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Understanding the Neural Bases of Implicit and Statistical Learning

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Abstract

Both implicit learning and statistical learning focus on the ability of learners to pick up on patterns in the environment. It has been suggested that these two lines of research may be combined into a single construct of "implicit statistical learning." However, by comparing the neural processes that give rise to implicit versus statistical learning, we may determine the extent to which these two learning paradigms do indeed describe the same core mechanisms. In this review, we describe current knowledge about neural mechanisms underlying both implicit learning and statistical learning, highlighting converging findings between these two literatures. A common thread across all paradigms is that learning is supported by interactions between the declarative and nondeclarative memory systems of the brain. We conclude by discussing several outstanding research questions and future directions for each of these two research fields. Moving forward, we suggest that the two literatures may interface by defining learning according to experimental paradigm, with "implicit learning" reserved as a specific term to denote learning without awareness, which may potentially occur across all paradigms. By continuing to align these two strands of research, we will be in a better position to characterize the neural bases of both implicit and statistical learning, ultimately improving our understanding of core mechanisms that underlie a wide variety of human cognitive abilities.

Keywords: Implicit learning; Statistical learning; Neuroimaging; fMRI; EEG; Neuroscience; Neuropsychology; Neural basis

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1. Introduction

The ability to detect patterns in the environment is central to many aspects of human cognition, ranging from perception to language, to decision-making, to the enjoyment of avant-garde music. Understanding this ability has been the focus of two traditionally distinct lines of research, centered on "implicit learning" (Reber, 1967) and "statistical learning" (Saffran, Aslin, & Newport, 1996). *Implicit learning* is defined as "the capacity to learn without awareness of the products of learning" (Frensch & Runger, 2003, p. 14). In contrast, *statistical learning* is more broadly defined as the ability to extract the statistical properties of sensory input across time or space (e.g., Frost, Armstrong, Siegelman, & Christiansen, 2015; Schapiro & Turk-Browne, 2015; Siegelman, Bogaerts, & Frost, 2017). Although these two lines of research use different tasks and procedures, they also share many commonalities and may in fact encapsulate the same underlying memory phenomena, as has been previously discussed (Christiansen, 2018; Perruchet & Pacton, 2006). Both implicit learning and statistical learning involve the extraction of structure from input and are generally thought to occur incidentally, through exposure to positive examples, without instruction, and without intention to learn. Both types of learning also then influence behavior in similar ways, for example, by making it easier to hear phoneme or word boundaries (statistical learning) or produce practiced motor sequences (implicit sequence learning). It has recently been suggested that these two literatures may be united under a single framework of "implicit statistical learning" (e.g., Rebuschat, 2015).

At this key juncture of increasing crosstalk and interaction between these two lines of research, working toward a better understanding of the neural bases of these learning phenomena is critical for continued progress in both these fields. By comparing the neural processes that give rise to implicit versus statistical learning, we may determine the extent to which these two learning paradigms do indeed describe the same core mechanisms. Deepening our understanding of the neural mechanisms of implicit and statistical learning will also continue to provide key insights into both these learning phenomena at a theoretical level, providing biological constraints to narrow the space of possible models that may account for observed learning behavior. For example, past research has shown that over the course of a typical paradigm, learning may occur in different ways, mediated by different neural memory systems (e.g., Poldrack et al., 2001, cf. Reber, 2013). Neural evidence can thereby provide a more accurate, nuanced view of how qualitatively different mechanisms underlying learning may wax and wane over time. Finally and more generally, neural measures can often provide a more sensitive index of processing than behavioral data alone and allow for the investigation of populations in which a behavioral response may be difficult to acquire (e.g., infants, certain groups of patients). By obviating the need for behavioral responses, data from neuroscience can enable us to address a wider variety of research questions. In sum, articulating the neural contributions underlying implicit and statistical learning is critical to reaching a deeper understanding of these learning mechanisms and provides a view of these capacities that could not be achieved by considering behavioral data alone.

With these goals in mind, this article reviews what we currently know about how the brain accomplishes implicit learning and statistical learning tasks. We first provide a brief primer on the memory systems of the brain. We then outline the concepts, research foci, and experimental paradigms that have been used in the two fields of implicit learning and statistical learning. Next, we review findings that shed light on how learning occurs at the neural level in these different paradigms. While we describe neuroscience studies on "implicit learning" and "statistical learning" in separate sections, this distinction is designed to reflect the separate historical trajectories and different paradigms used by each field, rather than to necessarily argue for a strong delineation between these two constructs at a mechanistic level. We conclude by considering key commonalities in the neural bases underlying learning among these different paradigms and possible future research directions to drive continued progress in both fields.

