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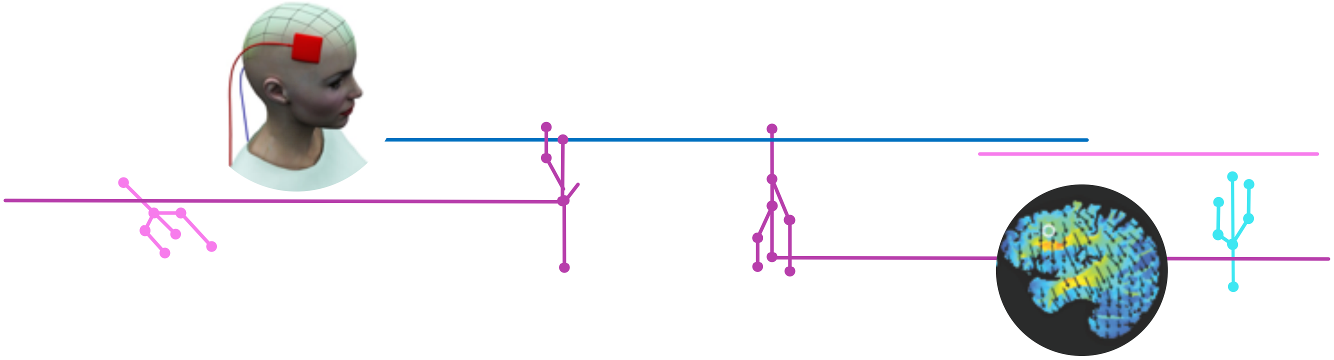

The Causal Neural Substrates of Statistical Learning

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Bachelor of Psychological Science (Hons 1)

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Abstract

Although humans often struggle to make rational decisions based on probability, there are types of information processing that appear highly sensitive to statistics. In fact, the human brain can extract information about complex statistical probabilities present in the environment through an automatic *statistical learning* process. Statistical learning is the primary way that human infants, with no developed frontal cortex or reasoing skills, can learn the complexities of language and grammar. As adults, statistical learning enables us to benefit from the many repetitive and predictable elements of our sensory environment, such as visual scenes or event sequences. Statistical knowledge is often implicit, but it can be used by the explicit system to facilitate other cognitive processes; such as decision-making, skill learning, and social capabilities. The reach of statistical learning across the cognitive landscape is broad, and this brings into question the nature of the neural substrates that govern this process. Neuroscientific research supports there being a critical role of the hippocampus, as it relates to long-term memory. But neuroimaging work suggests a role of higher-level cortical regions, within the frontal and parietal cortices. These areas are more commonly associated with explicit executive functions, and less so for implicit learning abilities. Recent advances in non-invasive brain stimulation allow is to directly control cortical brain acitvity in order to unearth causal relationships between the brain and behaviour. To date, there is little causal evidence regarding the neural substrates of statistical learning outside the hippocampus. In this thesis, I investigate how the direct manipulation of local activity in cortical brain regions is related to the incidental statistical learning process.

Chapter 2 examines task parametres that produce the most robust statistical learning behaviour using a well-known *contextual cuing* paradigm (Chun & Jiang, 1998). In this task, observers search through visual scenes containing statistical regularities. They typically have around 2000 ms to scan the displays. To investigate the speed of statistical processing, I briefly flashed displays for only 300ms and controlled further processing with backward masking. In a series of experiments, I found that learning could occur with briefly presented displays, but only for a reduced amount of information. These findings illustrate an efficient learning mechanism that can operate rapidly, but may be capacity limited at these speeds.

In Chapter 3 I report a large-scale tDCS study (n = 120) investigating the causal relationship between cortical activity and statistical learning. I compare bidirectional currents (i.e., anodal and cathodal) and two active brain regions (i.e., left prefrontal cortex and left

posterior parietal cortex) to a sham stimulation condition - a placebo control. The contextual cuing task was used to tap the statistical learning process, and the stimulation was delivered online, during exposure to regularities. Cathodal currents selectively affected learning, compared to sham and anodal currentsm and this was for both the frontal and pareital target regions. Specifically, cathodal stimulation disrupted the early cuing benefit, suggesting that stimulation delayed learning or the effects of learning on behaviour, but did not abolish it altogether. The effect was not explained by a general change in response times, a change in awareness or a speed/accuracy tradeoff. Instead, the impact of tDCS on performance was specific to the learning effect over time. This revealed a causal link between activity in frontoparietal areas and the evolution of statistical learning in this task.

Chapter 4 investigates the causal relationship using a different task believed to tap the same underlying process. Known as *Visual Statistical Learning* (Fiser & Aslin, 2001), this paradigm involves passive visual exposure to shapes with embeded probabilities, and learning is measured offline, in a recognition test after exposure. I focus on the cathodal effect, and compare stimulation of two brain regions (i.e., left posterior parietal cortex and left orbitofrontal cortex) to sham. Using the offline measure, I found no effect of stimulation (Experiment 1). This was despite having a large sample (n = 150) and observing robust learning at test. In Experiment 2, I develop an online measure of learning to investigate effects of stimulation that may be dynamic across time. Using a double-blind, pre-registerred design, I compare active (cathodal) stimulation to sham (n = 80) and observe that tDCS did influence statistical learning. As with chapter 3, the effect was selective to the early time-window. These findings provide converging evidence on the intervening role that cortical brain areas play in a visual statistical learning process.

The empiricle studies provide novel insights into the causal relationship that cortical areas have in producing statistical learning behaviours. The observation of direct cortical involvement has implications for theoretical accounts of statistical learning; and is consistent with the idea that statistical learning should be operationalised as a principal of processing similar to the Bayesian brain hypothesis. The work presented in this thesis broadens our understanding of the neural substrates that support implicit learning abilities, particularly those that involve extracting regularities from the visual scene and using them for implicit prediction.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications included in this thesis

Nydam, A, S., Sewell., D. S., & Dux, P. E. (2018). Cathodal Electrical Stimulation of Frontoparietal Cortex Disrupts Statistical Learning of Visual Configural Information. Cortex. 10.1016/j.cortex.2017.11.008.

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Nydam, A, S., Sewell., D. S., & Dux, P. E. (Submitted). Cortical Involvement in Visual Statistical Learning with Identity Structure.

Other publications during candidature

Peer-Reviewed Papers

Sale, M. V., **Nydam, A. S.,** & Mattingley, J. B. (2017). Stimulus Uncertainty Enhances Long-term Potentiation-like Plasticity in Human Motor Cortex. Cortex, 88, 32–41.

Kamke, M. R., **Nydam, A. S.,** Sale, M. V., & Mattingley, J. B. (2016). Associative Plasticity in the Human Motor Cortex is Enhanced by Concurrently Targeting Separate Muscle Representations with Excitatory and Inhibitory Protocols. Journal of Neurophysiology, 115(4), 2191–2198.

Conference Abstracts

Nydam, A. S., Sewell, D. S., & Dux, P. E. (Nov 2018). Cortical Involvement in Visual Statistical Learning of Shape Identities. Australian Cognitive Neuroscience Society Conference, Melbourne, Australia.

Nydam, A. S., Sewell, D.S., & Dux, P. E. (Aug 2017). Cathodal electrical stimulation disrupts incidental learning of visual configural information. International Conference on Cognitive Neuroscience (ICON), Amsterdam, Netherlands.

Nydam, A. S., Sewell, D. S., & Dux, P. E. (Sep 2017). Cathodal electrical stimulation disrupts incidental learning of visual configural information, Science of Learning Research Centre Conference, Brisbane, Australia.

Nydam, A. S., Sewell, D. S., & Dux, P. E. (Jul 2017). Cathodal electrical stimulation disrupts incidental learning of visual configural information. Model-based Neuroscience Summer School, Amsterdam, Netherlands.

Nydam, A. S., Sewell, D. S., & Dux, P. E. (Nov 2016). Statistical Learning of Irrelevant Visual Information is Disrupted by Electrical Stimulation of Frontoparietal Cortex. 6th annual Australian Cognitive Neuroscience Society Conference, Newcastle, Australia.

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Contributions by others to the thesis

My supervisors, Paul Dux and David Sewell, contributed significantly to the conception, design, and interpretation of each of the empirical studies. They also assisted by proofreading the manuscripts that resulted from the empirical chapters and the thesis as a whole. The resources, guidance and expertise they both provided were integral to the research program.

David Lloyd contributed by rendering computerised images of the tDCS montages used in the papers presented in Chapters 3 and 4. Kristina Horne, Dustin Venini and Ashley York assisted with data collection for a series of behavioural pilots for the paradigm used in Chapter 2. Jasmine Huang and Dustin Venini assisted in data collection for two behavioural pilots of the paradigm used for the tDCS experiments in Chapter 4. Michelle Hall provided MATLAB code for the Fiser task used in Experiment 1 of Chapter 4. Claire Naughtin and Michelle Hall provided assistance with generating data analysis scripts in MATLAB early on during the program.

Statement of parts of the thesis submitted to qualify for the award of another degree

No works submitted towards another degree have been included in this thesis.

Research involving human or animal subjects

The empirical research involving human participants that is included in this thesis was approved by the University of Queensland Medical Research Ethics Committee with the project code: 2009000335. A copy of the ethics approval letter has been included (see Appendix A).

Acknowledgments

When I began this journey, a foot extended and the black oxford heel met pavement
Shoes shined, I entered and was swiftly embraced by a lineage of Dux in a tree
A doe-eyed one gave me knowledge. Side-by-side we shared code and process
A stoic one gave me wisdom, eye-to-eye we stood hands to feet.
Back then I called you colleagues, lab members and my friends
Now I call you family, and hope to see you at camping or acro again.

When I began this journey, blue glass in my wake, I saw concrete and incognito
"Do the science you would believe in", you said, a call to arms from two years ago
Your mantra was quality in increments, do good work daily and results manifest
When needed, you guessed with one simple question, you cut through veneer and knew what was best
Back then I called you a supervisor, who worked as he dressed: consistent and bold
Now I call you a mentor, who doesn't look a day over 40 years old.

One year in to this journey, I sought a second advisor while out on a random walk
A welcome expedition into weeds of theory, with frequent libations we would talk and talk
You shared your abundant ideas with me, and taught me the greatest feedback and commenting style
Back then I saw you as mathematics and answers
Now I see questions are all the way down.

All along this journey, my pockets were full. I had gifts wrapped up in people
My big ideas guy was a constant companion; the contrarian gal bore more questions afoot
A pea and a pod gave nonsense as needed; the clear spoken thinker did help me a lot;
Two minds in small bodies brought 'offees and scheming, the laughs were loudest with you both.
Back then I called these science chats, a curios nerve cell being quenched among colleagues
Now I call this fulfillment, the exchange of ideas that are bigger than us.

When I struggled along this journey, there were always those, who helped to bare some load
Time slowed with reviews and dead-end experiments, and my song and dance lost its tune
The army General fought hard by my side, you gave depth and texture, my true gravity
Close to the end and Pop! Came some colour. a nerd in the expanse to re-tune perspective
Back then I called home when my luck got low, and outstretched palms would re-charge my chance
Now I call this love, and my gratitude is so that if I have the chance, I will always always dance.

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Keywords

statistical learning, incidental learning, visual search, decision-making, cognition, tDCS

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ANZSRC code: 170202, Decision Making, 20%
ANZSRC code: 170203, Knowledge Representation and Machine Learning, 10%

Fields of Research (FoR) Classification

1701 Psychology	50 %
1109 Neurosciences	50 %

Dedications

I dedicate this thesis to my dad, Associate Professor Kees Nydam. He is an MD, MBBS, FACEM, FAChAM, AFRACMA, MMEd, and MHMa. But not a real doctor. His words.

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List of Abbreviations Used in the Thesis

ANOVA:	Analysis of Variance
ARC:	Australian Research Council
ARC-SRI:	Australian Research Council Special Research Initiative
BF:	Bayes Factor
BOLD:	Blood Oxygen Levels Dependent
DLPFC:	Dorsolateral Prefrontal Cortex
EEG:	Electroencephalography
ERP:	Evoked Response Potential
fMRI:	functional Magnetic Resolution Imaging
IFG:	Inferior Frontal Gyrus
IPS:	Inferior Parietal Sulcus
ITI:	Inter Trial Interval
M1:	Primary Motor Region
MEP:	Motor Evoked Potential
MTL:	Medial Temporal Lobe
PFC:	Prefrontal Cortex
PPC:	Posterior Parietal Cortex
ROI:	Region of Interest
RT:	Response Time
SD:	Standard Deviation
SEM:	Standard Error of the Mean
tACS:	Transcranial Alternating Current Stimulation
tDCS:	Transcranial Direct Current Stimulation
TMS:	Transcranial Magnetic Stimulation
TMS-MEP:	Transcranial Magnetic Stimulation Motor Evoked Potentials
TPJ:	Temporal Parietal Junction
tRNS:	Transcranial Random Noise Stimulation

GENERAL INTRODUCTION

"Learning is an experience. Everything else is just information."

ALBERT EINSTEIN

The way we process information in a given moment is influenced not only by our current goals, but by experience that accumulates over time. In a game of tennis, your decision about how to serve the ball will be affected by the things that were important for past serves, along with aspects unique to the moment that may be goal-directed, like a strategy, or saliency-based, like an unexpected (and in appropriate) shout from the stands. Over the span of minutes to an entire lifetime, the history of sensory experience will amount to regularities that capture likely and less likely events, as well as more complicated patterns. Encoding the patterns in past experience can yield predictions about new experiences. Intriguingly, one need not be aware of any patterns for them to impact behaviour in a meaningful way. The impact of such regularities on the brain is believed by many to reflect an ability to learn the statistical characteristics of the environment (Aslin, 2016; Aslin & Newport, 2012; Chun & Turk-Browne, 2007; Fiser & Aslin, 2001; Perruchet & Pacton, 2006; Reber, 1967; 1989; Saffran, Aslin, & Newport, 1996). Individuals learn these statistics passively and automatically, without looking for patterns or being taught about them through feedback or reinforcement. They also tend to be unable to describe the knowledge gained, or that learning has taken place at all. For these reasons, the statistical learning process fits within a larger family of implicit learning abilities, characterised by experience-based learning without awareness (Batterink, Paller, & Reber, 2019; Perruchet & Pacton, 2006; Reber, 1989).

Encoding in a statistical manner is powerful. The representations exhibit a large capacity for storing information; much larger than any goal-directed or saliency-based mechanism would allow (Perruchet & Gallego, 1997). For this reason, statistical learning plays a critical role in the many aspects of cognition that require interacting with high-dimensional information, including language learning, maths learning, decision-making and social interactions. Beyond merely storing structured input, statistical encoding can become input itself and used for other cognitive operations or contribute to the dynamics of learning. Learning has been defined as the change in a stimulus-response pattern that occurs with task-specific training, practice, or repeated experience (Thorndike, 1931). The essence of this definition is how learning produces adaptive changes that unfold over time. The behaviour of learning is paralleled by changes in the brain, known most generally as neural plasticity (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). There is accumulating evidence that being sensitive to the structure of experience facilitates visual perception (Fiser & Aslin, 2002a; Orbán, Fiser, Aslin, & Lengyel, 2008), object recognition (Brady & Oliva, 2008; Otsuka, Nishiyama, Nakahara, & Kawaguchi, 2013), visuo-motor skills (J. H. Howard & Howard, 1997; Remillard, 2008), attentional operations (Chun & Jiang, 1998; Chun & Turk-Browne, 2007), decision-making (Sewell, Colagiuri, & Livesey, 2017) and predictive processing (Schapiro, Kustner, & Turk-Browne, 2012; Turk-Browne, Scholl, Johnson, & Chun, 2010a). Therefore, the fact that the brain both encodes and learns in a statistical manner is well-established. What is less well understood are the neural substrates that support this process, and how learning may be linked to the neural mechanisms involved in attention and memory.

This opening chapter outlines the recent theoretical and empirical work on statistical learning mechanisms in the human brain. I focus on statistical learning that applies to simultaneously presented items and how it facilitates visuospatial processing to do with scene recognition and visual search. I describe the breadth of the statistical learning phenomena and how this demonstrates a domain-general learning mechanism. I examine behavioural data showing how statistical cues are used to organise perception and guide cognitive operations to do with attention and decision-making. I present neuroscientific models that link statistical learning to memory systems in the brain, and contrast these against neuroimaging evidence that ties it to cortical regions that are thought to play a role in attention and decision-making. Finally, I outline how causal techniques may shed light on the underlying neural mechanisms, as has been done for other types of explicit learning. Along the way I highlight key experimental paradigms and identify issues in the literature that are yet to be resolved. This material sets the stage for the core research aim, which is to investigate a set of outstanding questions on the nature of cortical neural activity associated with a behaviour in statistical learning tasks: (1) Can brain stimulation be used to influence forms of statistical learning that are not purely stimulus- or response-based? (2) Is the cortical activity observed in fMRI directly involved in the statistical learning process? (3) To what degree may cortical involvement generalise across tasks that are believed to tap the same underlying process? The remaining chapters present three empirical papers that addressed each of these questions using a combination of psychophysics and brain stimulation approaches.

Statistical Learning – A Domain General Process

The current framing of statistical learning in the literature embodies a convergence of two historically distinct research fields: *implicit learning* (Reber, 1967; 1989) and *statistical learning* (Fiser & Aslin, 2001; Saffran et al., 1996; Turk-Browne & Scholl, 2009). The modern study of implicit learning was established by Arthur Reber following the discovery that individuals could infer grammar syntax rules from structured input without instructions and without awareness of the resulting knowledge (Reber, 1967). The concept of statistical learning was developed more recently, and stemmed from Jenny Saffran and Richard Aslin's research showing that infants learn words among continuous streams of syllables based on the transitional probabilities between neighbouring syllables (Saffran et al., 1996).

A number of recent reviews have highlighted commonalities between these two. These identified a shared set of principles that underlie both types of learning, and proposed the unifying term *implicit statistical learning* (Conway & Christiansen, 2006; Jost & Christiansen, 2010; Perruchet & Pacton, 2006; Schapiro & Turk-Browne, 2015). A variant *incidental statistical learning* has also been used (Fan & Turk-Browne, 2016; Hall, Naughtin, Mattingley, & Dux, 2018b; Schapiro & Turk-Browne, 2015; Turk-Browne, Johnson, Chun, & Scholl, 2008b), which sidesteps the issue of unconscious processes. The principles of both types of learning are that the process is:

- *automatic* – it occurs without instruction or supervision (i.e., reinforcement);
- *incidental* – it emerges as a result of exposure, rather than being a result of explicit analytical processes, such as hypothesis testing;
- *implicit* – observers are typically not aware of the resulting knowledge according to direct questioning or recognition tests; and

- *domain-general* – in that the learning mechanism can act on information formed by all types of input and then be used for a variety of perceptual and cognitive operations.

For ease of reference, this thesis will henceforth refer to incidental statistical learning more simply as *statistical learning* (SL). This process is still distinguished from the more general form of learning that was defined above (i.e., Thorndike).

The broad meaning of statistical learning deliberately reflects the ubiquitous nature of the phenomena. Statistical learning has been observed across all sensory modalities, including the visual, motor, auditory, olfactory and tactile domains, as well as cross-modally (Mitchel, Christiansen, & Weiss, 2014). It has also been observed for abstract information, such as semantic concepts (Goujon, Didierjean, & Marmèche, 2009) and illusory stimuli (Endress & Mehler, 2009), demonstrating that the process can be unbound to the sensory input itself. Statistical learning is not limited to spatiotemporal patterns in adjacent elements (Fiser & Aslin, 2001; 2002b),. It can apply to dynamics events, such as motion trajectories (Chun & Jiang, 1999; Experiment 2), and non-adjacent regularities (Newport & Aslin, 2004; Ono, Jiang, & Kawahara, 2005). This suggests the process may not be constrained to transitional probabilities alone. In fact, learners can infer a vast array of statistical characteristics, that include; covariation (Chun & Jiang, 1999); conditional probabilities (Fiser & Aslin, 2005); distributional elements such as variability and central tendency (Alvarez, Oliva, & Treisman, 2009; Chetverikov, Campana, & Kristjánsson, 2016); and more complex geographical structures that control for transitional probability (Schapiro, Turk-Browne, Norman, & Botvinick, 2016).

Statistical learning is present in both humans and non-human species, including rats, pigeons and primates (Santolin & Saffran, 2018). In humans, the abilities begin early in infancy (Kirkham, Slemmer, & Johnson, 2002; Saffran et al., 1996) and are maintained into adulthood (Rieckmann, Fischer, & Bäckman, 2010; Simon, Howard, & Howard, 2010), suggesting they are preserved across developmental stages. Thus, the nature and extent of this process appears impressively broad across the dimensions of stimulus type, relationships and species. This breadth supports the notion that statistical learning is fundamentally about processing the structure of experience. Likewise, the underlying neural mechanism should be similarly capable of representing a diverse range of inputs for a diverse range of functions.

Statistical Learning in Vision

Learning to represent statistics found in visual input has been investigated using a variety of stimuli and types of regularities. The earliest and most well-characterised demonstration of this phenomena was a set of experiments by József Fiser and Richard Aslin about visual scene segmentation. These authors sought to understand a function; how do observers deal with visual information that comes from a continuous stream of input with no explicit markings about what will be relevant for future behaviour. Recall the computational problem of extracting words among unmarked speech streams faced by infants in Jenny Saffran’s original work. This was an analogous problem in vision. Learners were presented with a series of visual scenes. Each was comprised of multiple shapes presented simultaneously (Figure 1). The shapes in the scenes contained embedded probabilities whereby some shapes were more likely to appear adjacent to a certain other shape, in space or time (Fiser & Aslin, 2001; 2002a; 2005). Participants simply viewed the scenes. There was no task and subjects were not informed about the patterns. Over the span of eight minutes, observers viewed 144 scenes, each presented for 1 second. Afterwards, a surprise recognition test was used to assess whether visual encoding was sensitive to the statistics of experience. Across a number of experiments, Fiser and Aslin observed recognition rates between 60 to 70%, which were above-chance at the group level. These findings illustrated automatic learning of the embedded statistical structure that affected visual recognition.

The phenomenon was named *visual statistical learning,* and the experimental paradigm is commonly referred to as *the Fiser task.* It has been replicated many times in other behavioural and neuroscience work (Conway, Goldstone, & Christiansen, 2007; Covington, Brown-Schmidt, & Duff, 2018; Karuza et al., 2017; Luo & Zhao, 2017; Roser, Aslin, McKenzie, Zahra, & Fiser, 2015; Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Zhao, Ngo, McKendrick, & Turk-Browne, 2011). Follow-up experiments confirmed that subjects learn the transitional probabilities between shapes in the pairs above frequency or joint probability alone. Altogether, Fiser and Aslin’s work on visual statistical learning was critically important to the field for two reasons. It provided an ecologically valid demonstration that the mere existence of structure in visual input allowed observers to represent statistics that would be required for learning higher-order features in real-world scenes through experience. It also demonstrated that statistics are spontaneously used by the perceptual system to bind objects in the service of recognition.

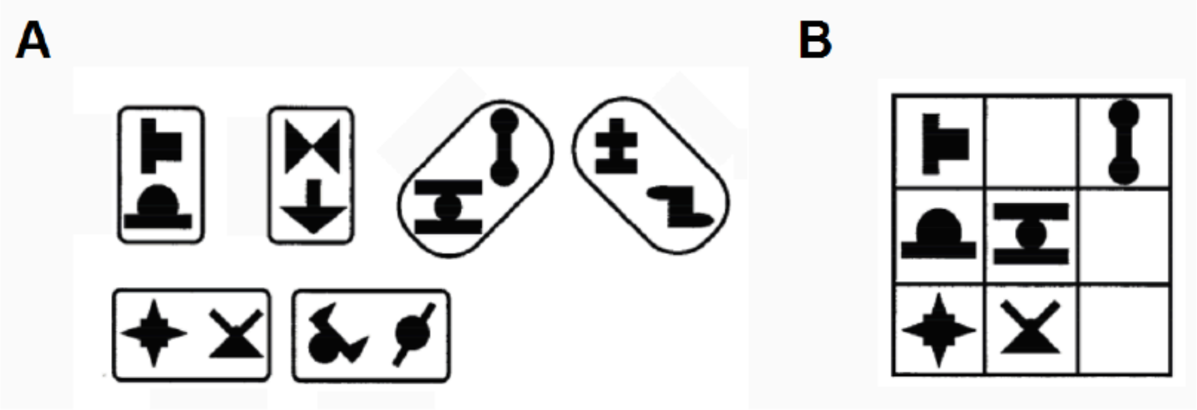


Figure 1. Schematic illustration of the stimuli in the Visual Statistical Learning task by Fiser and Aslin (1998). A set of twelve abstract shapes are organised into six base pairs that contain two shapes with a given spatial arrangement (A). Base pairs are combined in a grid-like array to form a visual scene (B). Each scene contains three of the possible six base pairs. Note that the grid lines are not visible to participants. During exposure, observers view a series of visual scenes in which the base pairs are recombined in all possible locations within the grid, and in all possible combinations of other base pairs. This means that after exposure, the shapes in the base pairs are identifiable because they have a higher conditional probability of appearing together, in a fixed spatial arrangement, than other shape pair combinations that were formed during exposure.

Since then, a number of tasks have developed to tap the statistical learning process in vision. Many employ this basic design where a series of arrays are presented that contain relationships among elements, and then the representations that result from passive learning are measured in a subsequent test phase. Findings concur that observers extract a variety of relationships passively or while performing a range of cover tasks (e.g., Turk-Browne, 2014). In some cases, aspects of attentional selection imposed by the task may affect which regularities are learned or represented (Turk-Browne, Jungé, & Scholl, 2005). Similarly, detecting one type of regularity can sometimes interfere with detecting other types of regularities (e.g., Hall, Mattingley, & Dux, 2015; Zhao, Ngo, McKendrick, & Turk-Browne, 2011). In other cases, two types of regularity can be learned in parallel, as was the case for spatial and sequential patterns in a visual task (Jiménez & Vázquez, 2011), and for adjacent and non-adjacent structures in an artificial grammar task (Romberg & Saffran, 2013). The latter observation has also been observed with linguistic input, and has led some authors to propose a multiple component view of statistical learning abilities (see Arciuli, 2017; Thiessen, 2017; Thiessen, Kronstein, & Hufnagle, 2013).

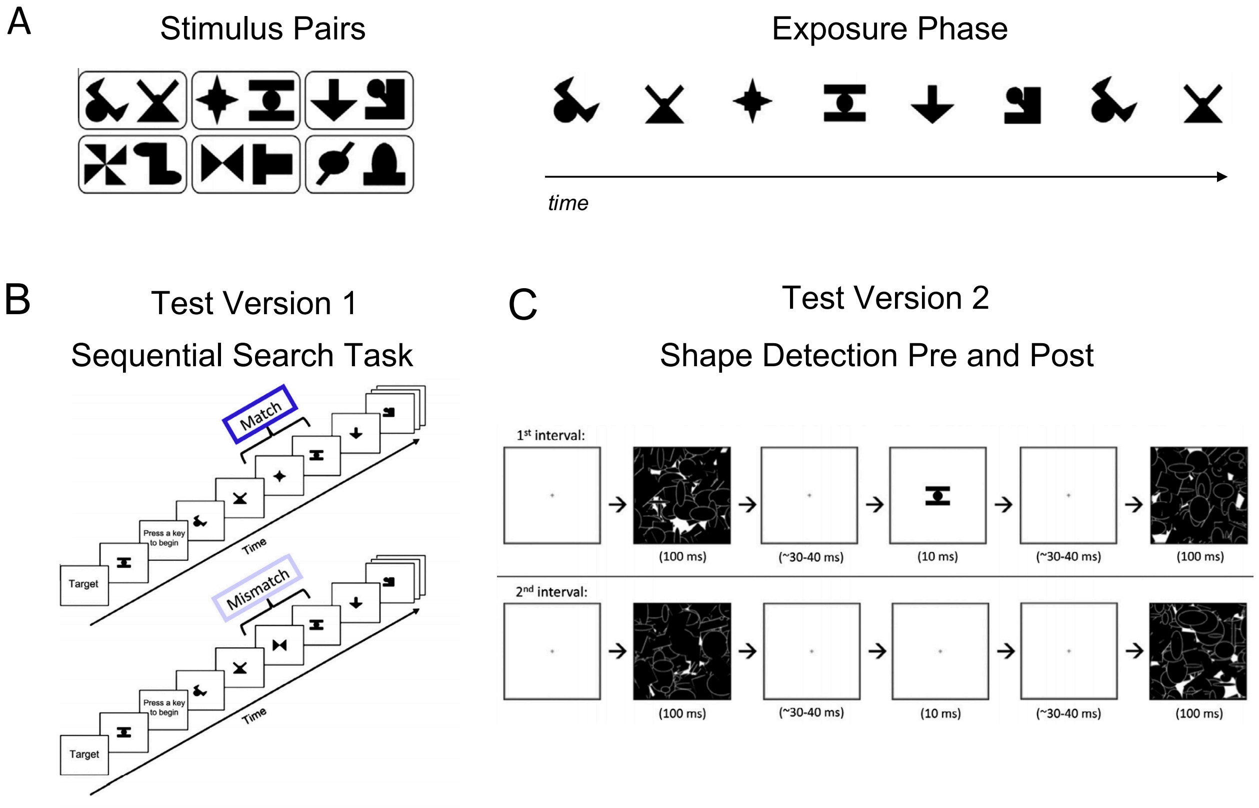


Figure 2. Summary of methods used to show how passive statistical learning affects representations across test methods. (A) Using a set of shape pairs (or auditory pairs, not shown), observers were exposed to a sequence of the shapes or tones. (B) In one experiment, the test of learning was a sequential search task. (C) In another experiment, the measure was pre and post sensitivity on a shape detection task wthat used forward and backward masking to obscure shape items. Both types of tests were sentitive to the pair learning, showing statistics chance visual representations even when not predicted in the current task. Reprodued with permission from Barakat et al., 2013.

Such ideas are compatible with a domain-general learning process that can act on multiple types of inputs to be used for a variety of behavioural outputs. Clear evidence for how the same structured input can alter different outputs comes from experiments that used different tasks in the test phase. After exposure to a sequence of shapes with embedded pairs, observers were tested on two tasks (Barakat et al., 2013). One test involved a sequential search task and one involved detection of individual shapes (Figure 2). More importantly, neither test task involved making predictions about the shape sequences themselves, but rather used a task orthogonal to the predictions. Learning generalised to both test tasks. This, among other work (Turk-Browne et al., 2010), shows how multiple cognitive processes, in this case temporal search and discrimination, may draw on a common representation that comes from passive statistical learning. Granted, the way statistical learning draws on underlying components may not be uniform across all tasks, modalities or individuals (see Thiessen et al., 2013). Yet overwhelmingly, empirical literature supports the idea that statistical learning can produce robust representations that are capable of being accessed by many cognitive operations, from familiarity judgements, to perceptual discrimination to sequential expectations.

Subsequent lines of research investigated how statistical regularities are represented. A number of elegant manipulations in the Fiser task revealed they recalled patterns to differing degrees depending on the hierarchical structure of the overall input. For example, pairs of shapes embedded among larger triplets were recalled to a lesser degree than the triplets themselves (Fiser & Aslin, 2005). The authors proposed a principal of constraint in statistical learning based on the embeddedness of the broader structure. Complementary work using visual sequences revealed that embeddedness of the features *within* an object (such as colour and shape) also constrained which statistics were learned (Turk-Browne, Isola, Scholl, & Treat, 2008a). The idea of constraint has been important for understanding the process that gives rise to statistical learning and how it could overcome the curse of dimensionality: how representing all probabilities in an environment would rapidly exceed the capacity of the system. Instead, it this idea suggested that the system adaptively scales the computations based on information that will be most meaningful given the broader structure of the environment. This assertion also describes how the process of representing visual covariation could be scaled up to increasingly complex scenes, such as those that may contain dynamic objects, features, timescales and meaning.

A dominant set of models that attempt to explain the learning process are known as chunking models. While differing in their details, the key assertion is that information from the input itself is being represented in the brain. According to these frameworks, the detection of statistical regularities occurs by randomly grouping the input into “chunks” of information, which are stored as exemplars in memory (Perruchet & Gallego, 1997; Thiessen et al., 2013).

Over repeated encounters, the original elements are combined into new chunks that represent a single, more complex, element in the higher-order structure. The simplest of these frameworks, the PARSER model (Perruchet, 1998), proposes that processes inherent to memory formation, such as activation, decay and interference, give rise to representations that are statistically coherent. For example, elements within a chunk that are presented frequently will be strengthened in memory based on activation, whereas chunks that appear rarely will decay and become weakened. Data from a sequence learning task was successfully fit to such a model (Slone & Johnson, 2015). The notion of interference in the model predicts that if elements from one chunk appear in another chunk, this will cause a suppressive effect. This aspect predicts the findings of Fiser (2005) where embedded pair items were remembered to a lesser degree than the larger triplets. It is also consistent with evidence of weakened memory representations for competing items found with behavioural (Otsuka & Saiki, 2016) and neuroscientific measures of representations (Kim, Norman, & Turk-Browne, 2018) after statistical learning.

Another model that fits the data well was based on the Bayesian computational framework. The Bayesian perspective views the brain as an unconscious inference machine (Knill & Pouget, 2004). The system attempts to make the most accurate predictions in the face of noisy sensory input, by using internal models of the environment (known as priors) combined with current sensory input (likelihoods) to continually update the model (posterior) in order to generate optimal predictions (Friston, 2010). Data from a series of experiments using the visual statistical learning phenomena were fit to models that made different assumptions about how statistical representations could be made (Orbán et al., 2008). The data were most consistent with a Bayesian model over other counting-based or purely associative models. In addition, the Bayesian model was fit to new data that captured two important theoretical predictions about statistical learning. Namely, that the system does not rely on pair-wise associations, but that objects are grouped into larger hierarchies. And that statistical learning is near optimal in capturing complex patterns with a flexible degree of generalisation. This work does not conclusively rule out other models of the learning process, however it does show that behavioural data on visual learning was consistent with what a Bayesian model predicts. Furthermore, Bayesian models are inherently probabilistic, and therefore refer to the relationships between items not sensory units directly, which is consistent with the original idea that statistical learning captures relationships (e.g., by Fiser &

Aslin, 2001). This finding sets the stage for exploring biologically plausible Bayesian models that could compare predictions about how this mechanism could be instantiated in the brain.

The work reviewed above identifies a powerful visual statistical learning mechanism that operates via mere exposure. It demonstrates how regularities in sensory input come to affect visual perception by structuring representations of visual sequences and visual scenes. The work conducted by Fiser and Aslin offered ecological validity and suggested observers spontaneously learn and represent the statistical relationships between elements in input. However, popular chunking models (e.g., Perruchet & Gallego, 1997) explain the learning process as emerging from representing the input itself rather than the relationships. The preferred fit of a Bayesian model to data from the Fiser task (Orbán et al., 2008) was consistent with the idea that information is stored in a statistically optimal manner. Further work is needed to align different model predictions about the mechanism for representing statistical information with the vast empirical data on statistical learning phenomena. Stepping away from the issue of how representations are formed by statistical input, we see a learning process that extends beyond bottom-up perception.

Once the statistical information is extracted, it becomes available as top-down input itself – in the form of implicit knowledge – to produce a variety of downstream effects (Chun & Turk-Browne, 2007; Turk-Browne, Johnson, Chun, & Scholl, 2008b). For instance, statistical learning can produce mid-level perceptual effects in the form of neural anticipation of the associated stimulus (Turk-Browne, Johnson, Chun, & Scholl, 2008b). It can also constrain the emergence of rule-learning based on the computed statistics (MacKenzie & Fiser, 2008). When regularities are embedded in task-irrelevant locations, they can draw spatial attention to those locations, demonstrating an effect of statistical regularity on selection mechanisms (Zhao, Al-Aidroos, & Turk-Browne, 2013). Likewise, when task-irrelevant regularities are associated with a task-relevant object, statistical learning can expedite procedural learning during visual search (Chun & Jiang, 1998). Thus, the notion of a domain-general learning process also resides in how the extraction of statistical cues can affect a variety of functions in the cognitive domain.

When Statistical Learning Guides Top-Down Cognition

The literature reviewed thus far has examined the form of statistical encoding; and form heralds function. Statistical cues are not only represented in the brain (i.e., in memory) but have a functional role when they are used to make predictions and shift behaviour. This occurs when the mental representations about statistics influence ongoing cognitive process, such as attention, prediction or response-selection. To appreciate the functional effects of statistical learning on behaviour, one must briefly understand what is meant by an underlying cognitive process. In the broadest sense, cognition is everything that occurs between the arrival of a stimulus in the brain and a response by the organism. At this level, cognition is the black box between input and output. And so, the effects of statistical cues on familiarity judgements (i.e., Fiser & Aslin, 2001) would surely involve cognition. But in order to understand the complex process that is cognition, researchers have broken it down into modules. And a number of meaningful modules have been identified (Sternberg, 1969; Anderson et al., 2016). While the specific modules may depend on the process being studied, cognition, otherwise known as information processing, tends to involve a few key subprocesses, namely: perception, selection (or attention), storage (or working memory), evaluation (or decision-making) and output preparation (response selection and inhibition). Early frameworks viewed these modules as a series of stages (i.e., Donders, 1868); arranged sequentially in time. Since then, many different combinations of sequential, parallel and overlapping stages have been put forth (e.g., McClelland, 1979; Triesman and Gelade, 1980); with each viewing the components as either discrete or continuous in time. Disregarding the temporal organization of cognitive stages, the dominant view across models is that there are separate processes (Sternberg, 1969). They are separate in the sense that manipulating one or more factors of an experiment will produce distinct effects on a given process, while not affecting another process; this is known as the additive factors approach (Sternberg, 2011). Recently, neural imaging signals from EEG and fMRI have helped to assert the idea of separate processes (Ratcliff, Philiastides & Sajda, 2009; Anderson, 2016). Indeed, some processes, like visual search, appear to be complex; involving many subprocesses and stages. Only by appreciating the separateness of cognitive processes (or stages) can one start to look for commonalities in the way statistical learning affects behaviour, and therefore cognition, more generally.

