

Towards an explicit account of implicit learning

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Purpose of review

The human brain supports acquisition mechanisms that can extract structural regularities implicitly from experience without the induction of an explicit model. Reber defined the process by which an individual comes to respond appropriately to the statistical structure of the input ensemble as implicit learning. He argued that the capacity to generalize to new input is based on the acquisition of abstract representations that reflect underlying structural regularities in the acquisition input. We focus this review of the implicit learning literature on studies published during 2004 and 2005. We will not review studies of repetition priming ('implicit memory'). Instead we focus on two commonly used experimental paradigms: the serial reaction time task and artificial grammar learning. Previous comprehensive reviews can be found in Seger's 1994 article and the *Handbook of Implicit Learning*.

Recent findings

Emerging themes include the interaction between implicit and explicit processes, the role of the medial temporal lobe, developmental aspects of implicit learning, age-dependence, the role of sleep and consolidation.

Summary

The attempts to characterize the interaction between implicit and explicit learning are promising although not well understood. The same can be said about the role of sleep and consolidation. Despite the fact that lesion studies have relatively consistently suggested that the medial temporal lobe memory system is not necessary for implicit learning, a number of functional magnetic resonance studies have reported medial temporal lobe activation in implicit learning. This issue merits further research. Finally, the clinical relevance of implicit learning remains to be determined.

Keywords

artificial grammar learning, basal ganglia, functional neuroimaging, implicit learning, prefrontal cortex, serial reaction time task

Abbreviations

ACS	associative chunk strength
AGL	artificial grammar learning
FMRI	functional magnetic resonance imaging
MTL	medial temporal lobe
REM	rapid eye movement
SRT	serial reaction time

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Introduction

Implicit acquisition of knowledge about structured patterns embedded in stimuli can occur as an unintentional consequence of human experience. This phenomenon can be found in, for example, the sensorimotor domain, language, and music [1]. Seger [2], following Reber [3–5], suggested four characteristics for the phenomenon of implicit learning: limited explicit accessibility to the acquired knowledge (i.e. subjects typically cannot provide sufficient, in many cases, any explicit account of what they have learnt) the nature of the knowledge acquired is more complex than simple associations or based on simple exemplar-specific frequency counts; implicit learning does not involve explicit hypothesis testing but is an incidental (automatic) consequence of the type and amount of processing performed on the stimuli; and implicit learning does not rely on declarative memory mechanisms that engage the medial temporal lobe (MTL) memory system. Thus, to characterize implicit learning it is necessary to address issues related to the nature of the acquisition process (e.g. implicit versus explicit, automatic versus controlled, incidental versus intentional), the nature of the acquired knowledge and its representation (e.g. implicit versus explicit access, abstract versus concrete, structural versus surface-based, complex versus simple), and to characterize their functional role (e.g. implicit versus explicit strategies, automatic versus controlled processing). From a cognitive neuroscience perspective it is also of interest to characterize the neural infrastructure sub-serving these aspects of implicit learning and how the knowledge is put to use.

The serial reaction time task

Implicit learning is typically investigated with three different stimulus structures (patterns, sequences, or functions) and three different response modalities (conceptual fluency, efficiency, or prediction and control) [1,2]. Besides artificial grammar learning (AGL), one of the most intensely investigated implicit learning

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paradigms is the serial reaction time (SRT) task [6], in which implicit learning is inferred from faster reaction times in responding to reoccurring versus, for example, random sequences, while the participants typically report no or little awareness of reoccurring sequences. There are several proposals for how knowledge of sequence structure is acquired, including the acquisition of stimulus–stimulus, stimulus–response, response–response associations, or perhaps more abstract representations [1]. The learning of sequences with a fixed order can be viewed as a special case of acquiring knowledge about more general structural regularities or temporal contingencies in stimuli. These regularities can be deterministic, probabilistic, or non-deterministic as in the case of AGL.