1.1. Memory systems of the brain

All types of learning, including implicit learning and statistical learning, can be understood in terms of the underlying contributions made by the two basic memory systems of the brain. Although memory performance may be mediated predominantly by one memory system alone, often performance is a function of interactions between two. Declarative memory refers to the recall and recognition of facts and events and depends on the medial temporal lobe (MTL) and various cortical regions, particularly the prefrontal cortex and the parietal lobes (Gabrieli, 1998; Scoville & Milner, 1957; Squire, 2004; Squire & Zola, 1996). The MTL consists of the hippocampus and adjacent perirhinal, entorhinal, and parahippocampal cortices (Squire, Stark, & Clark, 2004). In contrast, facilitated processing that occurs independently of recognition or recall is referred to as *nondeclarative memory* (Squire & Zola, 1996) and does not require the MTL system. Nondeclarative learning capacities are heterogenous and include skills, habits, procedures, priming, and simple types of memory like habituation and sensitization, and as such do not rely on a single, coherent memory system (Reber, 2013). Rather, nondeclarative memory reflects an accumulation of changes that take place directly within the neural circuits that were activated during the initial learning process, in processing areas such as the basal ganglia (which contains the striatum, which in turn contains the caudate and putamen, among other structures), cerebellum, and neocortex (e.g., Eichenbaum & Cohen, 2001; Gabrieli, 1998; McClelland, McNaughton, & O'Reilly, 1995; Reber, 2013; Squire, 2004; Squire & Zola, 1996). For example, perceptual repetition priming—which refers to facilitation in processing a repeated stimulus—is driven by changes in sensory cortical areas that are directly involved in initial perception (Squire & Zola, 1996). The lack of hippocampal involvement, which allows for the flexible relational storage of information (Eichenbaum & Cohen, 2001), may explain why perceptual priming effects are often found to be highly stimulus specific.

Seminal evidence for the existence of these two separate memory systems came from Scoville and Milner's (1957) observations of a hippocampal amnesic patient known as H.M. Following bilateral temporal lobe resection for intractable epilepsy, H.M. showed complete loss of declarative memory for events subsequent to his surgery, together with

partial retrograde amnesia for 3 years leading up to his operation. Despite this dramatic impairment in his ability to form memories for new episodes and facts, H.M. showed preserved learning on other memory tests, such as mirror drawing and the Tower of Hanoi puzzle (Cohen, Eichenbaum, Deacedo, & Corkin, 1985; Corkin, 1968; Milner, Corkin, & Teuber, 1968). Subsequent research substantiated these early observations, demonstrating that amnesic patients can achieve normal performance on many other memory tasks, such as artificial grammar learning, prototype learning, probabilistic category learning, perceptuomotor skill learning, and perceptual priming (e.g., Cohen & Squire, 1980; Goshen-Gottstein, Moscovitch, & Melo, 2000; Graf & Schacter, 1985; Keane et al., 1997; Knowlton & Squire, 1993, 1994, 1996; Nissen & Bullemer, 1987; Reber & Squire, 1994, 1998). These types of learning do not require a normally functioning hippocampus and came to be known collectively as nondeclarative memory (Squire & Zola, 1996), as performance on these tasks demonstrates memory storage while not requiring the conscious retrieval of any knowledge. Thus, declarative and nondeclarative memory can be dissociated on the basis of both conscious awareness and reliance on the MTL system, although there is not a perfect one-to-one correspondence between awareness and MTL dependence (Hannula & Greene, 2012; Henke, 2010).

1.2. Competition between memory systems

As we will see, a common theme that emerges across implicit learning and statistical learning paradigms is that there is frequently interaction or competition between the declarative and nondeclarative memory systems of the brain. This is particularly evident in implicit learning research, which, relative to the statistical learning literature, has traditionally placed a much stronger emphasis on characterizing the neural basis of learning. Even in paradigms that have been specifically designed to isolate "implicit learning" per se, healthy learners completing these tasks may show behavioral evidence of having acquired both declarative and nondeclarative memory (e.g., Perruchet, Gallego, & Savy, 1990; Perruchet & Pacteau, 1990; Servan-Schreiber & Anderson, 1990). The finding that declarative and nondeclarative memory systems are often both active during learning, and may compete with one another, also appears across findings from the statistical learning literature. Thus, investigating *interactions* between implicit and explicit memory, rather than how each system functions in isolation, is critical to understanding how humans actually learn.

Equipped with a basic understanding of the two dissociable memory systems of the brain, we now turn our attention to reviewing the conceptual definitions, research foci, and experimental paradigms used in the two parallel literatures of implicit learning and statistical learning.

1.3. Overview of implicit learning and statistical learning fields: Research foci and experimental paradigms

A strong focus of implicit learning studies is on the nature of the representations acquired during learning (i.e., whether conscious or unconscious). Paradigms used to

study implicit learning in a laboratory setting include the artificial grammar learning task (AGL; Reber, 1967), the serial reaction time task (SRTT; Nissen & Bullemer, 1987), and the weather prediction task (Knowlton, Squire, & Gluck, 1994). Learning in all these tasks is typically measured indirectly, without making direct reference to prior studied items, and the knowledge supporting performance on these tasks has generally been assumed to be unconscious (Reber, 1989).

For example, the AGL task—the hallmark paradigm of implicit learning research (Reber, 1967)—requires participants to memorize strings of letters generated by a finite-state artificial grammar. After exposure to numerous letter strings, participants are told that the strings were based on specific rules, and then asked to categorize new letter strings as either grammatical or ungrammatical. Despite having little verbalizable knowledge about the underlying rules, participants are typically able to categorize new strings at above-chance levels (Reber, 1967, 1976).

Similarly, in the SRTT, learning can occur in the absence of awareness of the underlying sequence (Destrebecqz & Cleeremans, 2001). In the canonical version of this task, participants respond to sequential visual cues that appear in one of four locations by pressing one of four corresponding response buttons. After each response, the next cue appears in a new location after a brief delay. Unbeknownst to participants, there are both sequential trials, which follow a repeating sequence, and random trials, in which the visual cues no longer follow a repeating pattern. As participants learn the hidden pattern, their response time to the repeating cues gradually decreases over and above the general response time reduction that occurs to randomly ordered cues as a function of task practice effects.