In our complex and often dynamic visual world, spatial navigation and goal-directed search are important processes for every-day functioning. Visuospatial search may be guided by voluntary operations, such as top-down attention, as well as by involuntary functions, such as bottom-up salience. Visual search is also guided by prior experience. This is because visual environments, like language, contain spatiotemporal regularities. All beaches tend to look alike, as do kitchens, as do roads. Regardless of the specifics, one can efficiently recognize scenes by identifying a common set of items or layouts. In a kitchen, you can expect to find items like a kettle, fridge, and toaster, regardless of where they are or what they look like. These repeated patterns can be exploited by the information processing system to produce adaptive gains in familiar environments. The situational arrangement of objects in an environment is known as a *context*, and research shows that contextual information can facilitate visual-spatial processing (Biederman, Mezzanotte, & Rabinowitz, 1982).

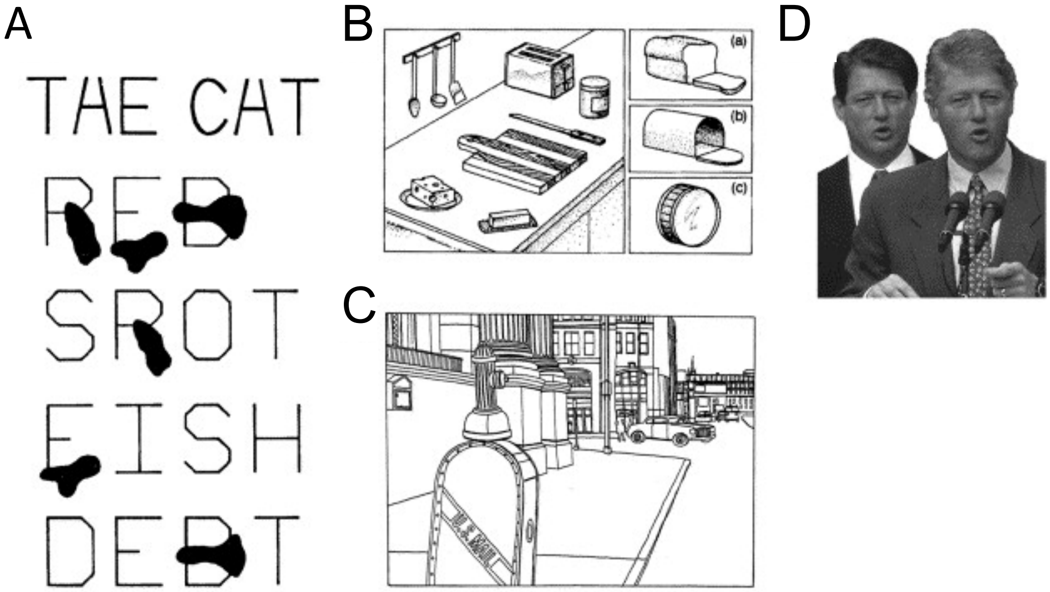


Figure 3. Top-down varieties of visual context effects. (A) Knowledge about word context disambiguates the identity of embedded letters obscured by inkblots. (B) Knowledge about a kitchen context facilitates identification for an appropriate object (loaf of bread in inset a), compared with a visually similar, misleading object (mailbox in inset b) or inappropriate object (drum in inset c). (c) Automatic knowledge about positional constraints in scenes, such as a fire hydrant on the ground, means that when violated, such as by having the fire hydrant on the mailbox, objects are difficult to detect. (d) Context about visual features influences face recognition. Observers can readily discriminate the two figures based on contextual cues such as hairstyle and speaking position, but interestingly, the faces are identical in this digitally altered image. Reprinted with permission from Chun, 2000.

Early on, contextual information processing was studied using explicit, semantic forms of knowledge, which operate in a top-down manner. The examples of a beach and a kitchen were Research showed that identifying an object in an expected context, such as bread in a kitchen scene, was faster and more accurate than identifying an unexpected object in that scene, such as a post box in a kitchen. A variety of visual context effects support the idea that context facilitates a number of cognitive processes, including recognition, identification and discrimination (summarized in Figure 3). In a similar sense, statistical learning helps to constrain predictions based on context. Implicit knowledge about statistical cues can guide where, when or what to expect in the environment. But unlike contextual processing that occurs in a top-down manner, contextual processing of statistical cues occurs through an incidental learning process.

At its heart, all forms of contextual inference (top-down and implicit) are based on knowledge about regularities in the environment. It was Chun and Jiang (1998) who first proposed that the development of contextual knowledge in the brain should itself be explained by exposure to regularities. The context would be built up over the course of an experimental session, rather than be based on pre-experimental information that had been used in the studies of visual context effects to date (i.e., schema processing). As a result, Chun and Jiang ran a set of experiments that provided the first confirmatory evidence of such an incidental learning mechanism for visual context. The phenomenon is known as *contextual cuing* (Figure 4).

In their task, individuals performed visual search for a target ‘T’ among an array of distractor ‘Ls’. In one condition, the distractor context was novel, meaning that for a set of configurations the distractors were always randomly located across blocks. In another condition, the distractor contexts repeated, meaning a given array of distractors was associated with a given target location across the blocks. In this way, visual context - defined by configural regularities - came to cue the target’s location. In the novel condition, performance became increasingly faster over the blocks, in line with procedural learning in visual search. Critically, in the repeat condition, visual search performance became increasingly faster and more accurate compared to the novel condition. This display × block interaction (Figure 5) captures the contextual cuing effect. Since observers were not instructed to pay attention to the distractors or their configurations, regularities affected performance in an incidental manner. Furthermore, when individuals performed a forced-choice recognition test on the repeated contexts, they did not show any explicit memory or awareness of learned contexts, showing the knowledge about context was implicit.

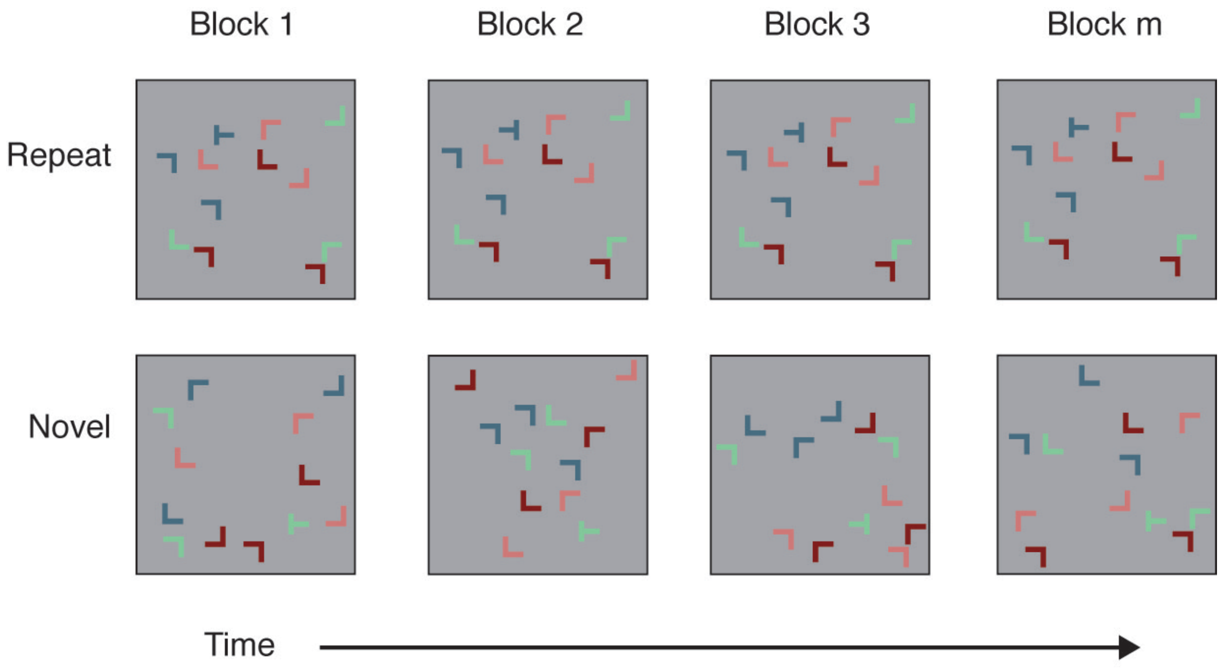


Figure 4. Schematic illustration of the repeat and novel displays in the contextual cuing paradigm (Chun and Jiang, 1998). In repeat displays (top panel) the location of the target “T” and the location and orientation of distractor “Ls” is constant over time so that the distractor context predicts the target location (but not the required response). In novel arrays (bottom panel) the target location is constant but the distractor configurations vary across blocks. Over the course of exposure, faster responses to the target are produced by the effect of repeating distractor configuration. Note that the repeated context does not predict the orientation of the target, and so learning of location is dissociated from the button-press response.

Contextual cuing is an example of how spatial regularities can affect visual search performance in an incidental manner. Note that the repeating configurations predict the location of the target but not the target’s orientation, which remains random on any given trial. This is a critical element of the paradigm because it separates the learned target-context association from the response outcome itself. Thus, learning the regularities comes to influence a decision-making process (e.g., searching for a target and determining a feature of the target); distinct from influencing a stimulus-response pattern (e.g., SRT tasks) or stimulus-location pattern (e.g., perceptual SRT tasks and categorization tasks) in motor learning and perceptual learning, respectively. Therefore, contextual cuing demonstrates effects of statistical learning on a process that is distinct from motor-related and perception-related processes.

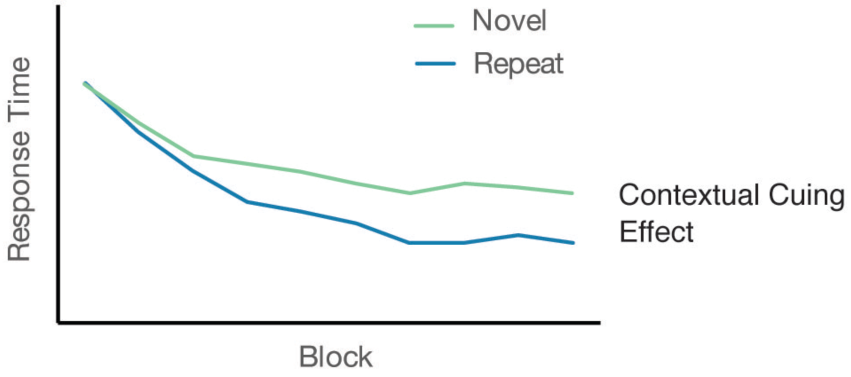


Figure 5. Typical response time effect observed in the contextual cuing task. Responses to the target decision become increasingly faster for Repeat displays comared to Novel displays over blocks, indicative of the contextual cuing effect.

Since it was first reported, the contextual cuing paradigm has been modified in an impressive number of ways by inserting a variety of regularities (Figure 6). These variations firmly establish that the learning in contextual cuing is fundamentally about extracting covariation with experience and using it to inform task-relevant decisions. Types of covariation have included, but are not limited to: using object identity independent of spatial location (Chun & Jiang, 1999; Endo & Takeda, 2004); global features of the display like colour or background (Hyun & Kim, 2002; Kunar, Flusberg, & Wolfe, 2006); motion trajectories (Chun & Jiang, 1999); order effects between trials (Ono et al., 2004; 2005); as well as categorical distinctions that supersede the input itself (Goujon et al., 2009; Goujon, Didierjean, & Marmèche, 2007; Yang & Merrill, 2014). Such breadth along the dimension of stimulus and regularity type is consistent with a domain-general account of statistical learning.

A number of features place contextual cuing within the broader statistical learning framework (for a review see: Goujon, Didierjean, & Thorpe, 2015). Learning emerges rapidly since a reliable difference between repeat and novel arrays can be observed after just three repetitions of the displays (Chun & Jiang, 1998; Jiang & Chun, 2001; Jiang & Wagner, 2004; Tseng & Lleras, 2012; Zellin, Mühlenen, Müller, & Conci, 2014), convergent with other statistical learning phenomena (e.g., Chun & Turk-Browne, 2007; Hall, Mattingley, & Dux, 2018a; Turk-Browne, Johnson, Chun, & Scholl, 2008b). The magnitude of the cuing benefit is between 20 ms and 100 ms, depending on the complexity of the displays. The effect cannot simply be explained by perceptual learning because a benefit still occurs when the exact locations of repeating distractor items are jittered or altered across repetitions (Chun & Jiang, 1998). The cuing behaviour is primarily associative. No improvements occur if the distractors repeat but with random target locations as per the "repeated search" literature (Kunar, Flusberg, & Wolfe, 2008). Cuing exhibits a large capacity, as people are capable of learning 60 individual configurations over 5 days (Jiang, Song, & Rigas, 2005). There have been reports that a cuing benefit asymptotes after 30 exposures (Tseng & Lleras, 2012; Zellin et al., 2014), although this requires further investigation.

A number of studies show that memory for spatial context tends to be implicit. When participants were asked to recognize the repeating displays, either by forced-choice (e.g., Chun & Jiang, 2003) or by target-location generation tests (e.g., Smyth & Shanks, 2008), observers perform at chance (Assumpção, Shi, Zang, Müller, & Geyer, 2015; Chua & Chun, 2003; Chun & Jiang, 1998; Colagiuri & Livesey, 2016; Goujon et al., 2015; Pollmann & Manginelli, 2009; Zellin et al., 2014). There is some evidence of above chance recognition when using extended exposure (Smyth & Shanks, 2008) or real world displays (Brockmole & Henderson, 2010; Brockmole, Castelhano & Henderson 2006; Rosenbaum & Jiang, 2013), and the nature of implicit memory has been disputed by some (Conci & Muhlenen, 2009; Geyer, Baumgartner, Müller, & Pollmann, 2012; Rosenbaum & Jiang, 2013). One aspect of this debate concerns the nature of recognition tests themselves and how they may lack sensitivity as a measure of awareness (Schlagbauer, Muller, Zehetleitner, & Geyer, 2012). Another element is the nature of variability in recognition across individual displays and individuals (Schlagbauer et al., 2012). These exceptions encourage some authors to focus on the incidental nature of learning per se rather than the involvement of implicit memories itself. Overwhelmingly, the collective evidence suggests that contextual cuing with abstract T and L displays occurs without awareness.

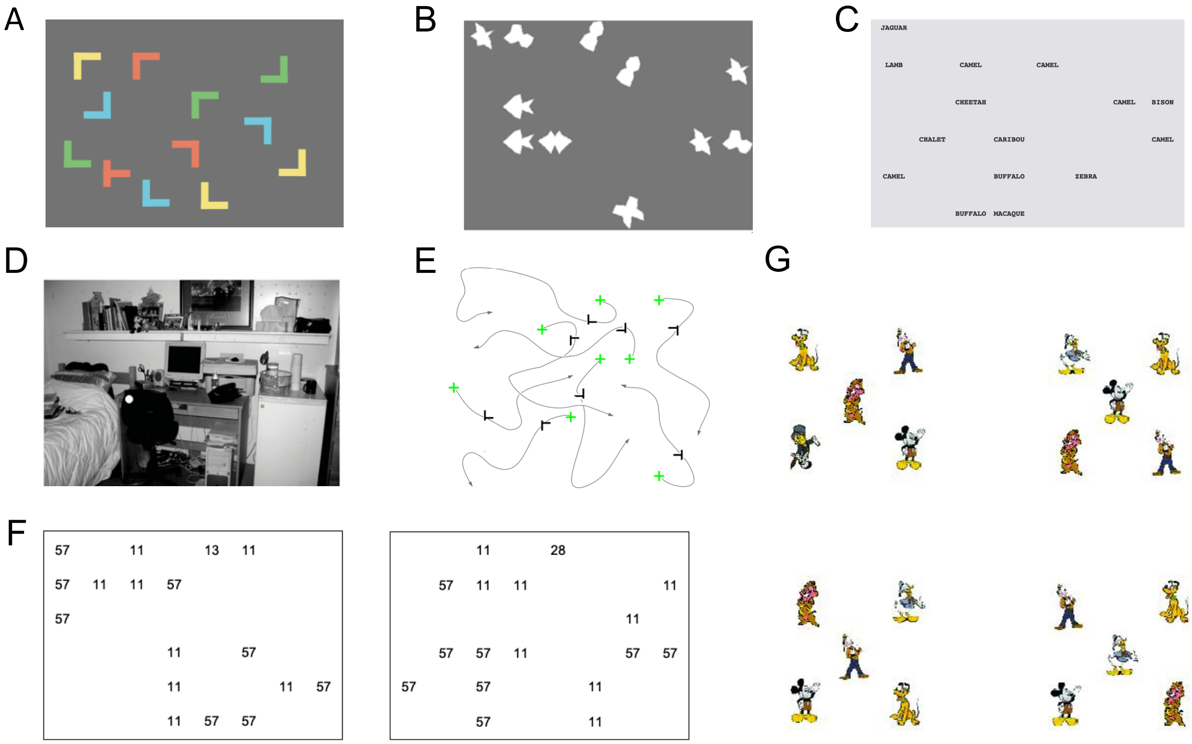


Figure 6. Variations of contextual cuing paradigms. (A) Spatial contextual cuing, where the location of distractors cues the location of a target in the configuration. Reproduced with permission from Chun, 2000. (B) Identity cuing, where the idendity of distractors cues the target identity, while the location of items remains random. Reproduced with permissions from Chun & Jiang, 1999. (C) Semantic cuing, where category knowledge, such as the distractors being mammal words, serves as the context to cue the location of a target word, either 'Blouse' or 'Chalet'. Reproduced with permissions by Goujon, Didierjean & Marmeche, 2009. (D) Real world scenes as context for locating a white dot target. Reproduced with permissons from Brockmole & Le-Hoa Vo, 2010. (E) Dynamic context where the trajectories of distractor items cued a target trajectory. Reproduced with permissions from Chun & Jiang, 1999. (F) Numerical contextual cuing where the category of odd numbers (57 and 11), regardless of their location, cued the location of a target number (either 13 or 28). Reproduced with permission from Goujon, Didierjean & Marmeche, 2007. (G) Cuing task used to test children and older adults where cartoon characters cued a target character, jimeny cricket. Reproduced with permissions from Merrill et al., 2013.

A substantial portion of the contextual cuing literature has focused on the nature of the representations being learned. It is generally agreed that associative mechanisms are responsible, but different hypotheses on the 'how' make distinct predictions regarding the level at which the associations are formed. As with other forms of statistical learning, a dominant hypothesis has been chunking. This reduces cuing to a bottom-up learning effect, driven mostly by local features around the target. There is some evidence in support of this idea, since cuing is sensitive to perceptual grouping principles (Olson & Chun, 2002), and local items near the target seem to be more important for learning than distractor items distant from the target (Brady & Chun, 2007). What is more clear is that subjects learn a number of different associations that include: item associations that make up a context, target-distractor associations, and target-context associations (Beesley, Vadillo, Pearson, & Shanks, 2016; Brady & Chun, 2007; Ogawa & Kumada, 2008). Studies that show a target needs to be recognized within the global context to facilitate learning run counter to the bottom-up chunking accounts (Tseng & Li, 2004; Zhao et al., 2012). Thus, statistical learning in contextual cuing most likely involves representing multiple statistical cues.

An ongoing debate concerns the role of attentional guidance or decision-making in producing the RT benefit for repeat displays. The two leading accounts postulate that the RT effect is due to: (1) faster or more efficient visual search for the target (Chun & Jiang, 1998); or (2) a reduced response threshold when selecting the appropriate motor response once the target has been acquired (Kunar, Flusberg, Horowitz, & Wolfe, 2007). These accounts differ whether they implicate effects at the level of decisional processes (i.e., the left or right judgment), or non-decision components (i.e., locating the target during visual search). The debate is alive and well, with a recent review being published this year (see Sisk, Remington, & Jiang, 2019).

The attentional guidance account holds that the effect of regularities speeds attention towards the likely target location, meaning it affects processing before the target is found. Support for the attentional guidance account largely comes from studies using search slopes (Wolfe, 1998) which measure RT across different set sizes to index the efficiency of locating the target. The original Chun and Jiang (1998) study observed reduced search slopes for repeat arrays; evidence of increased attentional guidance to the target. This was challenged in a study by Kunar and colleagues (2008) that showed contextual cuing effect when the search process was already optimal by using pop-out targets. Additionally, the same group pooled data across 10 experiments and failed to show a reliable slope effect (Kunar, Flusberg, Horowitz, & Wolfe, 2007). The evidence on search slopes has remained mixed since then, with three studies showing a slope effect and eight failing to show such an effect (Kunar et al., 2007; Sisk et al., 2019). These inconsistencies may reflect how the representation of a repeated configuration is not equal across distractor items (as modelled by Brady & Chun, 2007) and so may not scale with set size in a linear fashion. And so, it appears the evidence is not yet definitive regarding whether context repetition influences attentional guidance.

Response-related accounts offer a disparate view. They suggest the benefit to processing occurs after the target has been located, at the decision and response stage. This stems from two key lines of enquiry. The earliest support came from a finding that contextual cuing interacted with response congruency (Kunar et al., 2007). For colour-singleton targets that were either an A or an R, when the identity of the target was congruent with the distractors (e.g., a red 'A' among green 'A's), contextual cuing was observed. But cuing was not observed when targets were incongruent with distractors (e.g., a red A among green Rs). However, this task altered the demand characteristics from traditional cuing in that the search was for a colour singleton rather than a conjunction search, as used in Ts and Ls displays. Also, the motor response to the target (A or R) was confounded with the identity of the target itself, rather than being a decision about a target feature. Thus, it is difficult to integrate this congruency effect with the broader instantiation of the contextual cuing phenomena. For statistical learning more broadly, studies of motor skill learning using the SRT task have used congruency effects for a different purpose. After learning a sequence, items were inserted that were incongruent with the predicted sequence and the resulting congruency effect was used to infer the degree of learning that occurred across individuals. When encoded regularities predict a motor response, congruency effects are expected, but when the regularities guide a cognitive process, such as in visual search, the picture is more complex.

A third approach has recently shed light on the conflict between the attentional –related and response-related accounts. By adopting a computational approach, the different theories about how cuing affected behaviour could be directly compared (Sewell et al., 2017; Weigard & Huang-Pollock, 2014). In response-time modelling (also known as sequential sampling models), the raw response-time data (or "reaction times") are used to separate the time taken for the decision process from the time taken to perceive the stimulus and execute a response; termed non-decision time (Figure 7). Conceptually, the decision stage is modelled as a process of continuously sampling evidence from a noisy input until a threshold is reached for making a decision, at which time the motor output is initiated (Ratcliff & Rouder, 1998). The decision process may in terms of the speed at which evidence is accumulated over time (i.e., drift rate). It can vary in terms of the amount of evidence needed to reach a decision (i.e., threshold). This is conceptually similar to the criterion in signal detection theory. Finally, decisions can vary in terms of the bias in the system prior to the decision starting (i.e., start point). These parameters of accumulation of evidence, threshold and bias can be compared between experimental conditions or population groups to describe the characteristics of the underlying cognitive mechanism. Models such as these have been validated in a number of theoretical papers. And biologically plausible models of behavior and neural activity are now emerging

When a diffusion modelling approach was applied to contextual cuing data (Sewell et al., 2017), is was used to distinguish between the three theoretical accounts of cuing behavior. These were: (a) the attentional account, (b) the response threshold account, (c) and a new perceptual evidence account. The attentional account was modelled as a change in the non-decision time parameter for repeat relative to novel trials. This was because attentional shifts occur before the target is fixated on, and the RT reflects a decision about a target orientation. The response threshold account was modelled as a change in decision thresholds for repeat displays. A reduced threshold would produce a RT faster with more errors; thereby changing the distribution of RT responses. Finally, the perceptual account was mapped to the evidence accumulation parameter, since predictive information speeds processing. Put differently, they compared a non-decision account (attention) to two decision-related accounts (perceptual evidence and threshold) of cuing behavior. When the models were fit to data, they could compare a goodness-of-fit measure for each of the three models, to evaluate evidence for the three theoretical accounts. The results, foremost, showed that all three mechanisms were present across individuals. However, the majority of individual data was best characterized by a decision-making account, either the evidence accumulation model or the response threshold model (Sewell et al., 2017). A similar effect on the decision parameters over the non-decision time was observed in other data (Weigard & Huang-Pollock, 2014), providing converging evidence against a purely attentional account of cuing. It is most likely multiple mechanisms (for a review see Sisk, Remington, Jiang, 2019).

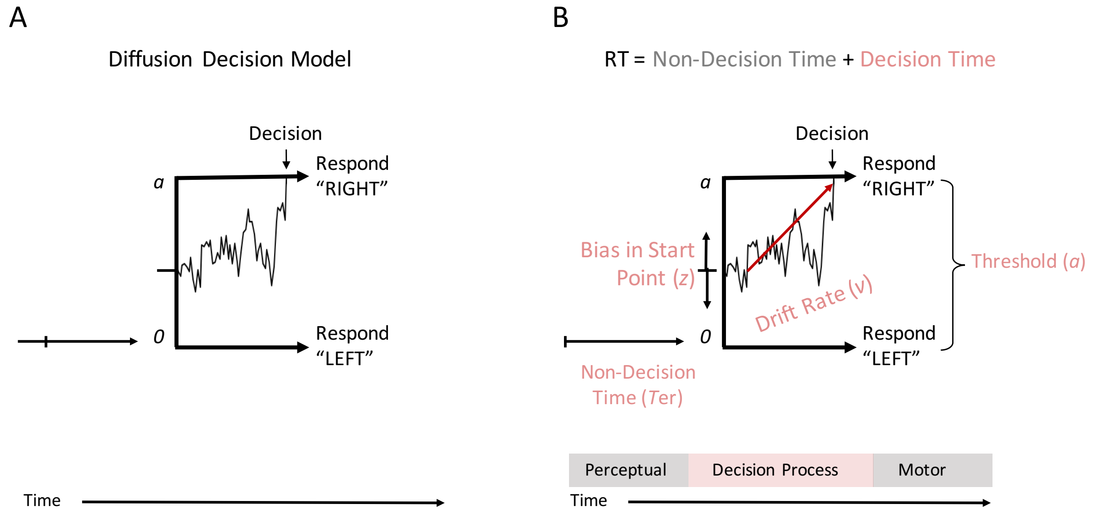


Figure 7. (A) Schematic representation of the diffusion model of the decision process (i.e., Ratcliff and Rouder, 1998). ((B) Annotated schematic representation with parametres colour coded for decision-time (red) and non-decision time (grey).

One caveat when relating the modelling results (Sewell et al., 2017) to implicit learning more generally is that the learning was most-likely explicit in their paradigm. They used a large number of trials (required for modelling) and only eight repeat configurations and eight novel configurations. It is therefore likely that individuals recognized the repeat displays on some level by the end. No data on recognition was collected. Whether different mechanisms would be observed for implicit cuing is yet to be empirically tested. A strength of the method was that it did not require altering the nature of the search task (such as using target absent search) or manipulating set size (to measure slope effects). Noting the caveat, the application of response-time modelling to contextual cuing provided the first and most direct test of different mechanisms that support incidental learning of regularities.

Visual search is a multifaceted process. It is probable that implicit cuing involves multiple mechanisms that unfold over different time scales in a continuous manner. Some mechanisms are to do with attentional selection, some are to do with speeding a decision, and some are to do with the response process. Conceptualizing cuing as a shift in a decision-process, and not solely a shift in pre-target attention or post-target response, is helpful on many accounts. In the service of parsimony, it avoids getting bogged down in the mechanistic details of a paradigm, especially when those details are hotly debated (e.g. attention vs threshold accounts). Theoretically, it would predict the findings of a search benefit when attention is already optimal (e.g., Harris & Remington, 2017; Ogawa & Kumada, 2008; Kunar et al., 2007). Adopting a decision-making framework can unify theory across paradigms to better understand how statistical encoding contributes to adaptive behaviours through implicit learning. Modelling research will therefore be highly important for investigating the domain-general theory of an incidental statistical learning process in the brain. One of the significant challenges will be to obtain sufficient trial data from an individual while keeping the learning implicit. While evidence from electroencephalography shows that attention does shift in contextual cuing tasks (e.g., Johnson et al., 2007), the involvement of attention is not incompatible with the decision-making framework. Rather, when the time before the eyes land on the target (i.e., attention) is not measured using eye-tracking or inferred using search slopes, we can reason that the cumulative effect of attention (before the target is found) and the decision process (including information processing and response selection) are encapsulated in the RT data. Moving forward, this thesis will refer to cuing as an effect on attention and decision-making moving forward. At the level of measured behavior, the cuing effect is an RT benefit that emerges over time.

Summary of Behavioural Literature

The psychophysics research reviewed thus far demonstrates how the statistical learning process is pervasive throughout the brain, being observed across multiple levels of the information processing hierarchy, from perception to cognition. Visual statistical learning phenomena have clear functions linked to representing complex scenes. This mechanism is capable of binding features into objects (Turk-Browne, Isola, Scholl, & Treat, 2008a), objects into scenes (Fiser & Aslin, 2005; Orbán et al., 2008), scenes into contexts (Chun & Turk-Browne, 2007) and abstracting these into broader categories (Brady & Oliva, 2008). In particular, I have illustrated how passively extracting structure from visual input helps define objects in time and/or space; and that this contributes to a degree of visual familiarity to such objects in recognition tests. I have also discussed how knowledge about regularities can be used adaptively by the system to inform the *what, where* and *when* of visual events and contribute to incidental learning behaviour. I explained that visual statistical learning (e.g., Fiser & Aslin, 2001) and contextual cuing (e.g., Chun and Jiang, 1998) are two prominent examples of the same underlying process manifest at different levels of information processing. As per the work of Fiser, the building blocks are automatic and hierarchical, and may be explained by Bayesian learning principles (Orbán et al., 2008).

While the models of statistical learning for visual perception have been well characterised; models to describe how regularities are utilised by the cognitive system, such as in cuing tasks, are an active area of investigation. As described, there is current debate about whether incidental cuing tasks involve a shift in attention (e.g., Chun & Jiang, 1999) or a shift in response-selection (e.g., Kunar, 2007), and likely affects both (e.g., Sisk et al., 2019). I described how clarity can been gleaned by adopting a unifying decision-making framework (e.g., Ratcliffe, 2008; Sewell et al., 2019) to describe adaptive changes in choice behaviour tasks. It can sidestep tedious mechanistic questions. It avoids demarcating search behaviour into pre- and post-target operations using adapted paradigms. After-all, the nature of cognition is that of a cascade of operations. By viewing the target decision as a read-out of a decision process, is more consistent with a construct that embraces how cognition is a cascade of operations, represented as the black box between input and outputs. Theoretically, statistical learning is purported to be a domain-general black box between structured input and many types of outputs (e.g., Reber, 2018). Yet despite the considerable empirical and theoretical work, important questions remained unanswered about how statistical learning is formed in the brain. I turn next to this question.

Neural Models of Statistical Learning

Statistical learning is pervasive, and the mechanisms are complex. To date, a cohesive understanding of the systems-level neural architecture is largely missing. Much of the early neuroscience was motivated by a desire to map statistical learning abilities on to the known systems for learning and memory. That is, they wished to known whether the neural activity better aligned with a slow capacity-limited learning system governed by the cortex or a fast flexible system supported by the hippocampus and surrounding medial temporal lobe structures (O'Reilly, Bhattacharyya, Howard, & Ketz, 2014). Later, studies of the neural correlates unearthed a broad functional network including both systems (Batterink et al., 2019; Giesbrecht, Sy, & Guerin, 2013; Hall et al., 2018b; Karuza et al., 2017). Yet much of the neuroimaging work has taken a modular view, looking at hippocampal activation rather than network wide activation. There has also been a focus on sequential learning and how this relates to procedural learning supported by frontal-striatal networks. Far less imaging work has been done with spatial regularities and a more central cognitive process. In order to understand how the brain learns regularities, at any level of cognition, one must consider memory.

Learning and memory are inherently linked; and all types of learning, including the statistical and incidental forms, can be understood in terms of the underlying contributions made by two classically distinct memory systems in the brain. A declarative (or explicit) system for facts and events that is consciously accessible. And a non-declarative (implicit) system for procedures and information that is automatic or unconscious. The seminal report was nearly 60 years ago. Patient H.M. (Scoville & Milner, 1957) suffered damage to his medial temporal lobe (MTL) including bilateral hippocampus, and was unable to remember new facts and events. H.M. was able to remember new information via implicit learning; evident in performance measures, such as in faster responses to items in a sequence (see Clark & Maguire, 2016). This curious profile of impaired explicit memory but intact implicit memory was soon corroborated by evidence from hippocampal-amnesia patients and animal studies (Squire, 1992). We now know that hippocampal amnesia patients have normal performance on a range of implicit learning tasks, including artificial grammar learning, probabilistic category learning, perceptual skill learning, and some priming tasks (Clark & Maguire, 2016). Yet show impairments on a range of explicit tasks. The classification of memory systems in the brain has forked into two distinct faculties: an explicit system that depends on the MTL, and an implicit system that does not and instead recruits cortical areas. Aside from the anatomy, explicit and implicit learning are distinguished by other features, such as the speed of learning and the reportability (McClelland, McNaughton & O’Reilly, 1995). The implicit/explicit dissociation in memory was foundational for the field of cognitive neuroscience because it provided the first indication that memory was not a unitary process, but rather memory incorporated functionally specialized sub-processes. However, one cannot make generalisations from the patient work alone. Many findings relied on failing to find a difference in the preserved abilities (like implicit learning) but using null hypothesis significance testing (NHST; such as Bayesian analysis) was not routinely done. The degree of reorganization after damage is difficult to characterise, as is the degree to which behaviour may reflect compensation by intact regions. Nevertheless, the impact of this work can be still felt today in the neuroscience models that have been applied to study statistical learning today.

The Complementary Learning Systems theory (McClelland, McNaughton & O'Reilly, 1995) summarizes the idea of separate memory systems for MTL and a slow cortically-based mechanism. It provides a computational framework to understand the tradeoff between functions that require memorizing distinct experiences (e.g., where I parked my car today versus yesterday), and memorizing regularities across multiple experiences (e.g., where is a good place to park my car generally). It posits distinct roles of the hippocampus and cortex in representing each type of memory. It also distinguishes these types of memory based on explicit or implicit representations and the speed of acquiring the knowledge. However, this literature has not had a focus on statistical learning, and it falls short of being able to explain the finding of impaired contextual cuing with MTL damage (Chun & Phelps, 1999). On a conceptual level, behavioural studies show that both implicit and explicit memory are often acquired alongside one another during statistical learning (Batterink, Reber, Neville, & Paller, 2015; Preston & Gabrieli, 2008; Taylor, Krakauer, & Ivry, 2014) which means that isolating implicit behaviours may be problematic. As such, these memory models have evoked controversy by some (e.g., Shanks, David & John, 1994), and others have proposed abandoning the terms entirely in favour of a model based on learning characteristics (see Reber, 2013 for a review).

One such alternative framework was proposed by Paul Reber, who frames statistical learning as a principle of the brain, rather than a system in the brain, thereby rejecting the dissociation between explicit and implicit memory. Instead, statistical learning is framed as an emergent property of a general and pervasive plasticity (Reber, 2013). This posits that all neural circuits lead to adaptive reshaping of function to match experience. This framework is useful to understanding domain-generality since it integrates the results from a variety of statistical learning phenomena, based on how the learning proceeds (i.e., as a result of structured experience). According to this framework, encoded statistics reflect changes in brain activity that are intrinsic to the retrieval process. Further, this type of storage could be operating via a neurobiologically simpler mechanism than the one presented in the complementary systems theory. Specifically, it does so by allowing for implicit learning that operates on the representations formed by the MTL memory system via a distributed system. This ties back to the distinction made between what is learned and how it is used by the system. Critically to the field of statistical learning, it explains how contextual cuing without awareness may still involve the MTL, whereas the Complementary Learning Systems theory disallows MTL involvement in implicit contextual cuing.

