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Motivated Learning: The Influence of Reinforcers

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Psychology

by

Russell Cohen Hoffing

September 2018

Dissertation Committee:
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The Dissertation of Russell Cohen Hoffing is approved:

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Committee Chairperson

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Dedication and Acknowledgements

I want to dedicate this thesis to the brain, in all its awe-inspiring complexity and frustrating incomprehensiveness. To my brain in particular, and all that has shaped it: evolution and environment. To my advisor, and lab mates for giving me the best brain training I could have hoped for. Thank you for caring, and for your patience. To my professors, mentors, and the field of psychology for all the time, obsession and brilliance put into understanding human nature. These efforts have given me a deep appreciation for the complexity and elegance of how the brain creates even the most banal of human behaviors. To the luck that I was born to a caring and uplifting family. To my mother who inspired me and whom my appreciation of her badassery took way too long to develop –I can't believe we wrote a grant together. To the opportunities to create enduring relationships with my friends. To all those that accompanied my journey to this day and to those that will accompany me henceforth. I will forever be grateful for your presence, and awe inspired by you. Thank you. <3.

ABSTRACT OF THE DISSERTATION

Motivated Learning: The Influence of Reinforcers

by

Russell Cohen Hoffing

Doctor of Philosophy, Graduate Program in Psychology
University of California, Riverside, September 2018
Dr. Aaron R. Seitz, Chairperson

Extant research suggests a number of systems, including reinforcement and attentional systems, contribute to learning. The overall goal of this dissertation is to expand our understanding of how reinforcement systems contribute to learning. Chapters 1 and 2 use a task-irrelevant learning paradigm, which has been used to study the role of reinforcement systems in learning. To first understand how reinforcement systems influence learning, Chapter 1 tests the hypothesis that task-irrelevant learning is mediated by the norepinephrine reinforcement system, by using pupillometry as an indirect measure of norepinephrine system activity. Consistent with this hypothesis results indicate an increased change in pupil size accompanying learning. Chapter 2 investigates how emotion stimuli, which are thought to activate distinct reinforcement systems than the norepinephrine system, influence learning. Consistent with this hypothesis, results indicate that learning, found to be influenced by the norepinephrine system, is moderated by emotion stimuli. Chapter 3 used a task-switching training task manipulating explicit feedback (i.e. points), to investigate how reinforcement systems influence learning in the executive function domain. Consistent with the hypothesis that reinforcement systems 'tag' task-relevant brain states, results indicate that feedback schedules which favored speeded

responses, biased response strategies to sacrifice accuracy for speed. In conclusion, this dissertation furthers our understanding of the role of reinforcement systems in learning by providing a method of measuring norepinephrine reinforcement system activity during learning as well as provides a novel framework to understand how multiple reinforcement systems contribute to learning.

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General Introduction

How do we learn?

From the time we are born, each second our sight, smell, hearing, taste and touch are bombarded with a vast amount of sensory input. Yet, from this vast amount of stimulation we are able to make sense of the world. It is clear that to do this sense-making we select some input over others. Extant research implicates a multiplicity of systems that are involved in the selection and subsequent learning process (Seitz & Dinse, 2007), though the manner in which each system influences learning and how they interact is still not well understood. This dissertation aims to further our understanding of a key set of systems that influence learning: reinforcement systems. Here, techniques and theories derived from the field of perceptual learning, are used as a framework to formalize how reinforcement systems influence learning.

Chapters 1 and 2 use a task-irrelevant learning paradigm (Seitz & Watanabe, 2005; further discussed below), which has been used to study the role of reinforcement systems in learning. In Chapter 1, we test the hypothesis that the norepinephrine reinforcement system mediates task-irrelevant learning, by using pupillometry data as an indirect measure of the norepinephrine reinforcement system. Chapter 2 investigates how emotion stimuli, which are thought to activate a distinct reinforcement system than the norepinephrine system, influences task-irrelevant learning. Chapter 3, investigates how the role of reinforcement systems differ across cognitive domains by investigating how explicit feedback (i.e. points) influences learning in a task-switching paradigm. Overall, this dissertation furthers our understanding of the role of reinforcement systems in learning by

providing a method of measuring norepinephrine reinforcement system activity during learning as well as providing a novel framework to conceptualize how multiple reinforcement systems contribute to learning.

Dissertation Structure

The overarching goal of this dissertation is to further our understanding of how reinforcement systems contribute to learning. First, the introduction briefly reviews reinforcement learning. Then, current models of perceptual learning are discussed and a novel framework –the perception-reinforcement-action framework—is introduced to further elaborate on the role of reinforcement systems in learning. Next, three Chapters investigating how reinforcement systems contribute to learning are presented. Finally, in the discussion we interpret results from the Chapters in context of the aforementioned conceptual models of learning and discuss implications for the field of perceptual learning.

A brief history of reinforcement

The term "reinforcement" was first coined by physiologist Ivan Pavlov to describe how associations are formed (Pavlov, 1928). Specifically, he used the classical conditioning paradigm, where pairing of an unconditioned stimuli with a conditioned stimulus reinforces (i.e. strengthens) the association between the two stimuli. Other researchers have investigated how associations are made, including Edward Thorndike, who investigated how stimuli can reinforce responses via instrumental conditioning paradigms (Thorndike, 1898). B. F. Skinner investigated the relationship between stimulus-response-outcome relationships using operant conditioning paradigms (Skinner, 1958).

This research has expanded to include a vast field studying the role of reinforcement in perceptual learning (Seitz, Kim, & Watanabe, 2007; Seitz & Watanabe, 2005; Seitz & Dinse, 2007; Seitz, Kim, & Watanabe, 2009; Seitz & Watanabe, 2009), cognitive training (Deveau, Jaeggi, Zordan, Phung, & Seitz, 2015; Deveau, Lovcik, & Seitz, 2014; Deveau, Ozer, & Seitz, 2014; B. Katz, Jaeggi, Buschkuehl, Stegman, & Shah, 2014; Benjamin Katz, Jones, Shah, Buschkuehl, & Jaeggi, 2016), clinical psychopathologies (Graybiel, 2008), behavioral economics and others (Gershman & Daw, 2017; Montague et al., 2006). With the development of electrophysiological and imaging techniques, the initial animal work done by Pavlov has expanded to investigate the neurobiological mechanisms underlying reinforcement including neurochemical systems and neural circuits. For example, multiple neurochemical systems have been identified, which may underlie the process of reinforcement, including systems that release dopamine (Bao, Chan, & Merzenich, 2001; Schultz, 2002), acetylcholine (Bakin & Weinberger, 1996; Kilgard & Merzenich, 1998; Thiel, Friston, & Dolan, 2002), and norepinephrine (Bear & Singer, 1986; Gordon, Allen, & Trombley, 1988; Witte & Marrocco, 1997). These neurochemicals systems are candidate reinforcement systems due to their diffuse connectivity throughout the brain. It has been hypothesized that these neurochemical systems act as a mechanism of reinforcement via the release of neurochemicals throughout the brain to "tag" activity to be learned (Seitz & Dinse, 2007; Seitz & Watanabe, 2003). Imaging techniques have also identified multiple reinforcement systems that respond to more abstract stimuli than primary reinforcers including money, beliefs, social responses, art, and bodily states (Montague et al., 2006; Ochsner & Gross, 2014). For example, the orbital frontal cortex has been implicated in the

processing of more abstract reinforcers (Ochsner & Gross, 2014) while subcortical structures like the striatum and insula are thought to be more involved in concrete reinforcers (Ochsner & Gross, 2014).

Overall, the crucial observation made by this body of research is that there exist multiple interacting reinforcement systems. To account for this, the role of multiple reinforcement systems is conceptualized in context of evidence that a multiplicity of systems contribute to learning. First, two conceptual perceptual learning models are reviewed, which account for a multiplicity of systems contributing to learning. Afterwards, a novel framework –the Perception-Reinforcement-Action processing framework—is introduced to expand on these models to understand how reinforcement systems influence learning.

A Learning Threshold Model of Perceptual Learning

Perceptual learning is typically defined as the improvement in the perception of a stimulus, such as improvement in the discrimination of orientation, spatial frequency or contrast, following training (Ahissar & Hochstein, 2004; Fahle & Poggio, 2002; Gibson, 1963). Over the past three decades of perceptual learning research, models of perceptual learning have suggested that there is a multiplicity of systems involved in learning. A model proposed by Seitz & Dinse (2007) takes into account perceptual learning found in conditions with attention, without attention and passive stimulation. Attention has been thought to act as filter on sensory input and select relevant information that is subsequently encoded into memory (Seitz & Dinse, 2007). For example, in Ahissar and Hochstein (1993)

participants trained on an array of oriented lines that could either be categorized by one of two tasks: its global orientation (i.e. vertical or horizontal) or whether an aberrant line was present (i.e. missing or present). When participants were trained on one task (e.g. global orientation) and subsequently switched to train on the other task (e.g. line detection), no transfer of learning was found, despite using the same stimuli. This result indicated that attentional mechanisms, were influencing learning. A number of studies have replicated findings of the influence of attention in perceptual learning (Seitz & Dinse 2007).

