signal changes and behavioral measures revealed that younger and older adults recruited areas within the same network to different degrees. Specifically, older adults drew more heavily on parietal regions, whereas younger adults recruited prefrontal and striatal regions to a greater extent. Similarly, in an SRTT, early stage PD patients and controls both showed successful IL after pre-training on the repeating sequence before scanning commenced, although PD patients showed slower rates of learning (Werheid et al. 2003). When participants continued the SRTT during a subsequent scan, patients and controls performed at similar levels during scanning, but activation patterns for repeating sequences differed: Whereas IL correlated more strongly with frontal activation in the controls, bilateral parieto-occipital activation was predictive of performance in the patient group. Moreover, as expected, striatal activation was observed in the control, but not in the patient group.

From the research discussed above, it appears that impaired striatal functions in healthy aging and PD are compensated for by an increased reliance on extrastriatal areas, and the MTL emerges as a strong contender for such compensatory activity. As of yet, there is no evidence that the striatum can compensate for MTL damage, and in this way the compensatory recruitment may be unidirectional. This likely reflects the fact that MTL activation is associated with the acquisition of more flexible and associative information, whereas striatal learning is restricted to the acquisition of constant stimulus-response mappings (Poldrack et al. 2001; Rose et al. 2002). This account posits that the differential involvement of MTL and striatum in IL does not reflect the explicit-implicit distinction, but rather the structural complexity of the to-be learned material.

The hypothesis that older adults might recruit the MTL during IL is also in line with the behavioral pattern we have identified earlier. To reiterate, IL deficits in older adults have only been observed under conditions when (a) highly complex patterns are used, (b) learning is explicit, or (c) an explicit task is performed concurrently. This may be related to the fact that MTL activation during EL by means of, for example, dual-task requirements interferes with IL because of the concurrent load on the MTL in both IL and EL. In younger adults, however, the striatal and MTL systems work competitively during IL, and thus, concurrent MTL load does not interfere with IL to the same degree.

Taken together, research suggests an increased reliance on extrastriatal brain regions during IL when striatal functions are impaired. Nevertheless, neuroimaging studies on IL when striatal functions are compromised have been somewhat inconsistent with different studies implicating posterior cortical areas (Fera et al. 2005; Werheid et al.
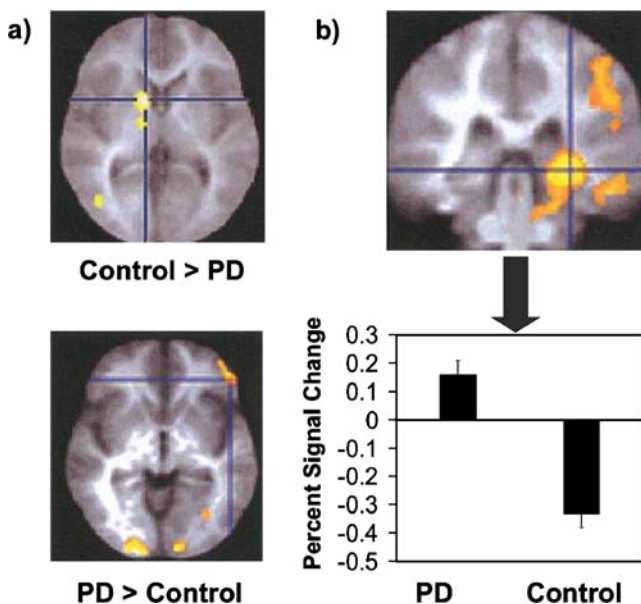
Fig. 2 **a** Activation in healthy controls and PD patients during the weather prediction task. Healthy controls recruited the caudate, whereas PD patients activated prefrontal and occipital areas. **b** Signal change in the MTL by group. In this region, PD patients showed an increase, whereas controls showed a decrease in BOLD response for weather prediction compared to baseline blocks. Adapted from Moody et al., 2004

2003), frontal regions (Aizenstein et al. 2005), and medial temporal areas (Beauchamp et al. 2008; Moody et al. 2004; Rauch et al. 2007; Rieckmann et al. 2009; Voermans et al. 2004), as well as no change in activation (Daselaar et al. 2003). Hence, more research is needed to substantiate the ideas put forward here.

Summary and Future Directions

Behavioral research demonstrates that IL is normally spared in old age but there are limits to IL ability that may be related to the demands on forming higher-order associations. Further, these constraints appear to affect IL in older adults more so than in younger adults. Relatively little research has addressed behavioral IL findings in aging from a neuroscientific perspective. Notably, research has largely ignored findings that the striatum, which appears central to IL, shows steady age-related volumetric and neurochemical decline. Integrating evidence from behavioral and neuroscientific studies suggests that spared IL in old age reflects neural compensation. Specifically, older adults may rely more heavily on cortical and MTL recruitment to compensate for age-related decline in striatal functions. The costs of the compensatory process show when cortical and MTL resources are highly taxed during IL, such as when sequence complexity or explicit strategies require higher-order association between several items.

Future research should seek to identify more precisely the characteristics of compensatory mechanisms for impaired striatal functions across a variety of tasks. This line of inquiry holds several important implications, but is yet largely a hypothetical model derived from combining behavioral and neuroscientific evidence. The hypotheses resulting from this review imply that imaging research into age-related neural compensation in IL should be directed toward changes in negative correlations between regions, such as the striatum and the MTL. Often, meaningful deactivations in fMRI studies remain undetected because of a lack of a priori hypotheses. Identification of compensatory mechanisms for impaired striatal functions in the healthy and diseased brain can lead to the development of specific cognitive test batteries that are tailored to identify early warning signs of disease, which may otherwise be masked by functional compensation.

On a more general note, understanding brain compensation in old age could also facilitate the understanding of those functions that do show drastic decline in aging. In this review, the focus has been on compensatory mechanisms and their limits from the perspective of IL. However, it is likely that there are costs of compensation also for cognitive functions other than IL, as compensation might draw more globally on the availability of neural resources. As described above, evidence suggests that medial temporal and frontal areas may compensate for striatal impairment, but not the other way around. Note, however, that the separation of IL and EL in experimental settings likely does not reflect everyday life situations, where the two systems are closely linked and simultaneously involved. Increased MTL recruitment in old age may result in an advantage for IL and disadvantage for EL, because of competition for available neural resources. Moreover, the costs of compensation might be especially marked in aging, as compared to focal striatal lesions, because age-related volumetric decreases are global and also occur in parts of the brain that are involved in compensation.

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