Neural Correlates in fMRI Studies

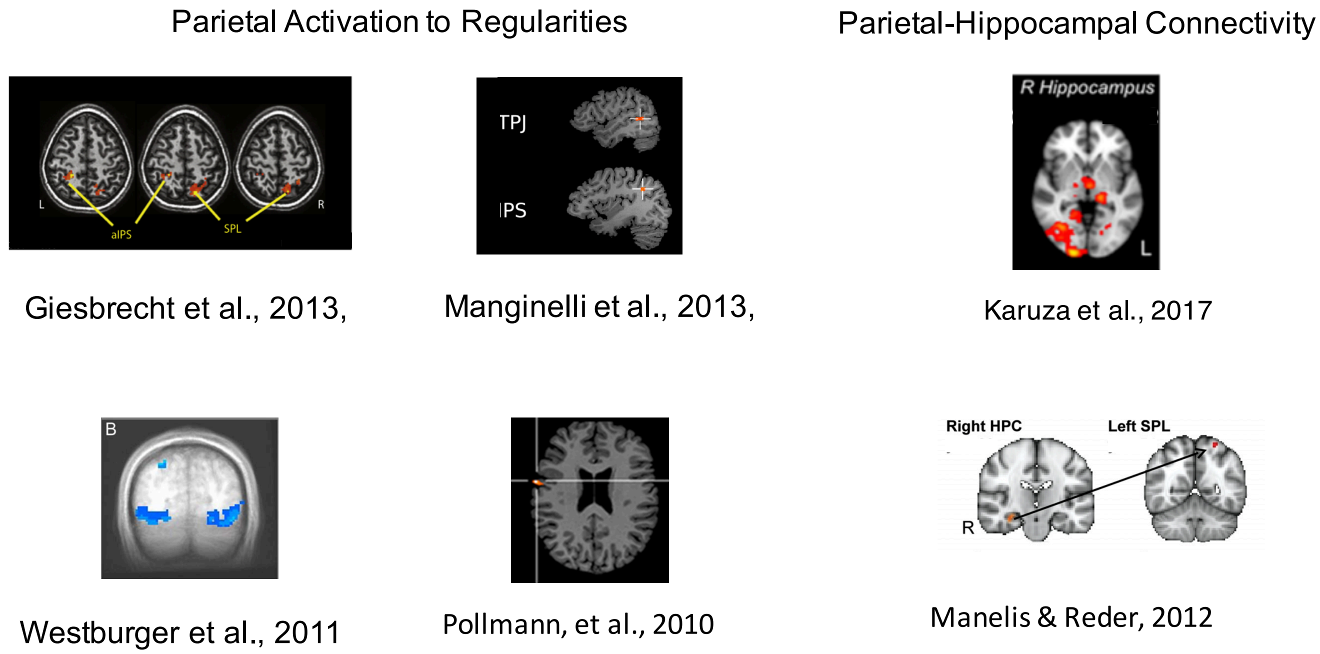
These learning and memory systems have been observed directly in healthy individuals using functional-MRI (fMRI). This approach assesses fine-grained spatial dynamics of neural activity via measuring blood-oxygen-level-dependent (BOLD) activation patterns within different regions of interest. Across the statistical learning literature, different authors have focused on different neural regions, but there are consistently widespread patterns of activation across the brain. Integrating across neuroimaging studies of implicit and statistical learning, processing structure relative to random or unlearned input is associated with activation of the following areas: sensory cortex; MTL and hippocampus; striatum and basal ganglia; the prefrontal cortex; and the posterior parietal cortex. There is some evidence that sensory areas are recruited in a domain-specific manner (see Conway & Christiansen, 2006; Frost, Armstrong, Siegelman, & Christiansen, 2015), with visual tasks recruiting higher visual areas (e.g., Karuza et al., 2017; Pollmann & Manginelli, 2010; Turk-Browne, Scholl, Chun, & Johnson, 2009) and language tasks recruiting linguistic areas, such as Broca's area in the left Inferior Frontal Gyrus (IFG: Karuza, 2014; McNealy, Mazziotta, & Dapretto, 2006). However, a number of cortical and subcortical brain areas are commonly activated across a range of tasks that have included: artificial grammar learning (AGL), serial reaction time (SRT) tasks, probabilistic classification, and visual statistical learning (see Batterink et al., 2019) in line with the notion of a domain-general mechanism.

The neuroimaging findings generally agree that the hippocampus is involved, and particularly for spatial relationships. For example, changes in hippocampal activity are associated with viewing repeat vs. non-repeat arrays in contextual cuing (Geyer et al., 2012; Giesbrecht et al., 2013; Greene, Gross, Elsinger, & Rao, 2007; Preston & Gabrieli, 2008; Westerberg, Miller, Reber, Cohen, & Paller, 2011). Convergent evidence has been observed across a number of statistical learning paradigms, such as for viewing scenes with embedded probabilities between shapes (Karuza et al., 2017), learning covariation in visual sequences (Turk-Browne, Scholl, Johnson, & Chun, 2010b), and in complex versions of the SRT task

(Albouy et al., 2015; Rieckmann et al., 2010). Thus, MTL involvement is consistent with the patient work, and appears somewhat domain-general but with the hippocampus being recruited for spatial regularities and the striatum recruited for sequential regularities in motor learning (Goldfarb, Chun, & Phelps, 2016; Rieckmann et al., 2010).

The time course of hippocampal activation tends to follow an early-to-late pattern where activations are often observed early on during exposure then reduce over time (Geyer, Baumgartner, Müller, & Pollmann, 2012; Giesbrecht, Sy, & Guerin, 2013; Greene, Gross, Elsinger, & Rao, 2007). In some studies, the magnitude of learning positively related to early hippocampal activation, though the sample sizes were small for conducting correlation analyses (Giesbrecht et al., 2013; Karuza et al., 2017; Turk-Browne, Scholl, Johnson, & Chun, 2010b). This pattern was also observed for sequence learning in the SRT task (Albouy et al., 2015; Rieckmann et al., 2010). One explanation of the disengagement of the hippocampus with exposure is that it reflects competition between the striatal and MTL systems. This is discussed in relation to models of habit or skill learning that propose practice (or exposure) leads to increased processing efficiency and reduced reliance on the MTL system. This evidence paints a nuanced picture of a domain-general statistical learning mechanism that is supported by interactions between the declarative and non-declarative systems (Batterink et al., 2019; Reber, 2013).

Beyond subcortical structures, the neuroimaging evidence points to a contribution from higher-order cortical regions, notably within dorsal prefrontal and parietal regions. While these areas are well-described in models of voluntary attention and memory retrieval (Corbetta, 1998; Summerfield et al., 2006) and explicit learning (Fuster, 2001), their involvement in implicit memory and attention is less clear. Importantly, fMRI studies show increased activity in dorsal frontoparietal networks during implicit learning tasks (summarized in Figure 8). The involvement of DLPFC and PPC has been linked to domain-general information processing for attention and memory that is biased by encountered regularities. For example, activation of cortical control regions has been observed in spatial statistical learning tasks (Giesbrecht et al., 2013; Karuza et al., 2017; Manginelli, Baumgartner, & Pollmann, 2013a), probabilistic sequence learning tasks (Turk-Browne et al., 2009), and artificial grammar tasks (Forkstam, Hagoort, Fernández, Ingvar, & Petersson, 2006). The ubiquitous involvement over a range of types of tasks, structures and inputs would be consistent with a domain-general mechanism. A number of studies have focused on the contextual cuing paradigm. These tend to show increased BOLD activation to repeat displays; particularly in areas such as the temporal parietal junction (TPJ), inferior parietal sulcus (IPS), superior parietal lobe (SPL), medial prefrontal (mPFC), and IFG (Giesbrecht et al., 2013; Manginelli, Baumgartner, & Pollmann, 2013a; Pollmann, 2012).


Parietal Activation to Regularities

Parietal-Hippocampal Connectivity

Giesbrecht et al., 2013,

Manginelli et al., 2013,

Karuza et al., 2017

Westburger et al., 2011

Pollmann, et al., 2010

Manelis & Reder, 2012

Figure 8. Summary of fMRI findings showing activation in cortical areas, such as the TPJ, IPS and SPL within the left posterior parietal respond to structure or regularities in spatial statistical learning tasks. Contrasts show activity for predictive structured displays compared to novel, non-predictive displays. Red indicates increased activity to structure. Blue indicated reduced activity.

An early and often cited study by Manginelli and colleagues (2013a) focused on the cortical areas that are linked to working memory functions. They used a localizer task to map brain areas that responded to capacity limits in a working memory. In the same participants, functional activity was recorded during spatial contextual cuing and the regions of overlapping activity were identified. These were a number of regions including the temporal parietal junction (TPJ) and inferior parietal sulcus (IPS). To investigate the time course of learning there were two groups: An fMRI-last group was scanned after six epochs of cuing, and an fMRI-first group was scanned at the beginning of the first epoch before learning had occurred. For the fMRI-first group, there was no activation during initial learning (in epoch 1) that related to cuing behaviour later on. In the fMRI-last group, repeat displays were associated with increased BOLD signal in the left IPS, and this correlated with the magnitude of cuing across individuals (Manginelli et al., 2013a). The authors related this finding to the role of the PPC in memory maintenance where information retrieved from long-term memory to guide top-down attentional by retrieval (Manginelli et al., 2013a). Also, in the fMRI-last group, the right TPJ and ventral occipital areas had greater activity for repeat than novels - the opposite pattern to IPS. But since TPJ activity was not modulated by the change in cuing magnitude over time, the authors proposed it may have reflected bottom-up processes to do with memory-cue detection that were constant across time (Manginelli, Langer, Klose, & Pollmann, 2013b). The correlations between evoked activity and cuing magnitude may be spurious, due to a small sample size. Also, the failure to detect activity changes in the fMRI first group could suggest a lack of sensitivity of BOLD signal early in learning, or that working memory areas are only recruited later in the learning phase, during exploitation rather than formation of implicit context memories. Regardless of these caveats, other work corroborates a pattern of increased activity in posterior parietal cortex for repeat displays compared to novel displays (Giesbrecht et al., 2013; Kasper, Grafton, Eckstein, & Giesbrecht, 2012; 2015). En masse, this work collapses over all epochs, and so does not capture the temporal dynamics of learning in contextual cuing.

Only a limited number of fMRI studies have examined how repeats and novel conditions relate to patterns of brain activity across time. These show increasing IPS activity to repeat displays with exposure (Giesbrecht et al., 2013; Preston & Gabrieli, 2008). Other studies show activation in prefrontal areas, when using the contextual cuing task (Manelis & Reder, 2012; Pollmann, 2009) or the Visual Statistical Learning task (i.e., Fiser and Aslin, 1991) to tap statistical learning (Karuza et al., 2017). Moving beyond BOLD activation, a recent study measured functional connectivity during passive exposure to visual structure (Karuza et al., 2017). A network involving the precuneus and the frontal cortex was identified, which reduced connectivity during exposure, and this reduction predicted recognition of the pair structure at test. Together, this work highlights the importance of dynamic changes in brain activity during statistical learning, consistent with the suggestion frontoparietal circuits interact with one another in a time-varying manner to adapt brain function in support of behaviour (Bassett & Mattar, 2017; Bassett, Yang, Wymbs, & Grafton, 2015).

As a whole, the neuroimaging work has been successful in providing fundamental knowledge about patterns of brain activity evoked by statistical learning in healthy individuals. The findings point to a role of the hippocampus and sensory cortices, along with downstream association regions within the prefrontal and parietal cortices (also known as cognitive control regions). The work is important because it extended on early competition models of memory (McClelland, McNaughton & O'Reilly, 1995) to implicate a distributed network that involves both cortical and subcortical processing regions shared by explicit and implicit forms of learning (Frost et al., 2015; Reber, 2013). An early notion was frontal and parietal activation during implicit learning related to working memory circuits that were recruited to retrieve memories for voluntary behaviour; consistent with the account of a domain-general system that operates across a variety of tasks and inputs. However, the fMRI work has not conclusively identified a cortical mechanism that directly interferes with the statistical learning process. Across the brain, the activity changes associated with processing learned displays have not reflected a signal signature, in terms of the temporal dynamics (early or late, and static or dynamic over time) or the direction of activity change (increase or decrease in key areas). Some studies reported increased activity to structure, and some report repetition suppression effects (see Westburger et al., 2011). Some activity appears to be fixed across time, such as in the right TPJ (Manginelli et al., 2013a), and some activity appears to be associated with the dynamics of learning (i.e., the interaction in the left IPL). Whether the activity predicts learning behaviour across individuals is short on definitive evidence. To date, the direct contribution of cortical activity for learning is an open question.

The positive evidence for frontal and parietal activation raises the question: Does the activation of cortical control regions play a *causal* role in the statistical learning process, or does it reflect concurrent processes that operate on the learned material, or the task more generally, that are not critical for learning itself? The evidence provided by fMRI studies is correlational. Therefore, it remains possible that the frontal and parietal activation was produced by changes in attention and working memory operations that were not central to the emergence of incidental learning about regularities. This was especially unclear in the many studies that averaged brain activity over conditions or were not designed to measure changes over time (low power to assess the interaction or to compare early and late stages). As a technique, fMRI has poor temporal resolution and so it is not well suited to questions about learning dynamics. The few studies that did characterize the time course of neural changes (either via the interaction or by splitting the data into stages) may have observed changes to do with explicit practice on the task or operations that tracked exposure, like attentional engagement, but did not contribute to statistical learning directly. Of note is that the changes in frontal activation may reflect procedural learning of motor responses, which are correlated with the structure in SRT tasks and category learning tasks. Causal evidence is now needed to advance our understanding of cortical involvement in implicit statistical learning.

Causal Methods for Understanding Brain Activity

With its ability to influence neural activity directly, non-invasive brain stimulation is well-placed to help elucidate the cortical locus of implicit statistical learning. Brain stimulation approaches can provide novel insights into the causal brain-behaviour links that govern an underlying cognitive process (Bestmann, de Berker, & Bonaiuto, 2015; Filmer, Dux, & Mattingley, 2014). Techniques such as transcranial magnetic stimulation (TMS) or transcranial direct-current stimulation (tDCS) can be used to modulate or perturb a target brain region and the resulting changes can be measured at different levels of activation; spanning from local changes in neural activity to larger networks and effects on cognition and behaviour directly). The effects are painless and temporary, and direct current stimulation has been used in human research for over 40 years now. Delivering TMS involves a coil held against the scalp that uses the fast switching of a magnetic pulse on and off to produce an electrical current that elicits action potentials in the targeted cortical tissue. For example, with the TMS coil placed over the motor cortex, a single pulse over the thumb area will elicit a finger twitch 25 ms later or a leg twitch 80 ms later. The timing and intensity of the pulses can be manipulated to produce changes to synaptic plasticity. A common example is repetitive TMS (rTMS) which is used to disrupt neural excitability in a given region for up to 60 minutes.

Another popular technique is transcranial direct current stimulation (tDCS). This type of stimulation also affects cortical excitability and function (Filmer et al., 2014), but without directly producing action potentials (Nitsche et al., 2008). Instead, tDCS changes the likelihood that neurons will fire, which in turn has a measurable effect on excitability, firing rates, and other indices of neural activity (Filmer et al., 2014). It works by delivering a weak electrical current, usually between .5 to 2 mA, through the brain tissue via electrode pads attached to the scalp. Conventional tDCS involves two electrodes: an anode and a cathode.

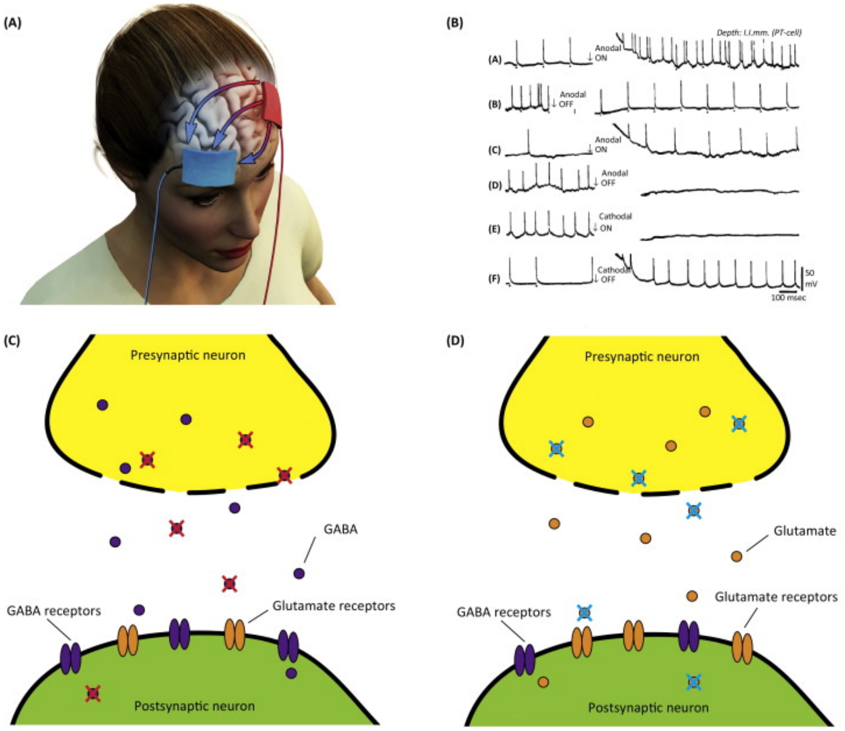


Figure 9. Neurobiological mechanisms of tDCS. (A) Schematic of the application of tDCS via two electrodes on the scalp and the induced current flow from the anode (red) to the cathode (blue). (B) Modulation of neuronal spike-timing by tDCS. (C) Inhibitory effect of tDCS by increasing GABA receptors. (D) Excitatory effect of tDCS via an increase in Glutamate. Adapted with permissions from Filmer et al., 2014.

One electrode is placed over the site of interest and another electrode used as a reference; although other electrode arrays have also been used (Datta et al., 2009). The effects of tDCS can be measured online, during active stimulation, or offline, such as with a pre-post design. And stimulation can have either a depolarising (excitatory) or hyperpolarising (inhibitory) effect on excitability depending on type of stimulation being used. For example, placing the anode over a targeted motor area caused an increase in excitability (Nitsche & Paulus, 2000); and reversing the direction of current flow by placing the cathode over the target region (cathodal tDCS) caused a decrease in excitability (Wagner et al., 2007). However, such polarity-dependent effects are not guaranteed, and other patterns are increasingly being observed in the literature (Batsikadze, Moliadze, Paulus, Kuo, & Nitsche, 2013; Esmaeilpour et al., 2017; Monte-Silva, Kuo, Liebetanz, Paulus, & Nitsche, 2010; Ohn et al., 2008). Yet by delivering bidirectional currents to the cortex (Figure 5), one can infer involvement of a target brain area in a measured process (Bestmann et al., 2015).

Compared to TMS which is relatively focal, tDCS can influence activity in large cortical areas. For this reason, along with its affordability and low risk profile (Nitsche, Liebetanz, et al., 2003a), the methodology has proven useful as a therapeutic technique in the treatment of neurological and psychiatric conditions (e.g., depression; Fregni et al., 2006). The technique has also gained momentum as a way to augment cognitive training, with evidence that combined tDCS and training improves outcomes over training or tDCS alone (e.g., Filmer et al., 2017a; 2017b). In a research context more broadly, tDCS is being used to investigate the interfering roles of key neural circuits in a given cognitive process. These have included processes related to motor learning (Nitsche, Schauenburg, et al., 2003c; Stagg, Jayaram, et al., 2011b), visual perception (Antal, Nitsche, & Paulus, 2001), attention and working memory (Fregni et al., 2005; Jacobson, Koslowsky, & Lavidor, 2012; Kang & Paik, 2011), and decision-making context (Filmer, Varghese, Hawkins, Mattingley, & Dux, 2017). As a foundational step, the results of these studies provide causal evidence that a given brain region is involved in a given cognitive process. Further to this, when designed well, they can expose the relationship between a neural mechanism, such as consolidation, and a cognitive process, such as motor learning.

Precisely how tDCS is able to alter performance across a variety of tasks is not yet fully understood, although there are theories about its underlying mechanisms. A dominant perspective is that tDCS changes the resting membrane potential of neurons near the stimulation site which leads to an increase or decrease in the likelihood of an action potential firing (e.g., Nitsche et al., 2003; 2008). Supporting evidence comes from in vitro animal studies showing that tDCS altered the firing rates of neurons (Bikson et al., 2004; Bindman, Lippold, & Redfearn, 1964). Much of what we know about tDCS in humans comes from studies of the motor cortex, which used TMS-evoked potentials as an index of neural excitability (Nitsche & Paulus, 2000; Nitsche et al., 2004). A recent meta-analysis found that the polarity-dependent effect whereby anodal tDCS leads to excitation and cathodal produces inhibition was reliable in the motor cortex (Jacobson, Koslowsky, & Lavidor, 2011). But that effects were far more heterogeneous outside the motor domain.

At a cellular level, tDCS mechanisms have been investigated in pharmacological studies. These suggest that the online effects of tDCS depend on sodium and calcium channels (Nitsche, et al., 2003b), since sodium channel-blocking drugs prevented the anodal excitability increase in humans (Liebetanz, 2002). Both the online and offline effects appear to be mediated by N-methyl-D-aspartate (NMDA) receptors, which respond to the excitatory neurotransmitter glutamate (Luft, Pereda, Banissy, & Bhattacharya, 2014; Nitsche et al., 2008). When drugs that block NMDA receptors were administered before stimulation, tDCS was less effective at modulating MEP amplitudes (Nitsche et al., 2003), and the long-term effects were reduced (Liebetanz et al., 2002). These NMDA receptor-dependent changes are believed to be a key mechanism that may explain learning effects observed with tDCS (Clark, Coffman, Trumbo, & Gasparovic, 2011; Hunter et al., 2015). There is also evidence that GABA receptors are involved; a major inhibitory neurotransmitter (Stagg, Bestmann, et al., 2011a; Stagg et al., 2009). And emerging evidence suggests the balance between excitation and inhibition, mediated by these neurochemicals, may provide a more meaningful explanation of tDCS effects across individuals.

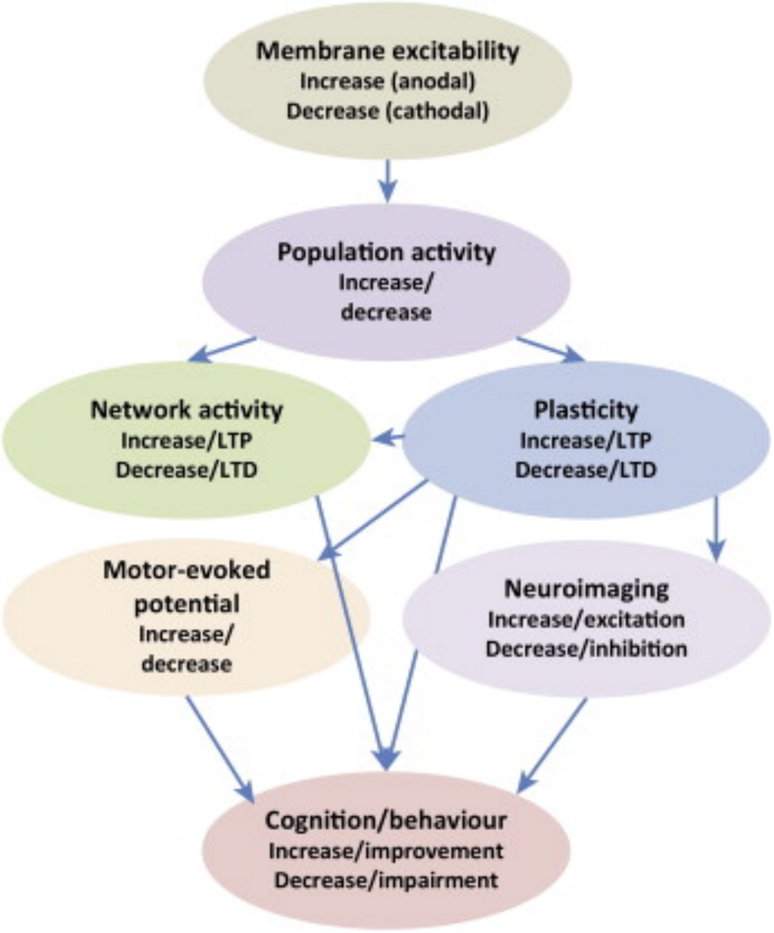


Figure 10. Levels of action for understanding tDCS effects on behaviour. Used with permissions from Bestmann, et al., 2014.

The totality of tDCS-effects on the brain can be classified into different levels of action (Figure 10). Modulation of membrane excitability in a target region produce net changes to population activity, which can be heterogeneous and may not be in the same direction as the induced current. Reviews have shown that outside the motor cortex, the anodal-excitation/cathodal-inhibition account is varied (Batsikadze et al., 2013; Rosenkranz, Nitsche, Tergau, & Paulus, 2000), which has led authors to argue for a ‘perturbation’ account of tDCS-effects (Bestmann et al., 2015) in place of the earlier excitation/inhibition framework. According to the perturbation view, tDCS is a method for disrupting normal brain function by leveraging bi-directional currents applied to target regions and measuring resulting changes to cognition or behaviour. This means that having appropriate active control conditions is key when using tDCS to understand aspects of cognitive function. Unfortunately, such levels of control have not been consistent across the literature, as you will see in the section below. Put in the context of statistical learning, tDCS can provide a much-needed test of the idea that cognitive control regions tied to explicit operations are also important for implicit statistical learning. Given the large number of regions that have been linked to statistical learning in spatial vision, tDCS is better suited to modulate behaviour compared to TMS, that may be too focal. Finally, the constant current delivered by tDCS modulates excitability in an activity-dependent manner. This means one can measure behaviour online, during the stimulation, and know that changes reflect an interaction between the induced electrical current and the endogenous task-evoked activity.

Using tDCS to Understand Cognition

The modulation of cortical activity by tDCS can influence performance measures that pertain to learning. This has been extensively studied in relation to motor learning, where tDCS targeting functional regions in primary motor and parietal cortex was found to improve performance on sequence learning tasks (Reis & Fritsch, 2011; Stagg, Jayaram, et al., 2011b). This effect was also found with implicit motor learning (Nitsche, Schauenburg, et al., 2003c), therefore showing the ability of tDCS to modulate behaviours not privy to awareness. Scaling up from sensory areas, research has shown facilitation of knowledge acquisition following stimulation of the PFC. For example, learning novel vocabulary was improved by five consecutive days of anodal tDCS targeting the left TPJ compared with sham (Meinzer et al., 2014), and by one session of anodal tDCS targeting Wernicke's area compared to cathodal and sham (Flöel, Rösser, Michka, Knecht, & Breitenstein, 2008). Training effects on a decision-making task were disrupted by online stimulation (anodal or cathodal) over the dorsolateral prefrontal cortex (DLPFC) compared to a region control, and to a montage targeting DLPFC with a different reference location (Filmer et al., 2013). In line with the role of the PPC in directing spatial attention, cathodal tDCS to the right PPC impaired visual search (Ball, Lane, Smith, & Ellison, 2013). These studies demonstrate the efficacy of tDCS for modulating explicit operations to do with learning, decision-making and attention.

There has been only limited work on implicit operations. In this domain, tDCS was found to alter implicit associations in language tasks. For example, cathodal stimulation of left post temporal gyrus, over Wernicke's area during a categorsation task led to reliance on high-dimensional solutions over low-dimension solutions, compared to stimulation over the vertex (Perry & Lupyan, 2014). Similarly, repetitive-TMS (rTMS) targeting the left inferior frontal gyrus (Broca's area) selectively altered accuracy in low- but not high-dimensional categorization (Lupyan, 2012). In probabilistic learning, rTMS over left DLPFC improved performance on weather prediction tasks compared to stimulating the vertex or visual cortex (Cho, Yoon, Lee, & Kim, 2012; Kincses, Antal, Nitsche, Bártfai, & Paulus, 2004; Vercammen et al., 2011). Anodal stimulation to the right but not left DLPFC affected complex sequence learning in the SART task (Janacsek, Ambrus, Paulus, Antal, & Nemeth, 2015). This work implicated activity in the targeted cortical areas during incidental learning. One of the major drawbacks of this work is that these types of implicit tasks often conflate learning with motor output. Similar to the imaging work on spatial regularity learning, these results do not differentiate between procedural learning in the task, believed to alter frontal-striatal networks, and statistical information processing that may be distinct from this. So, while parietal areas may be involved in explicit attentional operations, frontal areas have been implicated in explicit and implicit learning tasks to differing degrees.

To date, no studies have used tDCS to investigate statistical learning outside the sensory domain. Indeed, the efficacy for using tDCS to understand MTL supported learning processes remains unclear given the depth of these structures. An account of statistical learning that suggests a cortically-mediated learning mechanism would predict an effect of tDCS delivered to these regions. Based on the current idea that tDCS modulates the resting membrane potential of neurons (e.g., Nitsche's et al. (2008) theory), stimulation will be most effective when it is paired with an action or task that involves the brain area being stimulated, so that an action potential is initiated by that task. That means that a difference in statistical learning during active brain stimulation (either anodal or cathodal) compared to a sham-control would indicate causal involvement of that network. Substantiating cortical involvement across different paradigms will be important to provide causal evidence in line with a mechanism for extracting structure beyond task-specific effects. Thus, combining a brain stimulation technique that is suited to perturbing large cortical areas with behavioural measures of statistical learning may garner a deeper understanding of the neural substrates that are critically important for statistical learning in the context of cognition.

Project Motivations and Aims

The purpose of this thesis is to examine the causal role of frontoparietal activity in the statistical learning process. Based on the key themes that emerged from a review of the relevant literature, the central question was distilled into three research aims: (1) Explore whether causal modulation of the cortex by tDCS has an effect on forms of statistical learning that occur outside the motor domain (i.e., SRT tasks); (2) Investigate whether the associated activation of the left frontoparietal cortex observed by fMRI directly contributes to the emergence of learning dynamics produced by exposure to regularities, with a focus on behavioural change over time; (3) Interrogate the degree to which cortical involvement may generalises across tasks that tap the same statistical learning process, consistent with the evidence of a domain-general mechanism for extracting regularities with experience that operates across a variety of stimuli, structure and task domains.

The first aim will be achieved by leveraging recent technological advances in causal brain stimulation methods. The use of electrical brain stimulation in cognitive neuroscience has already been successful in shedding light on the neural networks that support explicit forms of learning, such as cognitive training (Filmer et al., 2013; 2017) and deliberate skill learning (Reis et al., 2009). The prefrontal cortex and the parietal cortex are higher-up in the information processing hierarchy (Treisman and Gelade, 1980), and are believed to represent information in a domain-general way that is abstracted from the lower-level sensory inputs that are domain-specific. Therefore, by directly modulating brain activity during the formation of statistical learning, we can investigate whether frontal brain areas are also important for implicit, memory-guided learning. Unlike rTMS or cTBS protocols that are delivered offline, prior to a behaviour being assessed, tDCS allows for measuring behavior *online*. This aspect of the methodology is helpful to avoid the contamination offline consolidation processes on measured learning behaviour. Critically, the direct current method allows us to look for causal evidence regarding activity in frontoparietal regions and the dynamics of statistical learning. Since fMRI cannot provide evidence that PFC and PPC regions are necessary, and the stroke work cannot rule out compensatory networks due to plasticity after brain damage, brain stimulation evidence is best suited to investigate the role of cortical regions in statistical learning. Issues in tDCS research, such as a lack of experimental controls, use of small sample sizes, and generalizations being made without testing a variety of tasks, have contributed to setbacks in the field (see Filmer et al, 2014 and Bestmann et al., 2014). Thus, the second aim will be achieved by following best-practice brain stimulation design by using large samples, bidirectional currents, active control regions (not simply the vertex or visual cortex) where appropriate. The third aim will be achieved by using a variety of tasks to tap the same underlying statistical learning process. Together, these will advance our understanding of the cortical contribution to a general statistical learning process in the brain.

Thesis Outline

Inherent to these long term-goals was using a paradigm that separated motor output from the learned regularities, namely the well-known contextual cuing paradigm. The first step was to determine the conditions under which robust contextual cuing behaviour would be observed. Specifically, Chapter 2 presents a behavioural study that assessed the role of visual exposure duration and context capacity in producing robust cuing behaviour. In Chapter 3, we turn to the key focus of causal neural substrates of statistical learning and present the first brain stimulation study investigating frontoparietal involvement in spatial statistical learning assessed via contextual cuing. Chapter 4 explored the issue of a domain-general mechanism of statistical learning and found that cortical involvement generalised to another well-known statistical learning task that used passive exposure, namely the Fiser task. Specifically, after failing to observe a tDCS effect with this exposure-test measure, we investigated online cuing again, but with identity-based regularities. To do so, a new task was developed that harnessed the strengths of a cuing task combined with the transitional probability structure that defined identities of distractor items, while controlling for spatial regularity. This last experiment did converge on causal cortical involvement early in learning across different types of structure and stimuli. The final discussion in Chapter 5 summarizes the key findings across all experiments and elaborates on the impact of the work as a whole by examining the broader implications and considering extensions of the work that could be beneficial to the field.

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CHAPTER 2:

THE SPEED OF PROCESSING CONFIGURAL REGULARITIES FOR LEARNING

This manuscript is under review at Attention, Perception and Psychophysics.

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Abstract

Past experience with invariant visual information plays an important role in statistical learning that affects the visual search process. This is captured by the contextual cuing where repeating spatial configurations produce a response time benefit to targets that is greater than the benefit when searching through novel configurations (e.g., Chun & Jiang, 1998). We investigated how rapidly these spatial regularities are extracted by the system to produce adaptive cuing behaviour that evolves over time. Typically, observers can process displays until a response is made, with up to 2000ms of visual processing time. We employed backward masking to limit processing to 300 ms, enough time for one fixation. Previous work had shown intact cuing with short presentations, but that was after learning had taken place. We showed that the formation of contextual cuing can occur with briefly presented displays. However, this was only for a situation where there were 12 configurations to learn, but not when there were 30 configurations to learn. In light of this surprising finding, we conducted two successful replications of the effects, and ruled out the possibility of latent learning being blocked by the mask. Our results highlight a powerful statistical learning mechanism that can rapidly extract predictive spatial information and use this to guide ongoing behaviour in under 300ms. The results dovetail with work showing rapid, high-capacity, gist extraction in real-world scenes.

Statistical learning plays a key role in many aspects of complex cognition. This includes those to do with language (Reber, 1989; Saffran, Aslin, & Newport, 1996), procedural skills (Howard & Howard, 1997; Nemeth, Janacsek, & Fiser, 2013; Simor & Nemeth, 2019), abstract categorization (Ashby & Maddox, 2005; Brady & Oliva, 2008; Kruschke & Johansen, 1999), and processing visual scenes (Aslin & Newport, 2012; Fiser & Aslin, 2001; Turk-Browne, Jungé, & Scholl, 2005). One of the most intriguing areas in the current statistical learning literature concerns the relationship between contextual regularities and spatial search. After only a few repetitions of a complex visual scene, the human brain extracts contextual information based on regularities in the layout of objects. When the regularities are associated with a target during visual search, target responses improve relative to conditions that don not contain regularities. This phenomenon is known as contextual cuing (Chun & Jiang, 1998; 1999; 2003) and research has shown it emerges rapidly (Chun & Jiang, 1998; Jiang & Chun, 2001; Jiang & Wagner, 2004), is robust to noise (Jungé, Scholl, & Chun, 2007; Zellin, Mühlenen, Müller, & Conci, 2014) and exhibits a high-capacity (Jiang, Song, & Rigas, 2005), all of which helps to position it in a broader framework of statistical learning abilities. However, there is little empirical work examining temporal exposure parameters that produce robust contextual cuing. A key issue is the speed with which observers can extract the regularities from a display to promote learning, and to date, direct manipulations of exposure duration remain limited. This study aims to investigate the emergence of learning in contextual cuing when backward masking is used to control viewing times.

A number of lines of research highlight how contextual cuing is both rapid and powerful. For example, the response time benefit to repeat arrays is reliable by the third set of repetitions (Chun & Jiang, 1998; Jiang & Chun, 2001; Jiang & Wagner, 2004; Zellin et al., 2014), and is preserved even if only half the items are repeated (Song & Jiang, 2005). At least 60 individual configurations can be learned across multiple days (Jiang et al., 2005), and contexts acquired on later days do not interfere with cuing for contexts learned earlier, indicating the learning is relatively unrestricted across time. The rapid cuing benefit is met by early differences in processing time as indexed by eye-tracking measures of first fixations (Peterson & Kramer, 2001), and scalp recordings in EEG (Johnson, Woodman, Braun, & Luck, 2007) and MEG (Chaumon, Drouet, & Tallon-Baudry, 2008) that show effects as within 300ms of display onset. Together, this work suggests a rapid and high-capacity mechanism for statistical learning. However, the learning conditions in these studies are limited only by how quickly the observer finds and responds to a target. So, while learning may induce differences early on, the time taken to process a display is often longer. This leaves open the question of how temporally efficient the incidental learning mechanism is itself.

Sufficient processing time appears important for robust cuing behaviour. This comes from evidence that longer display durations are associated with larger cuing magnitudes, defined as the difference between repeat and novel displays (Geyer, Shi, & Müller, 2010a; Kunar, Flusberg, & Wolfe, 2008; Ogawa & Kumada, 2008). This observation has been related to the role of eye movements in successful memory retrieval (Geringswald, Baumgartner, & Pollmann, 2012).

Further to this, some have suggested cuing cannot emerge without search, based on findings of no benefit for repeat arrays when using target-absent displays (Jiang, Sigstad, & Swallow, 2012; Kunar et al., 2008). However, that work has faced criticism from some who believe search without a target produces a different decision strategy which explains the failure to observe cuing in no-target designs. Eye tracking work has shown that cuing has little effect on the early stages of search, namely the initial fixation to the target (Zhao et al., 2012), whereas later stages of search benefit more from repeated configurations. Together, these observations have led to an argument that the cuing effect is relatively sluggish (Schlagbauer, Mink, Müller, & Geyer, 2016) and requires additional time beyond a single fixation to produce behavioural changes that indicate learning. Yet a more nuanced picture emerges when reviewing other ways observers can engage with repeating configurations across different task demands.

Early evidence that repeated spatial configurations are processed quickly came from the initial studies published by Chun and Jiang (1998). In the standard version of the search task observers could move their eyes freely to locate and identify the target, being a rotated “T” among rotated “L” distractors. Later, in Experiment 5, the authors employed shorter display durations of 200 ms to investigate the role of eye movements in producing the response time benefit for repeated contexts. Contexts were learned with the typical long exposure duration (around 2000 ms) and then in a subsequent test phase using the short duration, intact cuing was observed via an accuracy effect, with higher accuracy for repeat displays. The authors concluded that the eye movements afforded by longer display durations may not be necessary to produce cuing by a learned context, in line with their broader argument that subjects learn the global spatial layout that can be matched within the time of an initial fixation. However, it must be noted that since encoding in this experiment took place using the long durations Chun and Jiang's results do not speak to whether the short displays are sufficient to produce incidental learning themselves. Only that the process of matching a learned configuration to the current display may occur rapidly. The authors also noted that without masking the displays, visual processing beyond the display duration may have contributed to the cuing observed at test. This was based on the seminal visual persistence work showing that information about a visual stimulus persists beyond its physical offset (Coltheart, 1980). By presenting a second stimulus shortly after the first, known as backward masking, the persistent processing can be disrupted (Bachmann, Luiga, & Põder, 2016). Thus, without using masking, direct evidence of rapid context processing has remained elusive.