However, follow up research paints a more complicated picture of learning with findings that indicate that perceptual learning can occur without attention. For example, pairing of stimuli with electrical stimulation of reinforcement systems, like the ventral tegmental area (Schultz, 2002; Bao, Chan, & Merzenich, 2001) and nucleus basalis (Thiel, Friston, & Dolan, 2002; Kilgard & Merzenich, 1998; Bakin & Weinberger, 1996), are sufficient to induce learning. Research using task-irrelevant learning (TIL) paradigms have found similar results where a subliminal stimulus (i.e. upward moving dots at 5% coherence) are paired with a target stimulus. After consistent pairing of the stimulus and targets, discrimination for the stimulus improves despite there being no overt target detection benefit for learning the stimulus, thus this phenomenon was dubbed 'task-irrelevant' learning (Seitz & Watanabe, 2005; Seitz & Dinse, 2007; Seitz et al., 2009; Seitz & Watanabe, 2009). TIL has been thought to be mediated by activation of reinforcement systems during target detection, leading to the release of a learning signal. The learning signal which would normally induce learning of the target, 'spills' over to tag the temporally paired stimulus. Overall, this phenomenon is similar to learning found in

operant conditioning paradigms where stimulus-response-outcome states are reinforced. In context of TIL, target detection acts as a reinforcer.

Finally, the learning threshold model takes into account findings of passive learning where coactivation of sensory systems in the brain with passive stimulation (i.e. where no decision is required) leads to cortical reorganization and learning (Schultz, 2002; Bao, Chan, & Merzenich, 2001; Seitz and Dinse 2007). Furthermore, direct stimulation of brain regions, using techniques such as transcranial magnetic stimulation, can also enhance learning (Seitz & Dinse 2007).

To explain the aforementioned results, Seitz & Dinse (2007) suggest that learning occurs only after a learning threshold is surpassed. Thus, sensory inputs are not typically sufficient to surpass the learning threshold, allowing behaviorally irrelevant information to be ignored. However, when sensory information interacts with reinforcement systems, attention or brain stimulation, sensory signals are pushed past a learning threshold and are subsequently learned. Below, a conceptual model which elaborates on the role of attention in perceptual learning is discussed.

An Attentional Gating Model of Perceptual Learning

A model proposed by Seitz & Watanabe (2009) expands on the learning threshold model by further elaborating how attentional mechanisms interact with task-irrelevant learning (TIL). Various studies have indicated that attention can enhance or impair TIL. For example, manipulations of exogenous attention been found to suppress TIL (Choi, Seitz, & Watanabe, 2009; Leclercq & Seitz, 2012b). In other studies attention manipulations have

led to the enhancement of TIL including increased TIL for stimuli presented after a cue (Leclercq & Seitz, 2012a) or a target (Cohen Hoffing & Seitz, 2015; Leclercq & Seitz, 2012a). TIL has also been found to vary by its spatial proximity to the task target, where irrelevant stimuli closer to the task target result in increased learning, indicating that the spatial profile of attention is modulating TIL (Nishina, Seitz, Kawato, & Watanabe, 2007).

To account for these results, Seitz & Watanabe (2009) suggests that there exist a multiplicity of reinforcement and attentional systems at work in shaping TIL. For example, the Petersen and Posner (2012) attention network model suggests that there exist three attentional systems: the alerting, orientation and executive attention networks. According to the Seitz & Watanabe (2009) model each of these attentional networks act on their own spatial and temporal time course to filter sensory input. Task-irrelevant learning suppression occurs because the irrelevant stimulus is distracting and is filtered out by attentional systems. Conversely, the presence of task-irrelevant learning suggests that the irrelevant stimulus is not filtered out by the attentional system and thus the task-relevant stimulus learning signal "spills over" to the task-irrelevant stimulus.

The Perception-Reinforcement-Action Processing Framework
The perception-reinforcement-action (PRA) framework aims to extend previous models by elaborating on how reinforcement systems influence learning. This model is adapted from the perception-valuation-action processing framework (Ochsner & Gross, 2014). While, the aforementioned perceptual learning models suggest that attentional systems and reinforcement systems may share a neural substrate, the PRA model assumes that they do

arise from the same neural substrates based on evidence that the same reinforcement systems are involved in downstream behavior. The PRA framework incorporates a 3-stage cycle (**Figure 1**): 1) the perception stage (P), 2) the reinforcement stage (R) and 3) the action stage (A). In the perception stage (P) external and internal sensory inputs from the world (W) are passed onto the reinforcement systems. The PRA process model unfolds in real time in a cyclical manner where the output of action informs the new state of the world. Furthermore, W_1, W_2, and W_n represent multiple reinforcement systems. Below, the task-irrelevant perceptual learning paradigm is first used to expand on the reinforcement stage of the PRA process and then second, the action stage is elaborated on by discussing how the reinforcement stage influences subsequent behavior.

The Reinforcement Stage

In the reinforcement stage (R), reinforcement systems are activated by reinforcers that create associations between the world and internal sensory inputs. Reinforcers range from primary to secondary reinforcers. Primary reinforcers are stimuli that activate basic survival functions, such as food, water, and bodily states (Gershman & Daw, 2017; Montague et al., 2006). Secondary reinforcers are stimuli which are associated with primary reinforcers, such as points in a game, money (Gershman & Daw, 2017; Montague et al., 2006), and social responses (Ochsner & Gross, 2014). Reinforcers can also be internal, as is the case in task-irrelevant learning (TIL) where target detection leads to activation of reinforcement systems (Cohen Hoffing & Seitz, 2015; Seitz & Watanabe, 2005; Seitz et al., 2009). In TIL, stimuli that are temporally paired with targets are learned

even when the learned stimuli are subliminal, and no task is associated with the stimuli (Cohen Hoffing & Seitz, 2015; Seitz et al., 2009). For example, in Seitz et al. (2009) participants viewed oriented gratings, while undergoing continuous flash suppression rendering the gratings imperceptible. One of the oriented gratings (e.g. 45 degrees) was continually paired with a water reward and resulted in learning of only the paired oriented grating. This result provided further support that TIL is mediated by reinforcement systems. The learning threshold and attention gating model predict that the norepinephrine reinforcement system mediates TIL (Seitz & Watanabe, 2005; Seitz et al., 2009).

The largest source of norepinephrine in the brain is located in the locus coeruleus (Aston-Jones, 2005). The fact that the locus coeruleus has diffuse connections throughout the brain is consistent with the hypothesis that release of norepinephrine can 'tag' a brain state to be learned. Aston-Jones (2005) proposes that the norepinephrine system has two modes: a phasic mode involved in exploitation of currently available information and a tonic mode involved in exploration of the environment. In a pupillometry study in humans, participants discriminated tones of increasing difficulty (Aston-Jones, 2005). At the end of each trial participants were given the option to reset difficulty. As hypothesized, large phasic changes in pupil size were seen at the beginning of difficulty sets and tonic baseline pupil size was greatest right before participants decided to reset difficulty. These results have been further replicated in animal studies which indicate increased engagement and accuracy during phasic activation of the norepinephrine system, while tonic activation of the norepinephrine system is associated with task-disengagement (Aston-Jones, 2005). Consistent with this hypothesis, studies investigating learning, have found evidence that

norepinephrine increases in a phasic manner during learning (Cohen Hoffing & Seitz, 2015; Nassar et al., 2012). In addition to the norepinephrine systems, extant research has implicated other neurochemical systems in learning including dopamine (Bao, Chan, & Merzenich, 2001; Schultz, 2002) and acetylcholine (Bakin & Weinberger, 1996; Kilgard & Merzenich, 1998; Thiel, Friston, & Dolan, 2002). Overall, the PRA conceptual model accounts for findings that suggest multiple reinforcement systems contribute to learning, by explicitly including multiple PRA cycles.

The Action Stage

After the reinforcement stage, reinforcement systems give rise to action. Actions can be either cognitive (i.e. attention processes, memory retrieval, mental imagery) or physical (i.e. eye movement, physiological responses like changes in pupil size or heart rate). To expand on this, two models which implicate the involvement of reinforcement systems in attention processes are discussed. Specifically, theories suggest that reinforcement, arousal and attention processes arise from the same neural substrates. As discussed above, Aston-Jones (2005) suggests that the norepinephrine system has phasic and tonic activation patterns, which encourage different forms of behavior to allow for optimized behavior. Petersen & Posner (2012) put forth a framework suggesting that reinforcement systems like norepinephrine and acetylcholine play distinct roles in attention. In this framework the norepinephrine system is hypothesized to be involved in the alerting of attention while the acetylcholine system is involved in the orientation of attention (Petersen & Posner, 2012). In context of the PRA model, these two theories suggest that the attentional systems put

forth by Peterson & Posner (2012) are actions that arise from engagement of the neurochemical reinforcement systems. For example, the norepinephrine system, when phasically activated, may give rise to activation of the alerting attention system, while tonic activation of the norepinephrine system may give rise to activation of the orienting attention system. Although, in the Petersen & Posner (2012) model, it is thought that the orienting of attention is mediated by the acetylcholine system. These conflicting accounts of the underlying neurochemical systems of attention suggest that these neurochemical systems are not fully independent.