Another standard implicit learning task is the weather prediction task (Knowlton et al., 1994). This task involves learning of associations between combinations of stimuli and outcomes and is also generally assumed to occur without requiring the involvement of the declarative memory system. The stimuli in this task consist of a set of cards. Each card contains a unique geometric pattern and is associated with one of two possible outcomes (sun or rain) with a fixed probability. On each trial, participants are presented up to four cards and asked to predict the weather outcome. The actual weather outcome is probabilistically determined by the individual cards, whereby each card is a partially accurate predictor of the weather. With each trial, learners receive feedback and become increasingly accurate at predicting the weather. This improvement can occur even though learners may have little explicit knowledge of the information they are using to improve their judgments.

In contrast to the field of implicit learning, statistical learning researchers have generally not focused on the nature of the representations acquired during learning (i.e., whether conscious or unconscious), but rather on the finding that learning appears to occur incidentally—without instruction to detect patterns. Statistical learning is most commonly studied within the context of speech segmentation, using the artificial speech segmentation paradigm (Saffran, Newport, & Aslin, 1996; Saffran, Newport, Aslin, Tunick, & Barrueco, 1997; Saffran et al., 1996). In this task, learners are exposed to a continuous speech stream made up of repeating three-syllable nonsense "words" (e.g.,

bupada + *babupu* + *tutibu* → *bupadababupututibu*. . .; Saffran et al., 1996, 1996, 1997). Learners must become sensitive to the co-occurrence statistics between neighboring syllables—which are higher within words than across word boundaries—in order to discover the underlying "word" units. After exposure, learning in adult participants is then typically tested using a forced-choice recognition measure, requiring the discrimination of words from the exposure steam (e.g., *bupada*) and nonword foil items (e.g., *pubati*). If performance on this forced-choice measure is above chance, statistical learning is inferred. Reaction times on a speeded target detection task have also been used, which measure the effects of learning on online processing (e.g., Batterink, Reber, Neville, & Paller, 2015; Batterink, Reber, & Paller, 2015; Franco, Eberlen, Destrebecqz, Cleeremans, & Bertels, 2015; Kim, Seitz, Feenstra, & Shams, 2009; Turk-Browne, Scholl, Chun, & Johnson, 2009). Statistical learning is also studied within the visual domain, using an analogous paradigm in which participants view a sequence of images or abstract shapes organized into repeating triplets (e.g., Fiser & Aslin, 2002; Turk-Browne, Jungé, & Scholl, 2005).

In sum, the paradigms used to study implicit learning and statistical learning appear to focus on the same core mechanism—the detection of patterns governing elements in complex stimulus domains (cf. Reber, in Rebuschat, 2015). Although these tasks differ in notable ways—including demands on perceptual and motor processing, use of auditory versus visual stimuli, and engagement of linguistic versus nonlinguistic processing—"learning" in all cases is defined as the participants' ability to extract regularities in input they are exposed to, without any instruction to do so. The overall similarities between the paradigms raise the possibility that similar neural mechanisms and substrates may be involved. In the next section, we review neuroimaging studies of healthy learners in order to characterize the specific brain areas activated in these different learning paradigms, providing a valuable perspective on the extent to which these different paradigms in these two literatures reflect similar neural processes.

1.4. Implicit learning paradigms

1.4.1. Artificial grammar learning (AGL)

Neuroimaging studies have implicated a number of different regions in AGL, including prefrontal cortical areas (most commonly left inferior frontal regions including BA 44/45), parietal areas, and the basal ganglia (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Petersson, Folia, & Hagoort, 2012; Petersson, Forkstam, & Ingvar, 2004; Skosnik, Gitelman, Parrish, Mesulam, & Reber, 2002). Different authors have focused on different neural regions when interpreting these widespread activation patterns. For example, activation of left inferior frontal gyrus or "Broca's area" has been interpreted as reflecting this region's role in linguistic processing, online sequence processing, and sequence learning (Forkstam et al., 2006; Petersson et al., 2004, 2012). Skosnik et al. (2002) found distinct neural correlates in posterior parietal areas for grammaticality judgments contrasted with letter

string recognition. This activity was interpreted as the letter strings becoming more word form like as learning proceeded.

Behavioral evidence in amnesic patients and controls suggests that performance on the AGL task can be supported by either exemplar-specific "chunk" knowledge that can in some cases be explicit (i.e., the bigrams and trigrams shared between the strings presented at training and at test) or by abstract grammatical rule knowledge (Knowlton & Squire, 1996). Neuroimaging evidence supports this notion of different explicit and implicit sources of knowledge on this task, and additionally suggests that these different sources of knowledge are supported by different neural substrates, with competitive interactions occurring between these memory systems. For example, Lieberman et al. (2004) found that test items with higher chunk strength elicited greater hippocampal activation relative to low-chunk-strength items. In contrast, processing of grammatical compared to ungrammatical strings (controlling for chunk strength) was associated with increased caudate activation. Furthermore, caudate and hippocampal activations were strongly negatively correlated ($r = -0.87$), suggesting a competitive relationship between basal ganglia and medial temporal areas. Petersson et al. (2012) also reported strong MTL deactivation, including the hippocampus, during classification of grammatical items. Again, this activation was dissociated from chunk strength. This finding converges with the negative correlation between hippocampal and caudate activation reported by Lieberman and colleagues, and further supports the idea that knowledge of chunk strength—mediated by the hippocampus—and knowledge of abstract grammar rules—mediated by the caudate—actively compete with one another during grammatical classification.