Another line of evidence that can speak to processing speed comes from modified versions of the cuing paradigm that use task demands that limit processing. For example, spatial configural learning was observed with a change detection task that used brief presentations of 400 ms (Jiang & Song, 2005; Experiment 2). Subjects were exposed to dot arrays that contained repeating spatial arrangements and had to detect a change in a target dot from a subsequent probe array. After training on 20 repetitions of 18 arrays, change detection was found to be more accurate for the repeat arrays compared to novel arrays, which were added at test. This indicated humans can encode context using brief presentations, at least for simple dot arrays. The set size of 11 items was comparable to standard T and L displays that typically use 12 items. Without masking the displays, this task was not a direct manipulation of exposure duration. In a similar design, cuing effects were observed in a test phase after training that used 500ms presentations and the Ts and Ls search task (Makovski & Jiang, 2011). Once again, only repeat displays were presented during training, and so there was no measurement of the learning process online. These authors also reported a cuing effect after using 150ms presentations, however it required changing display items to make the target more salient. Together, these findings imply that humans can form knowledge about a visual context using 400-500ms presentations. Although they fall short of testing this directly.

Rapid learning of context is also evident in studies that used pop-out search tasks to impose processing limits (Geyer, Zehetleitner, & Muller, 2010b; Kunar, Flusberg, Horowitz, & Wolfe, 2007; Ogawa & Kumada, 2008). Ogawa and Kumada (2008) employed the standard T and L displays but made the target a feature singleton; a white T among black Ls, thereby enabling efficient search. In a training phase, participants were exposed to repeat and novel arrays. Their response times were within 600 ms on average; indeed faster than serial search. In a test phase, the T was changed back to the same colour as the distractors, producing the standard search task. The researchers reasoned that transfer of learning from training to test would indicate that search without requiring attending to individual array items was sufficient for encoding context. Indeed, across three experiments they found evidence of learning at test after efficient (pop-out) search with context regularities. Unfortunately, analysis of the online training data was not reported. No visible difference was evident between repeat and novel contexts in the figures, therefore whether pop-out search could produce robust cuing behaviour itself remained unclear. Interestingly, they went on to investigate what type of information was learned by assessing transfer to recombined displays made from two repeat contexts that cued the same target. These preserved individual associations between items but created a new global layout. Using this method, they did not observe transfer, and concluded that the cuing afforded by an efficient search task was driven by configural learning of the global layout rather than non-configural learning of individual items. This supported Chun and Jiang's hypothesis that contextual processing is driven by encoding the global layout and may provide a mechanistic explanation as to how rapid context processing may occur.

The work reviewed above hints that contextual information processing can occur rapidly; possibly within the first few hundred milliseconds of viewing and may not require eye movements or attention to individual items. Yet, the rapid cuing benefit was often tested after training with longer presentation durations and so cannot speak to the learning process directly. Furthermore, the work on rapid cue utilization does not differentiate between direct visual processing of the display and indirect processing of an internal representation that survived beyond display offset. In their original paper, Chun and Jiang noted that without masking the 200ms displays, processing time beyond the presentation duration could have contributed to cuing at test. They cited seminal work on visual persistence that shows how information about a visual stimulus persists beyond its physical offset (Coltheart, 1980) and this contributes significantly to perception and cognition. Thus, the previous observations of cue learning with 300-500ms presentations (e.g., Makovski et al., 2011) may have been due to iconic persistence. But by presenting a second stimulus shortly after the first, known as backward masking, the persistent processing can be disrupted (Bachmann, Luiga, & Põder, 2016; Breitmeyer & Öğmen, 2006). To date, no studies have used masking to control processing time during the formation of context knowledge itself (i.e.., learning).

In the present study, we investigated how masking affects the temporal dynamics of statistical learning in spatial scenes. Our goal was to isolate the rapid components of information processing that may be associated with statistical learning (i.e., the emergence of a cuing benefit) by using brief visual exposure that was controlled by masking. The contextual cuing task followed the method of Chun and Jiang (1998) with a random presentation of repeat and novel displays across a number of blocks of a visual search task. Except that displays were presented briefly for only 300ms then backward masked using a random line array. Random patterns such as this are highly effective for masking visual stimuli (Coltheart & Arthur, 1972). Previous work has shown that contextual cuing is effective when using 12 repeat configurations and 12 novel (control) configurations (Chun & Jiang, 1998), as well as when using larger numbers of configurations such as 32 repeat configurations (Makovski et al., 2011; Ogawa & Kumada, 2008), and up 60 repeat configurations with extended training (Song & Jiang, 2005). To test the capacity limits of a rapid statistical learning process, we opted for a mid-point of 30 repeat and 30 novel configurations for Experiment 1a and 1b. Based on the previous observation of an accuracy benefit when using 300ms presentation durations at test (Chun & Jiang, 1998), we predicted that a contextual cuing effect during masking would similarly present as an accuracy benefit for repeat displays relative to novel displays over time.

Experiment 1a

Participants

Twenty participants (μ = 21.3 years, σ = 2.61, 11 female) from The University of Queensland community completed Experiment 1a. This sample size was determined based on an *a priori* power calculation that, given a medium effect size (*d* = .5), we could observe a within-subjects Cuing × Epoch effect with 85% power and an alpha level of .05. Participants were

18 – 35 years, had normal or corrected-to-normal vision and were psychiatrically and neurologically healthy. They were paid AU$20 for attending a one-hour session. The University of Queensland Human Research Ethics committee granted study approval.

Apparatus

Participants sat unrestricted approximately 63 cm from a 19″ CRT monitor (resolution 1024 × 768; 100 Hz refresh rate) connected to an Apple iMac-mini computer and a Macintosh keyboard. The experiment was programmed with MATLAB 2015b using the Psychophysics Toolbox 3 extension (Brainard 1997; Kleiner et al. 2007; Pelli 1997).

Stimuli

Search displays contained T and L shapes (.5° visual angle) presented in white against a grey background (RGB: 80, 80, 80). Participants searched for a target 'T' (rotated 90° to the right or 90° to the left) among 11 distractor Ls (rotated 0°, 90°, 180° or 270°). Items appeared in an invisible 13 × 13 grid (16° visual angle). The items were allowed to jitter in their cell upon each repetition of a given display so as to minimise perceptual learning effects to the grid and to item locations. Items were equally distributed across the four visual quadrants of the screen to avoid clustering that might make a given display more salient than another. To avoid biases for searching in a given quadrant, the target locations were evenly distributed across quadrants in the repeat and novel conditions.

Mask stimuli were created using a pattern array that contained 200 rectangular shapes (each subtending .5° × .1° visual angle) with a random orientation (0°, 15°, 45°, 75°, 90°, 105°, 135°, 165°). The locations of the T and Ls, which are composed of vertical and horizontal elements, were masked with lines of oblique orientations. The remaining mask lines were randomly determined. This kind of backward stimulus had produced effective masking in other work (Turvey, 1973).

Search Task

In the search task (Figure 1a) each trial began with a fixation cross for 500 ms, followed by the display for 300 ms, which was backward-masked with the line-array for 500 ms. There was a prompt screen ("?") until response for 2000ms, followed by a blank inter-trial-interval (ITI) for 500 ms. Participants responded to the orientation of the target 'T' using the 'z' and 'm' keys with index fingers on each hand as quickly and as accurately as possible. They received summary feedback about their performance after each block.

Each block contained two types of displays (Figure 1b). There were 30 repeat displays in where a given target location (but not the orientation) was associated with a particular distractor configuration (location and orientation) and this was fixed across block. In novel displays, the same number of target locations were used (30), but the targets appeared with ever-changing distractor configurations – participants were not informed of this manipulation. On any given trial, the orientation of the target, which was the decision-relevant feature, was random. This meant repeat displays did not cue the motor response, only the target's position in the display. Repeat and novel displays appeared once per block in a randomized order. Displays were generated at the beginning of each session and were not the same across individuals. Participants completed 12 blocks of 60 trials (720 trials in total), in which repeat displays and novel displays were presented in a random order, and the key dependent variable was accuracy.

Data Analysis

For all experiments, data were collapsed into epochs with four blocks in each and RTs were restricted to correct responses only. RTs were trimmed for outliers > 3SD above the mean, calculated for each condition. Trimmed or missing data did not exceed 5% for any individual participant. Frequentist statistics are reported using an alpha level of .05 and two tailed tests. The data were also examined by calculating Bayes Factors for each of the dependent variables (accuracy and RT). A Bayes Factor provides an index of the fit of the data under the alternative hypothesis (i.e., a cuing benefit), relative to that under the null hypothesis (i.e., no difference between repeat and novel responses). Bayes Factors above 1 represent more evidence in favour of the alternative relative to the null hypothesis, whilst Bayes Factors below 1 suggest relative evidence in favour of the null hypothesis. Whilst Bayes Factors represent a continuum of evidence favouring the null and alternative hypotheses, we adopted the Jeffrey's scheme (1961) cut-offs to facilitate their interpretation. A Bayes Factor above 3 or under 1/3 provides substantial evidence for the alternate hypothesis or null hypothesis, respectively, and a Bayes Factor between 1/3 and 3 provide only anecdotal evidence suggesting the data are insensitive.

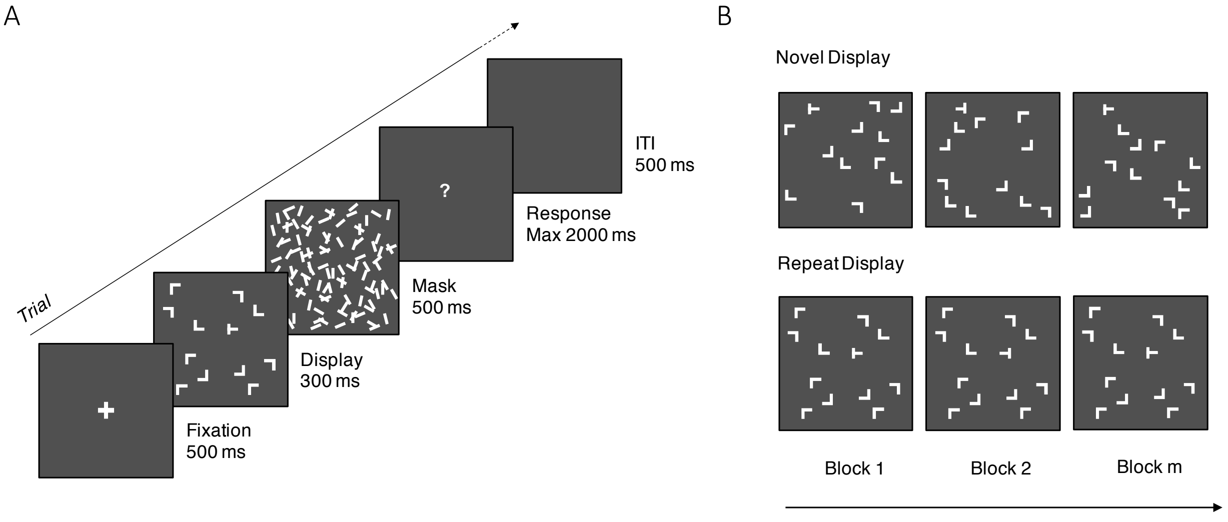

Figure 1. (A) A schematic illustration of the trial sequence used in the masked contextual cuing paradigm. (B) A schematic illustration of the repeat and novel display conditions. In novel displays, the target location was fixed, but the distractor configuration changed each block. In repeat display, both the target location and the distractor configuration were fixed across blocks, only the target orientation was random. Items are not drawn to scale.

Results

In Experiment 1a, there was no evidence to support contextual cuing from brief (300 ms) masked displays (Figure 2a). A repeated-measured ANOVA on accuracy with factors Display Type (repeat and novel) and Epoch (1 to 3) revealed a main effect of Epoch, $F_{2,38}$ = 5.273, p = .009, η_p^2 = .217, indicating a general practice effect over time. But no main effect of Display Type, $F_{1,19}$ = .455, p = .508, and no Display Type × Epoch interaction, $F_{2,38}$ = .329, p = .722. For the Bayesian ANOVA, we compared a model that included the main effect of Epoch (null model) to a model that also included the main effect of Display (single effect model), and to a model that included both the Display effect and the Display × Epoch interaction (interaction model). Since the models have a transitive relationship, the null model was compared to these two models by division. When looking at the accuracy data, the null model was preferred. The data were 4.1 × against the single effect model compared to the null model, and 148 × against the interaction model (Display × Epoch) compared to the null model. Counter to our prediction, the results support the null hypothesis whereby accuracy increased overall, but there was no cuing benefit.

Looking at the response time data, we observed the same pattern. A main effect of Epoch, $F_{2,38} = 32.737$, $p < .001$, $\eta_p^2 = .633$, but no effect of Display Type, $F_{1,19} = 1.925$, $p = .181$, and no Display × Epoch interaction, $F_{2,38} = .068$, $p = .935$. However, in this case, the null model was only preferred by a factor of 2.7 compared to the single effect model, and by a factor of 13 against the interaction model. It seems the RT data were insensitive to overall differences between repeat and novel displays that would indicate a robust cuing effect. Taken together, the results indicate that visual search performance was *not* influenced by embedded configural regularities that predicted the target location. Thus, by truncating visual exposure duration via the use of a mask, we were unable to produce the typical statistical learning effect.

Experiment 1b

In Experiment 1a, we used 30 repeat configurations and 30 control (novel) configurations each that were encountered 12 times by the participants. This design was based on evidence of a high-capacity statistical learning mechanism that underpins contextual cuing. However, it is more common to use fewer configurations. Indeed, Chun and Jiang (1998) presented 12 configurations encountered over 24 blocks in the original contextual cueing demonstration. Thus, perhaps the larger number of displays in our design in our first experiment exceeded the capacity of the system to produce a cuing benefit. However, it must be acknowledged, that counter to this, other studies have found a cuing benefit with 32 configurations encountered 20 times (Makovski & Jiang, 2011) or 60 configurations encountered 300 times over 5 days, (Song & Jiang, 2005). So, an alternative explanation is that the conditions of exposure with brief, masked presentations were insufficient to produce learning. To test this, we removed the mask and used the standard presentation time of 2000ms to investigate whether a cuing benefit would be observed using 30 repeat configurations encountered 12 times.

Method

All methods were identical to Experiment 1a except that the mask stimulus was removed, and search displays were shown for 2000 ms. Under these conditions, accuracy was expected to be near ceiling so, now response time was the key dependent measure. Participants were 20 first-year psychology students who received course credit. One was excluded due poor accuracy (below 75% cutoff) leaving a final sample of 19 participants (μ = 21 years, σ = 2.55, 12 female).

Results

Using this typical presentation time, we observed a robust cuing effect with the classic response time benefit for repeat displays relative to novel displays over time (Figure 1b). As expected, accuracy was close to ceiling with the mask was removed (94.77% ± 2.04*)*. There was a main effect of Epoch, $F_{2,36\cancel{1,18}} = 5.888$, $p = .006$, $\eta_p^2 = .246$, indicating accuracy improved over time. Bayes factors support the null (Epoch) effect model over the Display effect model ($BF_{10} = .216$) and the Display × Epoch Interaction ($BF_{10} = .038$) in the accuracy data. All other *p*s > .67.

In the RT data, there was no main effect of Display Type, $F_{1,18} = 2.437$, $p = .136$, but there was a significant Display Type × Epoch interaction, $F_{2,36\cancel{1,18}} = 4.145$, $p = .024$, $\eta_p^2 = .187$, and a main effect of Epoch, $F_{2,36\cancel{1,18}} = 45.284$, $p < .001$, $\eta_p^2 = .716$. Bayes Factors for the model effects were inconclusive regarding the Display effect model (BF10 = .707) and the Interaction model (BF10 = .707) compared to the null Epoch model. However, planned contrasts did shed light on the interaction. There was no cuing benefit in Epoch 1, $t_{18} = .875$, $p = .393$, $BF_{10} = .139$*,* with the data supporting the null effect. A reliable cuing benefit emerged in Epoch 2, $t_{18} = -2.386$, $p = .028$ ($BF_{10} = 4.37$), with support for the alternative hypothesis. In epoch 3, the data was trending in that direction, $t_{18} = -2.019$, $p = .059$, but the Bayes Factor was only anecdotal ($BF_{10} = 2.409$). This indicates that cuing did emerge when using 30 repeat displays with response-terminated presentations.

Experiment 2

The results of Experiment 1b confirmed we could observe contextual cuing in our paradigm when longer exposure durations (2000ms) were employed. Under the standard viewing conditions, we observed the typical response time benefit that indicated statistical learning about spatial context. This was consistent with previous research which found humans can learn target-context associations using a larger number of individual configurations. In that sense, the results argue against the idea that the number of configurations used in Experiment 1a exceeded the capacity of the system. A remaining possibility is that the number of configurations combined with the briefly presented displays in Experiment 1a was too taxing for context learning to occur. Experiment 2 returned to the main question of whether a contextual cuing effect could be observed using controlled brief exposure. We repeated the design with 300ms masked displays but used 12 repeat and 12 novel displays encountered in 24 blocks. This design reflects the most common implementation of the contextual cuing paradigm (i.e., Chun & Jiang, 1998). We expected a cuing benefit to emerge in accuracy and be robust by the end of exposure.

Method

All methods were identical to Experiment 1a except there were 24 trials each block (12 repeat and 12 novel) shown in a random order for 24 blocks. Twenty participants took part (μ = 19.1 years, σ = 2.29, 13 female); recruited from a first-year psychology pool receiving course credit. Note that reducing the number of configurations from 30 to 12 meant there were 48 trials per cell in the epoch-level analysis for Experiment 2 (12 trials per condition × 4 blocks per epoch) compared to 120 per cell for Experiment 1a (30 trials × 4 blocks).

Results

Here accuracy was affected by display type (Figure 1c). The critical Display Type × Epoch interaction was significant, $F_{5,38\cancel{1,19}} = 2.595$, $p = .030$, $\eta_p^2 = .120$, however, the main effects of Display Type and Epoch were not significant, $F_{1,19} = 1.419$, $p = .248$ and $F_{5,38} = 1.363$, $p = .245$, respectively. Planned contrasts revealed the interaction was driven by crossover effects indicating the cuing effect was variable across epochs. In epoch 1, there was no cuing benefit, with 10 × support for the null hypothesis (repeat = novel) over the alternate (repeat > novel; $BF_{10} = .097$). In epoch 2 there were suggestions of an accuracy benefit, but the data were unreliable ($BF_{10} = 1.96$). By epoch 5, the cuing benefit was reliable, with 3 × support for the alternate hypothesis over the null ($BF_{10} = 3.81$). However, the benefit was unstable, and not maintained in epoch 6 where the data were unreliable ($BF_{10} = .413$). This pattern may reflect task fatigue. Looking at the model effects in the ANOVA, the data was unreliable in terms of supporting the single effect model (Display × Epoch) relative to the null model (Epoch alone), $BF_{10} = 1.559$.

For RTs, there was no speed benefit for Repeat displays. Response times did become generally faster over time, $F_{5,38} = 32.75$, $p < .001$, $\eta_p^2 = .633$, but there was no main effect of Display Type, $F_{1,19} = .556$, $p = .465$, and no interaction $F_{5,38} = .745$, $p = .592$. Planned comparisons revealed no reliable effects across epoch (BF10 range .258 - .932). Overall, the data provided weak support for a cuing benefit that took time to emerge. When using 12 repeat and 12 novel displays, there was a reliable accuracy benefit in Epoch 5, but the data was not reliable when looking over all epochs. Thus, we decided to attempt to replicate this result.

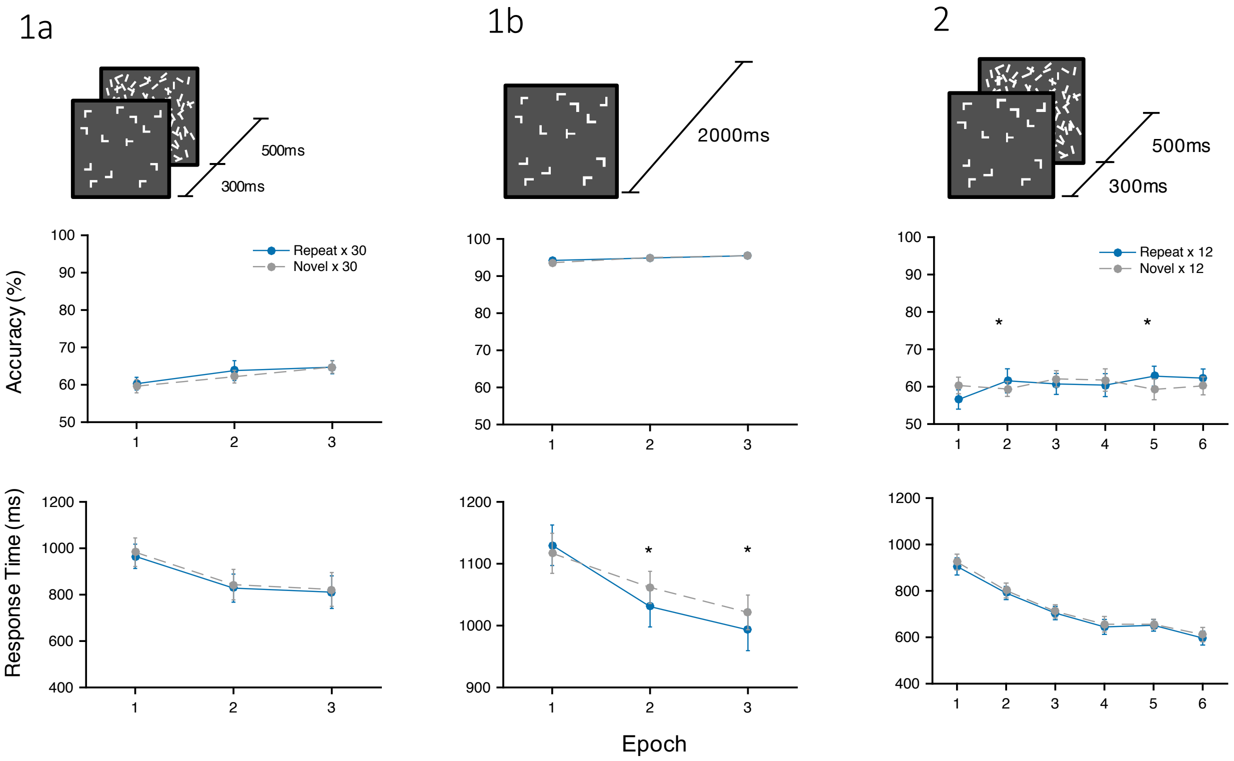

Figure 2. Response time and accuracy data for Experiments 1a, 1b and 2. (A) Experiment 1a used 300 ms masked presentations and found no accuracy advantage for repeat displays. (B) Experiment 1b used standard 2000 ms presentations and no mask and found a contextual cuing effect whereby correct response times increased for repeats displays over time compared to novel displays. (C) Experiment 2 reduced the number of repeat and novel configurations per block from 30 to 24 and reimstated the brief masked displays. Here, an accuracy advantage was observed for repeat displays, indicating statistical learning of the repeating contexts with brief presentations.

Experiment 3

The results of Experiment 2 showed that by reducing the number of individual configurations and increasing the number of exposures, we began to observe a statistical learning effect with brief masked presentations, but overall the data were somewhat insensitive to our key manipulation. Experiment 3 was an attempt to replicate the result in new data. Experiment 3 used the same design as Experiment 2 except that we increased the number of exposures from 24 blocks to 32 blocks. Given the previous benefit only appeared in Epoch 5, we hoped this change would allow time for learning to stabilize and be maintained.

Method

Twenty participants took part in Experiment 3 (μ = 22.21 years, σ = 2.74, 55 % female) from The University of Queensland. They attended a single 1-hour session and were paid $10 for their time. The task was displayed on a 23″ LCD monitor (ASUS, resolution = 1920 × 1080; refresh rate = 60 Hz). All other methods were the same as Experiments 1a and 2.

Visual Search Task

During the training phase, participants completed 32 blocks of the visual search task where 30 repeat displays and 30 novel displays were intermixed in a random order. The displays were presented for 300ms followed by the line mask for 500ms. The key outcome measure was accuracy on the search task as a function of display type across epoch.

Results

The results of Experiment 3 replicated the key findings of Experiment 2 (Figure 2). There was an overall accuracy benefit for repeat displays compared to novel displays (Main effect of Display Type, $F_{1,19} = 6.27$, $p = .022$, $\eta_p^2 = .25$). There was also the expected main effect of Epoch, $F_{7,133} = 4.86$, $p < .001$, $\eta_p^2 = .20$. The Display × Epoch interaction was not significant, $F_{7,133} = 1.02$, $p = .48$, in line with the common finding that contextual cuing emerges within the first epoch of the experiment (Chun & Jiang, 1998; Peterson & Kramer, 2001). When comparing the null model (Epoch effect) to the single effect model (Display Effect), Bayes Factor values were 305 × in favour of the main effect model, and were 22 × against including the interaction (Display + Display Type × Epoch), providing extremely strong evidence that an accuracy benefit best characterized the data.

To ensure the large accuracy benefit was not based on pre-existing differences between the conditions, we ran a paired-sampled t-test on the block 1 data. This revealed no difference between Repeat and Novel displays prior to learning, $t_{19} = .328$, $p = .373$, $BF_{10} = .135$, with the data 4.4 × in favour of the null hypothesis over the alternate. Thus, the accuracy cuing effect was not present initially, but emerged over time with exposure to regularities during the search task. Planned contrasts revealed the accuracy benefit in Epochs 4, 6, and

8, where Bayes Factors > 3 supported the alternate hypothesis (i.e., repeat > novel) over the null (Supplementary Table 1).

In the RT data, there was also a cuing benefit, evident in the main effect of Display Type, $F_{1,19} = 7.65$, $p = .012$, $\eta_p^2 = .29$, and Epoch, $F_{1,7} = 13.67$, $p < .001$, $\eta_p^2 = .42$, with no Display × Epoch interaction, $F_{7,133} = 1.87$, $p = .080$. Again, the single effect model (Display Type) was favoured 4.3 times over the null model (Epoch alone), and there was no support for the interaction model ($BF_{10} = .072$). Planned contrasts confirmed the speed benefit emerged early on, in Epoch 2, and was maintained over Epochs 4,5,6,7 and 8 (Table 2). These results are consistent with a robust cuing effect that emerged in both accuracy and RT.

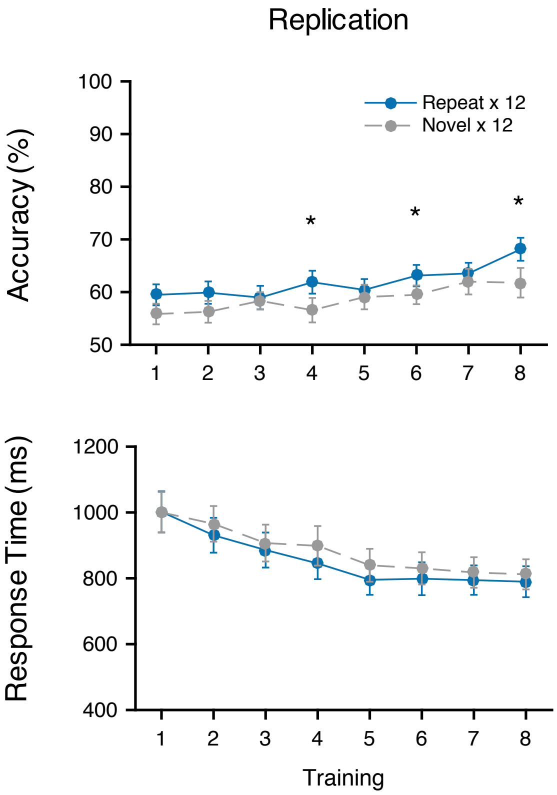

Figure 3. Results for Experiment 3 that replicated the cuing effect with brief presentations. Accuracy and Response time data are plotted as a function of display type and epoch. There was an accuracy benefit for repeat displays overall ($BF_{10} = 305$), which replicated Experiment 2. The cuing benefit emerged in Epochs 4, 6 and 8 where Bayes Factors > 3 are marked with an asterisk.

Comparing the Replication to the Original

Experiment 3 sought to replicate the cuing effect observed with brief displays in Experiment 2, using a reduced number of configurations (12) and more encounters (32). To allow a more a direct comparison with the original design (Experiment 2) we repeated the analysis on the first 24 encounters only. This revealed the same pattern of robust contextual cuing. Namely, there was a significant main effect of Display Type on Accuracy (p = .025, BF_{10} = 22.11), which was reliable. In the RT data, there were significant main effects of Display Type and Epoch (ps < .018, BF_{10} = 2.2). These results indicated that the data in the replication attempt were sensitive to differences between repeat and novel conditions when matching the number of encounters, and so support the alternate hypothesis that the replication data (Experiment 3) were consistent with the effect observed in Experiment 2.

Discussion

The results clearly demonstrated that incidental learning of spatial regularities can appear using brief, masked presentations. The results of Experiment 3 converge with those found in Experiment 2, showing that humans can benefit from regularities in the visual scene even when only afforded 300ms to view the stimuli. This is consistent with accounts of a rapid statistical learning mechanism that underpins contextual cuing effects. Previous research had observed the cuing benefit was intact when displays were presented for only 300ms after learning with longer display presentations (Chun & Jiang, 1998). This finding demonstrated that, after learning, subjects can match the current display to a learned display within the time of an initial fixation and supports the proposal that the global spatial layout is important for contextual cuing. The results of Experiments 2 and 3 build on this evidence to show that subjects can *acquire and use* the statistical spatial layout of a scene rapidly, even when additional processing is blocked by a visual mask. This suggests the statistical learning mechanism itself may be supported by an information processing system that is similarly rapid; able to encode and utilize regularities in a glance.

Experiment 4

As it stands, we have observed rapid context learning with 12 configurations (Experiments 2 and 3) but not with 30 configurations (Experiment 1a). One outstanding issue from the 30 configuration set up was that participants had fewer encounters in this experiment than in those that employed 12-configurations. Specifically, only 12 blocks were used, compared to 24 blocks in Experiment 2 and 32 blocks in Experiment 3. In Experiment 4, we upped the number of encounters to be 24. If the number of encounters explained our previous failure to observe cuing with 30-configurations, we expected an accuracy benefit to emerge here (alternate hypothesis). This would show the rapid statistical learning underpinning these effects has a high capacity.

Another reason why we might have failed to observe contextual cuing in Experiment 1a is because learning did, in fact, occur but the mask blocked learning from being expressed. This idea comes from earlier work that shows cuing is not expressed in some cases where resources are taxed by a demanding secondary task (e.g., Annac et al., 2013; Manginelli et al., 2013; Jiang et al., 2001). In these studies, latent learning (or encoding) is evident in the spontaneous emergence of a cuing benefit once the secondary-task manipulations are removed. For example, when working memory resources were taxed by a concurrent delay-match-to-sample task (e.g., Manginelli et al., 2011), no contextual cuing benefit was observed. When the memory task was removed in a test phase, an RT benefit spontaneously appeared for the repeat displays that were used during training. Similar latent learning effects were observed after training with an attention manipulation (Jiang & Song, 2005). When selective attention was directed to subset of items during search, no cuing was observed for the unattended items. But when attention was re-directed to the previously unattended items at test, cuing was immediately evident, suggesting learning did occur for the unattended items but was not being expressed. Both lines of work have been used to argue for a latent learning mechanism underlying contextual cuing, and that the ability to use regularities depends on attention and working memory resources (see also Annac et al., 2019).

Applying this idea to our experiments, it may be possible that latent learning occurred in the original 30-configuration experiment, but that the ability to express learning (via a cuing benefit) was impeded by the mask. If this were the case, a cuing benefit should be observed when the disruptive effects of the mask are removed. To investigate such a possibility, we included an unmasked test phase after training in Experiment 4. To limit additional learning that could take place once the mask was removed, we only measured 4 test blocks, consistent with the designs in previous work. This was collapsed into 1 epoch for analysis. We predicted that if latent learning occurred, we should see a cuing effect in the test phase. This could be either via an accuracy benefit or a speed benefit. These predictions, along with the analysis plan, were registered on the open science framework prior to data collection and have been made available here: https://osf.io/h38a9/.

Method

Twenty participants from the paid-participant pool at The University of Queensland took part in the study (μ = 23.15 years, σ = 3.17, 60 % female). The apparatus and stimuli were identical to Experiment 3, except there were 30 repeat and 30 novel displays intermixed over 24 blocks. For the training phase, displays were presented, as before, for 300ms followed by the mask for 500ms. For the test phase, we removed the mask and participants completed four blocks with the same repeat and novel configurations. Given that learning was successfully expressed within 300ms in a previous study (Chun & Jiang, 1998), we kept the displays duration to be 300ms, and just followed it with a blank screen for response. Considering properties of iconic persistence, it is highly likely that information about the displays would have remained accessible to the processing hierarchy after stimulus offset. The four test blocks were collapsed into one epoch for analysis, consistent with the design of previous literature. Accuracy and correct RTs were assessed as a function of display type. Responses beyond 2000ms were not recorded. Missing data did not exceed 5% for any individual.

Training Phase Results

As predicted, no reliable learning was detected in accuracy or RTs in Experiment 4 (Figure 4). For accuracy, there was a main effect of Epoch, $F_{1,5}$ = 6.78, $p < .001$, η_p^2 = .26, but no main effect of Display Type, $F_{1,19}$ = 1.26, p = .275, nor a Display × Epoch interaction, $F_{5,95}$ = .26, p = .932. Bayes Factors were 3.8 × in support of the null model (incl. Epoch) relative to the cuing model (Display type effect).

For correct RTs, there was likewise a main effect of Epoch, $F_{1,5}$ =19.34, $p < .001$, η_p^2 = .50, with no main effect of Display Type, $F_{1,19}$ = 1.98, p = .176. But the Display × Epoch interaction was significant, $F_{5,95}$ = 2.80, p = .021, η_p^2 = .13. On further inspection, this was due to inconsistent effects across epochs (see Supplementary Table 2). Specifically, the null effect (repeat ≠ novel) was favoured in Epochs 1 and 3, signifying no RT differences, and the data was unreliable in Epochs 4 and 6. There was, however, evidence of an RT benefit for repeat displays in Epochs 2 and 5 where the alternate hypothesis (repeat < novel) was favoured over the null. Looking at the omnibus effects in the ANOVA, the null model (Epoch) was supported 71 times over the interaction model (BF_{10} = .014) and 5 times over the main effect model (BF_{10} = .188). This suggests that when matching the number of encounters across experiments, we still failed to observe a contextual cuing effect with 30 configurations. The RT pattern looked similar to the unreliable accuracy benefit observed in Experiment 2 with 12-configurations, in that a benefit emerged occasionally but was not maintained.

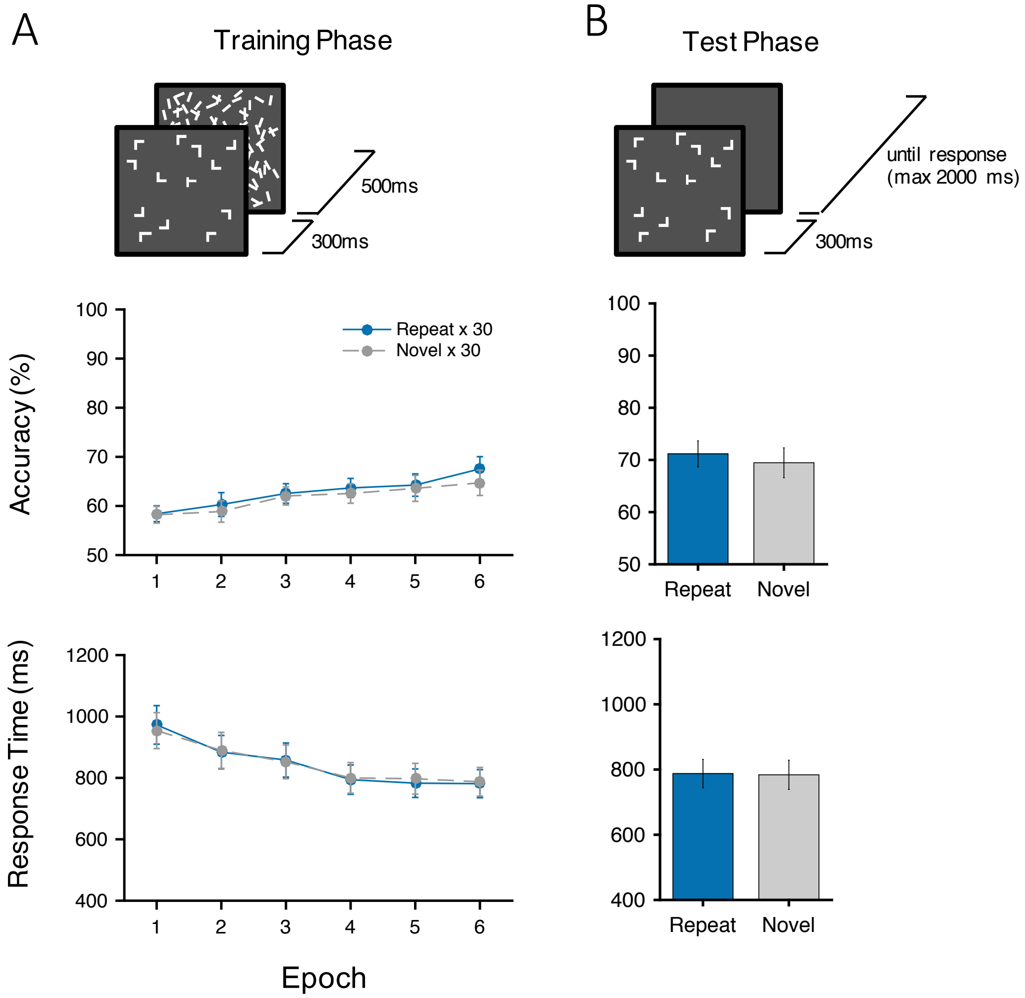

Figure 4. Schematic of the method used in Experiment 4. (A) During the training phase, there was strong support for the null hypothesis over the alternate. This was consistent with Experiment 1a showing statistical learning with brief presentations does not occur when using 30 configurations repeated over the same number of encounters. (B) In the unmasked test phase, there was no evidence of cuing, with strong support for the null hypothesis over the alternate.