Reinforcement, Emotion Stimuli, and Attention

There are other types of reinforcers that have been found to drive attentional systems. For example, emotion-laden stimuli have been found to be involved in learning by influencing memory encoding (Mather & Sutherland, 2011). One possible mechanism of influencing memory encoding is by acting as a reinforcer. Consistent with this hypothesis, research has found that emotion stimuli activate the orbitofrontal reinforcement system (Oschner & Gross, 2014; van Rooijen, Ploeger, & Kret, 2017). Positive emotions are thought to serve as social rewards which reflect a desirable setting that should be exploited. Consistent with the PRA model, emotion stimuli have been linked to actions, with positive emotions leading to a broadening of spatial attention (Fredrickson & Branigan, 2005; Gasper & Clore, 2002; Rowe, Hirsh, & Anderson, 2007; Srivastava & Srinivasan, 2010) while negative emotions lead to a narrowing of spatial attention (Easterbrook, 1959). Overall, the aforementioned evidence is consistent with the PRA model in that reinforcement systems

give rise to actions. Below, Chapters, which further our understanding of the role of reinforcement systems in learning, are introduced.

Research Questions

Chapter 1

Chapter 1 tests the hypothesis that norepinephrine reinforcement systems mediate task-irrelevant learning (TIL). A study using a standard TIL paradigm while collecting pupillometry was conducted. In the TIL paradigm images are paired with targets and distractors (Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d). Participants complete a dual task of detecting targets and memorizing the paired images. Pupillometry is used as an indirect measure of the norepinephrine system, (Aston-Jones, 2005; Rajkowski, Kubiak, & Aston-Jones, 1993; Steinhauer, Siegle, Condray, & Pless, 2004) based on evidence that recordings of neuronal activity in the monkey locus coeruleus, the main source of norepinephrine in the brain (Aston-Jones, 2005), are coupled with changes in pupil size (Rajkowski, Kubiak & Aston-Jones, 1993). Follow-up research, indicating that pupil size changes are correlated with learning, (Nassar et al., 2012) is consistent with the hypothesis that norepinephrine influences learning and pupil size. Based on the aforementioned results, we hypothesize that results will replicate previous findings of enhanced accuracy for targets compared to distractors (i.e. TIL; Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d) and that TIL will be accompanied by increased changes in pupil size.

Chapter 2

In Chapter 2 we investigated how emotion stimuli, which are thought to activate distinct reinforcement systems than the norepinephrine system, influence TIL. To test this hypothesis, we used a TIL learning paradigm where emotion stimuli were paired with emotion face targets (i.e. positive, negative and neutral faces) and distractors. Participants completed the dual task of reporting targets and memorizing images and were tested on recognition of the images and face targets. To further illuminate the influence of emotion stimuli on reinforcement systems we collected pupillometry data. Based on findings of a broadening of attention for positive emotion stimuli and narrowing of attention for negative emotion stimuli, we hypothesized that TIL would be enhanced for positive emotion stimuli and suppressed for negative emotion stimuli. Furthermore, we hypothesized that pupil size change patterns would reflect TIL patterns.

Chapter 3

The study in Chapter 3 was motivated by our interest in applying methodologies of perceptual learning, shown to increase transfer of learning, to create efficacious training paradigms targeting executive function abilities. To create an efficacious training paradigm, we first wanted to understand how reinforcement systems influence learning in context of other cognitive abilities such as executive functions. To study this, we investigated how various forms of explicit feedback (i.e. points) influenced performance on a task-switching training task. Participants received various feedback conditions that have been used in the literature but not systematically studied. We also used drift diffusion modeling (DDM) to understand how training altered decision processes.

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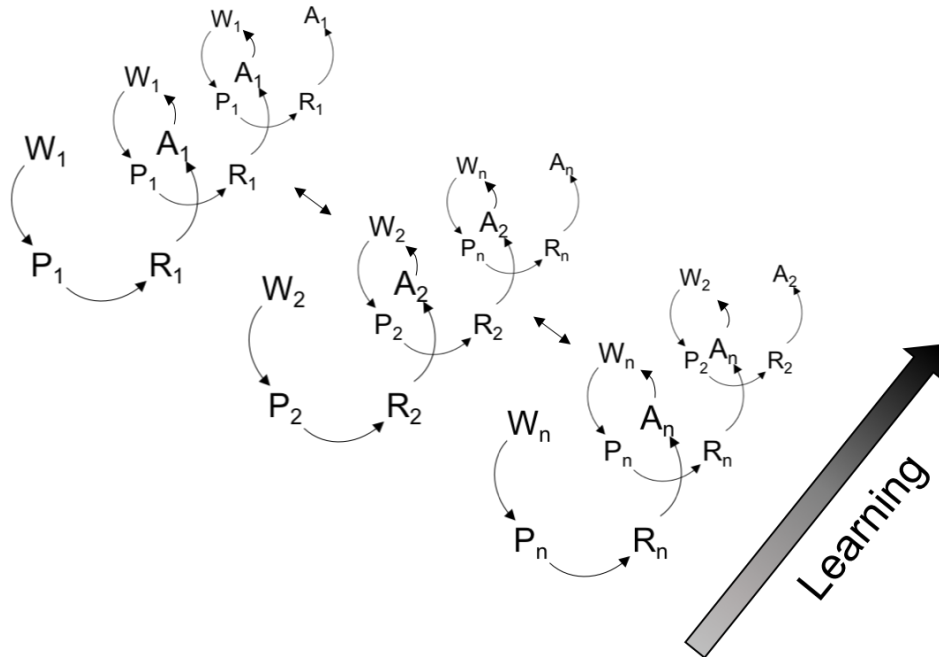
Figures

Figure 1: The perception-reinforcement-action cycle of the PRA process framework. The world (W) stage is processed by the perception stage (P) which then passes sensory input to the reinforcement stage (R) where associations between the internal and external states are created which then give rise to actions (A) which then further inform the current state of the world. Multiple PRA cycles interact to create learning. Adapted from Ochsner & Gross (2013).

Chapter 1

This chapter has been previously published as

Pupillometry as a glimpse into the neurochemical basis of human memory encoding

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Abstract

Neurochemical systems are well studied in animal learning, however ethical issues limit methodologies to explore these systems in humans. Pupillometry provides a glimpse into the brain's neurochemical systems, where pupil dynamics in monkeys have been linked with locus coeruleus activity, which releases norepinephrine (NE) throughout the brain. Here, pupil dynamics are used as a surrogate measure of neurochemical activity to explore the hypothesis that NE is involved in modulating memory encoding. A task-irrelevant learning paradigm is used, in which learning is boosted for stimuli temporally paired with task-targets. Results show that participants better recognize images that are paired with task-targets than distractors, and in correspondence that pupil-size changes more for target-paired than distractor-paired images. To further investigate the hypothesis that NE non-specifically guides learning for stimuli that are present with its release, a second procedure was used that employed an unexpected sound to activate the LC-NE system and induce pupil-size changes; results indicated a corresponding increase in memorization of images paired with the unexpected sounds. Together, these results suggest a relationship between the LC-NE system, pupil-size changes and human memory encoding.

Introduction

Converging evidence from animal research and theoretical models (Hassani, Cromwell, & Schultz, 2001; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; A. R. Seitz & Dinse, 2007; Yu & Dayan, 2005) suggest a key role of neurochemicals like dopamine (Bao, Chan, & Merzenich, 2001; Schultz, 2002), acetylcholine (Bakin & Weinberger, 1996; Kilgard & Merzenich, 1998; Thiel, Friston, & Dolan, 2002) and norepinephrine (NE) (Bear & Singer, 1986; Gordon, Allen, & Trombley, 1988; Witte & Marrocco, 1997) in the plasticity underlying learning; yet little is known about their role in humans. The study of neurochemical involvement in human learning is difficult because invasive methods are required to directly measure neurochemical release.

However, non-invasive measures such as pupillometry can provide clues into neurochemical activity. For example pupil-size changes have been suggested as surrogate measure of locus coeruleus (LC) activity and its release of norepinephrine (Nassar et al., 2012). This relationship is primarily supported by reports of a coupling of activity in the monkey LC and pupil dilation (Aston-Jones, 2005; Rajkowski, Kubiak, & Aston-Jones, 1993). However, recent studies in humans show that show that pupil-size changes were positively associated with a learning rate (Nassar et al., 2012; Silvetti, Seurinck, van Bochove, & Verguts, 2013) and increased task performance (Murphy, Robertson, Balsters, & O'connell, 2011). These data provide evidence that pupil dynamics are related to learning and are consistent with the hypothesized role of NE-LC activity in driving pupil-size dynamics and learning.

Here the hypothesis that NE causes learning for stimuli present during its release regardless of their relevance to the inducing stimuli is explored (A. Seitz & Watanabe, 2005; A. R. Seitz & Watanabe, 2009). To explore this hypothesis, pupillometry is collected in the context of task-irrelevant learning (TIL), in which learning occurs without attention being directed to the learned stimuli (A. R. Seitz & Watanabe, 2003, 2009; Watanabe, Nanez, & Sasaki, 2001). TIL is a robust learning phenomenon with demonstrations ranging from critical flicker fusion thresholds (A. R. Seitz, Nanez, Holloway, & Watanabe, 2005, 2006), motion (Watanabe et al., 2002), orientation processing (Nishina, Seitz, Kawato, & Watanabe, 2007), contour integration (Rosenthal & Humphreys, 2010), phonetic processing (Vlahou, Seitz, & Protopapas, 2009) and memory encoding (Leclercq, Le Dantec, & Seitz, 2013). Seitz and Watanabe (2005) suggested a model of perceptual learning where learning results from interactions between spatially diffusive task-driven signals (such as NE) and bottom-up stimulus signals.