Previous work suggests that implicit motor sequence learning is sensitive to the statistical structure of sequences. Lungu and colleagues [7•] investigated the effect of probabilistic patterns at the perceptual, stimulus–response, and execution levels, with the aim of identifying mechanisms by which these regularities are acquired. Their results suggest that both absolute frequencies and transitional probabilities are important, that these characteristics might be detected in different temporal order depending on the statistical properties of the stimuli, and they argued that different neural circuits are involved in detecting absolute frequencies and transitional probabilities. In addition to effector-independent learning, and consistent with the notion of parallel acquisition networks, Verwey and Clegg [8•] provided evidence for implicit effector (i.e. hand execution) dependent learning after extensive practice in an effector transfer SRT task (transfer generally refers to the transfer of knowledge acquired in one response modality to another response modality). These findings suggest that a hardwired and slowly adaptable local network might process effector specific information in addition to a more flexible global (i.e. interhemispheric) processing network.

It is likely that systems supporting both implicit and explicit learning can be engaged, and may perhaps also interact, during acquisition. Tubau and colleagues [9] provided evidence suggesting that relevant stimulus dimensions (location/symbol) engage different sequence learning mechanisms in the formation of internal representations and argued that a response–control shift (i.e. from stimulus–control to internal representational control) correlate with the emergence of explicit knowledge in the symbol condition. Wilkinson and Shanks [10] used a process dissociation procedure to separate automatic from intentional forms of processing [11] and argued that sequence knowledge can be brought under intentional control. Reinterpreting previous results [12], based on data from their inclusion–exclusion paradigm, they argued that participants can express (include) as well

as avoid to express (exclude) acquired sequence knowledge, which they suggest is consistent with the idea that information acquired during sequence learning is explicit in nature.

Recent studies suggest an age-dependent capacity to acquire higher-order regularities in the SRT task. Both Howard and colleagues [13•] and Dennis [14•] investigated this in young and older subjects. The former showed that second-order structure (i.e. the correct move depends on the previous two) could be acquired by both age groups (young more than old), while only the young group acquired third-order structure in an alternating SRT task (i.e. interleaved structured and random sequences). Similarly, Dennis [14•] demonstrated first and second-order deterministic sequence acquisition in both groups, while only young adults acquired sequences with second-order probabilistic structure. In another alternating SRT study, Negash [15] showed greater trial-type effects in young than in older patients. In a generation task (i.e. self-generated sequences) the young made more expectancy-based errors than the older group, suggesting greater implicit pattern knowledge. In a SRT study by Thomas and colleagues [16•], adults outperformed children (7–11 years; larger and more rapid learning effect). The functional magnetic resonance imaging (fMRI) results showed a significant overlap in the neural systems recruited by adults and children (including extrastriate, superior temporal/insula, basal ganglia, middle frontal, and anterior cingulate regions). The right caudate activity correlated with behavioral measures of implicit learning for both age groups, while learning-related developmental differences were observed in the right MTL (adults, sequence greater than random; children, random greater than sequence). Thomas and colleagues [16•] argued against the idea of developmental invariance in implicit learning and suggested that development in the implicit and explicit learning systems take place in parallel.

It is well-established that skill improvements not only occur during practice but also during off-line periods (i.e. between practice sessions), a so-called consolidation effect [17–19]. However, the contribution of rapid eye movement (REM) and non-REM sleep in consolidation of implicitly acquired sequence knowledge is still not well understood. Robertson and colleagues [20•] showed a sleep-dependent dissociation for implicit and explicit sequence learning; off-line improvement was sleep-dependent for explicit sequence learning and correlated with non-REM sleep, while off-line improvements in implicit learning seemed to be sleep-independent and only to depend on the time interval between practice sessions. Cajochen and colleagues [21] showed that the acquisition of different sequence structures improved after controlled sleep with multiple naps versus sleep

deprivation, in particular with naps that followed the circadian REM-peak.