Test Phase Results

The key question in the test phase was whether the typical response time benefit would emerge once the mask was removed (Figure 4b). Contrary to this prediction, a paired samples t-test supported the null effect of cuing on RTs, BF_{10} = .246. At the end of training, the RT benefit to repeat displays decreased from 20ms in Epoch 6 to 4ms in the test epoch, and this change was reliable, BF_{10} = 9.233. Thus, instead of the spontaneous cuing that was predicted, this pattern indicates that any speed benefit gained in training was not identifiable when the mask was removed.

In the accuracy data, neither the null nor the alternate hypothesis was favoured at test (BF_{10} = .976). Thus, we observed no evidence of latent learning in accuracy or RT after removing the mask in a test phase. Collectively, these results suggest a capacity limit for statistical learning under rapid viewing conditions that is not explained by the failure to express latent learning due to a mask being present.

General Discussion

We examined the processing dynamics of contextual cuing by masking visual displays to control processing time during search with repeating configurations. We observed evidence of a rapid contextual cuing process that occurred within 300 ms and produced greater accuracy when identifying targets embedded in configurations that repeated compared to novel configurations. This accuracy cuing effect was observed with a set of 12 repeating configurations but not when there were 30 repeating configurations. This larger set-size required longer processing times that allowed search to be complete and produced learning via a response time benefit. Taken together, these results indicate that contextual information based on spatial regularities can be processed rapidly in order to assist ongoing cognition. But it appears that the most robust cuing behaviour comes from longer durations. The set-size difference with short and long durations suggests that exposure time interacts with memory capacity during statistical learning of spatial configurations.

The rapid cuing we observed in Experiment 2 cannot be attributed to procedural learning of target locations alone, because the same number of target locations were used in the novels and repeat conditions, and the distribution of locations across quadrants was matched. This meant attentional prioritization of the target locations (Ferrante et al., 2017) would have been uniform across the display area for both conditions. Instead, the cuing benefit for repeat displays was a result of learned associations between a given configuration of items and a target location. And so, the distractor items needed to be processed in order to create the cuing benefit. We were similarly careful to match the distribution of distractors items across conditions, in terms of the number of items in each quadrant. Thus, learning is unlikely to be driven by conscious knowledge of one or more salient configurations in the repeat condition. Rather, our results tell of an associative, statistical learning mechanism that operated on a rapid timescale.

This finding builds on the previous work by showing that learning in contextual cuing can operate in 300ms of exposure. Experiment 5 in Chun and Jiang's initial study (1998) had shown that the cuing benefit could operate using 200ms exposure, but that was after learning had already occurred. It suggested the process of retrieving a learned display and matching it to the current display occurred rapidly, likely without eye movements, to produce an accuracy benefit. But it was not designed to investigate the formation of context learning directly. Similarly, the electroencephalography studies had observed the N2pc response, an indicator of selective attention to the target, differentiated repeat from novel displays at around 250ms after stimulus onset (Johnson et al., 2007; Olson, 2001), but learning occurred with longer, response-terminated displays and since the analyses averaged over the entire learning session, they could not distinguish rapid recognition of displays from rapid learning. Our findings are consistent with the hypotheses of Chun and Jiang (1998) that eye movements are not required for cuing to occur. But they add that the formation of spatial context memories may also not require in-depth visual processing. Instead, the evolution of learning itself, indexed by increasingly more accurate responses to repeat displays over time, can operate on a rapid timescale, and with minimal eye movements.

To the best of our knowledge, this is the first study to show contextual cuing with visual masking. Unlike the previous studies, the cuing benefit cannot be explained by iconic persistence of the displays after stimulus offset. We used visual masked to control processing time, yet the results have implications for theories of how cuing may rely on working memory resources. Working memory is often decomposed into stages, with Iconic memory being the retention or manipulation of information within 100ms, followed by visual short-term memory, and longer more robust forms of memory. Masking is known to disrupt iconic memory. Thus, observing cuing behaviour with 300ms masked exposure reveals two things. Firstly, that information about spatial context must be encoded rapidly in a way that survives iconic disruption. Secondly, that the cognitive system can use that encoded information to guide downstream attention and decision-making operations within that same timescale. This suggests that the integration of top-down operations (e.g., attention to a target) and bottom-up information (distractor information, potentially stored in memory) can occur within 300ms.

While other work has investigated the integration of top-down and bottom-up processes in this way (e.g., Sitwell & Vecera, 2020), the timescale of such integration has largely been overlooked.

If contextual information can be processed to affect decisions rapidly, the next question is how this behaviour may be distilled into different operations that play out over time. Based on first principals, the learning must first entail encoding of the displays, shown to occur through repetition. Encoding no doubt involves visual representations and some form of memory storage. Once stored, in order to benefit from the regularities, one must match the stored knowledge to the current display and generate predictions relevant to goal-directed behaviour. Attempts to distill the encoding from retrieval in incidental learning tasks are ongoing (see Batterink, Paller, & Reber, 2019; Thiessen, Kronstein, & Hufnagle, 2013). The sub-processes have also been referred to as the "learning" and "use" of implicit knowledge (Simor & Nemeth, 2019; Travis, Mattingley, & Dux, 2013). It appears the two components may be dissociable in terms of their reliance on working memory and selective attention. Learning (or encoding) can occur in the absence of an observable cuing benefit (Jiang & Chun, 2001; Jiang & Leung, 2005; Manginelli, Langer, Klose, & Pollmann, 2013; Travis et al., 2013). In these studies, a concurrent task was used to tax working memory or divide attention during exposure to repeat and novel displays. No cuing benefit was evident during dual-task mode. But a cuing effect emerged when the concurrent task was removed, suggesting the regularities were learned but not used (or acquired but not retrieved) during working memory load or divided attention. In a similar vein, we investigated whether the null effect with 30 configurations was explained by masking having an effect on the use of regularities rather than the underlying learning. Our results supported the latter; that no learning occurred with the larger set of configurations. It remains possible that learning may have emerged given additional exposure through more repetitions. So, an alternative explanation is that learning with a larger capacity was not completely abolished, but was rather slowed down, requiring more repetitions to see a benefit. For now, it is clear that when equating the exposure time (300ms), and the number of repetitions (24 blocks), statistical learning emerged with 12 configurations, but not 30 configurations. And this indicates a capacity limit.

Contextual information about the environment has been conceptualized in a number of ways. Another way that contextual information is represented is known as gist, which refers to generalizable information about a scene in terms of category and layout (Larson, Freeman, Ringer, & Loschky, 2014). Gist is most commonly investigated using real-world scenes, such as an office setting or a landscape, that are to be categorized as indoor or outdoor. A wealth of research has demonstrated that gist is extracted at incredible speeds. For example, using rapid serial visual presentations (RSVP), studies have observed gist extraction within a single fixation and as fast as 13 ms (Biederman, Mezzanotte, & Rabinowitz, 1982; Potter, Wyble, Hagmann, & McCourt, 2013; Rousselet, Joubert, & Fabre-Thorpe, 2005). Gist processing also exhibits a substantial capacity; capable of storing information about hundreds even thousands of individual scenes (Konkle, Brady, Alvarez, & Oliva, 2010; Standing, 1973). The majority of this work has measured simple categorization judgments to tap familiarity or recognition after exposure. Further, rates of visual processing in RSVP streams say little about absolute evaluation time, because there is no decision on each scene. More recently, gist extraction was found to impact downstream operations to do with attention and object recognition (Larson et al., 2014), suggesting the early processing of a scene may support adaptive functions of the visual system as they relate to learning from experience. The present results dovetail with this work to show that different types of context, either for gist or abstract regularities, may be processed rapidly to affect higher-level cognition. This has important consequences for theories about the temporal scale over which higher-level cognitive operations may benefit from implicit spatial predictions.

Unlike gist processing and typical contextual cuing, which both exhibit a large capacity, rapid contextual cuing was capacity limited. When using the same presentation duration (300ms), number of exposures (24 blocks) and opportunity to learn (based on 60% accuracy), we observed learning with 12-configurations but not with 30 configurations. The failure to learn with 30 configurations was not explained by latent learning that was blocked by the mask. A number of explanations for the capacity limit to learning with rapid exposure have been considered. The first pertains to the associative nature of learning. Studies show that cuing behaviour is driven by learning both the overall configuration and item-level associations, and this interacts with the type of exposure afforded by the task (Jiang & Wagner, 2004; Ogawa & Kumada, 2008; Song & Jiang, 2005). For example, in a pop-out search task, only configural learning was observed, but with typical exposure, both item-based and configural learning was observed (Ogawa & Kumada, 2008; Song & Jiang, 2005).

This is consistent with the notion that subjects learn multiple relationships between distractor-distractor items, target-distractor items and target-configuration elements during response-terminated search (Beesley, Vadillo, Pearson, & Shanks, 2016; Brady & Chun, 2007). The types of learning that occur in rapid viewing tasks has not been investigated. Thus, typical longer search appears to allow for processing multiple cues in concert, both local and global, to produce robust, high-capacity learning behaviour. Related is the way local and global learning may contribute to RT and accuracy effects. Since local items near the target constitute the largest contribution to the RT benefit (Brady & Chun, 2007), it is possible that global processing with rapid displays afforded an accuracy benefit more so than the typical RT effect. Furthermore, while repeating only local items near the target were enough to trigger retrieval once learned, repeating local items was not sufficient to establish a strong memory trace early in learning (Song & Jiang, 2005). This work implies that the formation of context learning requires both local and global elements to be encoded, but that some learning may be occur with incomplete encoding. In our study, the brief exposure duration and backward masking may have meant not all relational elements in a repeat display were processed (quantitative change). Or it might have meant that only global information was processed but not local (quantitative change). This change in *what* was being learned may explain the capacity limit. Future studies could investigate this by masking either local or global information during learning and use re-combined displays at test to see if configural or non-configural learning occurred (circa: Ogawa & Kumada, 2008; Song & Jiang, 2005).

A final possibility is that the capacity limit represented a slowing or delay in the emergence of learning, rather than abolishing it altogether. This is intuitive when considering there may have been less opportunity to learn given the lower accuracy in the masked experiments compared to a typical response-terminated experiment. Accuracy was 60% with brief presentations but is near ceiling at 90% or higher with longer exposures. With brief exposures, the number of trials where individuals did not locate the target was much higher than typical cuing tasks. This would explain the capacity limit as being related to a failure to locate the target. However, it cannot explain the capacity difference seen for the 12-configuration and 30-configurations experiments, because accuracy was comparable at 60% in each. So, the explanation about there being less opportunity to learn when using a higher number of configurations seems unlikely. More plausible is an explanation to do with opportunity to process distractors. Given enough repetition of a display, it becomes statistically more likely that any given subset of elements will be processed, including distractors and the target. Therefore, increasing the exposure, either in terms of presentation time or number of encounters over time, would provide an increased opportunity to learn, based on the statistics of experience.

Conclusions

We observed a contextual cuing effect with short, masked exposure. This reveals that spatial statistical learning can be effective even when information processing is truncated in a way that limits eye movements and processing beyond offset. The findings are consistent with the hypothesis that contextual processing is driven by encoding the global layout in a way that does not require eye movements, which may provide a mechanistic explanation as to how rapid context processing can occur. Unlike contextual cuing with longer processing times, this rapid processing of context regularities was capacity limited. The fast processing of context in terms of abstract spatial regularities dovetails with work on rapid, high-capacity gist extraction in real-world scenes. Understanding the rapid speed by which statistical learning can be formed contributes to a broader understanding of information processing in the human brain, and its capacity limits. Incidental learning about past experience supports many adaptive behaviours in humans and non-human animals. So characterizing ways that the brain can efficiently utilize past experience for behaviour is important for global theories of brain function.

Supplementary Table 1. Planned contrasts for the Accuracy benefit across epoch. Bayes factor values for paired samples t-tests comparing the alternate hypothesis (Repeat > Novel) to the null hypothesis across all experiments.

	Original		Replication	
	30-configuration (Exp 1a)	12-Configuration (Exp 2)	12-Configuration (Exp 3)	30-configuration (Exp 4)
Epoch 1	.250*	.10	1.20	.203*
Epoch 2	.364	1.97	1.37	.427
Epoch 3	.232*	.19	.28	.585
Epoch 4	-	.38	**23.95**	.373
Epoch 5	**-**	**3.82**	0.36	.467
Epoch 6	-	.42	**4.78***	.901
Epoch 7	-	-	.384	-
Epoch 8	-	-	**6.08***	-

Note: Bayes Factors in favour of the alternate hypothesis (> 3) are marked in Bold. Bayes Factors in favour of the null hypothesis (< 1/3) are marked by an asterisk. All tests used an uninformative Cauchly prior of .707.

Supplementary Table 2. Planned contrasts for the Response Time benefit across epoch. Bayes factor values for paired samples t-tests comparing the alternate hypothesis (Repeat < Novel) to the null hypothesis across all experiments.

	Original		Replication	
	30-configuration (Exp 1a)	12-Configuration (Exp 2)	12-Configuration (Exp 3)	30-configuration (Exp 4)
Epoch 1	.574	.279*	.233*	.108*
Epoch 2	.310	**2.474**	**4.085**	4.774
Epoch 3	.396	.474	.999	.256*
Epoch 4	-	.788	**3.904**	.617
Epoch 5	-	**3.978**	**25.589**	**6.887**
Epoch 6	-	.836	**6.778**	.538
Epoch 7	-	-	**3.522**	-
Epoch 8	-	-	**3.009**	-

Note: Bayes Factors in favour of the alternate hypothesis (> 3) are marked in Bold. Bayes Factors in favour of the null hypothesis (< 1/3) are marked by an asterisk. All tests used an uninformative Cauchly prior of .707.

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CHAPTER 3:

CATHODAL STIMULATION OF FRONTOPARIETAL CORTEX DISRUPTS STATISTICAL LEARNING

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Abstract

Attentional performance is facilitated by exploiting regularities and redundancies in the environment by way of incidental statistical learning. For example, during visual search, response times to a target are reduced by repeating distractor configurations – a phenomenon known as contextual cueing (Chun & Jiang, 1998). A range of neuroscientific methods have provided evidence that incidental statistical learning relies on subcortical neural structures associated with long-term memory, such as the hippocampus. Functional neuroimaging studies have also implicated the prefrontal cortex (PFC) and posterior parietal cortex (PPC) in contextual cueing. However, the extent to which these cortical regions are causally involved in statistical learning remains unclear. Here, we delivered anodal, cathodal, or sham transcranial direct current stimulation (tDCS) to the left PFC and left PPC online while participants performed a contextual cueing task. Cathodal stimulation of both PFC and PPC disrupted the early cueing effect, relative to sham and anodal stimulation. These findings causally implicate frontoparietal regions in incidental statistical learning that acts on visual configural information. We speculate that contextual cueing may rely on the availability of cognitive control resources in frontal and parietal regions.

Learning refers to a change in behaviour that occurs over time. There is converging evidence from neuroanatomical, neuroimaging, and lesion methodologies to show that the prefrontal cortex (PFC) is a critical neural substrate for many high-level functions that support advanced skill acquisition (e.g., when learning a language or musical instrument; Fuster, 2001). The PFC is also recruited for more basic forms of learning, such as when associating a visual stimulus with a particular button-press response (Fuster, 2001). Recent work using the non-invasive brain stimulation technique, transcranial direct current stimulation (tDCS), has begun to provide causal evidence regarding the prefrontal locus of learning and the effects of training on performance (Filmer et al., 2016; Filmer, Mattingley, & Dux, 2013a; Filmer, Mattingley, Marois, & Dux, 2013b). Yet it remains unclear whether other forms of learning that are believed to operate in a more automatic and incidental manner may also be modulated by brain stimulation.

During tDCS a subthreshold electrical current is passed from two electrodes – one anode and one cathode – through the scalp, and the resulting electric field is used to modulate neural activity. At the microscopic level, tDCS is believed to modulate cell membrane potentials. Anodal currents typically shift activity towards depolarization, whereas cathodal currents lead to hyperpolarization and a shift toward reduced overall activity (Bindman, Lippold, & Redfearn, 1964; Filmer, Dux, & Mattingley, 2014). While this polarity-dependent dichotomy appears to hold for stimulation targeting the motor cortex (Nitsche & Paulus, 2000; 2001; Rosenkranz, Nitsche, Tergau, & Paulus, 2000), tDCS induced changes to larger neural circuits are more complicated. In these cases tDCS effects depend on the stimulation parameters used (Bestmann, de Berker, & Bonaiuto, 2015); namely duration and intensity (Batsikadze, Moliadze, Paulus, Kuo, & Nitsche, 2013) but also whether or not it is paired with a concurrent task. For this reason, attempts to predict the direction of behavioural changes can be challenging. Nevertheless, by exploiting the capacity of tDCS to exert a bi-directional influence on a neural system, one can perturb a target region and explore the resulting influence on measured behaviour.

Previous research has predominantly examined explicit or intentional forms of learning. These are cases where participants are aware that information must be retained for later use (e.g., specific items or response mappings). Under such conditions tDCS to functional regions has been shown to influence both the time course and outcomes of learning. For example, in language learning tasks, online anodal and bilateral tDCS to temporal regions increased the rate of acquisition and led to more successful outcomes (Boggio et al., 2009; Flöel, Rösser, Michka, Knecht, & Breitenstein, 2008). In a concealed-object detection task, anodal tDCS delivered to the right inferior frontal cortex or the right posterior parietal cortex (PPC) also increased the learning rate and improved overall performance, compared to sham and to a lower intensity control (Clark et al., 2012). Conversely, Filmer et al. (2013b) found that the typical performance gains produced by sensory-motor training were disrupted by offline tDCS to the left PFC. This occurred for both anodal and cathodal stimulation, compared to an active control region (right PFC) and to sham (Filmer et al., 2013b). Using computational modelling, these authors also demonstrated that stimulating the left PFC during training influenced the efficiency of information processing for decision-making (Filmer et al., 2016), or put differently, the rate of evidence accumulation as formally characterised using the Linear Ballistic Accumulator model (Brown & Heathcote, 2008). In the context of evidence accumulation models of choice behaviour, decision-making refers to the process of selecting an outcome from a given set of alternatives based on the available evidence (Gold & Shadlen, 2007). Unlike the mechanisms that support sensory input or motor output, which are largely immediate, decisions evolve over time (Forstmann, Ratcliff, & Wagenmakers, 2016) by repeatedly sampling evidence from a stimulus and accruing information towards a given outcome until an internal decision threshold is reached (Ratcliff & Rouder, 1998).

While this work is important for understanding brain regions that support intentional learning, much of knowledge and skill acquisition occurs in an incidental manner by way of adapting to statistical regularities in the environment (Goujon et al., 2015; Perruchet & Pacton, 2006). Indeed, this notion of prediction leading to the optimization of cognition is central to the Bayesian brain hypothesis and the free energy principle (Friston, 2010). When learning about the environment in this way, some work has proposed that cognitive control mechanisms, supported by the PFC, preference certain aspects of learning at the expense of others (Thompson-Schill, Ramscar, & Chrysikou, 2009). This has been demonstrated in the domains of language categorization (Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012) and creativity (Chrysikou et al., 2013) where disrupting PFC function, via cathodal stimulation (but see discussion above regarding enhancement/inhibition in tDCS), benefited the incidental components of learning. Thus, contrary to the work of Filmer et al. (2013) on explicit sensory-motor learning, this line of work suggests that PFC involvement impairs learning (we return to this issue in the discussion). Nevertheless, collectively, the aforementioned work highlights the critical role of frontal and associated brain regions in an array of learning related operations. How these regions might contribute to uninstructed learning that affects other processes, such as visual attention and decision-making, remains an open question.

Statistical learning (Reber, 1967) and implicit learning (Saffran, Aslin, & Newport, 1996) both describe how exposure to regularities in the environment can produce sensitivity to the structured material as measured in behaviour, but without clear awareness or an ability to overtly express what has been learned (Conway & Christiansen, 2006; Perruchet & Pacton, 2006). Here, we use the term “incidental” to refer to the uninstructed property of the tasks, without making specific claims as to the “implicit” nature of the process or resulting knowledge. Incidental statistical learning is considered a domain-general learning mechanism (Perruchet & Pacton, 2006), and so it can exert effects at many stages of the processing hierarchy. For example, Visual Statistical Learning (Fiser & Aslin, 2001) refers to the facilitation of perceptual operations by passive exposure to object co-occurrences (see also Turk-Browne, Isola, Scholl, & Treat, 2008). Whereas, sequence learning affects motor processing, and is commonly assessed by the Serial Reaction Time (SRT) task (Nissen & Bullemer, 1987). In addition, functions such as attention and decision-making can also be influenced by incidental statistical learning. This is commonly demonstrated via contextual cueing in visual search paradigms (Chun & Jiang, 1998).

In visual search, typically, observers must locate a target item amongst an array of spatially dispersed distractors and make a decision about a given target feature (e.g., left or right orientation). Contextual cueing (Chun & Jiang, 1998) refers to the facilitation of Response Times (RTs) as a result of learned associations between a target’s location and the visual context created by the distractor configurations. In spatial contextual cueing, several target-distractor configurations are repeated during the experiment, and RTs reduce for these repeat displays compared to those with novel distractor configurations. Critically, the target identity (which maps on to the motor response) is not predicted by the context. Only the target’s location in the search display is predicted. Thus, contextual cueing does not reflect motor learning (e.g., Nissen & Bullemer, 1987; Nitsche, Schauenburg, et al., 2003b).

The contextual cueing effect describes the RT difference between repeat and novel displays (typically 100 ms), and the timecourse of learning is measured by the change in the contextual cueing effect across blocks or epochs (Chun, 2000). This means that learning can be measured online, rather than in a subsequent test phase, which is the case for other statistical learning paradigms. Observers are typically not instructed as to the existence of the regularities, and so the learning is deemed incidental. Several cognitive mechanisms have been put forward to account for the benefit in RTs observed for repeated contexts. Taken en masse, associative mechanisms are believed to influence both attention (Chun & Jiang, 1998) and decision related processes (Chun & Jiang, 1998; Kunar, Flusberg, & Wolfe, 2008; Kunar, Flusberg, Horowitz, & Wolfe, 2007; Zhao et al., 2012). A recent computational modelling study directly tested these accounts and found that cuing largely influenced the components of decision related processing (Sewell, Colagiuri, & Livesey, 2017).

At a neural level, incidental statistical learning is believed to rely on medial temporal lobe (MTL) structures and, specifically, the hippocampus. This was based on studies of amnesic patients who had intact perceptual and skill learning but impaired contextual cueing (Giesbrecht, Sy, & Guerin, 2013). This early work has found further support in neuroimaging findings that show hippocampal BOLD activity is related to performance in contextual cueing tasks (Geyer, Baumgartner, Müller, & Pollmann, 2012; Greene, Gross, Elsinger, & Rao, 2007; Preston & Gabrieli, 2008). The subcortical involvement links learning in contextual cueing to the storage of representations in long-term memory. Yet the same fMRI studies consistently report activation in cortical areas. In one study, BOLD activity for the repeat-novel contrast in the left inferior parietal sulcus (IPS) correlated with the final magnitude of the contextual cueing effect (Manginelli, Baumgartner, & Pollmann, 2013a). Activity relating to learning, assessed via BOLD contrasts for the context by epoch interaction, has also been demonstrated in the dorsolateral PFC (Manginelli et al., 2013a) and bilateral PPC (Giesbrecht et al., 2013). Given the correlational nature of these imaging results, it is possible that the frontal and parietal activation seen in these studies reflect concurrent processes that occur during contextual cueing, or act on the material as a consequence of cuing, without being directly related to the statistical learning per se.

Frontoparietal involvement is consistent with other forms of statistical learning (Janacsek & Nemeth, 2013; Rieckmann, Fischer, & Bäckman, 2010). Together, these brain regions may operate as part of a larger cortical-hippocampal network responsible for integrating sensory information into memory (Sestieri, Shulman, & Corbetta, 2017; Staresina, Cooper, & Henson, 2013). Indeed recently, Wang and colleagues (2014) delivered an excitatory transcranial magnetic stimulation (TMS) protocol to lateral parietal cortex during an overt associative learning memory task and found that stimulation improved memory performance and increased functional connectivity between parietal cortex and the hippocampus.

To date, no study has investigated the causal involvement of cortical regions in incidental statistical learning assessed via contextual cueing. Based on fMRI reports of increased PFC and PPC activity associated with learned repeat displays, here, we used tDCS to investigate the extent to which perturbing these brain regions may directly influence contextual cueing. Thus, the present work seeks to establish whether activity in PFC and PPC is causally involved in incidental statistical learning for visual configural information that comes to affect decision-making. Given the purported role of the DLPFC and PPC in various intentional learning and decision-making processes, tDCS to one or both regions may modulate learning. Alternatively, there may be a dissociation between tDCS effects for the frontal and parietal regions, based on their involvement in potentially interacting learning systems (i.e., Thompson-Schill et al., 2009).

Method

Participants

One hundred and twenty individuals participated in the study; 60 in the frontal region condition (mean age = 21 years, SD = 1.93 years, 17 male), and a different 60 individuals in the parietal region condition (mean age = 21 years, SD = 3.65 years, 16 male). For each brain region, participants were pseudo-randomly allocated to receive either anodal, cathodal or sham stimulation, with 20 participants in each group. The sample size was determined a priori based on an effect size ($\eta^2_p = 0.175$) taken from a previous single session tDCS study conducted by our group (Filmer, Mattingley, Marois, & Dux, 2013b). A power analysis using G-Power (Faul, Erdfelder, Lang, & Buchner, 2007) indicated that 18 participants per group would be required to achieve 80% power with an alpha level of .05. An additional two participants from the frontal condition and seven participants from the parietal condition were excluded for the following reasons: six for not responding on more than 5% of trials; two for failing to follow instructions; and one for performance below the minimum average accuracy cut off of 85% (determined pre–study).

Participants were screened for history of any neurological conditions or trauma; family history of epilepsy; metal in the body; and the current use of neuroactive medication. All participants met the tDCS safety criteria (Nitsche, Liebetanz, et al., 2003a), and had normal or corrected-to-normal vision. According to the Edinburgh Handedness Inventory (Oldfield,

1971) there were 49 right-handed, five left-handed, and six ambidextrous participants in the frontal condition. There were 57 right-handed, zero left-handed and three ambidextrous participants in the parietal condition. Participants gave informed written consent prior to the experiment and received $10 compensation for their involvement. The study was approved by The University of Queensland Human Research Ethics Committee.

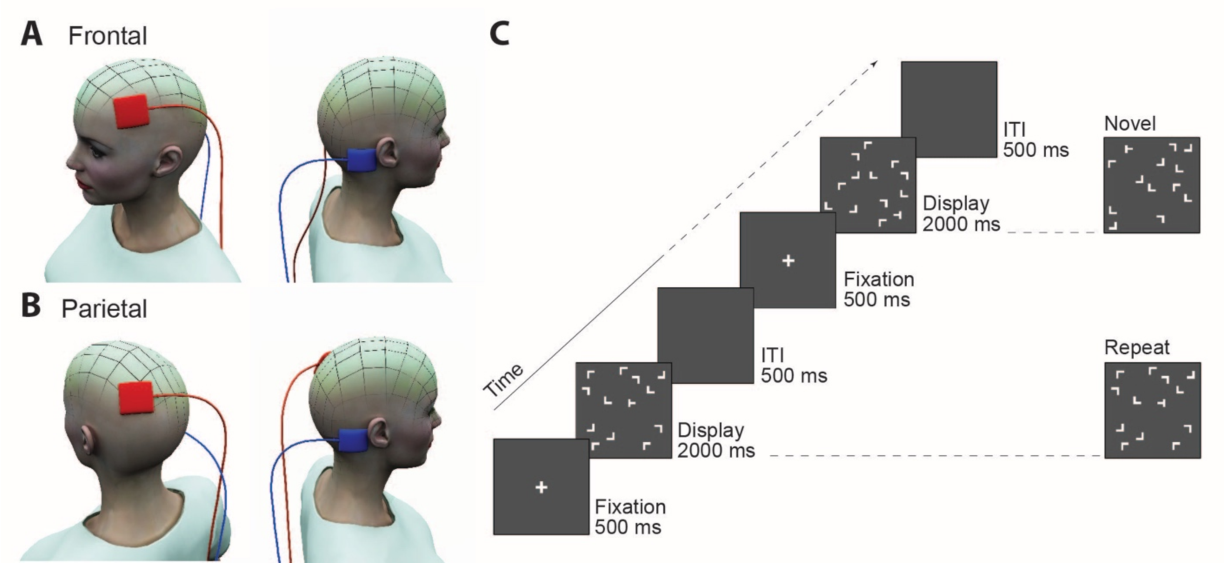

Figure 1. Experimental design. Electrode placement for the target electrodes (red) and reference electrode (blue) for the (A) frontal and (B) parietal regions. Each region was stimulated with anodal, cathodal and sham current types in a between-subjects design. (C) Stimuli and trial outline for the contextual cueing task. For repeat displays, the location and orientation of distractors, as well as the target location, was held constant across blocks, with only the target orientation changing randomly from trial to trial. For novel displays, all items in the display varied randomly. Note that displays were not response terminated.

Transcranial Direct Current Stimulation

Stimulation was delivered via a Neuro-Conn stimulator attached to two 5 × 5 cm electrodes. The electrodes were secured to the scalp using Ten20 electrode paste. In the frontal condition, the target electrode was placed over the left PFC, which corresponded to 1 cm posterior to the F3 site (see Figure 1b) according to the 10-20 Electroencephalography (EEG) system (Jasper, 1958). Previous work has shown F3 corresponds to the left DLPFC (Coffman, Clark, & Parasuraman, 2014; Herwig, Satrapi, & Schönfeldt-Lecuona, 2003; Utz, Dimova, Oppenländer, & Kerkhoff, 2010). In the parietal condition, the target electrode was placed over the left parietal cortex corresponding with the P3 site (see Figure 1a). This site has commonly been used to target the posterior parietal cortex (Sparing et al., 2009; Stone & Tesche, 2009), with proximity to the inferior parietal sulcus (IPS; Herwig et al., 2003). For both region conditions, the reference electrode was located over the contralateral (right) mastoid. This sought to minimise any confounding activation differences caused by the reference electrode. Current flow modelling was conducted a priori using HD-Explore software (Soterix Medical). As shown in Figure 2, the montages resulted in current flow localized to the target regions, being the left dorsolateral frontal lobe and left lateral parietal lobe.

During active stimulation constant currents (anodal and cathodal) were applied at an intensity of 0.7mA for 15 minutes (including a 30 second ramp up/ramp down). This protocol had been used in previous studies by our group investigating the modulation of learning with tDCS (e.g., Filmer et al., 2013a, 2013b, 2016). For sham stimulation, the electrodes were left in place for the full 15 minutes, however stimulation was turned off after 90 seconds (30 seconds constant current with a 30 second ramp up/ramp down). This procedure has been shown to reliably blind participants to the stimulation manipulation (Gandiga, Hummel, & Cohen, 2006). Current densities for all sessions were kept below the safety limit of 0.04 mA/cm^2 (Kessler, Turkeltaub, Benson, & Hamilton, 2012; Nitsche et al., 2008). In order to ensure adequate contact of the electrodes with the scalp, impedances were kept below 20 Ω prior to commencing stimulation.

Contextual Cuing Task

The contextual cueing task was adapted from Chun and Jiang (1998), and was programmed in Matlab 2015b using the Psychophysics toolbox extension (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, & Murray, 2007). The computer was connected to a 19” CRT monitor which had a resolution of 1024 × 768, and a refresh rate of 100 Hz. Participants were seated unrestrained approximately 63 cm from the monitor. Items were coloured white against a grey background (RGB: 80, 80, 80), and could appear within an invisible 15 × 15 grid that extended 10° × 10° visual angle. Displays consisted of one target stimulus, a T-shaped item, among a set of 12 distractor stimuli, L-shaped items. The orientation of distractors was determined randomly for each element and could be either 0°, 90°, 180° or 270° clockwise relative to vertical. Targets could be either 90° (‘right oriented’) or 270° (‘left oriented'). For each participant, a unique set of 12 configurations was generated in which the target location (but not its orientation), and the distractor locations and orientations were to remain constant across blocks – these we refer to as 'repeat' displays. For 'novel' displays, the target and distractor locations varied randomly across blocks.

On each trial, participants reported the orientation of the target T using the 'm' key for right oriented (90°) targets and the 'z' key for left oriented 270° targets. Responses were made via an Apple Macintosh keyboard, and participants were instructed to use their index fingers on both hands to respond. Each trial began with a white fixation cross (2.5° visual angle) presented for 500 ms, followed by the visual search display for 2000 ms, followed by a blank grey screen for 500 ms. The display time was held constant to ensure all participants viewed the configurations for the same duration, regardless of individual RTs. If no response was made during the display window it was recorded as a missed response and the program moved on to the next trial. Correct/incorrect feedback was provided during a practice block that comprised 12 trials of novel displays. The main task consisted of 10 blocks of 24 trials, with each block containing 12 repeat displays and 12 novel displays. Display type (repeat or novel), configuration (1 to 12) and target orientation (left or right) was pseudo-randomised for each block. After each block the program paused, and participants were required to press a key to continue. There was no feedback during the main task.

Self-Report Awareness

In keeping with previous contextual cueing paradigms, we probed for awareness any repetition in the task using computer administered questions immediately after the contextual cueing task. The questions followed the recommended procedure (Smyth & Shanks, 2008). Question one asked, "During the experiment, did you think any of the particular configurations of Ls were repeated?" Participants who responded 'yes' received two follow-up questions. Question two: "Approximately, when did you begin to notice this repetition?" Participants indicated a block number (being from 1 to 10) using the number keys on the keyboard. Question three: "After you realized particular configurations of Ls were being repeated, did you try to memorize these displays?" This required a yes/no response.

Recognition Test

Following the awareness questions, all participants were informed about the repetition of a portion of displays in the task, and that the next section would probe their ability to detect these regularities. The recognition test consisted of 4 blocks of 24 trials with each block containing the 12 repeated displays from the contextual cueing task, and 12 completely novel displays. The instructions were to respond as to whether a display was one that had previously been repeated (press ‘R’) or one that was new (press ‘N’). Participants were told that speed was not important, and to try to be as accurate as possible.

General Procedure

After completing the tDCS safety screening and filling out the pre-tDCS adverse effects questionnaire, participants’ heads were measured, and the stimulation pads were secured. Following the practice trials, stimulation was switched on and allowed to ramp up for 30 seconds before participants began the main contextual cueing task. Participants completed the task in 12 min on average, meaning that the stimulation was active for the entire task duration. Once the stimulation ended, the pads were removed, and the program proceeded to the awareness questions followed by the recognition test. Participants were monitored for 45 minutes following the end of stimulation as recommended by safety guidelines.

Data Analysis

Individual mean RTs were calculated for correct responses only. Outliers greater or less than 3 SDs from an individual’s mean RT were excluded for each display type condition separately. The mean number of discarded trials per participant was 1% in the frontal condition, and 0.9% in the parietal condition. The overall error rates for these groups were low, at 3.47% and 3.74%, respectively. In order to investigate how stimulation may have been influencing learning in contextual cueing, we investigated the contextual cueing effect at two stages of the task. Previous research has indicated that the contextual cueing effect emerges early, typically within the first three blocks (Chun & Jiang, 1998; Jiang & Chun, 2001; Jiang & Wagner, 2004), after which time the learning benefit stabilizes. We therefore defined two stages of learning: an early stage being blocks 1 to 3, and a late stage being blocks 4 to 10.

Results

Response Time Data

Response times decreased over the blocks and were faster for repeat displays compared to novel displays (Figure 2). To assess the effects of tDCS on contextual cueing, block data was collapsed into epochs (Table 1) and a 4-way ANOVA was run with factors: Display Type (repeat vs novel; within-subjects), Epoch (early vs late; within-subjects), Stimulation Type (sham, anodal and cathodal; between-subjects), and Stimulation Region (frontal vs parietal; between-subjects) on the RT data (see Table 1). There was an effect of Display Type ($F_{1,114} = 43.05$, $p < .001$) and Epoch ($F_{1,114} = 200.94$, $p < .001$); along with a

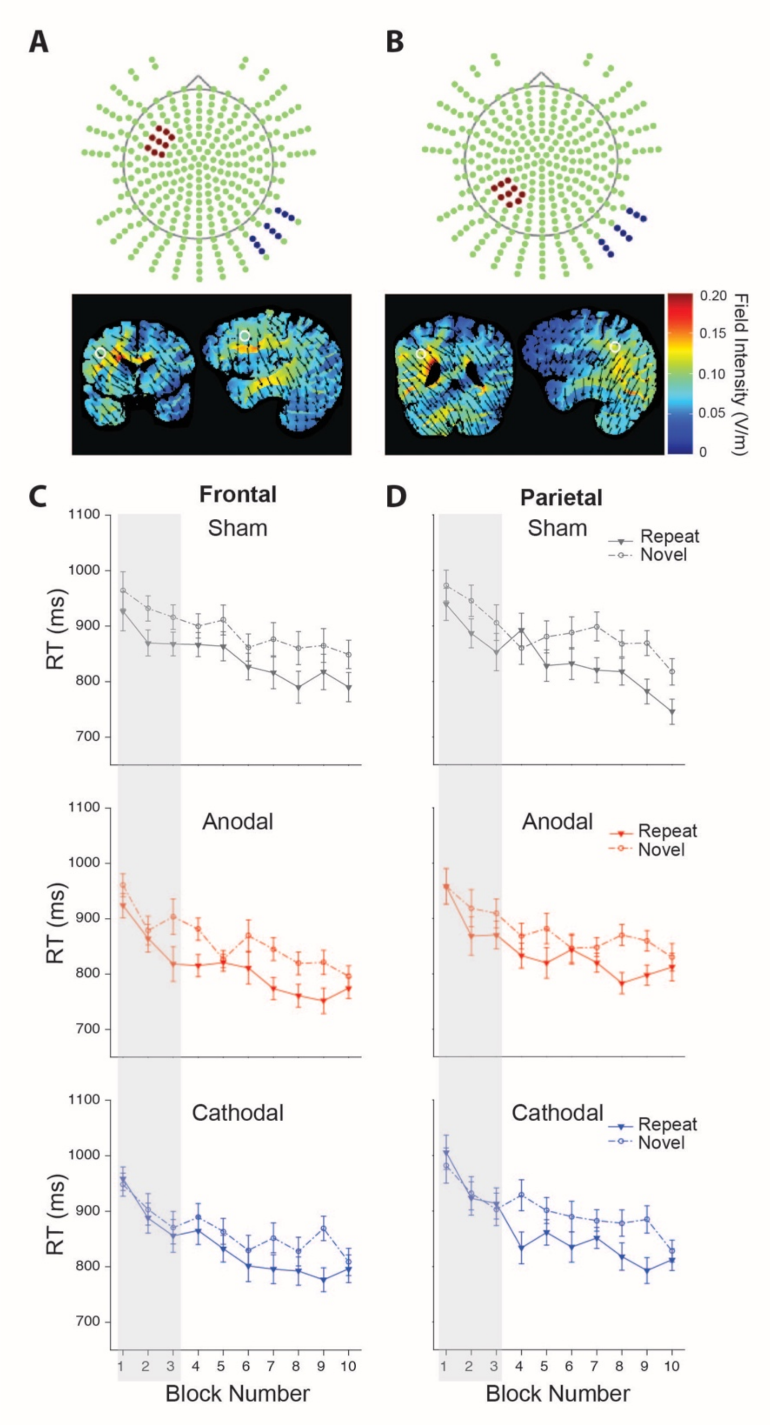

Figure 2. Current flow modelling and tDCS effects on behaviour. A) tDCS montage targeting the frontal region with the target electrode (red) 1 cm posterior to F3. Modelling shows the strongest field intensity localized to the

anterior prefrontal region in the left hemisphere. B) tDCS montage targeting the parietal region with the target electrode over P3 (red). The strongest field intensity was localized to the lateral parietal region in the left hemisphere. RT data for the contextual cueing task as a function of display type, block, and stimulation type (Sham, Anodal and Cathodal), with data shown separately panels for the (C) frontal and (D) parietal regions. Error bars reflect within-subjects confidence intervals (Loftus & Masson, 1994).