While TIL was discovered in low-level perceptual learning (A. R. Seitz & Watanabe, 2003; Watanabe et al., 2001), recent research of fast task-irrelevant learning (fast-TIL) (Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d; Lin, Pype, Murray, & Boynton, 2010; Swallow & Jiang, 2010) shows increased memorization of images even after a single pairing with a target of a target detection task. We note, that "task-irrelevant" in the context of fast-TIL is used to maintain consistent terminology with prior works on the topic and refers to the fact that the memorized images have no predictive relationship to presentation of targets of the target-detection task, nor are the targets informative of which scene will be tested in the scene-recognition task. Fast-TIL like effects have also been shown in other

studies, such as in Krebs et al. (2013) where increased recognition was found for faces paired with incongruent words.

Here the fast-TIL paradigm is adopted and used to examine the relationship between pupil dynamics and image recognition. We find that larger pupil-size changes correspond with improved image memorization through TIL. To further test the TIL model, a second study is conducted, in which novel sounds (following methods of Nassar et al., 2012 and Seitz et al., 2009) are paired with images to induce NE release. Results of this study are consistent with the first showing increased pupil-size changes and increased memorization for those images. These results suggest that TIL is a basic mechanism of learning in the brain and is a useful tool by which to understand the involvement of neurochemical signals in learning independent of task-related processing.

Materials and Methods

Participants

A total of 70 participants were run, 43 in Experiment 1 and 27 in Experiment 2. All participants had normal or corrected-to-normal visual acuity and received course credit for the 1.5hr session. Participants were excluded due to excessive eye-movement (12 in Experiment 1 and 7 in Experiment 2). This left a final sample of 31 participants (19.28 ± 1.4 y.o.; 20 females, 11 males) in Experiment 1 and 20 participants (19.85 ± 1.5 y.o.; 9 females, 11 males) in Experiment 2. All participants gave written informed consent, as approved by the University of California, Riverside Human Research Review Board.

Apparatus and Stimuli

An Apple Mac Mini running MATLAB (MathWorks, Natick, MA) and Psychophysics Toolbox Version 3.0.8 (Brainard, 1997; Pelli, 1997) was used for stimulus generation and experiment control. Stimuli were presented on a ViewSonic PF817 monitor with resolution of 1600 X 1200 resolution, and a refresh rate of 100 Hz. Display items consisted of 2112 scenes depicting natural or man-made environments to ensure that every trial contained a unique set of images. Scenes were obtained from the Massive Memory database (Konkle, Brady, Alvarez, & Oliva, 2010) at 256 X 256 pixels of resolution, then up-sampled and presented at 768 X 768 pixels (18.3° of visual angle). In Experiment 2, environmental sounds were obtained from an online library (Marcell, Borella, Greene, Kerr, & Rogers, 2000). We extracted the first 133ms of each sound and played them at a sampling rate of 22kHz through Sennheiser HD 202 headphones, which have a frequency range of 18Hz-18kHz. The background for all displays was a gray (luminance of $10cd/m^2$). Participants sat with their eyes approximately 57cm from the screen using the Eyelink 1000 tower-mount, which was used to track eye movement and pupil-size fluctuations of the right eye during every 10ms screen refresh. The eye tracker measured pupil diameter with a resolution of 0.2% of diameter, corresponding to a resolution of 0.01 mm for a 5 mm pupil, and has a spatial resolution of <0.01° RMS (S.R. Ltd, 2005). Pupil dynamics are known to be influenced by luminance levels (Winn, Whitaker, Elliott, & Phillips, 1994), thus each scene was matched to the average luminance distribution of the 2112 scenes using the histMatch function of the SHINE toolbox to control for luminance fluctuations across the image set (Willenbockel et al., 2010).

Procedure and Design

At the start of the experiment, a randomized target 9-point calibration and validation routine was performed using the EyeLink 1000 software to calibrate gaze and ensure accuracy of pupil dynamic readings.

Each trial consisted of an 8-scene Rapid Serial Visual Presentation (RSVP) stream, each presented for 133ms followed by an ISI (blank gray screen) of 1000ms (**Figure 1.1**). Targets or Distractors were randomly selected each trial and presented within a gray aperture presented in the middle of each scene. Each participant performed 120 trials of the main procedure (described below). Each trial began with the message, "Blink! Whenever you are prepared to not blink press any key to continue," to ensure participants were prepared for each trial. 15 Blocks of 8 trials each were separated at minimum by 10-second breaks. If a participant blinked or moved their eyes more than 1.5° from fixation during the RSVP stream they were alerted with the message "Please refrain from blinking or moving your eyes" and the trial was replaced with a new trial containing a novel set of images. Before each trial started participants were required to maintain fixation on a central red dot (0.1° of visual angle) for a random period of 300-600ms. To ensure that participants could conduct the task they performed a practice block of 8 trials prior to initiating the main procedure.

In Experiment 1, participants were instructed to complete two tasks (Target Detection and then Scene Recognition) in each trial. The Target Detection task was on the RSVP stream of alphanumeric characters; Targets (numbers '1', '2', or '3') and Distractors ('A', 'B', 'C', 'D', 'E', 'F', 'G', 'H', 'J', 'K', 'L', 'M', 'N', 'P', 'Q', 'R', 'S', 'T', 'U', 'V').

For the Target Detection task, participants had 1500ms to report the Target identity via the number pad keys '0' (if no Target presentation), '1', '2', or '3'. For the Scene Recognition Task participants were presented with two side-by-side scenes for 3000ms and reported which scene had appeared in that trial via the number pad keys '1' or '2'.

In Experiment 2, alphanumeric characters were replaced with environmental sounds, which were randomly selected from a list of 97 sounds. Participants were told that the sounds were irrelevant to the Scene Recognition task, which was their single task. In the place of Targets, a sound-change occurred (Novel Sound); in place of Distractors one repeating sound (Repeat Sound) was used. The trial retained the same statistical properties of Experiment 1.

In both experiments, three types of trial conditions were utilized: Distractor (n=48), Target (n=48), and Catch Trials (n=24). In Distractor (Repeat Sound) trials no target was shown and one random scene was tested in the Scene Recognition Task. In Target (Novel Sound) trials the Target-paired scene was tested. In Catch trials, a target was presented and one of the Distractor-paired (Repeat Sound) scenes was tested. Catch trials were introduced so that participants couldn't predict when a Target would occur or which scene would be tested. Tested scenes and Target presentation were counterbalanced across item positions 3-6 to avoid primacy and recency effects.

Data Analysis

We calculated accuracy on the Target Detection Task and the Scene Recognition Task by dividing the number of correct trials by the total number of responses made for each task,

excluding missed trials. In Experiment 1, 7.74 ± 0.93% (serr) of trials were missed in the Target Detection Task and 9.11 ± 0.96% in Scene Recognition Task. In Experiment 2, 13.67 ± 2.54% were missed in the Scene Recognition Task.

For the analysis of pupil dynamics, pupil diameter was normalized by dividing each data point by each subjects' pupil-size session mean. Analysis of pupil-size only examined Target and Distractor Trials, and excluded trials with eye-movements during the RSVP scene stream (6.77 ± 0.47 %) resulting in inclusion of 90 trials on average per participant. Baseline pupil-size (BPS) was defined as the trough-to-trough mean of pupil-size before stimulus presentation. This period was used because it provides an estimate of the pupil size immediately prior to the stimulus of interest, however it should be noted that it is not a stable baseline, due to the influence of processing the previous image. Alternative choices of baselines were more problematic because they were less temporally proximal to the stimulus of interest and eye movements and blinks contaminated pre-trial intervals. Pupil-size change (PSC) was defined as the difference between the trough and peak of pupil-size after stimulus presentation (**Figure 1.2**).

Results

Experiment 1 – Task Irrelevant Learning

To evaluate whether our procedure led to TIL recognition rates in the Scene Recognition Task were examined (**Figure 1.3**). As hypothesized, accuracy (**Figure 1.3a**) for Target-paired scenes (73.41 % ± 1.50%) was significantly greater than that for Distractor-paired (63.94 % ± 1.16%) scenes, t(30)= 3.7534, p=0.0004. Likewise, reaction-times were

significantly faster for Target-paired (1101 ± 13.2ms) compared to Distractor-paired (1147 ± 8.2ms) scenes, t(30)=-2.1947, p=0.0179 (**Figure 1.3b**). These increased memorization rates and faster reaction times for Target-paired scenes over Distractor paired scenes confirm a TIPL effect.

Pupillometry of TIL

A key question is whether there is a relationship between TIL and pupil-size changes during task performance **(Figure 1.4a)**. We observed that participants showed a larger pupil-size change (**Figure 1.4b**) for Target-paired scenes (6.01 ± 0.38%) over Distractor paired scenes (4.33 ± 0.35%), t(30)=9.5410, p<0.0001, which is consistent with our hypothesis that NE release is associated with Target-processing. On the other hand, we found no baseline pupil-size (t(30)=-1.1237, p=0.8650) differences (**Figure 1.4c)** between Target-paired scenes (99.91 ± 0.23%) and Distractor paired scenes (100.26 ± 0.18).