Although neuroimaging studies commonly find that the caudate is activated in AGL, patients with basal ganglia dysfunction due to Parkinson's disease or Huntington's disease show intact AGL performance (Knowlton et al., 1996; Meulemans, Peigneux, & Van der Linden, 1998; Reber & Squire, 1999; Witt, Nuhsman, & Deuschl, 2002). These findings suggest that the caudate is not critically involved in AGL. Nonetheless, one possibility is that the basal ganglia contribute to AGL in healthy participants, but that patients with impaired basal ganglia functioning may rely on their intact MTL memory system in order to achieve normal learning on this task (Moody, Bookheimer, Vanek, & Knowlton, 2004). Future studies will be needed in order to conclusively resolve this issue.

1.4.2. Serial reaction time task (SRTT)

In neuroimaging studies, learning of trained sequences relative to untrained sequences is associated with activation of the striatum as well as cortical areas related to motor planning (Daselaar, Rombouts, Veltman, Raaijmakers, & Jonker, 2003; Doyon et al., 1996; Grafton, Hazeltine, & Ivry, 1995; Hazeltine, Grafton, & Ivry, 1997; Rauch et al., 1995, 1997; Peigneux et al., 2000; Reiss et al., 2005; Seidler et al., 2005). In addition, early stages of exposure to the sequence are also often accompanied by hippocampal activation, which decreases gradually over the course of training (Albouy et al., 2008; Fletcher et al., 2005; Grafton et al., 1995; Rieckmann, Fischer, & Bäckman, 2010; Schendan, Searl, Melorse, & Stern, 2003). Learning success is positively related to activation in the striatum (Garraux et al., 2007; Peigneux et al., 2000; Rauch et al., 1997; Reiss

et al., 2005) and to deactivation in the MTL (Albouy et al., 2008; Rieckmann et al., 2010).

Two explanations have been proposed to account for the time course of involvement of the MTL in sequence learning (Rieckmann et al., 2010). One suggestion is that the MTL supports rapid initial acquisition of higher order associations in complex sequences (Doeller, Opitz, Krick, Mecklinger, & Reith, 2005; Fletcher et al., 2005; Schendan et al., 2003). This idea is supported by studies showing that the MTL seems to be especially recruited in complex versions of the SRTT, in which participants are forced to rely on second-order relationships (Curran, 1997; Schendan et al., 2003; Shanks, Channon, Wilkinson, & Curran, 2006). The MTL may be involved in making predictions about possible outcomes (Bornstein & Daw, 2012, 2013); as learning progresses, the associations between stimuli become more predictable, leading to concomitant decreases in MTL activation. An alternative explanation is that learning-related disengagement of the MTL is related to competition or functional suppression between the striatal and MTL memory systems, consistent with findings from other implicit learning tasks. According to this view, greater expertise is associated with increased involvement of the striatum and decreased reliance on the MTL system. This competition idea is supported by several studies showing that SRTT learning is enhanced when declarative memory function or top-down processing is disrupted (Brown & Robertson, 2007a,b; Galea et al., 2009; Nemeth, Janacsek, Polner, & Kovacs, 2013; Virag et al., 2015).

Recently, P. J. Reber and colleagues (Gobel, Parrish, & Reber, 2011; Sanchez, Gobel, & Reber, 2010; Sanchez & Reber, 2013) developed a modified version of the SRTT, the Serial Interception Sequence Learning (SISL) task. The SISL task may better encapsulate implicit learning compared to the standard SRTT, which is commonly accompanied by evidence of explicit knowledge in healthy participants (Reber & Squire, 1994, 1998; Willingham, Greeley, & Bardone, 1993). Although the SRTT requires participants to respond to the onset of stationary cues that appear at fixed intervals, the SISL task involves making responses at a much more rapid pace, which must be precisely timed to moving cues. The SISL task is more challenging and requires participants to continually engage in task performance, potentially leaving them with fewer resources to identify or memorize the repeating sequence. The idea that response speed makes learning more likely to be implicit is supported by the finding that decreasing the interval between the response and the next cue in the standard version of the SRTT selectively impairs explicit sequence learning (Destrebecqz & Cleeremans, 2001).

The SISL paradigm has been shown to produce robust implicit learning with low levels of conscious sequence knowledge even in healthy participants (Sanchez et al., 2010). In addition, providing participants with full explicit knowledge of the repeating sequence does not impact sequence learning, consistent with the idea that explicit knowledge does not normally contribute to performance on this task (Sanchez & P. J. Reber, 2013). Interestingly, while performance of known sequences in the SISL paradigm is associated with increased activity in the basal ganglia—pointing to the importance of this structure across sequence learning tasks—it does not modulate hippocampal activity (Gobel et al., 2011). As MTL activation is typically observed in the standard SRTT, this finding tentatively

suggests that competition between the basal ganglia and MTL systems may not occur during isolated implicit learning. It also raises the possibility that MTL activation during the standard SRTT may reflect the acquisition of parallel explicit knowledge of the sequence that does not actually contribute to implicit learning.