Table 1. Group response times (ms) by epoch for the contextual cueing task.

		Early Epoch		Late Epoch	
		Repeat	Novel	Repeat	Novel
Frontal					
	Anodal	868.83 (142.09)	914.35 (159.74)	786.86 (124.72)	837.03 (132.66)
	Sham	888.13 (155.68)	937.52 (140.01)	824.47 (158.38)	874.84 (143.12)
	Cathodal	900.67 (141.67)	907.25 (133.35)	808.65 (132.07)	848.56 (131.37)
Parietal					
	Anodal	899.06 (150.68)	928.59 (152.44)	815.76 (124.58)	857.82 (121.54)
	Sham	892.80 (145.50)	941.31 (143.73)	817.02 (120.80)	868.74 (125.27)
	Cathodal	947.41 (171.98)	938.95 (123.95)	829.26 (110.57)	884.71 (120.04)

Note: Values represent Means (SDs).

significant Display Type × Epoch interaction ($F_{1,114}$ = 7.64, p = .007), demonstrating robust contextual cueing at the omnibus level. Importantly, the 3-way interaction – Display Type × Epoch × Stimulation Type – was significant ($F_{2,114}$ = 4.135, p = .018), indicating that the contextual cueing effect was modulated by the stimulation. There was no effect or interacts with Stimulation Region ($F_{2,114}$ = .37, p = .693). All other ps > .168. We therefore collapsed across Region for the following analyses.

Our comparisons of interest regarding tDCS effects were the two active stimulation conditions (anodal and cathodal), compared to our sham control, and compared to each other. To follow up the 3-way interaction, we conducted separate 3-way ANOVAs with factors Display Type, Epoch and Stimulation Type to assess the following comparisons: cathodal vs. sham, anodal vs. sham, and anodal vs. cathodal. The critical interaction – Display Type × Epoch × Stimulation Type – was significant for cathodal compared to sham ($F_{1,78}$ = 7.85, p = .012) and cathodal compared to anodal stimulation ($F_{1,78}$ = 4.93, p = .039), but not for anodal stimulation compared to sham ($F_{1,78}$ = 0.16, p = .678). This indicated that cathodal stimulation to frontoparietal regions interfered with contextual cueing in the early stages of learning compared to anodal and sham stimulation.

Error Rates

Errors were low across all conditions (Table 2). There was a significant effect of Display Type ($F_{1,114}$ = 11.89, p = .001) and Epoch ($F_{1,114}$ = 9.62, p = .002), such that participants made fewer errors overall for repeated displays (3.31%) compared to novel displays (4.18%), and made more errors in the early epoch (4.15%) compared to the late epoch (3.33%). Repeated displays were therefore associated with both faster and more accurate responses over time. Collectively this indicates there were no speed/accuracy tradeoffs for learning related to contextual cueing. In terms of stimulation effects on errors, there was a significant interaction between Epoch, Stimulation Type and Stimulation Region ($F_{2,114}$ = 5.17, p = .007). Importantly, there were no main effects of Stimulation Type or Region, suggesting tDCS did not alter the ability to perform accurately. Lastly, there were no interactions between Stimulation Type or Region with Display Type ($F_{2,114}$ = .87, p = .421), indicating stimulation did not modulate errors related to our learning measure of interest, being the contextual cueing effect. (All other *ps* > .067.)

Table 2. Group percentage errors by epoch for the contextual cueing task.

		Early Epoch		Late Epoch	
		Repeat	Novel	Repeat	Novel
Frontal					
	Anodal	5.00% (7.48)	5.69% (9.35)	2.14% (4.23)	3.39% (5.59)
	Sham	3.06% (4.49)	4.44% (5.72)	2.98% (5.28)	3.99% (6.12)
	Cathodal	2.08% (4.35)	3.75% (6.00)	3.27% (5.48)	3.69% (5.75)
Parietal					
	Anodal	3.75% (4.91)	4.44% (5.62)	3.15% (5.34)	3.51% (5.19)
	Sham	3.75% (5.39)	3.33% (6.45)	2.80% (4.78)	4.05% (6.08)
	Cathodal	4.72% (6.09)	5.83% (5.75)	3.04% (5.25)	3.99% (6.86)

Note: Values represent Means (SDs)

No Group Differences in Awareness or Recognition

Around half the participants reported being aware of some form of repetition (Figure 3). Pearson's chi-squared test indicated there were no significant differences in the frequency of reported awareness between the stimulation types as assessed for each stimulation region separately (Frontal: $\chi^2 = 2.83$, $p = .243$; Parietal: $\chi^2 = .53$, $p = .63$), nor were there differences between overall ($\chi^2 = .53$, $p = .47$).

Accuracy in the recognition test was around chance, ranging between 48% and 59% across groups. To assess participants' sensitivity when distinguishing repeated displays from novel displays, *d'* (d-prime) was computed for each of the four blocks in the recognition test (shown in Figure 3B).

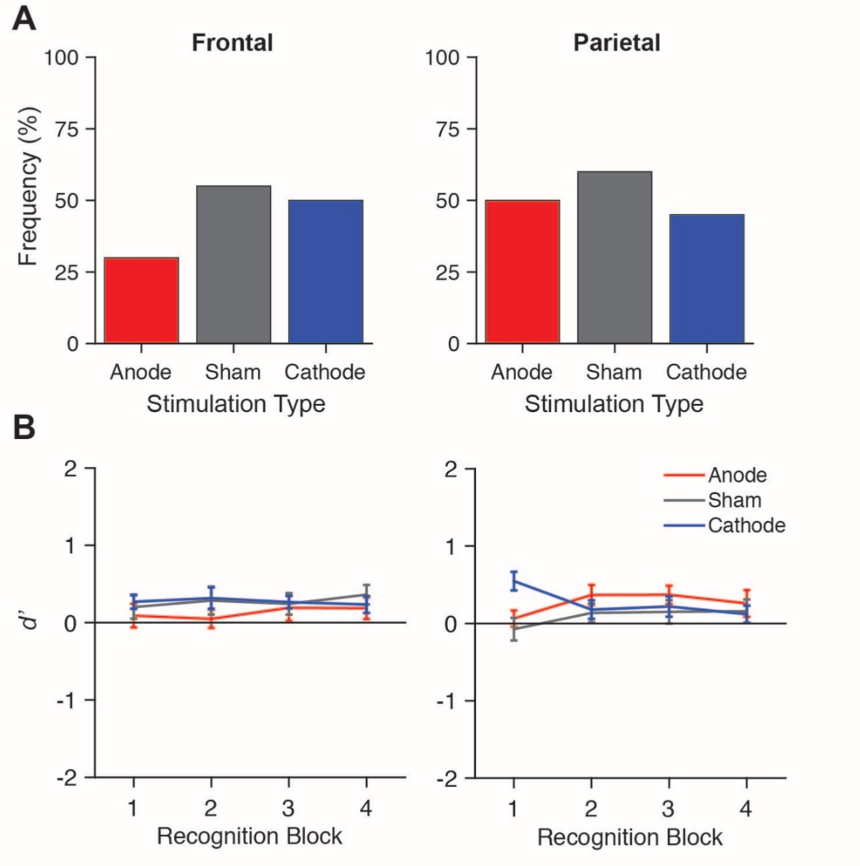

Figure 3. Reported awareness and recognition test results across stimulation groups. A) Percentage of participants who subjectively reported being aware of repetition following the contextual cueing task. This was approximately 50% of participants across all groups. B) Behavioural results from recognition test. Data represents mean *d'* for each recognition block, and error bars represent SEM.

A 3-way ANOVA with factors Recognition Block (1 to 4), Stimulation Type (anodal, sham, cathodal), Stimulation Region (frontal vs parietal) was conducted on the *d'* data. There were no significant effects of Recognition Block ($F_{3,342} = .226$, $p = .878$), Stimulation Type

($F_{3,114}$ = .744, *p* = .477), or Stimulation Region ($F_{1,114}$ = .069, *p* = .794), and no significant interactions (all other *p*s > .115).

While this indicates that recognition was not affected by stimulation, it may be worth noting that *d'* overall was reliably different from zero. A one-sample *t*-test on *d'* collapsed across the four Recognition blocks was significant, (t_{119} = 6.924, $p < .001$, *Mean d'* = 0.203). This is not surprising as it may reflect the ability of participants to learn the repetitions over the course of the four blocks once they have been made aware of the regularities. There was no difference in overall *d'* between those who reported being aware (*n* = 58) and those who were classified as unaware (*n* = 62), based on the probe awareness question after the contextual cueing task. An independent samples *t*-test on *d'* scores revealed no reliable difference in recognition performance between the groups (t_{118} = 1.519, *p* = .131).

Discussion

We sought to determine whether frontal and parietal brain regions are causally involved in statistical learning that occurs in spatial contextual cueing. We applied anodal, cathodal or sham tDCS online, either to the left PFC or left PPC. The contextual cueing effect, which is characterised by faster RTs for repeated relative to novel search displays, was disrupted in the early epoch by cathodal stimulation, relative to sham and anodal stimulation, for both the frontal and parietal conditions.

The current results extend previous neuroimaging findings regarding the cortical locus of learning during contextual cueing. Early investigations into the neural structures responsible for incidental statistical learning highlighted the importance of subcortical brain regions such as the hippocampus (Chun & Phelps, 1999) and striatum (Rieckmann, Fischer, & Bäckman, 2010). Since then, fMRI studies of contextual cueing corroborated the involvement of the hippocampus and its relation to learning performance (i.e., the typical interaction observed between display type and epoch/block). In addition, these studies consistently reported activity in cortical areas such as the dorsolateral PFC and regions within Posterior Parietal Cortex (PPC) that was associated with the repeat-novel contrast (Giesbrecht et al., 2013; Manginelli et al., 2013a; Pollmann, 2012). These correlational findings did not allow inferences about whether such cortical activity was necessary for learning to occur or was a by-product of other cognitive process operating on the learned repeated displays.

The present results provide the first causal evidence that both frontal and parietal regions are directly involved in the evolution of the contextual cueing effect, as evidenced by modulation of early learning observed here. Based on the functional and structural interconnectivity of these targeted regions with the hippocampus (Wang et al. 2014), one may question the contribution of hippocampal activity to the effects seen here. To comment on such dynamics would be speculative and is outside the scope of this study. Our tDCS modelling suggests that our stimulation protocol produced concentrated areas of current flow surrounding the left DLPFC and the left IPL. We therefore adopt the most parsimonious conclusion that frontal and parietal areas are critical for learning during contextual cueing.

Our results do not appear to be due to baseline differences in RTs. The variation in RTs for the first block was not reliable across stimulation region, stimulation type, or display type (all *p*s > .129). These differences are most likely attributable to inter-participant noise, rather than systematic differences between conditions. Looking at the two sham groups, there appeared to be a visual difference in the size of the contextual cueing effect between the frontal and parietal groups. Once again, these differences were not reliable (all *p*s > .526). It also seems unlikely that the effect of cathodal stimulation can be explained by modulation of general performance or response speed. If this were the case, why would stimulation selectively affect performance for repeat displays? Here, the novel trials constituted a control task in the form of standard visual search. If we take mean RTs for the novel displays to indicate baseline task performance, and hence arousal, we see no effects of Stimulation Type or Region (all *p*s > 0.359). Put differently, stimulation only affected performance when we included the repeat versus novel contrast – i.e. the contextual cueing/learning effect. This deems it unlikely that general changes in attention or responding could account for the pattern of results observed here.

Furthermore, while we argue that tDCS interrupted processes specifically related to the incidental learning of repeated configurations, one alternative explanation may be that tDCS affected generalized motor processes, rather than processes specific to statistical learning. We believe this is unlikely as any changes in motor processing should influence responses for repeat and novel displays to the same degree, as both display types required identical response mappings for the orientation judgment. Therefore, a purely motor account cannot readily explain the increasingly faster RTs seen for repeated contexts compared to novel contexts and the interaction with cathodal stimulation.

Given the apparent criticisms regarding the spatial specificity of tDCS, it is reasonable to question whether cathodal stimulation of any brain region might explain the modulation of contextual cueing seen here. We rebut this point based on the fact that we evaluated and selected our electrode configurations a priori using tDCS current-flow modelling software. The patterns of current flow were distinct for the two stimulation montages, and the areas of peak current density were located in the respective target regions. However, given the well-known structural and functional connectivity between the frontal lobe and parietal lobe as part of the frontoparietal network (Sestieri et al., 2017), it remains possible that targeting one region may have modulated activity in the other region, and these changing network dynamics may have contributed to the effects seen here rather than changes in a local brain region. Indeed, a study using resting-state fMRI found that anodal tDCS targeting the left prefrontal cortex increased coactivations between frontal and parietal regions (Keeser et al., 2011). Future studies should investigate how interactions between frontal and parietal regions may influence behaviours relating to incidental learning, and how these may be modulated by brain stimulation. For now, it seems plausible that frontoparietal regions may support statistical learning via activation of intervening cognitive control resources supplemented by these regions.

Contextual Cuing typically emerges quickly, with evidence of learning after only three repetitions (Chun & Jiang, 1998; Jiang & Chun, 2001; Jiang & Wagner, 2004; Zellin, Mühlenen, Müller, & Conci, 2014). The key finding in our study was that cathodal tDCS disrupted this early learning. At first, it may seem surprising that stimulation at a constant intensity caused behavioural changes in a limited time window of the task. Yet this makes sense when considering the non-linear dynamics of tDCS (e.g., Batsikadze et al., 2013), and the complexity of associated behavioural outcomes (Bestmann et al., 2015; de Berker, Bikson, & Bestmann, 2013).

We conceptualize our result as reflecting an impairment, or a delay in learning, rather than complete disruption of this process. Cathodal stimulation appears to make learning the repeating target-context associations more difficult to begin with, but does not render learning impossible, given sufficient exposure to the regularities. In behavioural studies of contextual cueing, there is evidence of delayed learning when concurrent WM tasks are administered during the early learning phase (Annac et al., 2013; Manginelli, Langer, Klose, & Pollmann, 2013b) and when displays are associated with certain types of feedback (Tseng & Lleras, 2012). At the neural level, reports of tDCS affecting a network without preventing it from operating are also consistent with our findings. Using computational modelling, a recent study showed that tDCS to left DLPFC altered network dynamics, which affected behaviour, yet did not prevent transmission of task-related neural activity (Bonaiuto, de Berker, & Bestmann, 2016). In our study, the temporal specificity of cathodal effects may have been due to the recruitment of other networks to compensate for the lost functioning. It is also possible that processing in the targeted regions was transient rather than sustained, and thus minimally affected. Alternatively, homeostatic mechanisms may have compensated for the effects of tDCS by returning network activity to its baseline levels after a sustained increase in excitability (Iyer, Schleper, & Wassermann, 2003; Turrigiano, Leslie, Desai, Rutherford, & Nelson, 1998; Wright & Krekelberg, 2014).

It should also be noted, that our finding of PFC involvement in contextual cueing is consistent with stimulation studies of other statistical learning processes. Repetitive TMS (rTMS) delivered to contralateral DLPFC was found to disrupt sequence learning in the SRT task compared to ipsilateral DLPFC and SMA controls (Pascual-Leone, Wassermann, Grafman, & Hallett, 1996). A later study replicated this finding showing that rTMS to DLPFC abolished learning compared to a parietal target, and further stipulated that this was specific to learning of spatial information, compared to a colour or a combined version of the SRT task (Robertson, Tormos, Maeda, & Pascual-Leone, 2001). Using a probabilistic category learning task, anodal tDCS to left PFC improved incidental learning compared to cathodal and sham stimulation (Kincses, Antal, Nitsche, Bártfai, & Paulus, 2004). While the processing demands of these tasks may be quite different from those that underlie contextual cueing, it appears PFC involvement is common across forms of statistical learning.

The present results must also be considered in relation to the proposed benefits of reduced frontal involvement for incidental learning. As described in the introduction, according to this work, reduced cognitive control, mediated by PFC disengagement, is advantageous for tasks that involve processing bottom-up stimulus-response information (Thompson-Schill et al., 2009). This account might predict that disrupting the left PFC with tDCS (either from anodal, cathodal, or both) would improve contextual cueing, whereas we found that cathodal stimulation disrupted learning by reducing the early cuing contextual cueing effect. The first point to make here, and as noted earlier, is that we cannot be sure that cathodal stimulation actually reduced activity in the target region (Batsikadze et al., 2013). Even if it did, there is fMRI work showing that reduced activity does not always indicate reduced involvement of a region (see Garner & Dux, 2015; Kok, Jehee, & de Lange, 2012), as it can also reflect sharper neural coding in a brain area and enhanced representations. Another point of difference concerns the type of tasks used. The work on hypofrontality has employed high-level conceptual or language-based tasks. These have involved generating verbal responses (Chrysikou et al., 2013) or categorizing stimuli based on abstract concepts (Lupyan et al., 2012), and were predominantly accuracy based. These tasks, no doubt, exert quite distinct processing demands from those recruited during visual search with speeded responses. Finally, this literature emphasizes a dissociation between the brain regions that support performance in line with current goals (e.g., distinguishing targets from non-targets) and those that underpin learning about the environment (e.g., forming target-context associations). Thus, this hypothesis might predict different response strategies for target and distractor processing when PFC function is disrupted. We see this as an avenue for future research into the potential ways that incidental learning for target-context regularities may be acted upon by the system.

Conclusions

In summary, we found that the evolution of statistical learning for configural visual information relies on activity in frontoparietal brain regions. These findings show for the first time that cortical areas are directly involved in the early emergence of the contextual cueing effect, and perhaps incidental learning generally. This result provides a common link between the frontal networks involved in explicit forms of learning, such as goal-directed training and intentional skill learning, and those tapped during incidental statistical learning that acts on higher-level information processing. Understanding the causal brain-behaviour relationships that support incidental statistical learning is important for developing more comprehensive models of how the brain computes associations between stimuli and uses this information to inform decisions in an automatic manner.

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CHAPTER 4:

A CORTICAL ROLE IN STATISTICAL LEARNING EFFECTS ON BEHAVIOUR

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Abstract

Visual statistical learning describes the encoding of complex patterns found in sensory material, and it has important functional consequences for cognition. Higher-order brain regions within the prefrontal and posterior parietal cortices are consistently implicated in neuroimaging studies of statistical learning. Yet causal evidence for this cortical contribution remains limited. In a recent study, we used transcranial direct current stimulation (tDCS) to perturb the left frontoparietal cortex while individuals learned location-based regularities in a spatial contextual cueing task. Here, we examined if the same tDCS protocol influences statistical learning of identity-based, rather than spatial, structure. Across two preregistered experiments using large samples (N = 150, and N = 80), we measured learning of shape co-occurrences (i.e., Fiser and Aslin, 2001) while the left posterior parietal cortex was perturbed by cathodal tDCS. In Experiment 1, we employed the standard recognition test to assess learning offline, after participants encoded the structure, but found no effect of parietal stimulation compared to a sham control or to an active control region. In a second experiment we developed a new task using the same identity-based structure but now included an online measure, during exposure, in order to assess the timecourse of learning. Under these conditions, we observed a stimulation effect that influenced the learning of identity-structure in early blocks of trials. This finding indicates that tDCS impacts statistical learning across distinct paradigms and stimulus dimensions. It adds to the imaging evidence that supports the hypothesis that there exists a domain-general neural mechanism, comprised of cortical areas, that underlies statistical learning that potentially works in concert with subcortical memory structures.

Through repeated experience the human brain can form incidental knowledge about complex patterns in the sensory environment (Fiser & Aslin, 2001; Turk-Browne, 2014). This ability, termed *statistical learning,* is believed to be supported by a neural mechanism that is domain-general; a mechanism that encodes structure-rich sensory input (Kirkham, Slemmer, & Johnson, 2002; Perruchet & Pacton, 2006; but see Conway & Christiansen, 2005). In support of this, there appears to be a common-list of brain areas that are associated with viewing or retrieving structure across different tasks and inputs (Batterink, Paller, & Reber, 2019). Yet statistical learning goes beyond tracking and storing such relationships since it can also facilitate ongoing cognition to produce learning. In vision, one of the key functions of statistical learning is to generate implicit predictions that can benefit decision-making in the context of visual search (Chun & Jiang, 1998; Goujon, Didierjean, & Thorpe, 2015). How neural activity directly supports these functions of statistical learning remains largely unknown.

A prime illustration of statistical learning in human vision concerns our ability to swiftly recognise scenes. After a single repetition, the way we recognise new objects will be based off incidental encoding of the underlying probabilities between the objects/features that constitute the scene (Biederman, Mezzanotte, & Rabinowitz, 1982; Friedman, 1979; Henderson, Weeks, & Hollingworth, 1999). In their seminal demonstration, Fiser and Aslin (2001) had participants view a series of arrays that contained shapes arranged side-by-side in a grid. Unbeknownst to observers, each shape belonged to a base-pair that had a fixed spatial arrangement over the course of the experiment. Each pair was shown alongside every other possible pair, and across multiple locations within the grid. The question was whether people encoded these higher-order statistics, in this case joint probabilities, that defined the base-pairs above the other shape-shape combinations.

In a forced-choice recognition test, participants did indeed reliably select the base-pairs over foil pairs, despite not being able to report the existence of any patterns. This was taken as evidence that novel objects are encoded based on statistical characteristics beyond mere frequency. In subsequent experiments (Fiser & Aslin, 2002a; 2005), these authors went on to show that humans extract multiple higher-order statistics in parallel and, critically, that they can do so without an active task or feedback, leading such learning to be described as “incidental”. This task been used repeatedly in other work (Conway, Goldstone, & Christiansen, 2007; Covington, Brown-Schmidt, & Duff, 2018; Karuza et al., 2017; Luo & Zhao, 2017; Roser, Aslin, McKenzie, Zahra, & Fiser, 2015; Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Zhao, Ngo, McKendrick, & Turk-Browne, 2011), and remains a prominent tool for assessing visual statistical learning.

Since this pioneering work, a number of paradigms have been developed to tap the extraction of different types of structure from visual arrays (Fiser & Aslin, 2002b; Orbán, Fiser, Aslin, & Lengyel, 2008; Turk-Browne, Johnson, Chun, & Scholl, 2008b). Another highly used example is contextual cuing (e.g., Chun and Jiang, 1998). Unlike the exposure-test format used in the Fiser and Aslin paradigm, contextual cuing makes use of implicit cuing behaviour; where learning is assessed online via a difference in response times (RT) for different types of arrays. In the standard version of the task, observers must locate a target (often a rotated “T”) among an array of distractor items (rotated “Ls”) and make a decision about how the target is oriented; either to the left or right. In half the arrays, the locations of distractors are random, and this forms a control condition that tracks typical visual search behaviour. In the other half of arrays, the distractor locations repeat and come to be associated with a given target location, though not the response associated with the decision, as target orientation varies randomly across trials. Over the course of exposure, response times to the repeating distractor arrays are expedited compared to the control, and this forms an online index of statistical processing. It is generally agreed that this form of contextual cuing reflects statistical encoding of the spatial relationships between elements in an array (Chun & Turk-Browne, 2008; Goujon et al., 2015). Thus, both the Fiser & Aslin paradigm and contextual cuing represent two prominent but distinct ways to measure visual statistical learning; one that uses identity-based structure, and another that uses location-based regularities. Both tasks have also been employed in neuroimaging work to assess the neural substrates of statistical learning.

The Neural Substrates of Visual Statistical Learning

The evidence to date suggests there may be distinct neural substrates for statistical learning depending on the types of structures that are being encoded. Much of the functional neuroimaging work has focused on temporal regularities of sequential regularities, such as in the serial reaction time task (SRT) or in artificial grammar (AGL) tasks (Abla, Katahira, & Okanoya, 2008; Aly & Turk-Browne, 2016; Gheysen, Van Opstal, Roggeman, Van Waelvelde, & Fias, 2010; 2011; Turk-Browne et al., 2008b; Turk-Browne, Scholl, Johnson, & Chun, 2010). These studies tend to report activation in prefrontal, motor and striatal areas which are regions associated with procedural learning. Passive processing of spatial structure appears to involve cortical regions in the posterior parietal cortex (PPC) (see Karuza et al., 2017). Using spatial structure for ongoing behaviour is also associated with these parietal regions as well as regions in the prefrontal cortex (PFC). For example, in the contextual cuing paradigm viewing repeat displays has been associated with increased BOLD activity in the left inferior parietal sulcus, the superior parietal lobe, and the temporal parietal junction compared to novel displays (Giesbrecht, Sy, & Guerin, 2013; Hall, Naughtin, Mattingley, & Dux, 2018; Manginelli, Baumgartner, & Pollmann, 2013; Pollmann, 2012; Pollmann & Manginelli, 2010), reflecting spatial learning of target-distractor regularities. In one study (Manginelli et al., 2013) this pattern of activity was also associated with larger cuing magnitudes across individuals, suggesting a functional relationship between the parietal activity and behaviour.

Parietal activation was similarly observed in the Fiser & Aslin paradigm. A recent fMRI study measured BOLD activity across three runs during passive exposure to arrays containing embedded pairs (Karuza et al., 2017). The researchers observed activity in a distributed network of bilateral parietal, occipital and subcortical areas. This converged with the imaging results mentioned above for contextual cuing and suggests a common neural mechanism for encoding structure from spatial arrays. But unlike contextual cuing, these changes in BOLD activity during encoding were not related to later recognition of the pairs. However, when looking at connectivity measures using task-based interregional correlations, Karuza and colleagues found correlations with functional behavioural outcomes. Specifically, they observed a functional change between the left superior parietal lobe and the right hippocampus during exposure that was predictive of stronger pair recognition at test. This network fits with the changes to frontoparietal and the parietohippocampal networks implicated in spatial contextual cuing (Manelis & Reder, 2012). Collectively, the neuroimaging work builds a case for the involvement of higher-cortical areas in the functional aspects of statistical learning beyond merely visual processing or task adaptation yet fall short of testing this directly.

Brain Stimulation Effects on Statistical Learning

Experiments using tDCS can uncover causal brain-behaviour links that govern learning-related operations (Filmer, Dux, & Mattingley, 2014). This technique involves placing electrodes on the scalp to deliver a weak electrical current to a target region, which has been hypothesised to alter membrane potentials in that area and thus the likelihood of neural activity (Bikson, Name, & Rahman, 2013; Dayan, Censor, Buch, Sandrini, & Cohen, 2013; Filmer et al., 2014; Nitsche & Paulus, 2000; Nitsche, Schauenburg, et al., 2003b), though it does not directly evoke action potentials (Ruhnau, Rufener, Heinze, & Zaehle, 2018). Therefore, combining tDCS with a task can be used to gain understanding of the causal neural dynamics that support a given process. The success of this technique is evident in the domains of cognitive training (Filmer, Lyons, Mattingley, & Dux, 2017a; Filmer, Mattingley, Marois, & Dux, 2013; Filmer, Varghese, Hawkins, Mattingley, & Dux, 2017b) and motor learning (Nitsche, Schauenburg, et al., 2003b; Reis et al., 2009) where targeting key processing regions influenced learning by altering processes related to consolidation in the case of motor learning, and evidence accumulation in the case of decision-making training. Whether similar effects may be observed for a type of incidental learning that occurs outside the motor domain has undergone limited investigation.

To this end, and in the first study of its kind, we previously employed online tDCS to investigate direct cortical involvement in visual statistical learning (Nydam, Sewell, & Dux, 2018). In this experiment, participants completed a standard contextual cuing task while we targeted the left posterior parietal cortex or the left prefrontal cortex with anodal, cathodal or sham tDCS. In the sham control, cuing manifested early and was maintained throughout the task. However, under cathodal stimulation this early cuing effect was disrupted, indicating a delay to learning by stimulation. This was interpreted as evidence of direct frontoparietal involvement in processing location-based regularities. These results aligned with two other stimulation studies that looked at target-context processing in contextual cuing that argued for a direct role of the frontal cortex (Pergolizzi & Chua, 2017; Zinchenko, Conci, Taylor, Müller, & Geyer, 2019). However, those studies focused on operations to do with change detection after encoding the arrays, rather than the evolution of learning itself. Based on this evidence that parietal regions process structural redundancies in spatial arrays, here, we seek to investigate whether tDCS of these parietal structures influences statistical learning of identity information that is spatial variant.

In two pre-registered experiments, we investigated whether perturbing neural activity with online tDCS influences visual statistical learning applied to identity-based contingencies (i.e., the Fiser & Aslin paradigm). Given the recent finding of the superior parietal lobe being predictive of pair recognition in the Fiser & Aslin paradigm (Karuza et al., 2017), we focused on this as our target region. In addition, based on our previous findings (Nydam et al., 2018) we compared cathodal currents to a sham control, and to an active control region; selected to be the left orbitofrontal cortex (OF) because it had not been associated with visual statistical learning in past fMRI work. In Experiment 1, statistical learning was assessed using the traditional Fiser & Aslin (2001) method. Brain stimulation was delivered online for 15 minutes during both exposure and test. If tDCS was affecting a common statistical learning process, we expected stimulation to influence learning regardless of the task used to measure it. Specifically, we predicted that pair learning, indexed by above-chance recognition, would be modulated by tDCS indicated by a difference between the group receiving active (cathodal) stimulation over the left posterior parietal cortex, when compared with the sham control group and with the region control group (over orbitofrontal cortex).

Experiment 1

Preregistration

The method and analysis were registered prior to data collection at: osf.io/7hqxe. The materials and data have also been made available online.

Participants

We recruited 150 healthy participants aged 18 – 40 years from The University of Queensland community, and randomly assigned them to three stimulation groups: cathodal-PPC, sham control, cathodal-OF (active control). All were right-handed, with normal or corrected-to-normal vision and were eligible to receive non-invasive brain stimulation based on the international safety guidelines (Nitsche et al., 2008). The sample demographics were; mean age = 21.1 years, 63% female, 66% glasses or contact use and mean Oldfield handedness score = 86%. Prior to commencing the stimulation, the average impedance was 8.47 mA. The study was approved by The University of Queensland Human Research Ethics committee and participants were paid AU$20 for a one-hour session. The sample size of 40 was chosen from power calculations that indicated 38 participants would be sufficient to achieve a power of 85%, given a medium effect size (Cohen's d = .5) for a between-subjects effect of group. The sample size was later amended to 50 per group due to an error in our randomisation procedure where we over assigned to one group. This was logged in the project registration at the time of discovery.

Visual Statistical Learning Task

Participants were seated approximately 63cm from a 19″ CRT monitor (resolution 1024 × 768; 100 Hz refresh rate) connected to an Apple iMac computer with a Macintosh keyboard. The experiment was run using custom code programmed in MATLAB 2015b using the Psychophysics Toolbox 3 (Brainard 1997; Kleiner et al. 2007; Pelli 1997). Due to constraints in lab availability and scheduling, a portion of participants were run in a different room with a 24″ ASUS nVidia LCD monitor (resolution 1920 × 1080, 60 Hz refresh rate) connected to the same computer, and stimuli had the same visual angle. There was no difference in learning based on monitor type or room.

Exposure Phase

The visual statistical learning task closely followed the exposure and test method developed by Fiser and Aslin (2001). As shown in Figure 1, visual displays contained black shape-silhouettes (3.6° visual angle) arranged in an invisible 3 × 3 grid (16° visual angle) on a grey background (RGB: 80, 80, 80). For each participant, 12 shapes were randomly selected from a pool of 24 shapes used previously (Fiser & Aslin, 2001; 2002b) and each shape was assigned to one of six base pairs that each had a fixed spatial arrangement; horizontal, vertical, or oblique (left or right oriented). Each array contained three base-pairs that were recombined with the constraint of having one from each arrangement per array. This formed eight possible pair combinations that appeared in different cell locations within the grid to create 144 trials. Exposure trials began with a fixation dot for 1000 ms (with up to 500 ms jitter) followed by the display for 2000 ms and lasted eight minutes. There was a self-paced break at the half-way point where participants pressed the space bar to continue. Since no responses were required during the exposure phase, participants were simply instructed to view the slideshow with eyes open and to be awake.

Test Phase

After exposure, there was a surprise two-interval forced choice recognition test. On each trial two pairs were shown sequentially at fixation. Participants indicated whether the first pair or the second pair was more familiar using index fingers to press the ‘z’ and ‘m’ keys after the second pair was displayed. Participants were instructed to focus on accuracy. Each of the six base pairs (e.g., AB) were compared against two foil pairs (e.g., AC and DB; as per Experiment 1, Fiser & Aslin, 2001) in a counterbalanced order. This produced four recognition trials for each of the six base pairs (24 test trials in total). Test trials begin with a fixation dot for 1000 ms, followed by the first pair for 2000 ms, a blank ISI of 1000 ms, the second pair for 2000 ms, and a screen with the key prompts that terminated upon response. It lasted two minutes on average, and critically, no participant finished before the stimulation was completed.

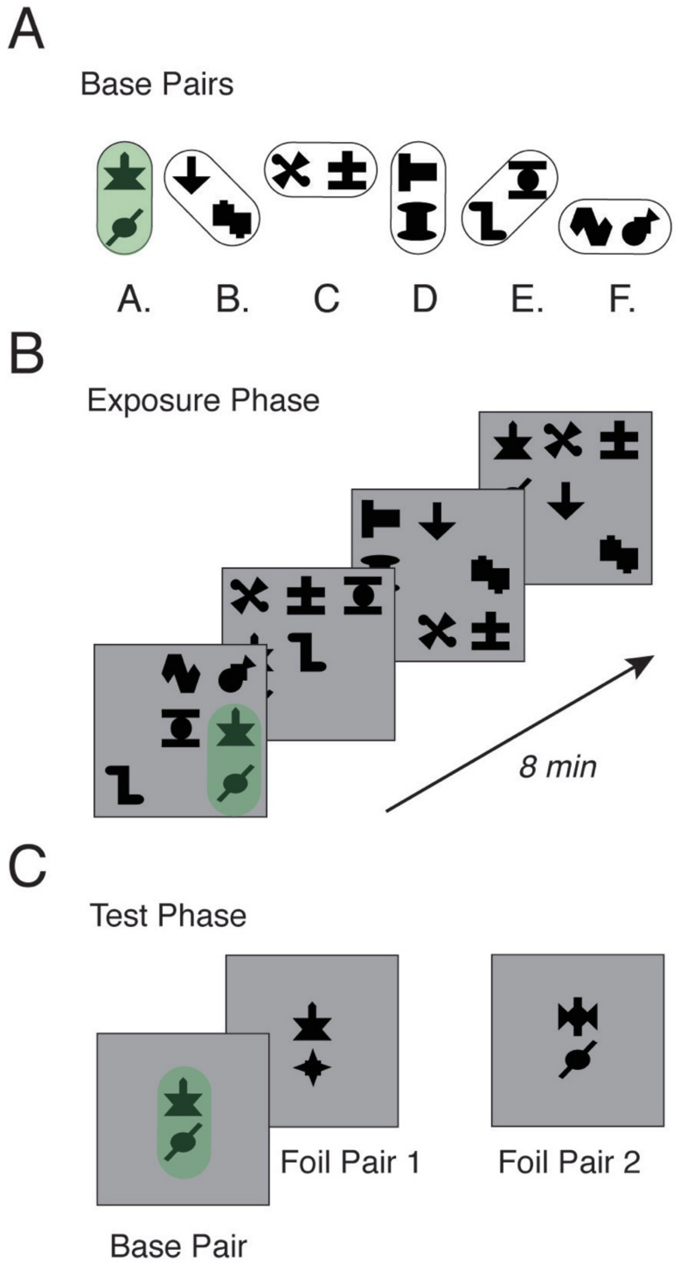

Figure 1: Visual statistical learning task following the method of Fiser and Aslin (2001; Experiment 2). (a) Each spatial arrays contained three of the six base pairs. (b) Participants viewed 144 arrays over eight minutes with passive exposure. (c) In a surprise recognition test that followed, participants were shown two pairs, presented sequentially, and had to select the more familiar pair. Note the green shading included here was for emphasis and was not part of the stimulus.