While we failed to find a relationship between baseline pupil-size and TIL, previous studies (e.g. Murphy et al., 2011), have shown that baseline pupil-size is related to performance outcomes. To test for this, we examined pupil-size and pupil-size changes as a function of Performance Outcome [Correct, Incorrect] **(Figure 1.4d)**. Consistent with previous findings, participants showed significantly lower (t(30)=-2.1386, p=0.0407, two-tail) baseline pupil-size **(Figure 1.4f)** for Correct trials (99.84 ± 0.20%) than Incorrect trials (100.44 ± 0.24%). On the other hand, we failed to find any significant differences (t(30)=-0.9283, p=0.3607) between pupil-size changes **(Figure 1.4e)** and Correct (5.09 ± 0.35%) vs. Incorrect scenes (5.22 ± 0.39%).

These results support a dissociation between pupil-size changes as regulating TIL, and baseline pupil in regulating overall performance, with lower baseline pupil-size leading to more accurate responses and greater Target-related pupil-size changes leading to TIL.

Experiment 2 - Memory Enhancement due to Alerting Sounds

While the results of Experiment 1 are consistent with our hypothesis for the role of NE in TIL, the dual task in Experiment 1 may recruit processes that may impact pupil dilation and thus confound the results. Thus to find independent evidence of the role of NE in TIL, we adopted an approach suggested by (Nassar et al., 2012) where alerting sounds were played as task-irrelevant stimuli drove learning on a numerical inference task. This is consistent with Seitz and Watanabe's model of TIL which predicts that rewarding or alerting signals are sufficient to induce TIPL (A. Seitz & Watanabe, 2005); this is also consistent with research that unexpected stimuli have been shown to phasically drive LC neurons (Sara & Bouret, 2012) and pupil dynamics (Murphy et al., 2011). We thus hypothesized that unexpected (alerting) sounds would lead to larger pupil size changes than expected sounds and that these alerting sounds would also lead to greater memorization of the paired scenes. To test this hypothesis, we replaced the Target Detection Task with a stream of task-irrelevant sounds, where one sound (Repeat Sound) replaced Distractors and a set of Novel Sounds replaced Targets (**Figure 1.1b**).

Results on the scene memorization task showed significantly increased accuracy for Novel Sound paired scenes (73.35 % ± 1.38%) compared to Repeat Sound paired scenes (69.15% ± 1.15%) (t(19)=1.84, p=0.039) (**Figure 1.5a**) and also significantly faster RT (t(19)=-2.85, p=0.0051) for Novel Sound paired scenes (1213 ± 14.4ms), compared to

Repeat Sound-paired scenes (1291 ± 14.2ms) (**Figure 1.5b**). This significant increased memorization and faster RT for Novel Sound paired scenes over Repeat Sound paired scenes suggests a TIL effect.

Pupillometry due to Alerting Sounds

Examination of pupil-size dynamics revealed significantly increased pupil-size change for Novel Sound paired scenes (4.74 % ± 0.15%) compared to Repeat Sound paired scenes (3.67% ± 0.13%) (t(19)=4.2147, p=0.0002) (**Figure 1.6b**) and no difference (t(19)=0.913, p=0.19) between baseline pupil-size for Novel Sound paired scenes (99.93 ± 0.21%), compared to Repeat Sound-paired scenes (99.66 ± 0.21%) (**Figure 1.6c**). These replicate the pattern of results seen for TIL.

Interestingly, we also found a relationship between Performance Outcome **(Figure 1.6d)** and pupil changes, with significantly (t(19)=1.99, p=0.031) increased pupil-size changes during the to-be-tested scene that was Correct (4.12 % ± 0.06%) compared to Incorrect (3.71% ± 0.15%) (**Figure 1.6e**). However, no difference (t(19)=0.873, p=0.20) between baseline pupil-size before scenes that were Correct (99.97 ± 0.12%), compared to Incorrect (99.97 ± 0.31%) (**Figure 1.6f**). While these results are different than those of the first experiment, the dynamics of the pupil-size changes were different in this experiment, with a faster initial rise in pupil-size and prolonged elevation of pupil-size after the Novel sounds. Furthermore, even Repeat sounds may have had a different impact on pupil-size changes than the Distractors in Experiment 1. While these differences between experiments are interesting and warrant further study, they don't strongly bear on our central observation that Novel sounds led to a TIL-like effect.

Prolonged Effects of Alerting

As stated above, the Novel Sounds produced a prolonged change in pupil size that persisted into the stimulus presentation periods following that of the Novel Sound. This prolonged effect is consistent with subjective observations of a prolonged "arousal/alerting effect" following the Novel Sounds which was experientially different from a more stayed effect following the Targets in Experiment 1. We hypothesized that a component of this effect was due to the prolonged release of NE that would in turn lead to improved memorization for scenes presented after the Novel sounds compared to scenes presented before the Novel sounds. To test this hypothesis, we examined performance in trials in which the tested scene was presented earlier or later in the image sequence relative to the Novel Sound.

Results of the Scene Recognition Task revealed a significant main effect of accuracy as a function of Trial-Type [Pre-Novel Sound, Novel Sound, Post-Novel Sound] with Pre-Novel Sound paired scenes having significantly ($F(2,38)=4.78$, $p=0.014$, one-way ANOVA) lower accuracy ($66.12 \% \pm 4.04\%$; **Figure 1.7a**) and significantly slower ($F(2,38)=58.702$, $p<0.0001$) RTs (1340 ± 23.5ms; **Figure 1.7b**) compared to Novel Sound-paired scenes ($73.35\% \pm 1.38\%$; 1213 ± 14.4ms) and Post-Novel Sound paired scenes ($79.95\% \pm 3.10\%$; 1264 ± 28.1ms). These results show that Novel Sounds not only benefited the paired scene but also had a prolonged effect that lead to increased accuracy and decreased RTs for scenes presented after the Novel Sound. 1

Discussion

Our results show that pupil-size dynamics are associated with increased memorization of images. In Experiment 1 pupil-size change was related to the performance advantage that arises from Target-processing in a standard TIL paradigm. Experiment 2, further tested this model by testing whether Novel sounds, which also stimulate the LC, would lead to TIL. Consistent with the model, Novel Sounds led to increased pupil-size changes and learning. Together these data support the hypothesis that NE release guides human memory.

These results are consistent with a model of TIL put forth by Seitz and Watanabe (2005) where "phasic" activation of the LC, which results in NE release throughout the nervous system (Bouret & Sara, 2005; Harley, 1987, 2004; Sara, Vankov, & Hervé, 1994) was hypothesized to lead to both task-relevant and task-irrelevant learning. This idea was built upon extant models of arousal and alerting, for which Petersen and Posner (2012) hypothesized to rely upon NE release, and also upon models of unexpected uncertainty in learning (Yu & Dayan, 2005) where NE release occurs for unpredictable stimuli, such as the unpredictable onset of a target in the stimulus stream. However, until now, there was no experimental evidence testing this hypothesis. Here, building upon findings of a connection between NE release and pupil dilation (Aston-Jones, 2005; Rajkowski et al., 1993) we find that pupil-size changes are transiently related to the difference in accuracy for the Target and Distractor paired scenes.

Apart from phasic changes in the LC, longer-term "tonic" changes in the LC have been shown to relate to performance reflective of the Yerkes-Dodson curve (Yerkes & Dodson, 1908). The Yerkes-Dodson curve has provided evidence of LC activation in which the low and high ends of the curve are associated with low performance and low task engagement whereas activation in the middle of the curve is associated with optimal performance and increased task engagement. Previous studies have suggested that baseline pupil-size reflects the tonic activation of the LC. In Experiment 1, correct trials exhibited lower average pupil-sizes, while incorrect trials had higher average pupil-sizes. However, this pattern was not replicated in Experiment 2. Still it is difficult to directly compare Experiments 1 and 2 since the tasks (dual vs. single) and stimuli were different. Further, in Experiment 1 the pupil-size change is transiently associated with an increase in TIL while in Experiment 2 there is a prolonged effect of an increase in pupil-size change, which may have contaminated our estimates of baseline pupil size. This transience may also explain why it has no relation to overall accuracy (regardless of condition) while baseline pupil-size is related to overall accuracy. Moreover, given that the Yerkes-Dodson curve is non-monotonic, we are left without the ability to make strong conclusions regarding the relationship between baseline pupil-size and performance as the full range of baselines is unknown and was not manipulated in this experiment.

An important factor in learning research is one concerning the impact of individual differences. Previous studies have found that significant individual differences can occur in the fast-TIL paradigm (Leclercq, Hoffing, & Seitz, 2014; Leclercq & Seitz, 2012c). As such, one question to address is whether these individual differences in TIL also contribute

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to differences in pupil dynamics. We first examined whether there were significant group-wise differences when participants in Experiment 1 were separated into those who showed TIPL (Learners Group, n=14) and those who didn't (Non-Learners Group, n=17). Learners performed at least 60% on Target paired scenes and at least 10% greater on tested Target over tested Distractor paired scenes; cut-offs were determined through a binomial cumulative distribution fit. A significant interaction between Group and Trial-type shows that the pupil-size changes differ as a function of condition between groups ($F(1,29)=5.12$, $p=0.031$) and this interaction was driven by a greater difference between Target and Distractor pupil-size changes in the Learners compared to Non-learners ($t(29)=2.26$, $p=0.016$). However, we didn't have sufficient power to conduct this same analysis in Experiment 2, where only 6 (of the 12 participants who showed better performance on novel compared to repeated paired sounds) met our strict criteria of "Learners". Furthermore, there were no correlations between the difference scores of Target-Distractor Accuracy and Target-Distractor Pupil Size change (Experiment 1: $r=0.21$, $p=0.26$; Experiment 2: $r=-0.01$, $p=0.96$). Thus, while we are intrigued by larger pupil sizes changes in Experiment 1 for the Learners, this relationship wasn't highly consistent. Similarly, previous studies (Murphy et al. 2011) have shown negative correlations between pupil size change and baseline pupil size. In the present study we failed to observe a consistent pattern across experiments between Target and Distractor pupil size change and baseline pupil size (Experiment 1, $r=-0.35$, $p=0.26$; Experiment 2, $r=0.11$ $p=0.49$). Altogether, it is difficult to know whether the lack of consistencies of the quantitative relationships between TIL, pupil-size and pupil-size-changes at the individual subject level reflect the noise in the

estimates of each of these measures or that we are failing to take into account non-linear interactions between these factors. An issue may be that fast-TIL relies upon a single pairing between an image and a target and that this may not produce as reliable of an induction of learning as found in slow TIL experiments, which involve many thousands of stimulus-reinforcement pairings.