Functional neuroimaging and lesion studies

FMRI and lesion studies implicate several cortical and subcortical structures in the SRT task [22–25], including motor regions, parietal regions, the basal ganglia, and the cerebellum. Implicit learning of the SRT task appears to be independent of the MTL memory system including the hippocampus [26], although a recent study [27] suggested that the MTL may be involved in both implicit and explicit learning of visuomotor sequences. Similarly, in a FMRI study of the number reduction task with performance feedback, Rose and colleagues [28] argued that the MTL plays a role in implicit acquisition of complex as opposed to simple relations (i.e. digit-strings with or without response–sequence mirror symmetry). This and several other studies, also using performance feedback, have reported MTL activation during learning of material generated from artificial grammars/languages [29–31]. In a recent study of the weather prediction task (a category learning task in which good/bad weather is probabilistically determined by card sequences), MTL activity was associated with receiving positive feedback but not with correct classification [32], suggesting that the MTL might be involved in associative feedback prediction, perhaps based on sequence recognition at some level. Results from an important case study of a densely amnesic patient with bilateral MTL lesions [33••] indicate that this region has a limited role in implicit learning of recurrent sequences, both in the SRT and Hebb's supra-span learning tasks (subjects echo digit strings in a series in which every third string is identical; learning is quantified in terms of increased accuracy on repeated strings compared with non-repeated). These findings are consistent with previous work on implicit sequence learning [34,35] and AGL [36] in amnesic patients as well as a recent rat model of the SRT task [37•]. Similarly, using a computer version of the radial-arm maze [38], Hopkins and colleagues [39•] found that amnesic subjects with selective MTL (hypoxic) lesions learned procedural sequences to the same degree as controls when compared with random sequences. In contrast, the controls performed significantly better than the amnesic patients on declarative sequences.

Whereas MTL lesions typically impair explicit but not implicit learning and memory, cases of implicit impairment and explicit sparing following basal ganglia lesions have been less consistent. It has been suggested that implicit and explicit sequence learning can proceed concurrently without interference [40], although explicit processing can interfere with implicit learning [41], suggesting that explicit and implicit processes can interact during learning. Aizenstein and colleagues [42•] found support for a multiple systems view on implicit

and explicit learning, which generate complementary representations. Decreased cortical activation was observed during processing of implicitly acquired patterns, while explicitly acquired patterns were associated with increased activation. Interestingly, they observed striatal activation in both conditions. They argued that this might be due to task-overlap (i.e. an implicit component in the explicit condition) or that both explicit and implicit learning involve processes supported by the striatum. In another study of standard and alternating SRT tasks, Fletcher and colleagues [43•] investigated the interaction between implicit and explicit learning. The results suggested right prefrontal, caudate nucleus, thalamus, and MTL engagement during sequence learning. The right prefrontal engagement seemed to be related to the explicit acquisition of alternating sequence structure. They suggested that explicit attempts to learn the alternating sequence reduced implicit learning and behavioral data indicated that the reduction in implicit acquisition was related to the suppression of learning itself rather than the expression of acquired knowledge. While they observed a negative fronto-thalamic interaction irrespective of task instruction with the standard SRT task, they observed a positive correlation between the right prefrontal region and the left thalamus in the explicit compared with the implicit alternating SRT condition. Finally, Kincses and colleagues [44•] report that transcranial direct current stimulation of the left prefrontal cortex, which probably increases neural excitability, improved implicit probabilistic classification.

The role of the subcortical structures

Implicit motor learning as indexed by the SRT task has been shown to be impaired in Parkinson patients and most convincingly for sequences that require the acquisition of second-order information. Smith and McDowall [45••] showed impairment on both first and second-order sequences in a verbal version of the SRT task with reduced motor demands in Parkinson patients. Using dual-task conditions to reduce influence of attention and strategic learning, Kelly and colleagues [46•] showed that both Parkinson patients and controls acquired sequences including both first and second-order information, while neither group acquired sequences including only second-order. Kim and colleagues [47•] found no implicit learning in early stage Huntington patients. A direct comparison between groups (FMRI) suggested reduced activation of the bilateral middle frontal, and the left middle occipital and precuneus regions in the Huntington group. Another study of patients with basal ganglia lesions (stroke; focus in the putamen) suggests explicit instructions to disrupt acquisition (this was not the case in the controls) [48]. Boyd and Winstein [48] argued that the basal ganglia are important in determining the efficacy of explicit information for implicit motor sequence learning, related to the increased task demands