1.4.3. Probabilistic category learning

Neuroimaging studies have demonstrated activation of the basal ganglia, in particular the striatum, during probabilistic category learning (Aron et al., 2004; Moody et al., 2004; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Poldrack et al., 2001). In addition, activity was also observed in a broad network of prefrontal, parietal, and occipitotemporal cortical regions. Mirroring findings from other implicit learning tasks, neuroimaging studies of probabilistic category learning also consistently find a decrease in MTL activation versus baseline (Aron et al., 2004; Moody et al., 2004; Poldrack et al., 1999, 2001). This finding again suggests a competitive interaction between these two memory systems.

Particularly relevant to the competition idea is the study by Poldrack et al. (2001), who used fMRI to compare neural activation during probabilistic category learning under two different conditions. In the version designed to engage implicit memory (i.e., the typical version of the task), subjects learned on the basis of trial-by-trial feedback; in contrast, in a modified version of the task designed to engage explicit memory, subjects learned on the basis of category labels, without making a categorization decision. Relative to the standard task version, the "explicit" version resulted in reduced activation of the basal ganglia and increased activation of the MTL, indicating that engagement of these two memory systems is modulated by whether the task encourages use of implicit or explicit memory strategies. In addition, activity in the MTL correlated negatively with activity in the striatum across learners. Furthermore, MTL and striatum showed reciprocal changes over time; the MTL was initially active and the striatum inactive, but as learning progressed, the striatum quickly became activated while the MTL became deactivated. These findings suggest that the MTL plays a role in learning during early stages of training, but that the basal ganglia subsequently "take over" learning, leading to disengagement of the MTL. A similar pattern of results was found by Foerde, Knowlton, and Poldrack (2006), who compared probabilistic category learning under dual-task versus single-task conditions. Equivalent levels of learning were found under the two conditions, but distraction by a secondary task reduced the involvement of the MTL and increased the involvement of the striatum. These results again point to a competitive interaction between memory systems during probabilistic category learning, as has been shown for other implicit learning tasks.

1.4.4. Statistical learning paradigms

We will now turn our attention to what is known about the neural basis of statistical learning. In contrast to the implicit learning literature, understanding the neural bases of learning has not been a central focus of statistical learning research. In addition, the field

of statistical learning as a whole is younger, as can be seen readily by comparing the publication years for the two seminal papers of each field (Reber, 1967; Saffran, Aslin, et al., 1996; Saffran, Newport, et al., 1996). Thus, whereas there is a rich and decades-old literature on the neural mechanisms underlying implicit learning, parallel topics in the area of statistical learning have only recently come under investigation. Nonetheless, recent findings from statistical learning seem to converge with previous results from implicit learning, suggesting additional parallels between these two literatures.

A handful of neuroimaging studies have investigated the neural basis of this type of statistical learning, contrasting activation evoked by speech streams with repeating words with that evoked by random syllable streams (Cunillera et al., 2009; Karuza et al., 2013; McNealy, Mazziotta, & Dapretto, 2006). These studies have consistently found that statistical regularities produce enhanced activation of higher level auditory networks, in regions that have been previously implicated in auditory and/or linguistic processing, such as the left superior temporal gyrus and the left inferior frontal gyrus (Broca's area; BA 44/45), extending to premotor cortex (BA 6; McNealy et al., 2006; Cunillera et al., 2009; Karuza et al., 2013). In addition, activation of left IFG/ventral PMC correlates with behavioral performance on postexposure tests of statistical learning (Cunillera et al., 2009; Karuza et al., 2013).

Thus, statistical learning underlying speech segmentation seems to be at least partially supported by unimodal auditory cortical regions.

In the visual domain, at least one neuroimaging study has revealed analogous results to what has been found using the speech segmentation paradigm, showing that processing of visual statistical structure is associated with enhanced activation in high-level visual networks (Turk-Browne et al., 2009). Participants viewed sequences of abstract shapes, which were either organized into repeating triplets or randomly ordered. Compared to random blocks, blocks containing visual regularities yielded greater activation in category-specific visual regions, namely object-selective lateral occipital cortex and word-selective ventral occipitotemporal cortex.

Taken together, these results have led to the proposal that statistical learning is largely supported by modality-specific learning mechanisms (Frost et al., 2015). According to this view, local computations are performed in separate neural networks in different cortical areas (e.g., visual, auditory, and somatosensory), each of which operates on modality-specific representations and is governed by its own set of constraints. For example, because auditory information unfolds over time, the auditory cortex displays greater sensitivity to temporal information. In contrast, relationships between items in the visual domain can be processed simultaneously, and thus, the visual cortex displays enhanced sensitivity to spatial information but lower sensitivity to temporal information. This model of statistical learning is supported by behavioral evidence showing a lack of correlation within individuals across different types of statistical learning tasks (e.g., syllables versus geometric shapes; Siegelman & Frost, 2015). This idea of modality specificity also echoes what has been demonstrated for different types of implicit learning—namely, that implicit learning results from experience directly shaping neural circuits within specific sensory cortical areas (Reber, 2013).