An interesting finding in Experiment 2 was that scenes tested after the Novel Sound also showed enhanced memorization. These results are consistent with previous findings of fast-TIL where prolonged benefits for scenes were found after the presentation of a target-arrow, which was similarly thought to alert participants to the RSVP stream of scenes (Leclercq & Seitz, 2012d). This result is also in line with findings from Murphy et al. (2011) where large pupil-dilations led to an increase in performance followed by a diminishing baseline pupil-size and decreased performance in the context of an oddball task where a key was pressed when an unpredictable sound occurred. They proposed that this pattern of task reengagement and disengagement was reflecting norepinephrine's role in regulating task engagement levels.

It is possible that eye movements made within the 1.5-degree fixation window may have influenced Target or Novel Sound mediated pupil measurements through direct influence on the pupil or through measurement error. Recent research has detailed that pupil-size can be confounded by eye-position with standard eye-trackers, such as the Eyelink that we used here (Gagl, Hawelka, & Hutzler, 2011). To avoid this potential confound, all experiments were conducted using a gaze-contingent display where fixation was required during all points of task-performance. Errors induced by gaze-position are

minimal within the central 2 degrees (Gagl et al., 2011) and are unlikely an influence in our data. To address whether there were movement differences we conducted a 2x2 repeated measures ANOVA on Condition [Target, Distractor] by Coordinate [X, Y] using the mean X and Y position during the Target and subsequent ISI presentation across trials for each subject and found no interaction in either Experiment 1 ($F_{(30,90)}= 1.875$ p=0.1811) or Experiment 2 ($F_{(19,57)}=2.177$ p=0.1565). Another concern is that even though luminance was equated across all images, Targets and Distractors may have exhibited local scene content and luminance differences, both of which have been demonstrated to influence pupil dynamics (Naber & Nakayama, 2013). While unlikely, as Target and Distractor scenes were randomly selected from a set of 960 scenes and randomized across participants, we confirmed that Targets were equally likely to be Distractors by computing the conditional probability of an image being a Target given it was tested. Out of the 2112 scenes that could possibly be presented (including the Blink set) and tested participants were tested on 1,315 of these scenes. A one-sample t-test on the Tested Target conditional probability from .5 (whether it was equally likely to be tested as a Distractor) ($t_{(1314)}= 0.3388$, p= 0.7348) fails to find any difference in probability that a given image was tested as a Target or as a Distractor. As such we are reasonably confident that our findings of pupil size are not simple confounds of eye-movements or image content.

Our results suggest that pupillometry combined with TIL, in which task-factors can be manipulated independently from the stimuli that are being learned, provides a useful approach to study the mechanisms of learning and memory. While these results are

consistent with the effects of arousal or alerting on learning, we suggest that a mechanistic model that relates arousal and learning to neurochemical systems like the LC-NE system provides a more parsimonious model of the processes involved. However, while our results demonstrate a relationship between pupil dynamics and TIL, there are substantial individual subject differences and further work will be required to clarify the quantitative relationship between pupil dynamics and TIL and ultimately, further research such as psychopharmacological and fMRI studies is required to confirm that the underlying mechanism is indeed NE.

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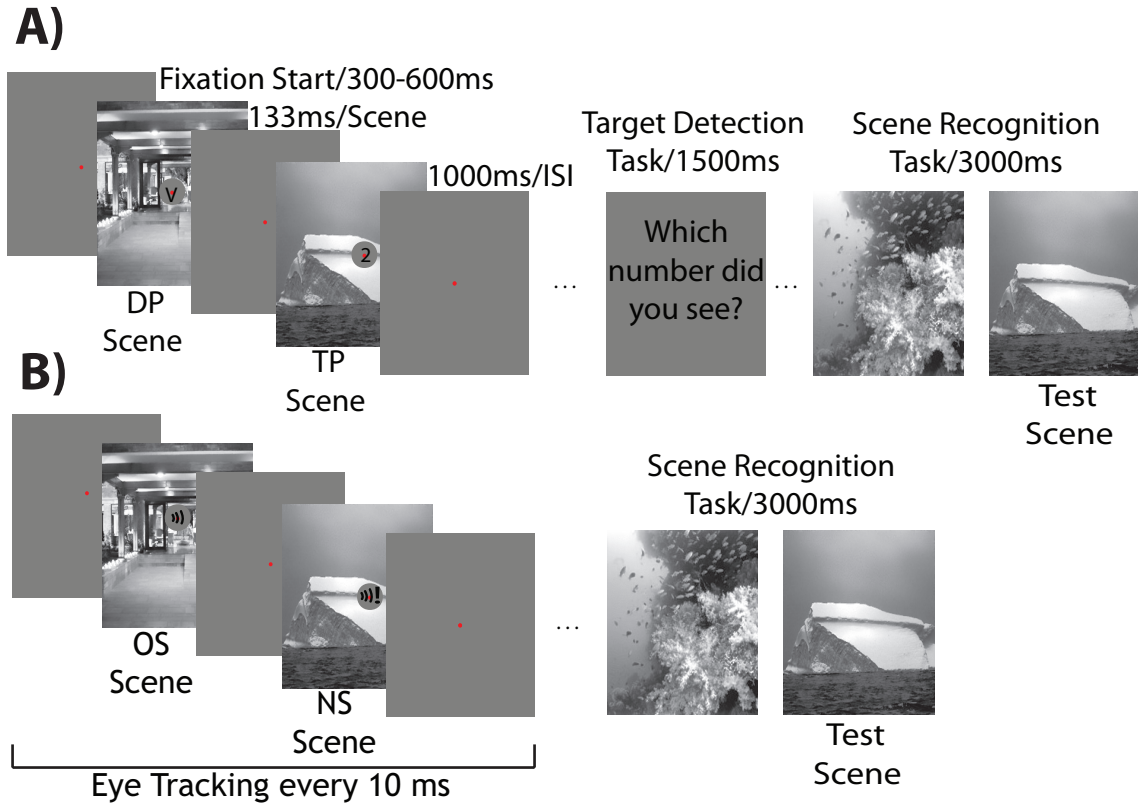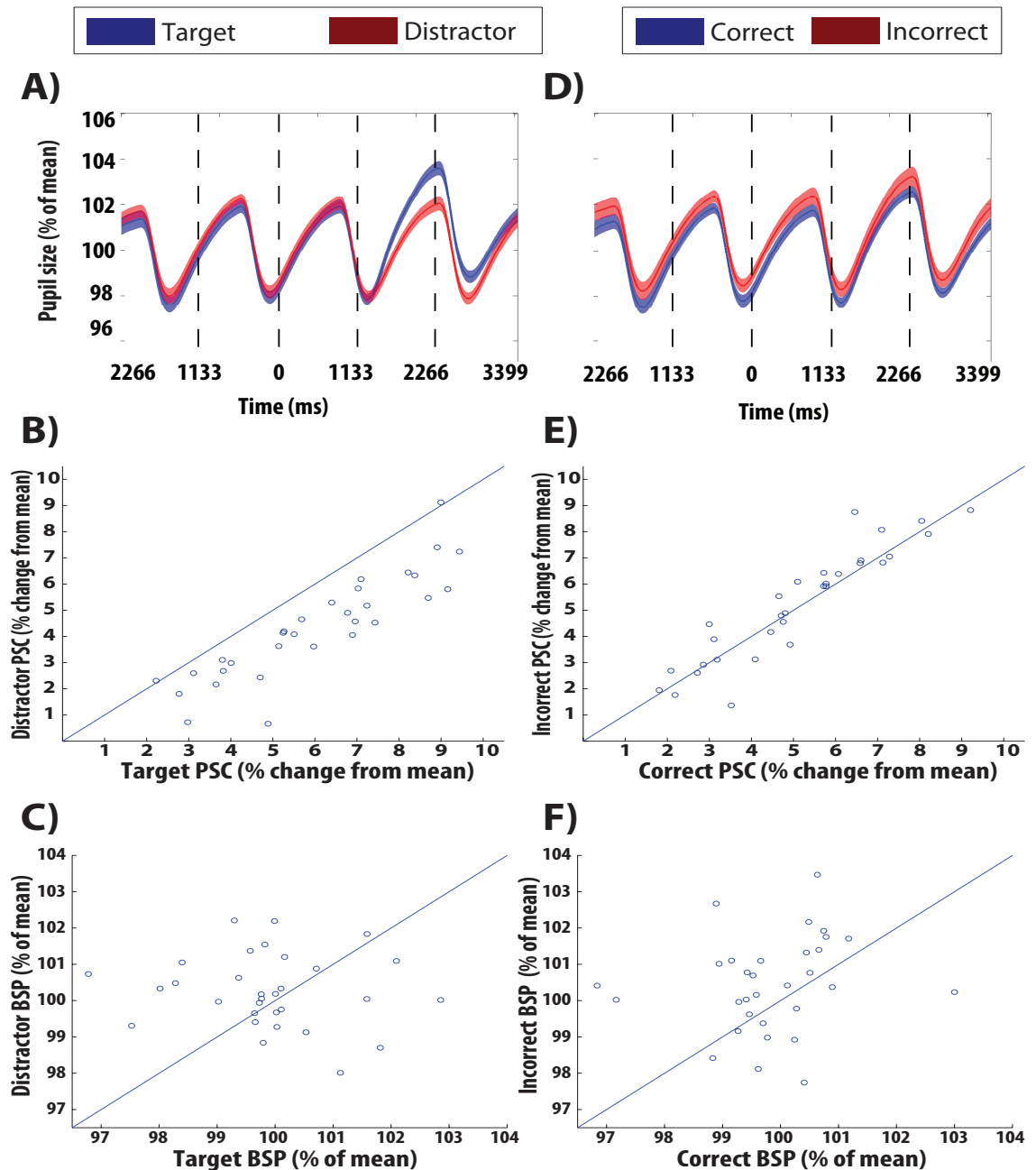
Figures