placed on working memory by explicit information. In a fMRI study, van der Graaf and colleagues [49[•]] investigated prolonged skill practice in a bimanual variant of the SRT task (simultaneous finger movements in response to randomly ordered pairs of visual stimuli). Extended practice resulted in a gradual reaction time decrease associated with the putamen, globus pallidus, and the posterior cingulate region. Decreased anterior cingulate and left occipito-temporal activations observed in parallel suggest attentional requirement reduction. They interpreted their findings as a shift from neocortical to basal ganglia involvement associated with learning the random order stimulus–response task.

Boyd and Winstein [50[•]] provided evidence for a cerebellar role in implicit motor learning in a study of individuals with unilateral cerebellar lesions (stroke) on an implicit motor learning task (sequence tracking). They suggested that the cerebellum supports the formation of predictive strategies for the timing of motor responses and that this function is not lateralized but that cerebellar output may affect the formation of an internal model for timing movements in both extremities. Moreover, Torriero and colleagues [51[•]] showed that repetitive transcranial magnetic stimulation of the lateral cerebellum interferes with the acquisition of SRT task sequence knowledge and provided some evidence for hemispheric cerebellar differences with respect to the expression of learning.

Representation of sequential structure can occur with respect to the order of perceptual events or the order in which actions are linked. Bischoff-Grethe and colleagues [52] showed with event-related fMRI that transfer type (motor versus perceptual) interacted with sequence retrieval (sequencing versus rest) which revealed significantly greater activation in the bilateral supplementary and cingulate motor areas, ventral premotor cortex, left caudate, and inferior parietal lobule for participants in the motor group, suggesting successful sequence retrieval at the response level. Based on these results, Lungu and colleagues [7^{••}] suggested that cortical brain regions including the prefrontal and motor regions encode the transitions from one element to the next early in learning, while the basal ganglia encode the full sequence structure toward the end of learning.

Artificial grammar learning

Previous work on AGL suggests that participants implicitly acquire both rule-based and exemplar-specific knowledge. In the typical AGL experiment, participants process (e.g. in a short-term memory task) a sample of grammatical strings during the acquisition phase and are subsequently informed that the strings were generated by a complex set of rules after which new strings are classified as grammatical or non-grammatical on the

basis of the immediate intuition ('guessing'). Participants typically perform reliably above chance with little, if any, explicit knowledge about their classification capacity.

The results of Chang and Knowlton [53^{••}] showed that the sensitivity to grammaticality status was not affected by a change in low-level visual features (font/case), while this change reduced the sensitivity to associative chunk strength (ACS) (i.e. the similarity of the classification items to the acquisition set in terms of two and three letter substring frequencies). The addition of a secondary task (articulatory suppression) during the acquisition phase eliminated font sensitivity and reduced the contribution of ACS to the classification performance. Consistent with fMRI data, showing reduced activation levels for high versus low ACS items in early visual regions [54[•]], some aspects of classification performance might be related to perceptual fluency (e.g. repetition priming), since changes in surface features reduced the ACS sensitivity. In an event-related fMRI study, using a balanced chunk strength design, Lieberman and colleagues [54[•]] reported several brain regions that may contribute to AGL classification. The main findings suggested that the caudate nucleus was more active for grammatical versus non-grammatical items, while the MTL seemed to be more active for high versus low ACS. Moreover, they reported some evidence for a negative correlation between the caudate and hippocampal activations, which they interpreted as suggesting a competitive relationship between the two regions. However, the observation of a negative correlation does not necessarily imply a competitive relationship and there is also some evidence suggesting that the MTL and the caudate nucleus can interact cooperatively [55].