Although there appear to be important modality-specific contributions to statistical learning, some neural regions may play a domain-general role. For example, while the left IFG (i.e., "Broca's area") has been previously implicated in statistical learning of structured speech as described previously (Cunillera et al., 2009; Karuza et al., 2013; McNealy et al., 2006), it may also contribute to other types of statistical learning. In the visual domain, activation of the left IFG was found to correlate with behavioral familiarity with shape triplets (Turk-Browne et al., 2009). In addition, in a nonlinguistic auditory statistical learning paradigm using tone stimuli, left inferior frontal cortex showed enhanced activation to structured tone sequences, but not to random sequences of tones (Abla & Okanoya, 2008). Although the left IFG appears to contain subregions that are truly language specific, other subregions within this general area may contribute to domain-general processes, such as the processing and integration of sequential information (Fedorenko, Duncan, & Kanwisher, 2012). Interestingly, processing of artificial grammar rules in the AGL paradigm is also associated with left IFG activation (Forkstam et al., 2006; Petersson et al., 2004, 2012), suggesting a shared neural basis for the processing of structure in AGL and statistical learning tasks.

Neuroimaging evidence also indicates that there are contributions to statistical learning from domain-general memory systems, notably the striatum and the MTL systems, just as has been found for diverse types of implicit learning tasks (e.g., Bischoff-Grethe, Martin, Mao, & Berns, 2001; Lieberman et al., 2004; Rauch et al., 1997; Seger & Cincotta, 2005). Striatal activation has been observed to statistical structure in both the auditory domain (Karuza et al., 2013; McNealy et al., 2006) and the visual domain (Turk-Browne et al., 2009). In this latter study, by excluding data from subjects who performed above chance on the familiarity test, the investigators focused on extracting neural correlates of implicit statistical learning. Caudate activation (but no hippocampal activation) was observed even in learners who exhibited no subsequent familiarity, suggesting that this region may contribute to implicit statistical learning, dissociable from explicit knowledge. In contrast, when all learners were included in the analysis, both caudate and hippocampal activation were observed. The involvement of the MTL in statistical learning is also supported by a finding by Schapiro, Kustner, and Turk-Browne (2012). By presenting participants with a continuous stream composed of hidden pairs of objects and applying pattern similarity analysis, these authors found that the representations of objects presented in pairs became more similar to one another after exposure compared to before exposure in the hippocampus and MTL cortex. The right hippocampus may be particularly important for making predictions about upcoming stimuli, as it shows increased activation to predictive stimuli compared to non-predictive stimuli (Turk-Browne, Scholl, Johnson, & Chun, 2010).

The observed activation of the MTL system during statistical learning raises the same question that has been central to the study of implicit learning: Does the MTL play a *necessary* role in statistical learning, or does activity in this region merely represent the acquisition of parallel (explicit) representations that do not centrally contribute to learning? Although a few studies have examined amnesic patients' performance on statistical learning tasks, this question cannot yet be answered conclusively. Schapiro, Gregory,

Landau, McCloskey, and Turk-Browne (2014) found that patient LSJ, who suffered complete bilateral hippocampal loss and broader MTL damage, showed widespread deficits in statistical learning across a range of visual and auditory stimuli (Schapiro et al., 2014). However, given that many normal, healthy participants also do not show above-chance performance on statistical learning tasks (e.g., Siegelman & Frost, 2015), it is difficult to unambiguously attribute patient LSJ's deficits to neurobiological impairment. Building on this work, Covington, Brown-Schmidt, and Duff (2018) studied a larger group of patients with MTL damage and reported that patients exhibit less learning overall compared to healthy controls. Nonetheless, these patients still exhibited above-chance learning, and their performance fell within the distribution of healthy participant performance. In addition, lesion size did not reliably predict performance. These results suggest that the hippocampus may contribute to statistical learning but is not strictly necessary for statistical learning to occur. Thus, the question of whether the MTL is necessary for statistical learning has not been conclusively resolved and awaits further investigation.

To summarize this small but growing literature on the neurobiological basis of statistical learning, there appear to be both modality-specific and domain-general neural mechanisms that contribute to learning. One class of findings indicates that statistical learning occurs within modality-specific sensory cortical areas, according to the stimuli presented during learning. For example, visual sequences activate higher level visual cortex, whereas word segmentation tasks activate higher level auditory areas. In addition, statistical learning also appears to be supported by domain-general memory systems that are involved regardless of stimulus modality. Both the striatum and MTL are activated to statistical structure across different modalities (audition and vision). This finding corresponds to what has been observed across many different types of implicit learning tasks —that multiple memory systems may be active under normal learning conditions in healthy learners, acquiring separate representations in parallel.

Using these findings as a point of departure, in the next section, we consider some outstanding questions and potential directions for future research on the neural bases of statistical learning and implicit learning. Many of the same methods, research questions, and conceptual approaches that have been productive in one field may be equally valuable when applied to the parallel research field (e.g., applying implicit learning concepts to statistical learning and vice versa).

2. Directions for future research

2.1. Statistical learning

2.1.1. Testing interactions between memory systems over the course of exposure

One important acknowledgment that has driven progress in the field of implicit learning is that implicit and explicit learning systems often operate in parallel in healthy learners, sometimes competing and sometimes interacting. In the domain of language learning, it has also been proposed that these two types of memories contribute and interact (e.g.,

Ullman, 2004, 2005). Given neuroimaging evidence demonstrating both hippocampal and striatal involvement in the same statistical learning task (e.g., Turk-Browne et al., 2009), interactions between these two different memory systems may also play a role in statistical learning generally, *with different neural systems engaged at different points in time throughout the learning process*. One possibility is that the hippocampus may contribute to statistical learning early during the exposure period, consistent with its role in making predictions about upcoming stimuli (Bornstein & Daw, 2012, 2013; Turk-Browne et al., 2010). As learning progresses, the striatum may become more involved, while the hippocampus becomes disengaged. Such a finding would echo results from different implicit learning tasks showing reciprocal engagement of these two memory systems over the course of learning (e.g., Albouy et al., 2008; Fletcher et al., 2005; Poldrack et al., 2001).