Figure 1.1: Cartoon of trial structure. Each scene was presented for 133ms with an ISI of 1000ms, eye tracking is recorded every 10ms. **A)** In Experiment 1 each scene could either be Distractor Paired (DP) or Target Paired (TP). For the Target Detection Task, after the RSVP stream, participants reported the number if presented, or 0 if not. In the Scene Detection task, participants reported which of the two images was shown in that trial. The Test Scene could either be a DP or TP scene. **B)** In Experiment 2, each scene could be a Repeat Sound paired (RS) scene or a Novel Sound paired (NS) scene. The Target Detection Task was removed but the Scene Recognition Task remained the same.
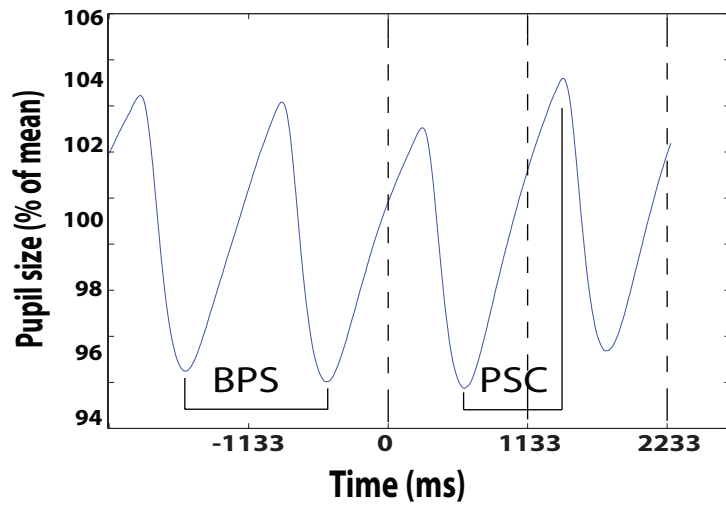
Figure 1.2: Quantification of Pupil dynamics. Baseline pupil-size (BPS) defined as the average of the period denoted by BPS. Pupil-size change (PSC) defined as the difference from the peak minus the trough denoted by PSC.
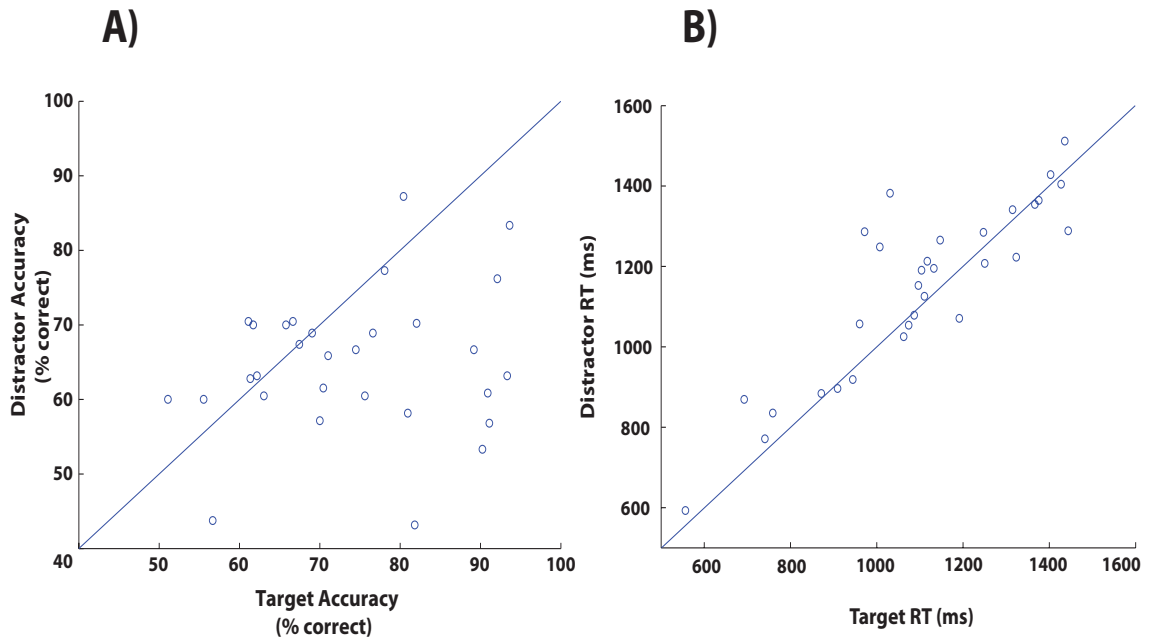
Figure 1.3: Scene Recognition Task Performance. Participants exhibited **A)** increased accuracy for Target-paired scenes over Distractor-paired scenes and **B)** decreased RTs for Target-paired scenes compared to Distractor-paired scenes.