In four AGL experiments, Zizak and Reber [56^{••}] examined the links between the classic and structural mere exposure effects (i.e. the preference of previously encountered to novel items and the acquisition of syntactic/structural regularities by being exposed to stimuli, resulting in a positive correlation between preference and grammaticality status on new items, respectively). In these experiments, subjects either classified stimuli based on grammaticality or rated them in terms of likeability. The grammar was instantiated with familiar and unfamiliar symbols, and participants showed standard AGL effects in all cases. However, whether the two exposure effects emerged was dependent on symbol familiarity (high familiarity produced the structural mere exposure effect; moderate familiarity produced only the classic mere exposure effect; unfamiliar symbols produced neither exposure effect). In another series of behavioral experiments, Domangue and colleagues [57] argued that learners can use at least two types of knowledge: an explicit model or instance memories. The subject performance was characterized in terms of

response times and accuracy with respect to their ability to generate letter sequences. The acquisition conditions were experimentally controlled in order to manipulate the availability of the two types of knowledge. The memory-based condition yielded rapid response times but less accuracy compared with the model-based acquisition condition.

A complementary perspective on AGL, which recently has received some attention, views this as a model for investigating certain aspects of language acquisition [58,59,60^{*}] as well as exploring differences between human and animal learning relevant to the faculty of language [61]. Already Reber [1] proposed implicit learning as intrinsic to natural language acquisition. In an event-related fMRI study, Petersson and colleagues [60^{*}] investigated the role of Broca's region in grammaticality classification, after implicit acquisition. The results suggested that Broca's region is specifically activated by artificial syntactic violations, consistent with similar observations with respect to natural language. In a follow-up study, using repeated acquisition sessions, serial string presentation, and a balanced chunk strength design, Forkstam and colleagues [62] observed that Broca's region was the only frontal region sensitive to artificial syntactic violations and not sensitive to ACS (C. Forkstam *et al.*, in preparation). In addition, a significant cortico-striatal processing network, including frontal, cingulate, inferior parietal, and middle occipital/occipito-temporal regions as well as the caudate nucleus, was observed.

In a study of implicit acquisition of acoustic regularities (transition probabilities between timbres), Tillmann and McAdams [63] extend previous implicit learning results to the domain of complex nonverbal auditory material. Their results suggest that listeners become sensitive to statistical regularities independent of acoustical surface characteristics in the stimulus material. A recent study [64] showed that readers are able to acquire an artificial script both with explicit and implicit acquisition instructions. In a follow-up study, Bitan and Karni [65^{*}] provided data suggesting that letter decoding can evolve from implicit training on whole-word recognition and that the acquired knowledge was independent of explicit letter knowledge (measured by declarative recognition). They concluded that both implicit (procedural) and explicit (declarative) knowledge contributed to letter decoding and word-specific recognition, suggesting the dependency on explicit knowledge as related to the possibility that both routines become proceduralized with practice.

Conclusion

A number of emerging themes can be discerned in the recent study of implicit learning. These include the

interaction between implicit and explicit processes, the role of the MTL, developmental aspects of implicit learning, age-dependence, the role of sleep and consolidation. The attempts to characterize the interaction between implicit and explicit learning are promising although the nature of this interaction is not well understood. The same can be said about the role of REM/non-REM-sleep and consolidation in implicit learning. Despite the fact that lesion studies have relatively consistently suggested that the MTL memory system is not necessary for implicit learning, a number of fMRI studies have reported MTL activation in various implicit learning paradigms. The role of the MTL in these activation studies is unclear and needs further investigation. At least two fMRI studies of AGL have related the MTL activity to the recognition of superficial substring features (i.e. ACS). In addition, and confirming previous results, a number of lesion studies suggest that the basal ganglia play an important role in implicit learning, while the MTL generally appears to have a limited role in implicit acquisition and performance. One possibility, however, is that the MTL might have a role in acquiring long-distance dependencies. Finally, the clinical relevance of implicit learning remains to be determined, for example, whether and to what degree implicit learning paradigms may serve as sensitive predictors of therapeutic outcome in the treatment of diseases affecting in particular the basal ganglia.

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