Transcranial Direct Current Stimulation

Stimulation Parameters

Across three groups we manipulated: (1) the type of current; cathodal (active) or sham (placebo control); and (2) the target region; the left posterior parietal cortex (PPC) or the left orbital frontal cortex (OF: active control). To target the left PPC, the cathodal electrode was placed over the CP3 location according to the international 10-20 EEG system and the reference was placed over the contralateral (right) mastoid bone. To target the orbitofrontal (OF) control region, we used the same reference location, but positioned the cathodal electrode just above the left eyebrow in line with the outer edge of the eyebrow.

Stimulation was delivered via a Neuro-Conn stimulator connected to 5cm × 5cm rubber electrodes secured to the scalp with Ten20 conductive paste. For the active conditions, stimulation was delivered at .7 mA intensity for 15 minutes, plus an additional 30 second ramp up and ramp down (900 seconds total). We chose this stimulation protocol based on Nydam et al. (2018). It produced a maximum current density of .028 mA/cm^2 under each electrode, well within the safe limits (Nitsche, Liebetanz, et al., 2003a). Sham stimulation involved 30 seconds of constant current plus a 30 second ramp up and ramp down (90 seconds total). To ensure adequate contact of the electrodes, the scalp was lightly abraded with alcohol wipes to remove oil and dirt, and stimulation only went ahead if an impedance below 20 μA/cm^2 could be achieved.

Current-flow modelling was conducted apriori using HD-Explore software (Soterix Medical) to confirm distinct cortical electrical fields were produced by our two electrode montages. The estimated field-intensity was concentrated in the intra parietal sulcus (IPS) within the left posterior parietal region (Brodmann Area 7) with the current directing up and outward. This was distinct to our control montage that showed concentrated currents within the anterior frontal region (Ba9 and Ba10), as well as the ventromedial frontal (Ba25) and inferior frontal gyrus (Ba45 and Ba47).

Procedure

Participants attended a single one-hour session. Stimulation was left to ramp up for 30 seconds before commencing the visual statistical learning task and never finished before a participant had completed all trials in the recognition test. Afterwards, participants were asked to self-report: (1) whether they recognised any shape patterns during the exposure phase, (2) whether they noticed the existence of shape pairs during exposure, (3) and to guess whether they were in the active stimulation condition or the placebo condition. We also recorded demographics variables of age, gender, Edinburgh handedness score (Oldfield, 1971), and whether they wore glasses or contacts.

Data Analysis

Our primary DV was accuracy on the familiarity test, indexed as the mean proportion correct. All frequentist statistics were run as two-tailed tests with an alpha of .05. Bayes factors were calculated using an uninformative prior, namely a zero-centered Cauchy distribution with a scale of .7. We considered (a) a non-directional stimulation effect since active stimulation could produce either facilitation or disruption (Filmer et al., 2014); (b) tDCS effect sizes are typically small in the literature; (c) and since we could not estimate an effect size with much precision we permitted a large credible interval. We interpreted the Bayes factors according to Jeffrey's classification scheme (Wagenmakers et al., 2017) whereby values between 1/3 and 3 indicate inconclusive evidence, and values greater than 3 (or less than 1/3) indicated moderate evidence. Finally, to assess successful learning in each group separately, we built null distributions pertaining to chance performance and compared this to the 95th percentile. The distributions were built by converting individuals' accuracy at test to deviance scores from chance (i.e., 65% accuracy becomes +15% deviance), randomly assigned a sign (+ or -) and calculated the mean over 1000 samples.

Results

Planned Analyses

Learning Across the Groups

All three groups displayed above change accuracy on the recognition test (Figure 2), illustrating robust a visual statistical learning effect. Accuracy was highest in the Cathodal-PPC group (μ = 62.90%, σ = 9.6, SEM = 0.14), followed by Sham (μ = 60.60%, σ = 13.3, SEM = 0.19), and was lowest in the Cathodal-OF active control group (μ = 58.80%, σ = 12.9, SEM = 0.18. The null distribution tests revealed performance well above the 95th percentile cutoff in all cases. For consistency with the visual statistical learning literature, we ran one-sample *t*-tests comparing performance to chance (50%) in each group. All were significant, $t_{(49)}$ = 9.471, 5.631, and 4.854 for Cathodal-PPC, Sham and Cathodal-OF respectively. Since the sham group consisted of half the participants having had the PPC montage and the other half having had the OF montage, we checked for baseline differences and observed evidence favouring the null, $t_{(48)} = .132$, $p = .896$, $BF_{10} = .287$ (log $BF_{10} = -1.248$), and so the following analysis were performed on the sham group as a whole, across both montages.

Stimulation Effects on Learning

Having established recognition of the pairs in all three groups, we turned to our key hypothesis regarding stimulation effects on learning. Using three independent samples *t*-tests, we compared: Cathodal-PPC with Sham (to assess the cathodal PPC effect); Cathodal-OF with Sham (to assess the control region effect); and Cathodal-PPC with Cathodal-OF (to assess any region effects). Overall, we found no group differences. Pair recognition was not significantly different between the Cathodal-PPC group and the Sham group, $t_{(98)} = 1.00$, $p = .318$, $d = .201$, $BF_{10} = .330$ (log $BF_{10} = -1.1$), with the data providing weak support for the null hypothesis over the alternate. Similarly, recognition in the region control group (Cathodal-OF) was not significantly different from the Sham group, $t_{(98)} = -0.669$, $p = .505$, $d = -.134$; $BF_{10} = .259$ (log $BF_{10} = -1.349$); the data indicating weak support in favour of the null. There data were uninformative regarding the region effect that compared Cathodal-PPC to Cathodal-OF, $t_{(98)} = 1.795$, $p = .076$, $d = .359$, $BF_{10} = .897$ (log $BF_{10} = -0.129$). Overall, the results favoured null effects of stimulation.

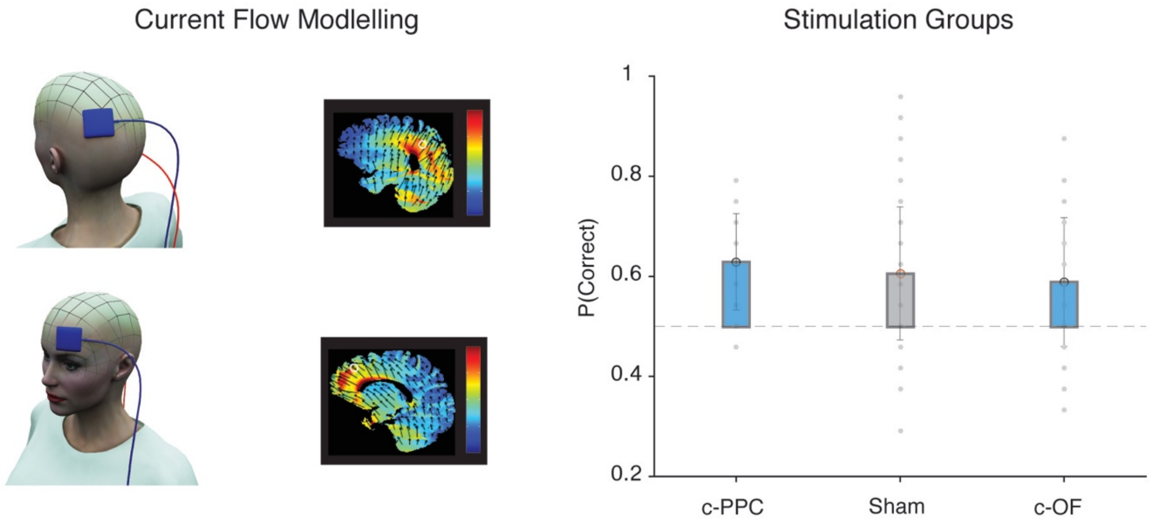

Figure 2. Current flow modelling and Experiment 1 results. Modelling shown for the two electrode montages targeting the left PPC as the region of interest and the left OF region for the active control. Sham stimulation

was used as a placebo control (not shown) applied to half the group using the PPC montage and half using the OF montage. Accuracy on the recognition test for each stimulation group shown with the individual (dots) and means (bars) data. The dotted line represents chance performance (50%) and the error bars indicate the standard error of the mean.

Exploratory Analyses

Removal of Non-learners

Despite robust learning at the group level, a portion of participants failed to recognise the pairs above chance, which was 14% of the total sample. This was compatible the broader VSL literature in which roughly one third of people do not show recognition (Arciuli, Torkildsen, Stevens, & Simpson, 2014; Siegelman, Bogaerts, & Frost, 2017; Turk-Browne & Scholl, 2009; Turk-Browne, Jungé, & Scholl, 2005). Some have argued that a more representative measure of learning would be the total number of individuals who exhibit above chance performance (Siegelman et al., 2017; Siegelman, Bogaerts, Christiansen, & Frost, 2016). In our study, a chi-squared test indicated no group differences on this measure (four in Cathodal-PPC, six in Sham, and 11 in Cathodal-OF), $\chi^2 = 4.319$, $p = .115$; $BF_{10} = 1.699$. Since our main hypothesis concerned *learning* we removed these individuals and re-ran the one-way ANOVA on mean accuracy, since this test is robust to differences in sample size. It was not significant, $F_{(2,\ 126)} = .108$, $p = .898$, $BF_{10} = .082$ (means: Cathodal-PPC: 64.4% > Sham: 63.4% > Cathodal-OF: 63.8%), and the data strongly favoured the null hypothesis over the alternative. Therefore, constraining the analysis to learners did not change the pattern of null results but arguably led to proportionally stronger support for the null over the alternative.

Awareness Questionnaire

It is possible that tDCS may have affected awareness of the pairs. Upon questioning, 59 individuals (39%) self-reported they were aware. Fewer people were aware by this measure in the Cathodal-OF group (26%) than the Cathodal-PPC (42%) and Sham (50%) groups, according to a significant chi-squared test, $\chi^2 = 6.258$, $p = .044$, $BF_{10} = 2.503$. Awareness related to accuracy as expected, with higher accuracy in aware individuals (65.5%) than unaware (57.7%), $t_{(148)} = -4.084$, $p < .001$, $BF_{10} = 285.4$. Critically, when entered into a two-way ANOVA on accuracy, awareness did not interact with group, $F_{(2,\ 144)} = .546$, $p = .580$, $BF_{10} = .185$, with strong support for the null over the alternate. While fewer people reported being aware in the orbitofrontal stimulation group, stimulation did not affect accuracy based on awareness.

Discussion

Here we used the seminal paradigm developed by Fiser and Aslin (2001) to assess VSL, and observed robust learning of the pairs, but there was no influence of stimulation on this learning. Thus, these results stand in contrast to the stimulation effect we observed for spatial contextual cueing (Nydam et al., 2018). However, there are two reasons why we may have failed to observe a stimulation effect here, the most obvious pertaining to how learning was measured.

By asking observers which pair was more familiar at test, the Fiser & Aslin paradigm involves an overt familiarity judgment. Some authors have noted limitations of using such explicit tests to gauge implicit knowledge (Turk-Browne et al., 2005) suggesting they may tap conscious knowledge that is stimulus-specific (Turk-Browne, 2014) and distinct from implicit knowledge which involves integrating information across stimuli (Thiessen, Kronstein, & Hufnagle, 2013). Experimental work has also demonstrated that statistical learning produces both implicit and/or explicit knowledge depending on how the task is implemented (Batterink, Reber, Neville, & Paller, 2015; Kim, Seitz, Feenstra, & Shams, 2009; Otsuka & Saiki, 2016). Perhaps the clearest support this is that in contextual cuing, explicit judgments about the repeating arrays are dissociated from cuing behaviour since observers typically do not perform above chance on recognition tests (Chun & Jiang, 1998; 2003), but see (Smyth & Shanks, 2008). Indeed, we previously observed that tDCS influenced contextual cuing but had no effect on recognition. It is possible a testing method that instructs participants to recognise structure may tap a different aspect of statistical knowledge compared to cuing, and this may explain differences in stimulation effects across the two tasks.

A second more parsimonious explanation is that the recognition test lacked sensitivity to changes in learning that evolve over time. The exposure–test format represents a persistent shortcoming in statistical learning paradigms across the visual, motor and language domains that has been noted by other authors (Siegelman et al., 2016; Turk-Browne, 2014). When learning is only assessed once at the end of the trials, an offline measure may miss critical aspects of learning that are dynamic, operate earlier in time, or are transient. Indeed, Nydam et al. observed only transient disruption, with cuing eventually reaching the same magnitude across all stimulation conditions. Therefore, it seems plausible that the recognition test may have missed an influence of tDCS on pair learning that occurred early during exposure and may have similarly reached an asymptote by the time learning was measured. Given our primary interest in the functional consequences of visual statistical learning, we decided to create a new task using the same shape-pair stimuli but with an online measure of learning that would be sensitive to the potentially dynamic nature of tDCS effects.

Experiment 2

The second experiment set out to determine whether an online measure of learning of identity structure would reveal causal involvement of cortical areas where an offline measure could not. To do this, we borrowed from the contextual cuing paradigm since it provides an online index of learning that is dissociable from practice effects and motor learning. Furthermore, the gap between cuing for spatial and identity structure has already been bridged by existing variations of the paradigm that used identities to define distractor and/or target features (Chun & Jiang, 1999; Endo & Takeda, 2004). Thus, we married the probability structure from the Fiser & Aslin paradigm with an incidental cuing task to create our new online measure of VSL.

The new task retained the same pair-structure from Experiment 1 by making the Fiser & Aslin arrays serve as distractors. A target was added so that observers could perform a visual search task to provide a response time measure across 12 blocks (collapsed into 3 epochs). To measure how statistical learning affected ongoing behaviour, we associated the distractor identity arrays with a given target location. Each array was defined by a unique set of three base pairs that formed a subset of identities where the locations of the items was would change for each repetition. In this way, it was the identity of distractor items that was predictive, rather than their locations. From piloting, we observed robust cuing in epochs two and three that was approximately 80 ms in magnitude, comparable to spatial contextual cuing studies. With tDCS, we targeted the same region, the left posterior parietal cortex, using cathodal currents applied with the same parameters and compared this to a sham control. Our primary hypothesis the same as in Experiment 1, namely that learning under active (cathodal) stimulation would differ from learning under sham; indicative of a stimulation effect. With our task now designed to be sensitive to a learning trajectory we also made a second hypothesis, informed by the results from contextual cuing: that the effect of tDCS would be different early on compared to later in the task.

Method

Participants

Once again, our design, hypotheses and analysis plan we registered prior to data collection [osf.io/7hqxe]. A total of 84 participants were recruited, but four were excluded prior to analysis: two failed to learn the appropriate key mappings; two experienced technical errors with the stimulator, one ran out of battery and the other could not achieve sufficient electrode contact on the scalp to begin stimulation. This left a final sample of 80 participants (mean age = 20.43 years, 65% female, 36.25% glasses or contact use, mean Oldfield handedness score = 84.49%, mean Impedance = 16.95 mA).

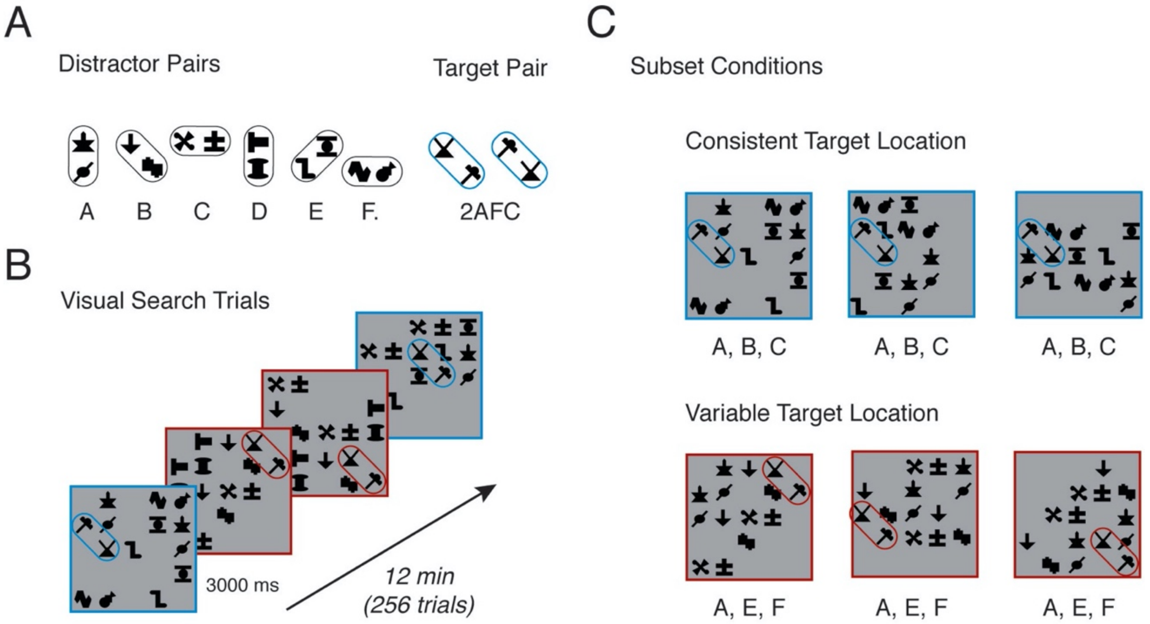

Figure 3. The online VSL task used in Experiment 2. (A) The stimuli were the same as Experiment 1 involving six distractor pairs (A, B, C, D, E, F) plus a seventh target-pair assigned to each individual. (B) Participants performed a visual search task where they had to locate the target-pair (shown circled in red or blue) and respond to its orientation using a 2AFC. On each trial, the target pair appeared among three different distractor pairs, each presented twice, to form a distractor subset that was defined by item identities. (C) In the repeat condition, a given distractor subset (e.g., A, B, C) was consistently associated with a target location. In the novel condition, the association between subset (e.g., A, E, F) and target location was inconsistent meaning the subsets did not cue any information about the target. Note that while each shape item belonged to a single pair, each pair belonged to multiple subsets – meaning it was the specific combination of distractor pairs in a subset that was predictive (or non-predictive) of the target location. Red and blue circles and borders are for illustrative purposes and were not visible in the task.

Online Visual Statistical Learning Task

Stimuli

In order to make search appropriately difficult, we doubled the number of items in each array which required enlarging the grid from 3 × 3 to 5 × 5 cells. The visual displays contained back shape-silhouettes arranged into six distractor-pairs and one target-pair (Figure 3). The shapes used across participants were randomly selected from a pool of 24 shapes. Because the shapes had different surface areas, it was important to prevent equate size for shape sin the target pair, so that one shape was not more salient than the other, which could produce a pop-out effect for one shape in the target. To address this, we sorted shapes based on total pixels before generating the target-pairs. The task was to find the target-pair and report the arrangement of shapes which was always on a diagonal with; either "shape A above B" or "shape B above A", responding with the 'z' and 'm' keys using index fingers on each hand. (Note an observer could conceptualize this task as to report whether "shape A was above" or "Shape B was above" once they found the target pair. Regardless, task was to find two adjacent shapes and respond to a feature of that object pair (integrated across the space of two objects). Participants practiced the response-mapping across 24 practice trials.

While searching for the target pairs, observers encountered sets of distractors that were comprised of the sets of three base-pairs on each array in the Fiser & Aslin paradigm used in Experiment 1). To make the display more crowded, each base-pair was shown twice. This formed 8 distractor sets for repeats, and 8 for novel. Over the course of blocks, the repeat sets appeared with the fixed identities, but in ever changing locations., and the set cued the location of the target pair. In non-predictive displays, the same sets repeated but varied in relation to the target position. The number of target locations used in the predictive and non-predictive conditions was matched.

To create cuing, contingencies were embedded between the target's location and the distractor identities. As with the Fiser & Aslin task, each array contained one base-pair from each spatial arrangement - horizontal, vertical, diagonal - which were recombined to form sixteen possible subsets. Eight of the subsets were assigned to the repeat condition, where they appeared with a fixed target location. The other half of subsets was assigned to the novel condition where the relationship between subset and target location was variable. It is worth noting that the novel condition contained the same six base-pairs as in the repeat condition, it was the specific subset of pairs that defined a repeat or novel context. This meant that simply learning the pair structure alone was not sufficient to produce cuing of the target location. Number of target locations was matched in repeat and novel conditions.

Trials began with a fixation cross for 500 ms (jittered between 100 and 500 ms), followed by the search display for 3000 ms. If participants had not responded in the allotted time, a prompt screen appeared until response, followed by a blank ITI for 500 ms. Trials were arranged into 16 blocks of 16 trials (eight repeat and novel per block). The script would pause every second block for a break and provide accuracy feedback. Participants were encouraged to maintain accuracy above 85%. The apparatus was the same as Experiment 1: a 19″ CRT monitor (resolution 1024 × 768; refresh rate of 100 Hz) connected to an Apple iMac computer, with participants seated unrestrained approximately 63 cm from the screen.

Brain Stimulation

Given the null effect for orbitofrontal stimulation, we removed this group and focused on cathodal currents over the left posterior parietal cortex compared with sham stimulation. We used same stimulation montage and parameters from Experiment 1, namely .7mA for 15 minutes delivered online. This design with only one stimulation montage meant we could employ a double-blind procedure where the experimenter did not know the type of stimulation being delivered. Participants were randomly assigned to receive cathodal or sham stimulation upon arrival using a custom MATLAB script that output a secret 5-digit code which the experimenter used to run the stimulator without having to know the group allocation.

Procedure

Participants attended a one-hour session where they completed a brief practice of 15 search trials before commencing 16 blocks of the online statistical learning task with concurrent (online) stimulation for 15 minutes. After the stimulation, the electrodes were removed from the scalp, and participants completed the same recognition test on the embedded pairs as in Experiment 1. Note that the familiarity test done was offline. Finally, participants answered some open-ended questions that probed their awareness of the subset patterns, the stimulation type (sham control or active), then were debriefed and paid $20 for time and travel.

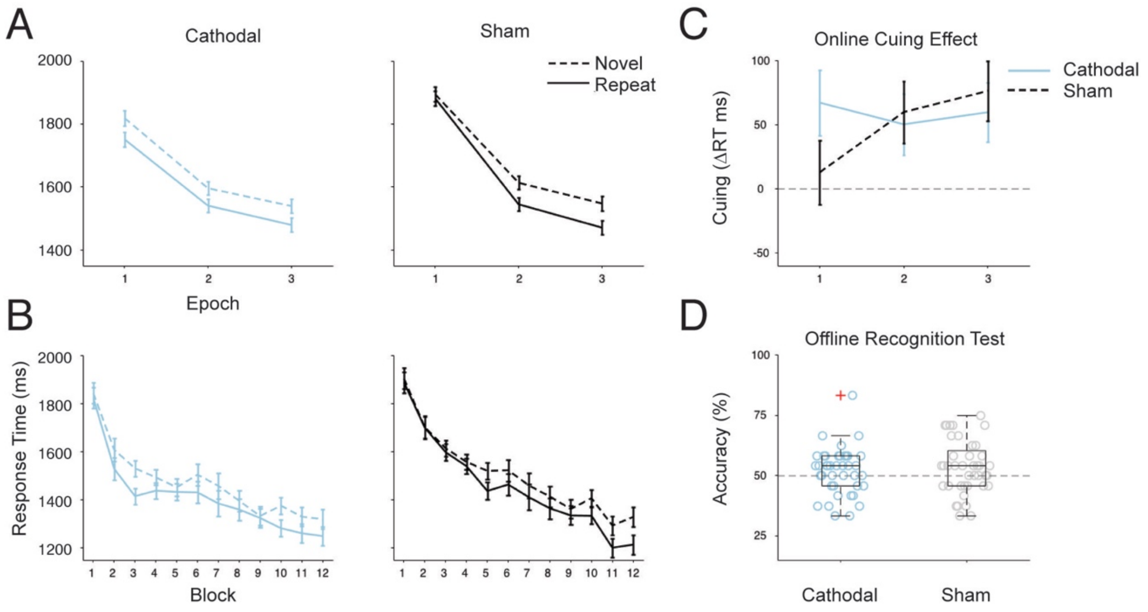

Figure 4. Experiment 2 results. Online visual statistical learning in the two stimulation groups with the data shown across (a) epoch and (B) block. (C) Cuing magnitude each across epoch for stimulation group. (D) Recognition of the base-pairs after stimulation was not affected by stimulation. Error bars indicate within-subjects standard error of the mean.

Results

Planned Analyses

Stimulation Effects on Learning

Looking across the blocks (Figure 4, panel B), we saw that response times became increasingly faster in the repeat condition relative to the novel condition. This pattern was observed in both the active (cathodal) stimulation group and the sham control group in line with the expected identity-cuing effect. As per our preregistration, the data were collapsed into epochs for analysis (Figure 4, panel A) and a 3-way ANOVA was run with the factors: Trial Type (Repeat or Novel), Epoch (1 to 3), and Stimulation (Active or Sham). There were main effects of Trial Type, $F_{1,\,78} = 17.05$, $p < .001$, $\eta_p^2 = .18$, $\mathrm{BF}_{10} = 2.47$, and Epoch, $F_{2,\,156} = 67.10$, $p < .001$, $\eta_p^2 = .46$, $\mathrm{BF}_{10} = 1.29\mathrm{e}{+}42$ and, critically, the Trial Type × Epoch × Stimulation interaction was significant, $F_{1,\,78} = 17.05$, $p < .001$, $\eta_p^2 = .18$, $\mathrm{BF}_{10} = 12.67$. This indicated an effect of stimulation on the temporal evolution of learning (i.e., the Trial Type × Epoch effect) as predicted. To follow-up how stimulation was influencing learning, we ran planned 2-way ANOVAs with factors Trial Type and Epoch for each group separately.

In the sham group, learning was characterised by a Trial Type × Epoch interaction, $F_{2, 78} = 5.023$, $p = .009$, $\eta_p^2 = .114$, along with main effect of Trial Type, $F_{1, 39} = 8.473$, $p = .006$, $\eta_p^2 = .178$, a main effect of Epoch, $F_{2, 78} = 33.19$, $p < .001$, $\eta_p^2 = .460$. The interaction reflected that cuing was not present in Epoch 1, $t_{39} = -.604$, $p = .549$, $BF_{10} = .291$, but emerged later and was robust in Epoch 2, $t_{39} = -3.531$, $p = .001$, $d^2 = -.558$, $BF_{10} = 56.905$, and Epoch 3, $t_{39} = -3.459$, $p = .001$, $d^2 = -.547$, $BF_{10} = 47.502$. The magnitude of the cuing benefit was 61 ms for Epoch 2 and 78 ms for Epoch 3, and both were accompanied by Bayes Factors that strongly favoured this effect over the null.

In comparison, learning in the active stimulation group followed a different pattern. There were main effects of Trial Type, $F_{1, 39} = 8.595$, $p < .001$, $\eta_p^2 = .181$, and Epoch, $F_{2, 156} = 34.761$, $p < .001$, $\eta_p^2 = .471$, but no Trial Type × Epoch interaction, $F_{2, 78} = .202$, $p = .817$. Instead, identity-cuing was already robust by Epoch 1, $t_{39} = -2.571$, $p = .014$, $d^2 = -.406$, $BF_{10} = 6.042$, and remained so for Epoch 2, $t_{39} = -2.726$, $p = .010$, $d^2 = -.431$, $BF_{10} = 8.424$, and Epoch 3, $t_{39} = -2.545$, $p = .015$, $d^2 = -402$, $BF_{10} = 5.732$. The magnitude of cuing was comparable to sham, being 65 ms, 50 ms and 58 ms across the epochs, and the Bayes Factors favoured a cuing effect over the null in all cases.

In summary, the results show that there was an effect of stimulation on learning, and the effect was driven by earlier emergence of identity-cuing during active stimulation compared to the sham control.

No baseline differences between groups

There were no baseline differences between groups, either in terms of mean RTs in block 1, $t_{78} = .342$, $p = .733$, or the cuing effect in block 1, $t_{78} = -.0007$; $p = .994$. This suggests the tDCS effect cannot be explained by existing differences between the groups.

No effect of stimulation on overall RTs

When collapsing across Trial Type to look at overall RT effects, there was an increase across block, $F_{2, 78} = 25.563$, $p <.001$, but no main effect of stimulation, $F_{1, 78} = .184$, $p =.669$, nor an interaction with stimulation, $F_{2, 78} = .381$, $p =.683$. This means the effect of tDCS on behaviour could not be explained by a general effect on procedural learning in the visual search task. Instead it was selective to statistical learning, being the difference between predictive and random conditions. Furthermore, the overall RTs for Epoch 1 did not differ across the stimulation groups, $t_{78} = .342$; $p = .762$, and so only the cuing magnitude was affected by stimulation in Epoch 1.

No effect of stimulation on Errors

Accuracy was at ceiling being consistently above 90%, and no individuals were below the 75% exclusion cutoff. There was a main effect of Trial Type, $F_{1, 78} = 8.021$, $p =.006$, $\eta_p^2 = .093$, and Epoch, $F_{1, 78} = 5.670$, $p = .004$, $\eta_p^2 = .068$, to show that performance became more accurate over time and was both faster and more accurate for Repeats than Novels. Stimulation did not affect accuracy, as no other effects were significant (all other *p*s > .215). This confirmed there was no speed accuracy tradeoff with cuing or with the stimulation effect.

General Discussion

We investigated the causal involvement of cortical brain activity that had been associated with the process of statistical learning in spatial arrays. Across two experiments we used cathodal tDCS to perturb the left posterior parietal cortex while participants were exposed to visual arrays that contained an identity-based structure, while controlling for location-based regularities. When the learning was assessed offline, using a recognition test after passive exposure, we could not detect a cathodal tDCS effect compared with a sham control or an orbitofrontal region-control. However, when statistical encoding was assessed online, over the course of exposure, tDCS *did* influence learning with identity-based structure. This demonstrated a generalisation of our previous tDCS effect observed using a different location-based paradigm. These results support the hypothesis that activity in the left PPC is causally involved in a functional visual statistical learning mechanism.

Experiment 2 investigated whether the null finding in Experiment 1 related to the "one-shot" test used at the end of exposure. By creating an online measure, we observed that tDCS *did* influence the statistical learning process. Specifically, cathodal stimulation over the left PPC produced an earlier cuing effect compared with sham. The effect of active stimulation cannot be explained by persisting differences in RTs or cuing between groups at block 1. Nor do they reflect a speed/accuracy tradeoff, since stimulation had no effect on accuracy. Our results do not reflect the impact of stimulation on general task performance, since tDCS did not affect overall RTs. Rather it specifically altered the *difference* between RTs to repeat and novel arrays and how this difference evolved over time. We therefore conclude that administering tDCS over the left PPC influences a general statistical learning process given a behavioural measure that is sensitive to behaviour over time.

This result is consistent with the finding that frontopatietal areas were directly involved in statistical learning that was assessed by spatial contextual cuing (i.e., Nydam et al., 2019). Attempts by other authors to generalise findings about statistical learning across different tasks and testing methods have been criticised in the literature largely because such aspects may change what is being learned about an underlying structure (Bays, Turk-Browne, & Seitz, 2016; Turk-Browne et al., 2005; Turk-Browne, Isola, Scholl, & Treat, 2008a). Considering these criticisms, it was important to empirically examine whether tDCS would influence statistical learning using a different measure. The combination of both results strengthens the causal evidence that cortical activity is directly implicated in a general visual statistical learning process. Such evidence supports claims from the imaging literature that higher-order cortical regions in the posterior parietal lobe process information in a way that directly contributes to the functional aspects of incidental learning. The current work also extends on this by suggesting a critical time window for when such perturbing activity may have the greatest impact on behaviour.

Stimulation affected learning early on. This mirrored the early time window observed for contextual cuing (Nydam et al., 2018), although the finding was in the opposite direction here (i.e., benefit vs. disruption). It is worth considering how such a selective or a dynamic effect may arise when tDCS delivers a constant current throughout. Despite this fixed parameter, tDCS effects on excitability measures, such as motor evoked potentials using TMS, tend to be non-linear across time (Bonaiuto, de Berker, & Bestmann, 2016). So one explanation for the present results is that they reflect changes to excitability that were dynamic in the relevant regions. Such changes may also be produced by task-based activity related to the encoding of statistical structure itself. Functional connectivity measures in fMRI identified a hippocampal-parietal network that had a similar profile. Compared to baseline, there was an early increase in connectivity, followed by a later decreased, and this was reported independently for two different statistical learning tasks (Karuza et al., 2017; Manelis & Reder, 2012). A similar network dynamic has been reported using temporal regularities (Turk-Browne et al., 2010), possibly as part of a domain-general mechanism (Batterink, Paller, & Reber, 2019). Moreover, in one study, learning behaviour was more strongly related to the early activity change (Manginelli et al., 2013), pointing to the functional role that would be in line with the present result. What do these early dynamics mean for statistical learning more generally? There are two models of statistical learning that could explain such a dynamic trajectory. The two-stage model offers a potential explanation based on a role of selective attention (Turk-Browne et al., 2005) which has been found to have a decreasing role over time. A more recent but related framework proposes that statistical learning can be decomposed into an early extraction stage followed by a later integration stage (Thiessen et al., 2013). Relating these ideas back to the present work, stimulation may have produced the most noticeable changes during such an early active stage. This could be manipulated experimentally in future work, by commencing tDCS after different amounts of learning have been allowed to see if stimulation still exerts an early effect after which time an active stage should be completed.

Despite both contextual cuing and identity-structure showing an early effect, the direction of the effect was opposite. Cathodal stimulation reduced or delayed contextual cuing but facilitated or expedited learning in Experiment 2 of this study. Such variability is consistent with the broader tDCS literature since cathodal currents may produce both facilitation and impairment. For example, studies have reported enhancements for cathodal tDCS in the domains of visuospatial attention (Bolognini et al., 2010; Sparing et al., 2009), language acquisition (Flöel et al., 2008; Meinzer et al., 2012), working memory (Fregni et al., 2005; Ohn et al., 2008; Zaehle et al., 2011), and recognition (Luo, 2017). Meanwhile, disruption has been shown for decision-making tasks (Filmer et al., 2013). Adding to this complexity is the fact that tDCS-induced changes interact with task-generated activity. Meaning the task-based activity recruited by spatial-structure versus identity features may be distinct. Broadly speaking, the difference in directionality embodies active and open debate concerning how to relate tDCS effects to measured behaviour (Bestmann, de Berker, & Bonaiuto, 2015) that is beyond the scope of the present study.

So far, we have pitched visual statistical learning as an umbrella term for how encoded statistical characteristics come to alter cognition in meaningful ways (Conway & Christiansen, 2006; Perruchet & Pacton, 2006; Thiessen et al., 2013). Yet we acknowledge there is ongoing deliberation about whether statistical learning represents as a single, unitary construct (Erickson, Kaschak, Thiessen, & Berry, 2016) or one involves multiple, independent operations (Bays et al., 2016; Frost, Armstrong, Siegelman, & Christiansen, 2015). What has become apparent is that statistical encoding draws on a range of cognitive processes and associated neural mechanisms. In search displays, statistical encoding has been found to be modulated by selective attention (Turk-Browne et al., 2005), top-down control of eye movements (Ball, Lane, Smith, & Ellison, 2013; Bardi, Kanai, Mapelli, & Walsh, 2013), factors relating to grouping (Baker, Olson, & Behrmann, 2004; Olson & Chun, 2002) and working-memory (Berryhill, Wencil, Branch Coslett, & Olson, 2010; Marián, Szőllősi, & Racsmány, 2018). Whether or not stimulation was exerting its influence via such moderators remains unclear. Alternatively, stimulation may alter explicit goal-directed behaviours that interact with statistical encoding. In line with this, cathodal stimulation of the right parietal cortex has been found to influence visual search (Ball et al., 2013; Ellison et al., 2014). We see these as avenues for additional enquiry.

Experiment 2 employed a double-blind procedure for the stimulation intervention. This meant we could be confident that the results were not due to extraneous systematic differences between active stimulation sessions and the sham control sessions. That being said, we cannot yet make definitive conclusions about the specificity of the parietal region without an active regional control. One possible alternative explanation may be that anodal currents from the reference electrode were producing the increased cuing compared to sham. We find this unlikely for the following reasons. Firstly, the mastoid is considered an appropriate non-brain reference in tDCS studies as it sits over a thick bony part of the skull where fewer currents may penetrate. Indeed, our current flow modeling supports this since the areas with the most concentrated current were under the cathodal electrode not the anodal reference. Also, a selective influence of cathodal currents in this montage was evident from our previous study which directly compared anodal currents and found they were not different from sham. Thus, it is parsimonious and valid to argue that changes in the target area under the cathodal electrode were responsible for the effects observed here.

An interesting implication of our results for understanding brain function concerns the complexity that is characteristic statistical learning. An important contribution of the Fiser and Aslin experiments were that they demonstrated the capability to encode high-dimensional patterns beyond mere frequencies, such as combinations of joint probabilities, transitional probabilities, and hierarchical relationships (Fiser & Aslin, 2001; 2005). In spatial contextual cuing, the structure comes from multi-object layouts that repeat. Relying on this instantiation of statistical structure alone may be limiting since we know that statistical learning is optimised for complex relationships found in real world events, a prolific example being language. Thus, by showing the same tDCS effect applied to joint probability relationships, our results instantiate a key feature of statistical encoding that concerns complexity beyond marginal probabilities (i.e., frequencies) or repetition. An important direction for future work would be to probe whether the same cortical activity remains important beyond joint probabilities to more complex community structures – as has been successfully applied to understanding hippocampal involvement (Aly & Turk-Browne, 2017; Schapiro, Kustner, & Turk-Browne, 2012; Schapiro, Turk-Browne, Norman, & Botvinick, 2016). This would relate statistical learning to some recent work on the functional organisation of the frontal cortex for representing abstraction of spatial regularities (Wang et al., 2019).