Future neuroimaging studies may address this idea by using more fine-grained measures to assess the time course of learning over the exposure period. To specifically target learning-related neural changes, time-course information could be combined with behavioral measures of learning collected over the exposure period, using approaches such as concurrent RT tasks (e.g., Batterink, 2017; Siegelman et al., 2017; Turk-Browne et al., 2010) or intermittent offline testing (Karuza et al., 2013). This sort of paradigm would allow for the assessment of whether reliance on one system over the other—across exposure or potentially even at different stages of exposure—predicts behavioral performance on tests of statistical learning. If positive evidence indicates that one memory system is optimally suited for extracting structure from the environment, a further step would be to test whether inhibiting the competing memory system enhances statistical learning, as has sometimes been found for different types of implicit learning tasks (e.g., Filoteo, Lauritzen, & Maddox, 2010; Foerde et al., 2006; Galea et al., 2009; Nemeth et al., 2013).

2.1.2. The role of the hippocampus in statistical learning

A related outstanding question with many parallels to the implicit learning literature is whether the hippocampus plays a necessary, causal role in statistical learning, or whether it merely acquires nonessential or redundant (explicit) knowledge in parallel. Yet a third possibility is that statistical learning may operate on declarative, MTL-dependent memory representations. Under this scenario, explicit memory traces would be initially acquired by the MTL system, with statistical learning mechanisms then operating on these representations to guide behavior (without necessarily requiring awareness).

As described previously, evidence from two prior studies suggests that patients with MTL damage on average perform more poorly on statistical learning tasks than healthy controls, including a case study failing to find above-chance performance (Covington et al., 2018; Schapiro et al., 2014). However, a potential limitation of these two studies is the use of only an offline recognition measure to assess learning. One possibility is that MTL patients show intact statistical learning when assessed through implicit measures, but they are impaired at tests involving explicit recognition, similar to dissociations that have been found for implicit learning (e.g., priming versus recognition; e.g., Keane et al., 1997; Goshen-Gottstein et al., 2000). To test this hypothesis, learning in these patients could be assessed using more implicit measures, such as RTs (Batterink & Paller, 2017;

Batterink et al., 2015, 2015; Siegelman et al., 2017), statistically induced chunking recall (Isbilen, McCauley, Kidd, & Christiansen, 2017), or EEG-based neural entrainment to the underlying structure (Batterink & Paller, 2017). The use of neural measures (e.g., EEG or fMRI) in these patients could also potentially reveal evidence of learning even in the absence of above-chance recognition performance (cf. Turk-Browne et al., 2009). In addition, neural measures would allow for direct comparisons of learning in patients and healthy controls, circumventing the potential confound of impaired retrieval and recognition processes in the patient group. Clarifying the role of the hippocampus in statistical learning would also provide important evidence on hippocampal computations, potentially contributing to the growing body of work demonstrating hippocampal involvement across a wide range of diverse tasks (e.g., Duff & Brown-Schmidt, 2017; Greene, Gross, Elsinger, & Rao, 2006, 2007; Rubin, Watson, Duff, & Cohen, 2014; Westerberg, Miller, Reber, Cohen, & Paller, 2011).

2.1.3. Understanding components of statistical learning

Evidence about the neural basis of statistical learning may also help to test current theoretical models and to better understand the substantial variability seen in statistical learning performance. As has been previously noted, individual performance on postexposure statistical learning tasks varies substantially, with at least one-third of a sample often failing to perform the task at above-chance levels (Frost et al., 2015; Siegelman & Frost, 2015). While statistical learning is often conceptualized as a single process, it in fact involves multiple dissociable neurocognitive components, and this individual variability in performance may be driven by differences in any number of these components.

This idea has been discussed previously in a number of different forms. For example, Frost et al. (2015) propose the individual variance in statistical learning performance can be split into two main sources: (1) ability to encode representations of individual elements in a stream, within the presentation modality and (2) ability to compute the distributional properties of the encoded representations (e.g., the transitional probabilities between syllables). Karuza and colleagues (2014) describe four essential components to statistical learning: (1) sensory input encoding, (2) pattern extraction, (3) model building, and (4) retrieval/recognition. Similarly, we have recently proposed that statistical learning in the context of speech segmentation can be dissociated into (1) "word identification," involving a transition from the perception and encoding of raw individual syllables to larger integrated words, and (2) subsequent memory storage and memory retrieval (Batterink & Paller, 2017). Regardless of how exactly these different processes are divided or described, logically they must all contribute to behavioral evidence of learning on postexposure tests. However, offline measures can only weigh in on whether that learning has (or has not) ultimately occurred, and they cannot dissociate these conceptually distinct components of learning.

In contrast, neural measures of learning have the potential to provide insight into the actual learning process itself, rather than merely the outcome of learning. Thus, these measures may allow us to empirically dissociate theoretically derived components of statistical learning and to identify their underlying neural mechanisms. For example, we

previously used an EEG-based measure of neural entrainment to track statistical learning online, *during* exposure. This measure also allowed us to separate the "word identification" component of statistical learning—that is, the perceptual binding of individual syllables into component words—from subsequent memory-related retrieval processes (Batterink & Paller, 2017). In future studies, these sorts of neural measures of online statistical learning could be synergistically combined with experimental manipulations designed to tease apart these different components of learning. As an illustration, Bogaerts, Siegelman, and Frost (2016) independently manipulated exposure duration and transitional probabilities to dissociate individual item encoding from higher order computations of distributional properties. These experimental manipulations impacted performance on an offline forced-choice recognition measure and may also impact neural signatures of learning in highly specific ways. For example, manipulations designed to target item encoding may modulate learning effects in sensory cortex, whereas manipulations that influence the computation of transitional probabilities may influence the neural signatures of learning in domain-general memory systems. Thus, understanding the neural basis of statistical learning may provide a powerful platform to tease apart different theoretical components of statistical learning.

2.1.4. Neural measures as sensitive indices of learning

Neural measures of statistical learning also hold great promise as tools to track learning in populations where behavioral responses may not be easily acquired. Using fMRI, Turk-Browne et al. (2009) found neural signatures of learning in the striatum even in observers who exhibited no subsequent explicit familiarity, suggesting that neural measures may provide more sensitive indices of learning than traditional behavioral measures. Online EEG-based neural entrainment (Batterink & Paller, 2017) could also potentially be used to track statistical learning without requiring a behavioral response. These types of measures could be used to assess statistical learning in different patient populations (e.g., hippocampal amnesia and Parkinson's disease), under different conditions of consciousness (e.g., sleep or anesthesia) and in different age groups (e.g., very young infants). By providing continuous data sampled over the exposure period, neural measures can also be used to track the time course of learning, rather than merely providing an assessment of the final outcome of learning.

2.2. Implicit learning

On the other side of the coin, insights from statistical learning research may also be applied to the field of implicit learning. Non-univariate neuroimaging methods such as representational similarity analysis (e.g., Schapiro et al., 2012, 2013) and functional connectivity analyses (Karuza et al., 2017) have recently been applied to understand statistical learning (2012), and they may be equally informative for understanding implicit learning. As previously described, using pattern similarity analyses, Schapiro et al. (2012) found that the representations of objects presented in pairs became more similar to one another in the hippocampus and MTL cortex after exposure to a structured visual stream.

A similar approach may be applied to implicit learning paradigms such as the AGL or weather prediction tasks to investigate whether similar MTL-mediated mechanisms may drive learning. For example, in the AGL task, letters or strings that occur together more frequently during training may come to be represented more similar to one another in the hippocampus, supporting a chunk-based model. An alternative (though not mutually exclusive) possibility is that grammatical sequences will be represented more similar to one another than ungrammatical sequences as a consequence of learning, reflecting abstract grammatical knowledge independent of chunk strength.

Other non-univariate neuroimaging methods such as functional connectivity analyses have also been used to explore neural changes associated with statistical learning. In a spatial statistical learning task, decreases in task-based connectivity were reported over the course of exposure to structured input, with greater decreases predicting better posttest performance (Karuza et al., 2017). Similar analyses could be applied to a variety of implicit learning paradigms to understand how changes in connectivity among different brain regions may support learning. Overall, taking advantage of continued advances in neuroimaging will provide additional insights into different learning mechanisms that drive performance in the various implicit learning tasks.

3. Conclusions

The neural events underlying implicit learning and statistical learning appear to share many commonalities. At the same time, these two fields have separate and distinct histories, and understanding these different trajectories and research approaches is critical to fostering synergy and continued progress in both areas. These separate research histories argue against the idea that these two terms may be combined under a single construct of "implicit statistical learning." Moving forward, we suggest that a reasonable approach to aligning these two strands of research is to discuss each type of learning by experimental paradigm, with an acknowledgment that learning across these different paradigms can often involve both declarative and nondeclarative memory systems in healthy learners. In this way, the term "implicit learning" may continue to be used to refer to learning "without awareness of the products of learning" (Frensch & Runger, 2003, p. 14), which may potentially emerge in any of these experimental paradigms, including the canonical triplet segmentation task typically used to study statistical learning as traditionally defined.

By taking advantage of what is currently known about the neural bases supporting learning in all of these related experimental paradigms, we may continue to make progress in these two historically separate fields of statistical learning and implicit learning. In particular, many decades of research have sought to uncover the neural mechanisms of implicit learning; however, in comparison, parallel research in the field of statistical learning is still in its infancy. To reach a better understanding of statistical learning, future research may help clarify issues such as how memory systems interact over the course of learning, and how the hippocampus may play a critical role. In addition, neural measures may yield valuable insight into theoretically dissociable components of

statistical learning, provide sensitive indices of learning to supplement behavioral measures, and track the time course of learning. By the same token, research using implicit learning paradigms may also benefit from recent advances in neuroimaging methods, which have already been successfully applied to shed light on statistical learning mechanisms. By continuing to align these two strands of learning research, we will be in a better position to characterize the neural systems that support the core human ability to acquire patterns in the environment, helping us to understand the neurocognitive mechanisms that underlie a wide variety of cognitive abilities.

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