Conclusions

Using online tDCS we have demonstrated how visual statistical learning for identity structure is altered by perturbing activity in a key parietal processing region. These findings further establish causal evidence of a broader cortical network, beyond the sensory and medial temporal lobe areas, that is directly involved in statistical processing, in line a domain-general memory system. Most interestingly, our findings converge on an early locus of influence that is overcome with continued exposure. These results add to our understanding about how the brain produces incidental learning across different types of visual input and task settings.

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CHAPTER 5:

GENERAL DISCUSSION

Summary of the Research Findings

The overarching aim of this thesis was to examine the neural substrates involved in incidental learning via experience with statistical regularities from the environment. It focused on the question of direct cortical involvement on statistical learning that applied to visuospatial input. I explored the causal modulation of cortical activity by tDCS and measured tDCS-induced changes to learning and the timecourse of these changes. Based on the neuroimaging data, tDCS was delivered over two key brain regions in the left frontal and left parietal lobes. The statistical learning process was assessed using a number of behavioural paradigms, including two paradigms that are highly popular in the literature – Contextual Cuing, introduced by Chun and Jiang and Visual Statistical Learning from Fiser and Aslin – and a new paradigm that combined elements of both to measure online cuing based on identity. The question of whether or not tDCS causally modulates incidental learning was addressed by comparing bidirectional currents (Chapter 3) targeting different brain regions (Chapter 3 and Chapter 4), and, where this was not feasible, a double-blind-sham-control procedure was employed (Chapter 4, Experiment 2).

In pursuit of the larger goal, the study reported in **Chapter 2** examined the temporal dynamics of information processing in the Contextual Cuing task. The key aim was to investigate the capacity of the system to learn regularities when processing time was controlled by masking. It also served to determine task parameters that could produce robust statistical learning within the time window required for online delivery of stimulation in the subsequent studies. Compared to standard contextual cuing tasks where visual displays terminate upon response at around 1000-2000 ms, I truncated visual exposure to 300 ms and disrupted further processing with masking. In Experiment 2, we observed evidence of a rapid statistical learning mechanism which could produce an increasing accuracy benefit for repeat displays. This complimented work showing that contextual cuing affected information processing and was effective at this timescale (e.g., Chun and Jiang, 1998; Experiment 5), after learning with longer displays. However, this rapid learning exhibited a capacity limitation (Experiment 1a) that was not observed with the typical 2000 ms display durations (Experiment 1b). Together, these findings implied that statistical learning could be robust and capacity limited. It was robust to disruptions in the time available to process information. But limited in the ability to benefit from set of larger set of information when given a brief glance.

The first tDCS study is reported in **Chapter 3** (Nydam, Sewell & Dux, 2018). It investigated cortical involvement in statistical learning with spatial regularities. This study had two key aims: to determine whether tDCS-modulation of cortical activity could affect statistical learning; and if so, determine how tDCS effects related to polarity and target region. Motivated by fMRI work on contextual cuing, which implicated the IPS, TPJ and IFG regions of the left Frontoparietal network, we explored whether targeting the left PFC and left PPC with tDCS would affect learning directly. Across six groups, we delivered cathodal, anodal and sham currents to two target regions. Cathodal currents disrupted the contextual cuing relative to the reverse polarity (anodal) and to the sham control. This provided the first causal evidence that brain activity in cortical areas was directly contributing to the dynamics of statistical learning in the contextual cuing paradigm. When exploring this tDCS-induced effect, it appeared to reflect a delay in learning rather than complete disruption. The early cuing effect, which typically emerges in the first 4 blocks, was attenuated during cathodal stimulation. But the cuing that emerged later on, in blocks 5-12, was unaffected by tDCS and of a comparable magnitude to the sham group. This finding built on the neuroimaging evidence to provide causal data on frontoparietal involvement in statistical learning.

In studying the process of statistical learning, it was important to use other tasks to demonstrate that effects can generalise and do not simply reflect a specific stimulus or response mapping. With this in mind, **Chapter 4** investigated casual modulation of cortical activity using the visual statistical learning task by Fiser and Aslin. This task also uses spatial arrays with simultaneously presented items, but the embedded regularities are derived from the identity of items (i.e., shapes in base-pairs) while controlling for their location. Taking the relevant neuroimaging work on this paradigm (i.e., Karuza, 2017), and combining it with the findings from Chapter 3, we focused on the effect of cathodal currents over the IPS region of the left parietal lobe. In a large sample, I compared three stimulation groups who received either cathodal currents over the left PPC, cathodal currents over the orbitofrontal cortex (OF: a region control), or sham stimulation (placebo control). Using the exposure-test design, Experiment 1 showed learning via above-chance recognition of the pair-identity structure at test. Learning was reliable in all three groups, being highest in the PPC group, followed by sham, followed by the OF group. However, learning was not modulated by tDCS. In fact, according to the Bayes Factors, the data favoured a null model for the cathodal effect of PPC stimulation compared with sham and was uninformative regarding the region difference between the PPC and OF stimulation.

Because learning is only assessed once and at the end of the trials in the standard Fisher and Aslin paradigm, Experiment 2 investigated whether this may have missed stimulation effects that occurred earlier, during exposure. I developed an online measure that would be sensitive to temporal evolution of learning. It was based on the cuing task used in Chapter 3. Active (cathodal) stimulation was compared to sham using a randomized, double-blind design. I predicted a differential effect of tDCS early on compared to later on based on the effects observed in Chapter 3. As predicted, stimulation did affect learning, and was selective to the early time window; consistent with the temporal dynamic observed for spatial contextual cuing. But unlike the delay caused with spatial-cuing, here the stimulation expedited learning, driven by earlier emergence of identity-cuing relative to sham. These results provided evidence that the tDCS-induced effects on statistical learning could generalise across tasks, though their effects may differ depending on the learning task. Furthermore, as cathodal tDCS over parietal cortex affected both location-based learning in contextual cuing, and identity-based learning here, this provided preliminary evidence to suggest the parietal cortex may be causally involved in visual statistical learning.

Implications of the Research Findings

The Frontoparietal Cortex Plays an Interfering Role in Statistical Learning

This thesis leveraged the known modulatory effects of tDCS to make causal links between brain function and behaviour. Across two studies, we found converging evidence that modulating activity in the frontoparietal network changed the way statistical regularities guide attention and decision-making. The studies in Chapter 3 and 4 show that the left PFC and the left PPC This finding expanded on fMRI studies showed associated activity in such regions by providing causal evidence to suggest a direct role of such activity in producing incidental statistical learning behaviours. Previous studies had used TMS to show frontal involvement in implicit sequence learning {PascualLeone:1996fj, Janacsek:2015bi} and related it to the role of fronto-striatal network in procedural motor learning {Goldfarb:2016ir, Rieckmann:2010ia}. We focused on learning that occurred outside the motor system. We targeted targeting the left IPS in the frontoparietal network, based on a mass of evidence showing related activity in this region. We did not investigate the effects of stimulating other parts of this highly connected system, and so it remains possible that tDCS-effects on visual statistical learning could be uniform across the cortex, regardless of the area targeted. However, when considering the neuroimaging evidence, and the surprising functional specificity of our effects on learning (and not on procedural learning or response operations), this becomes less likely.

The present findings expand scientific knowledge concerning the causal role of cortical activity in incidental forms of learning and memory. While both previous studies had focused on an imposed dualism between explicit and implicit learning and memory (O'Reilly, Bhattacharyya, Howard, & Ketz, 2014), the evidence from functional neuroimaging provided a link between cortical control areas and implicit learning. Using causal neuromodulation techniques, the present work builds on that evidence by showing that frontal and parietal activity contributes to directly learning dynamics. Our results could not be explained by a change in motor learning of response-mapping or a general change in procedural learning. Instead the tDCS effect was specific to the difference between repeat and novel responses over time. These observations provide novel evidence to support the proposal of a direct role for cortical control areas in implicit memory-guided behavior. The two observations that tDCS affected learning early on is consistent with an influence of these regions in the formation of statistical learning. This evidence is consistent with the idea that statistical learning is governed by a distributed network in the brain that involves hippocampal, sensory and cognitive control circuits.

What the tDCS Effects Reveal About a Cortical Mechanism

Stimulation modulated learning in a task-dependent manner. The same stimulation montage, with cathodal currents over left PPC and anodal currents over right mastoid, both disrupted and facilitated statistical learning depending on the task. Recall that in Chapter 3, tDCS delayed cuing by spatial regularities, but in Chapter 4, tDCS expedited cuing by identity-based regularities that controlled for spatial location. Observing opposing effects on cuing by the same stimulation protocol may point to some explanations for how the targeted brain region may be contributing to statistical learning. As stated throughout, the cathodal-inhibition model of tDCS effects on the brain is over-simplified and cannot explain such task-dependent results. Many empirical studies have observed non-linear effects of cathodal tDCS on brain activity across dose and time (for a review, see: Filmer, Dux, & Mattingley, 2014), and a number of authors have emphasized that the simplified model is inappropriate for explaining effects at the level of behaviour (Bestmann, de Berker, & Bonaiuto, 2015; Bonaiuto, de Berker, & Bestmann, 2016).

Instead, there is an emerging body of literature showing that tDCS effects are contingent on state-based or task-based activity. Studies that assess brain activity during or closely before and after stimulation reveal that way tDCS modulates network activity depends on the task (Li et al., 2019; Saiote, Turi, Paulus, & Antal, 2013). The present results would be consistent with such an account. Whether such cortical activity may reflect explicit knowledge that occurs alongside statistical learning is a question for future studies. This thesis focused on the way regularities come to be used incidentally, without instruction or feedback, and so such a discussion would be largely discursive and beyond the scope of the present findings which were not designed to test the nature of such knowledge. Instead, it is clear that tDCS over parietal regions affected the acquisition of regularities across two experiments (Chapters 3 and 4). According to the contemporary notion of tDCS effects on behaviour (i.e., beyond cathodal-inhibition accounts), there are two ways that stimulation over the same brain region could produce opposing effects on the operations it governs. One such way is by disrupting systems within the target region.

Rather than simply modulating the parietal cortex as a single, functional node, a sub-system account might suggest the regions within the targeted parietal cortex were differentially recruited by the task material. Systems within the parietal cortex are known to have different functional roles. Recall that the effects of tDCS on behaviour are a combination of task-based activity with tDCS modulations of excitability. According to this view, exposure to identity-based and spatial-based regularities may have engaged different functional systems within the parietal cortex, that when combined with the modulatory effects of tDCS, could have produced different net changes to activity and resulted in different behaviour. This sub-systems account would explain the effects we observed as a function of an interaction between task-evoked activity and tDCS-induced modulation. Such interactions are beginning to be explored in other work. For example, combining tDCS of the right-IFG and fMRI showed that the same polarity of stimulation had different effects on brain activity depending on the brain state (either simple choice task or no task; Li et al., 2019).

Was the Hippocampus Mediating Our Results?

It is worth considering the present results against a growing body of literature suggests the hippocampus is important for the rapid extraction of structure (Schapiro, Turk-Browne, Botvinick, & Norman, 2016a; Schapiro, Turk-Browne, Norman, & Botvinick, 2016b; Turk-Browne, Scholl, Chun, & Johnson, 2009; Turk-Browne, Scholl, Johnson, & Chun, 2010). One may wonder if tDCS may have produced current flow in subcortical regions, which would provide an alternative explanation for the observed results. The stimulation protocol placed the cathodal electrode over the left PPC and the return electrode over the contralateral mastoid and was delivered at .7mA. Studies show that 1mA applied to the scalp induces currents of .04V/m in the cortex (Huang et al., 2017) and that currents measured to be between .03 and .07V/m in monkeys have important effects on neural physiology and behaviour (Krause et al., 2019; 2017). It is unlikely that our stimulation produced sufficient current flow in deeper, subcortical structures to have had direct modulatory effects on the hippocampus. However, the effects of tDCS on brain function are more complex than originally thought (Batsikadze, Moliadze, Paulus, Kuo, & Nitsche, 2013), and stimulation over targeted areas of cortex can yield widespread changes in areas across the brain.

Studies that combine tDCS and fMRI are beginning to shed light on this issue. For example, tDCS to the motor cortex during an SRT task produced activation changes in different networks, and these depended on the polarity of stimulation (Stagg et al., 2009). Anodal tDCS increased activity in a motor network including the preSMA, whereas cathodal tDCS altered a motor network that included the PPC, suggesting intra-cortical effects. These changes can be in the same or opposite direction to activity changes in the target motor region (Antal, Polania, Schmidt-Samoa, Dechent, & Paulus, 2011), suggesting complementary dynamics may also be at play. While direct effects of the induced current on the hippocampus are unlikely, modulation of parietal activity by tDCS could have produced downstream changes to other functionally connected areas, which could have included the hippocampus. In fact, causal modulation of the hippocampus by cortical stimulation using rTMS has been reported (Wang et al., 2014). Using an associative learning task combined with rTMS to the left PPC, stimulation was found to produced offline changes to hippocampus that were specific to a functional network that involved the IPS in the parietal lobe and a sub-region of the hippocampus. Modulation of this network also affected associative learning. However, TMS may have a greater ability to modulate distal sites due to its ability to evoke action potentials directly. Modulation of the hippocampus or other subcortical regions by cortical tDCS has not yet been observed.

Impact of the Work in the Broader Field

Models of Learning and Memory Systems in the Brain

The question of cortical involvement in statistical learning abilities has important consequences for theories of memory and learning systems in the brain. Memory is not a unitary construct, and certain memory systems appear to represent certain types information (Henke, 2010; Preston & Gabrieli, 2008; Schapiro, Turk-Browne, Botvinick, & Norman, 2017; Squire, 2007). Many of these theories have sought to explain the functional tradeoffs between a fast, flexible system for encoding generalizable memories; and a slow, rigid system for encoding stimulus-specific memories. The current findings are not readily interpretable within the framework of dual-memory systems theory (O'Reilly et al., 2014). A prominent aspect of this model was the dissociation between a declarative memory system depended on the MTL (and hippocampus), and a non-declarative system depended on the cortex (O'Reilly et al., 2014). But incidental learning of statistical regularities has frequently been shown to involve the MTL and hippocampus (Chun & Phelps, 1999; Giesbrecht, Sy, & Guerin, 2013; Greene, Gross, Elsinger, & Rao, 2007; Karuza et al., 2017; Preston & Gabrieli, 2008; Turk-Browne, Johnson, Chun, & Scholl, 2008). The extent to which statistical learning may recruit either of these systems in isolation remains a subject of debate (Henke, 2010; Reber, 2013; Sestieri, Shulman, & Corbetta, 2017). And it remains possible that both implicit and explicit forms of knowledge are acquired in parallel during statistical learning tasks (Goujon, Didierjean, & Poulet, 2013; Rebuschat & Williams, 2012; Taylor, Krakauer, & Ivry, 2014). However, the statistical learning in our tasks occurred without explicit awareness of the regularities based on recognition tests. When attempting to characterize naturalistic learning that occurs during exposure to regularities, the interaction between learning and memory systems (Chun & Turk-Browne, 2007; Reber, 2013) may be more important than the dissociation.

A contemporary notion of statistical learning views it as a principle of processing in the brain, rather than a discrete system. According to this framework, the statistical learning process can operate on memories formed by either system (Reber, 2013), and can recruit neural resources based on the current demands. A related idea is the principle of Bayesian inference, which has been proposed to be a universal principal governing adaptive brain function (Friston, 2010). The underlying idea is that the brain constantly makes unconscious predictions based on an internal model of the world, and constantly updates that model based on experience. The system seeks to optimize sensory processing by applying a probabilistic model (i.e., Bayes theorem) to minimizing uncertainty. It uses what was most likely to occur previously (priors, and information about the current stimulus (likelihood) to compute what is most likely in a given environment (posterior). Learning is then based on the efficacy of these predictions over time. Optimization is said to manifest in the brain via a hierarchical model that enables reciprocal exchange of bottom-up predictions and top-down predictions to optimize predictions online. Both these frameworks suggest that downstream cortical areas can represent information about regularities while also explaining the involvement of the MTL. In this way, they both offer a parsimonious explanation for cortical involvement when using statistical regularities for learning.

Beyond the models, evidence is amassing that statistical learning recruits a distributed network of regions that include frontal, parietal, sensory and subcortical structures (Batterink, Paller, & Reber, 2019). Some research suggests that the involvement of sensory areas may be domain specific, and that the hippocampus is largely domain-general. The role of the brain areas outside sensory and memory systems has been overlooked. By and large, the extent of domain-generality has not been systematically investigated throughout the brain. There are well-known anatomical and functional connections between hippocampal, frontal and parietal regions that relate to attention, memory, and associative learning (Corbetta, 1998; Corbetta & Shulman, 2002; Staresina, Cooper, & Henson, 2013; Wagner, Shannon, Kahn, & Buckner, 2005). An important goal for future work is to understand whether learning statistical regularities happens independently and locally in the distributed brain regions, or whether changes in one region drive changes in the others.

The Early Impact of Stimulation and Network Dynamics

We observed an early locus of cortical involvement in statistical learning. Across Chapter's 3 and 4, the time-window in which stimulation modulated learning was selective to the first few blocks. We also observed an early locus of the masking effect, since cuing appeared to be delayed or diminished but not abolished all together. These findings could suggest a couple of things about the temporal dynamics of cortical involvement in a statistical learning process. Firstly, it may reflect a primacy effect of cortical involvement where such areas are recruited for the early stage of learning and reduce over time. This idea is supported by findings from the fMRI work. During contextual cuing, an area in the left IPS that was jointly associated with learning dynamics and working memory load decreased its activity over time, and the decrease was related to the way cuing by repeats increased over time (Manginelli, Baumgartner, & Pollmann, 2013a). The cortex along the IPS is commonly found to support working memory functions (Todd & Marois, 2004; Xu & Chun, 2006) as well as the interplay between memory and decision making, and tDCS studies find that stimulating this area affects performance in working memory tasks (Moos, Vossel, Weidner, Sparing, & Fink, 2012; Pergolizzi & Chua, 2015; Sandrini, Fertonani, Cohen, & Miniussi, 2012). These findings may suggest that cortical regions are involved early on, possibly related to the temporal dynamics of working memory involvement in the learning process. A related possibility is that these results reflects the temporal dynamics of a network involving the IPS and other brain regions that was affected by tDCS. The network idea is also supported by fMRI work showing that connectivity between parietal and hippocampal regions is initially high during statistical learning, then decreases over the course of learning or exposure (Giesbrecht et al., 2013; Karuza et al., 2017). This pattern was observed in the contextual cuing task and the visual statistical learning task, and the network activity correlated with behaviour in both cases. A parietal-hippocampal network may recruit cortical areas early on, then reduce involvement over time (Squire, 1992; McClelland, McNaughton & O'Reilly, 1995; Yamashita et al., 2009; Durrant et al., 2013). In both cases, the early effects of tDCS may have been in part due to functional activity patterns recruited by the tasks.

Alternatively, the early modulation of learning may reflect the temporal dynamics of tDCS on neural activity and functioning more generally. Until recently, the temporal evolution of tDCS-induced changes had been overlooked by the brain stimulation literature. Studies of tDCS effects on excitability had investigated temporal dynamics to some degree. Early on, studies showed that tDCS effects on excitability persisted for up to 90 min after stimulation had ceased (Nitsche & Paulus, 2000). Now, studies are showing that the changes can be dynamic across time (Batsikadze et al., 2013; Monte-Silva et al., 2013). Most relevant to the present work are results {Samani:2019kg} showing that cathodal stimulation over the primary motor cortex in humans produced long term depression-like changes to neural plasticity after 15 and 30 minutes, but produced the opposite changes (i.e., long term potentiation) after 20 minutes. This was one of a number of non-linear changes observed with TMS measures of neural activity over duration and dose. How such dynamic changes may relate to information processing or changes in non-motor regions is an open question. But some preliminary work combining tDCS and electroencephalography dovetails with these investigations. As was discussed in a recent review (Reinhart & Woodman, 2015), manipulating a cognitive function with a constant current via tDCS can produce temporally specific changes to ERP components that related information processing. This work has suggested a degree of temporal specificity at the scale of 3-5 seconds for tDCS effects. Thus, the effects of tDCS on both neural and cognitive function appear to have temporal consequences. The work done thus far suggests our early modulation of learning could, in part, relate to the temporal effects of stimulation.

It would be interesting to investigate whether the early locus of the tDCS effect could reflect either; working memory dynamics that are involved in statistical learning, or a stage-based effect on the initial acquisition of regularities for learning. To address the question of acquisition, one could deliver stimulation after learning has already taken place, or once learning asymptotes. If tDCS still modulates cuing or the dynamics of cuing after the regularities have been acquired, it could rule out a critical stage of cortical involvement in acquisition, and instead it may point to an effect of tDCS on the way latent learning of regularities were being used by the system to affect goal-directed behaviour. Such a distinction between latent learning (i.e., acquisition) and the expression of learning through behaviour (i.e., retrieval) appears to be important for understanding how statistical learning draws on other cognitive functions to do with selection. Behavioural studies of the contextual cuing phenomena and sequence learning in the SRT task have shown that loading working memory or manipulating attentional selection affects the expression of learning while leaving the acquisition process intact (Annac et al., 2013; Annac, Zang, Müller, & Geyer, 2018; Jiang

& Chun, 2001; Manginelli, Geringswald, & Pollmann, 2012; Manginelli, Langer, Klose, & Pollmann, 2013b; Pollmann, 2018). Given the exploratory nature of the initial tDCS work, we investigated the learning process as a whole (i.e., combining the acquisition of information about regularities with the use of this information to guide search). Moving forward, one can use our observation of selectively early cortical involvement across combined with the suggestion that learning expression may be distinguished from learning itself to ask more targeted questions about cortical involvement in aspects of statistical learning behaviour.

Statistical Learning Was Robust to Different Types of Disruption

This thesis examined the notion that implicit statistical learning recruits cognitive control regions in the frontoparietal cortex. Along the way, we observed that implicit memory-guided search (i.e., contextual cuing) was robust to different types of disruption: electrical and physical. When visual processing time was disrupted with masking, statistical learning still emerged (Chapter 2). When cortical processing regions were disrupted with tDCS, statistical learning still emerged. In both cases, learning was delayed or slowed, but appeared robust in the later blocks and was of a magnitude comparable to the control conditions without visual or electrical disruption. I am not the first to draw comparisons between the effects of masking and brain stimulation on visual processing. Similarities between the way a visual mask and a TMS pulse to the occipital pole modulate information processing were reviewed previously; in the context of conscious object perception (Breitmeyer, 2004). The work explains that masking and TMS can both limit the amount of information available for processing. More recently, the two have been compared experimentally to investigate the stochastic resonance account of visual detection mechanisms in the brain (van der Groen & Wenderoth, 2016). This experiment compared three levels of perceptual noise (via a stimulus) and electrical noise (via tRNS) and showed the same inverted “U” shapes relationship between noise and contrast thresholds. It showed that adding noise (either physical or electrical) during subthreshold and suprathreshold contrast reduced visual detection, but noise during optimal Both lines of work provide a proof of concept that physical disruption of a stimulus and electrical disruption of the brain can have comparable effects on behavior or a given process (i.e., detection). At least at the level of perceptual operations. Whether such a relationship would hold for more central cognitive operations, like visual search and decision-making, remains a question for future work. The present research was certainly not designed to compare the effects of masking to those of tDCS. However, the combined results of Chapters 2 and 3 are consistent with the notion that masking and tDCS placed limits on the amount of information available for processing, and that statistical learning was robust to these limits after a period of sufficient exposure to the regularities (i.e., the later epochs). In the case of memory-guided attention, assessed by spatial contextual cuing, it seems that different types of disruption only slowed learning, and did not abolish it completely.

In accordance with previous studies of the contextual cuing phenomenon, the advantages afforded by repeating arrays can manifest with incomplete information. For example, a complete spatial configuration is not necessary to produce a cuing benefit to repeat displays once learned (Olson & Chun, 2002). Likewise, a cuing benefit was still observed when displays were too brief for eye movements (Chun & Jiang, 1998; Makovski & Jiang, 2018). Our study presents novel results that the formation of context memories can still take place when processing of displays was disrupted by masking or modulating excitability in cortical control regions. The observation that implicit cuing can overcome such disruptions to the input is consistent with the idea that scene regularities provide rich information that is multi-faceted and extend these findings to processing networks in the brain (see below for more on networks).

In line with such an idea, studies show that statistical learning can adapt to distortions in distractor items, such as altered locations or removed items (Annac, Conci, Müller, & Geyer, 2017; Geyer, Shi, & Müller, 2010; Zellin, Mühlenen, Müller, & Conci, 2014), implying a flexible and efficient system that allows a learned display to be associated with variations in the input. Consistent with a statistical learning process (Turk-Browne et al., 2009). There is evidence that both local (Brady & Chun, 2007) and global (Peterson & Kramer, 2001; Tseng & Li, 2004) aspects of a display contribute to finding the target. While local regularities may be sufficient to produce cuing after learning has taken place (e.g., Olson & Chun, 2002), global regularities may be important for the formation of context memories early on (see Goujon, Didierjean, & Thorpe, 2015). This idea would predict different effects of disrupting local and global information (such as via masking) on the early and late stages of cuing. Masking global elements of a display should reduce early cuing benefits, while masking only local items near the target may not affect early cuing. These early and late stages refer to the learning period itself, such as early acquisition and later exploitation during the learning period (Thorndike, 1931). But the cuing benefit is also associated with early and late changes within a single search period during stimulus presentation (Jiang, Sigstad, & Swallow, 2012; Sisk, Remington, & Jiang, 2019; Zhao et al., 2012). These refer to information processing stages (i.e., Treisman and Gelade, 1980).

A more cohesive understanding of statistical learning mechanisms at the scale of information processing (during stimulus presentation) and the scale of learning (during acquisition and exploitation) is needed to move theory forward. This will help to explain how implicit learning may be robust to such a variety of forms of disruption. A key question concerns the relationship between statistical learning and distractor processing. Take the assertion that during visual search, top-down attentional control serves to boost the processing of target information and suppress processing of distractor information (i.e., Guided Search; Wolfe, 1994). At the same time, the literature on associative learning asserts that when a stimulus becomes a reliable predictor, such as through repetition, processing is biased towards that stimulus (e.g., Beesley & Le Pelly, 2010). These two predictions come to a head when regularities (learned over time) guide attentional processing (within a single event). Both operations predict a reciprocal relationship between statistical learning and attentional processing. When mapping this idea on to sequence learning paradigms, there is evidence of both aspects: that statistics modulate attention (e.g., Zhao & Turn-Browne, 2013); and that attention modulates statistical learning (e.g., Turk-Browne et al., 2009; Jiang & Chun, 2001). In the case of spatial learning paradigms, where the temporal sequence of spatial attention is harder to disambiguate, these relationships remain unclear. Might spatial regularities *increase* distractor processing? This would be predicted by an associative learning mechanism and was the observed previously where temporal regularities biased attention towards the distractors during search (i.e., Zhao & Turn-Browne, 2013). Alternatively, might spatial regularities suppress distractor processing? This would be in line with repetition-suppression effects or the “attentional efficiency” account of guided search (e.g., Beesley et al., 2018). Very recently, a study looked into this exact question proposes that distractor rejection may be a mechanism for spatial statistical learning (Stilwell & Vecera, 2020). At heart, these questions are about the nature of the representations that support a statistical learning process. And to understand mechanisms of disruption is to understand mechanisms of representation.

A related idea is that disruption may alter information processing through a mediator, namely that of utility. Predictive information in implicit learning tasks may be selected based on what will provide the most utility in given situation. There is evidence that the system does not always use all the regularities available to it, but prioritizes them based on utility (Endo & Takeda, 2004; Jiang & Song, 2005). When both the spatial location of objects and the identities of objects were predictive of a target (Endo & Takeda, 2004), spatial regularities were more influential than identity regularities. But when spatial regularities were no longer predictive (i.e., did not provide utility), identity regularities become influential. In other words, identity regularities were learned only when they provided an aspect of utility that spatial regularities did not. This suggests a hierarchy of information processing that can be flexibly adapted based on utility. A similar form of adaptation may have occurred during tDCS or masking, especially since these manipulations could have altered other operations involves in the cognitive cascade. The most obvious candidate is eye-movements. If eye movements were discouraged by the brief display durations used in Chapter 2, the system may have adapted to select information that did not require eye movements, based on utility, and this may have qualitatively altered what was learned in the task to produce slower, capacity limited cuing. To investigate this idea, one could use the method of recombined displays to assess global and local learning after contextual cuing with different task conditions (Ogawa & Kumada, 2008). In this design, each target would be associated with two repeat configurations during training. Afterwards, a test phases would measure cuing for repeat displays and recombined displays - made of two halves of the two repeat configurations. If individual items were learned, as was the case for standard visual search (Ogawa & Kumada, 2008), cuing should transfer to the recombined displays. If only global information was learned, cuing will not be transfer, as was the case for a pop-out search task (Ogawa & Kumada, 2008). Thus, this method can be used to infer whether local or global information was of greater utility during different task conditions. Likewise, during search with or without eye movements, cuing may be supported by a reliance on local and global information based on utility. Such an approach would get at the nature of the representations during various types of disruption.

Potential Mechanisms for Cortical Control Involvement

The key experiments in Chapters 3 and 4 provide novel evidence that cortical control regions play an interfering role in the statistical learning process. We show that modulating activity in DLPFC and PPC interferes with the early formation of statistical learning in a task dependent manner. I have considered the findings in terms of a direct role of cortical areas, as this was the most parsimonious explanation given the data. Until now, I have been agnostic about *how* these control areas may be involved. The present findings cannot strictly elucidate mechanisms on their own. But when considered alongside newly emerging evidence in the literature, a number of possibilities emerge. First off is the role of cognitive control governed by frontal regions and to a lesser extent, parietal regions. The DLPFC is important for a number of executive functions. Most notably it exerts top-down control over visual attentional processes (Miller and Cohen, 2001; Fuster, 2001). In the context of visual search, frontal regions are believed to exert influence over parietal areas in order to suppress unwanted distraction (e.g., see Feredoes et al., 2011). Some studies have suggested that DLPFC-governed control is actually detrimental to implicit statistical learning. This idea was touched on in the Discussion for Chapter 3. The notion takes a competition approach to learning. It proposes that disengagement of top-down control, through DLPFC deactivation, is beneficial for implicit processes.

Some evidence may support this account, since TMS protocols believed to decrease neural activation have produced an increase in contextual cuing (Rosero Pahi et al., 2020) and implicit recognition (Lee, Blumenfeld and d'Esposito, 2013). However, the assertion that a "decrease in excitability" caused the changes observed is not strictly supported by the data. Neural excitability was not measured in either case. Also, the TMS protocols were delivered offline, as a pre-treatment, before implicit learning was measured. So, the changes may have been contaminated by consolidation processes mediated by short-term plasticity. This explanation would be consistent with the fact that changes occurred in the later epochs of the tasks. One of the studies measured EEG-oscillatory activity induced by the TMS protocol and during the learning task (Rosero Pahi et al., 2020). And this was advantageous. It enabled them to show how task-related oscillations in the beta band were altered by DLPFC stimulation compared to the control region (vertex). The finding linked TMS-induced changes to a mechanism of top-down control; namely reduced beta-oscillations. It is possible that a similar reduction in cognitive control produced by tDCS in our studies can explain the facilitation of learning in Chapter 4, but it does not account for the disruption in learning we observed in Chapter 3. Whether facilitation may have been observed later on, after consolidation in Chapter 3 remains possible. Yet no causal, temporally specific evidence exists on whether PFC acts to suppress cognitive control or may also simultaneously enhance representations of the relevant statistical information. Also note that any observation of reduced activity in averaged BOLD signal may actually reflecting increased representational content (e.g., Garner & Dux, 2015; Kok, Jehee, & de Lange, 2012). Overall, the explanation that statistical learning relies on frontal control circuits via inhibition of top-down control is intriguing but requires further evidence. Combined methodologies, such as TMS-EEG and TMS-fMRI are now available and will surely prove useful for the needed investigations.

Another possibility is that cortical control regions were involved through a modulatory role of another process controlled by the same circuits. Two obvious candidates would be the dorsal fronto-parietal attention circuit (Summerfield et al., 2006; Rosen et al., 2016; Stokes et al., 2012), and the memory-retrieval circuit. Both are commonly known to be governed by the posterior parietal lobe and the dorsal frontoparietal network (Berryhill, Chein, & Olson, 2011; Corbetta, 1998; Sestieri et al., 2017) and both appear to play a role in gating the statistical learning process (Jiang & Chun, 2001; Turk-Browne, Jungé, & Scholl, 2005). Modulating parietal activity with tDCS can affect processes to do with visual search (Ball, Lane, Smith, & Ellison, 2013), spatial attention (Moos et al., 2012) and working memory (Berryhill, Wencil, Branch Coslett, & Olson, 2010; Sandrini et al., 2012). While modulating frontopolar activity has been related to memory retrieval processes after regularity learning and associative learning tasks (Chua & Ahmed, 2016; Pergolizzi & Chua, 2015; Ryals, Rogers, Gross, Polnaszek, & Voss, 2016). Therefore, an immediate question might be whether changes to attention or working memory processes can explain the pattern of results we observed with these statistical learning tasks.

To understand whether cortical modulation by tDCS may influence regularity learning through an intervening effect on attention, one could measure attentional changes directly; either using eye tracking, psychometric tasks, or known markers of attentional selection in EEG or fMRI. Alternatively, one could manipulate attention during exposure to regularities, to see whether attentional settings simply boost regularity learning during tDCS or may determine how tDCS influences learning. To address impending questions about the role of working memory, one may wish to focus on the opposing effect of stimulation for identity-cuing and location-based cuing. The expression of learning in contextual cuing appears to draw on working memory resources in a task-dependent manner. Studies show that holding items in working memory while searching displays impairs contextual cuing if the items were locations but not if they were colours or shapes (Annac et al., 2013; Manginelli et al., 2013b; Travis, Mattingley, & Dux, 2013). When the working memory task is removed, contextual cuing returns, suggesting the expression of learning requires working memory resources, not the learning itself. However, a recent study found that working memory load is not always detrimental and can even facilitate learning (and expression) in contextual cuing under certain conditions (Annac et al., 2018). Using the dual-task methodology, one could examine the relationship between different types of working memory load in learning different types of regularities. These research avenues serve to build on the current understanding of cortical involvement by investigating the nature of causal cortical involvement.

Concluding Remarks

The mechanism of cortical involvement in statistical learning is likely to be a complex one, but the contribution of the present work is clear. We provided much needed causal evidence on the role of cortical activity in producing statistical learning behaviours. These findings provide a novel and significant link between the modulation of cortical activity by tDCS and the process by which visual statistical regularities are learned. We identified the causal cortical locus across two different statistical learning tasks. We demonstrated that tDCS affected learning in a task-based manner early on, likely mediated by functional systems within the frontoparietal network. We proposed that the direct involvement of frontal and parietal activity in statistical learning can explain the observations in fMRI literature. Questions remain open as to the spatial specificity of our tDCS effects, and the effects of tDCS applied to areas outside this network. Whether task-based effect of tDCS on statistical learning occurred because of a mediating role of another function served by the same brain region is now an avenue for future work. To answer broader questions about the domain-general nature of cortical involvement, one can take what has been learned here with cuing tasks and apply it to other stimulus domains, tasks and regularities. Such an approach has already been taken for understanding hippocampal function in statistical learning across a range of tasks and phenomena (see: Schapiro et al., 2017).

The present work, together with the neuroimaging work, provides compelling evidence that statistical learning draws on distributed networks of brain areas in which both cortical and subcortical regions play an important role. Exploring the connections between statistical learning and brain regions that support higher-level cognition, such as attention and decision-making, can help answer important questions about the neural mechanisms that underlie statistical learning. It can also reveal new connections between statistical learning and other forms of learning that may draw on shared neural systems. The driving question is to understand how a sensitivity to statistical structure can be accomplished over so many stimulus types, tasks and timeframes. Such research also has the potential to inform models of diseases where aberrations in statistical learning have been observed, which include; Dyslexia, Parkinson's, Schizophrenia, Autism, as well as in healthy aging. The brain, after all, is not a passive machine; but is constantly generating predictions. And learning the structure of experience is a powerful way to form predictions. I believe there is much more to be gained by investing experience-based knowledge acquisition. Without these abilities, the dominant view is that you would not be able to read this thesis, and I would not be able to write it.

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APPENDIX A: ETHICAL CLEARANCE FROM THE UNIVERSITY OF QUEENSLAND HUMAN RESEARCH ETHICS COMMITTEE

THE UNIVERSITY OF QUEENSLAND

Institutional Human Research Ethics Approval

Project Title: The Ins And Outs Of The Central Bottleneck - 09/02/2016 - AMENDMENT

Chief Investigator: Dr Paul E Dux

Supervisor: None

Co-Investigator(s): Claire Kathleen Naughtin, Ms Rebecca King, Dr Hannah Filmer, Ms Angela Bender, Ms Kelly Garner, Mr Anthony Harris, Michelle Hall, Amy Taylor, Susan Travis, Elizabeth Varghese, Steffi Cook, Casey Lynch, Dr Ashika Verghese, Dr Warwick Rosebloom, Dana Schneider, Stephanie Goodhew, David Painter, Dr Andrew Bayliss, Abbey Nydam

School(s): School of Psychology, Faculty of Social and Behavioural Sciences

Approval Number: 2009000335

Granting Agency/Degree: James McKeen Cattell Fellowship; NHMRC

Duration: 31st December 2019

Comments/Conditions:

Note: if this approval is for amendments to an already approved protocol for which a UQ Clinical Trials Protection/Insurance Form was originally submitted, then the researchers must directly notify the UQ Insurance Office of any changes to that Form and Participant Information Sheets & Consent Forms as a result of the amendments, before action.

Name of responsible Committee:
Medical Research Ethics Committee
This project complies with the provisions contained in the *National Statement on Ethical Conduct in Human Research* and complies with the regulations governing experimentation on humans.

Name of Ethics Committee representative:
Dr Nancy Sturman
Chairperson
Medical Research Ethics Committee

Signature ______________ Date 2/3/2016