Figure 1.4: **Pupil Dynamics in Experiment 1. A & D)** Pupil-size fluctuates with each stimulus presentation with 0 representing the onset of the to-be-tested Target or Distractor-paired scene. Dashed lines represent times of stimulus onset. **B)** Significant t-tests indicated that Targets compared to Distractors induced larger pupil-size changes while **C)** no differences in baseline pupil-size were observed. Shading (**A**) represents within-subject standard error (Loftus & Masson, 1994). **E)** No difference was found in stimulus induced pupil-size change between Correct and Incorrect trials. **F)** Correct trials show a lower baseline pupil-size than Incorrect trials. Shading (**D**) represents within-subject standard error.
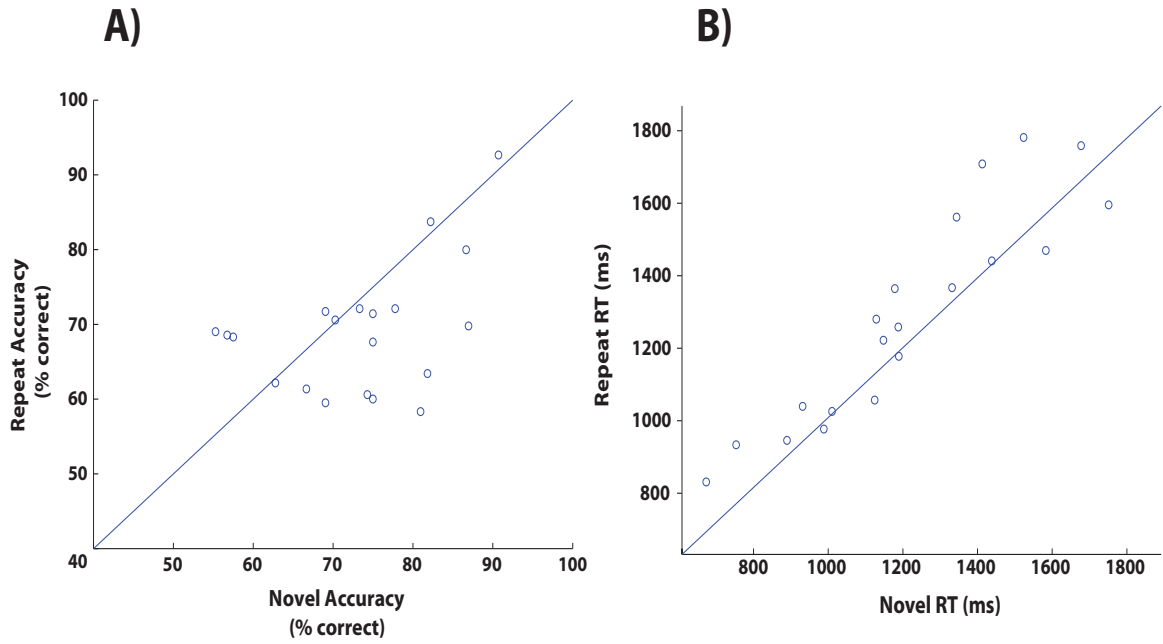
Figure 1.5: **Scene Recognition Task Performance.** Participants exhibited **A)** increased accuracy for Novel Sound-paired scenes over Repeat Sound-paired scenes and **B)** decreased RT for Novel Sound-paired scenes compared to Repeat Sound-paired scenes.
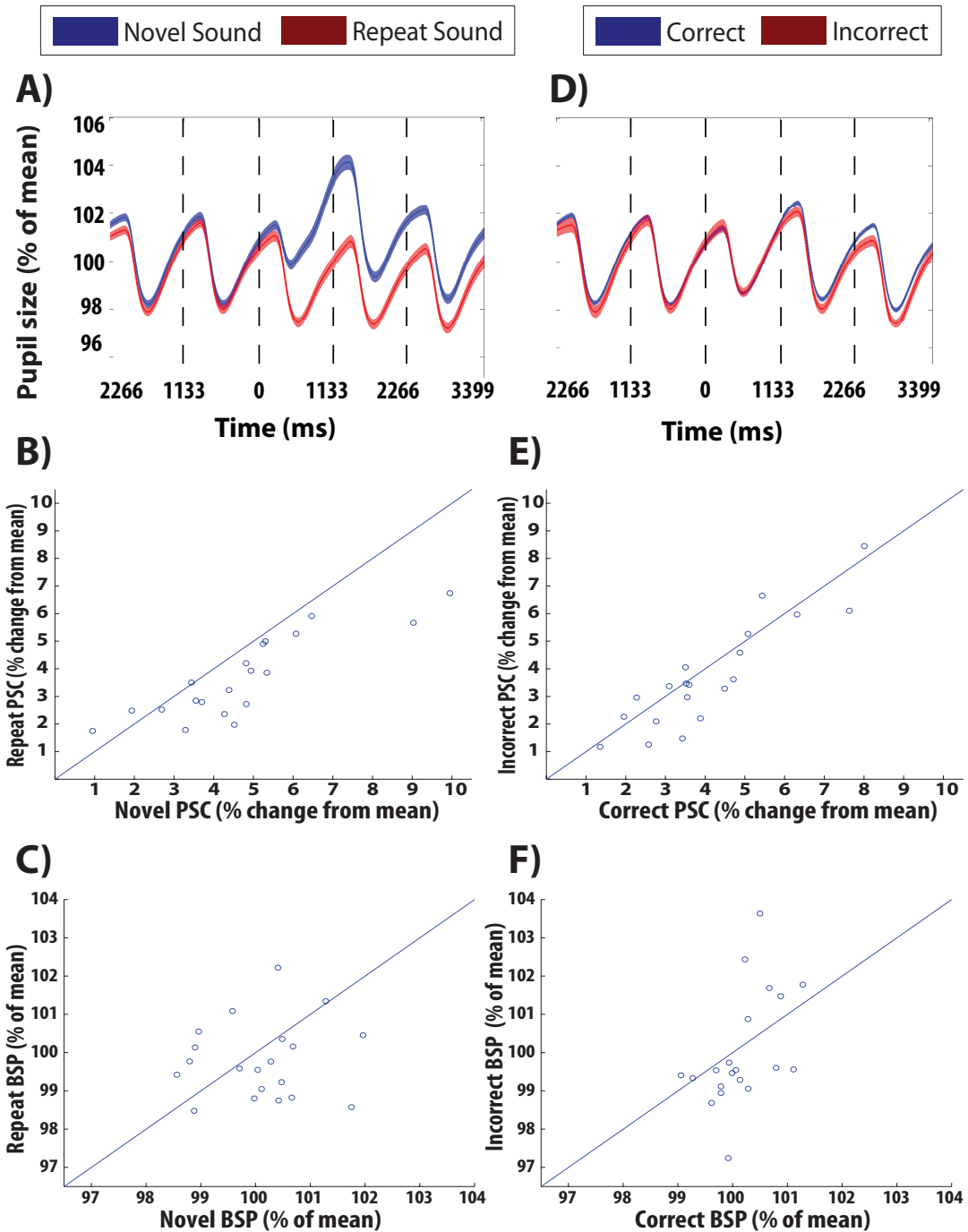
Figure 1.6: Pupil Dynamics in Sound Experiment . A & D) Pupil-size fluctuates with each stimulus presentation with 0 representing the onset of the to-be-tested Novel or Repeat Sound-paired scene. Dashed lines represent times of stimulus onset. **B)** Significant t-tests indicated that Novel compared to Repeat Sounds induced larger pupil-size changes while **C)** no difference between baseline pupil-size was observed. **D)** Pupil dynamics during Correct and Incorrect trials showed **E)** increased pupil-size change during Correct trials compared to Incorrect trials. **F)** No significant difference in baseline pupil-size between Correct and Incorrect trials was observed. Shading (**A, D**) represents within-subject standard error.
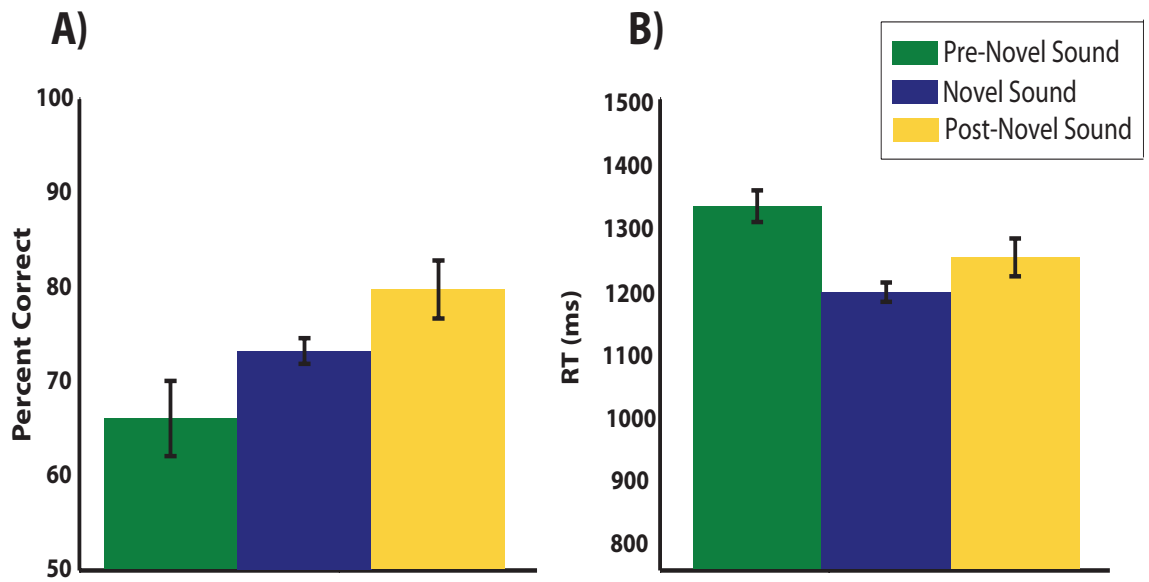
Figure 1.7: Catch Trial Accuracy and RT. Performance by condition before and after Novel Sound presentation during Catch trials indicates **A)** increased accuracy for Post-Novel Sound-paired scenes compared to Pre-Novel Sound-paired scenes and **B)** decreased RT for Post-Novel Sound-paired scenes, compared to Pre-Novel Sound-paired scenes. Error bars are within-subject standard error.

Chapter 2

The Influence of Emotion Reinforcers on Memory and Pupil Size

Abstract

How do we select which information to learn when our environment has an overwhelming number of stimuli? One way this selection process occurs is through reinforcement of stimuli that are behaviorally relevant. Research indicates that different types of behaviorally relevant stimuli lead to different patterns of behavior and subsequent learning. For example, positive and negative emotion stimuli have been found broaden and narrow attention respectively and influence learning accordingly. Here we focus on how emotion stimuli influence task-irrelevant learning (TIL). We tested they hypothesis that positive emotions lead to a broadening of attention, and subsequent increase in TIL, while negative emotions lead to a narrowing of attention and a reduction in subsequent TIL. In Experiment 1 we tested this hypothesis by presenting a rapid-serial visual presentation of images paired with emotion targets (i.e. positive, negative and neutral faces). Afterwards, we tested recognition of the paired images. Results indicate an increase in TIL for positive images, thus supporting the hypothesis that positive emotions lead to a broadening of attention, but we did not support the hypothesis that negative images lead to a narrowing of attention. To follow up on this result, we conducted Experiment 2, where we followed the same procedure as in Experiment 1 but additionally tested for recognition of the emotion targets. In addition, we collected pupillometry to investigate the role that reinforcement systems plan in the influence of emotions on TIL. Results indicate the opposite pattern of results with an increase in TIL for negative targets but not positive targets. A number of methodological differences between Experiment 1 and 2 contributed to an increase in

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difficulty in Experiment 2 and the discrepancy of results. Overall, these results suggest that

TIL is influenced by a number of reinforcement systems and further research is needed to

investigate these influences.

Introduction

Our cognitive systems do not have enough capacity to process the wealth of information in our environment. How then do we select which information to pay attention to? One manner in which selection occurs, is revealed in the task-irrelevant learning (TIL) paradigm. In this paradigm, stimuli, which temporally co-occur with goal-related tasks, are better encoded (A. R. Seitz & Watanabe, 2009). For example, stimuli presented with a task-target are better learned than those presented with task distractors (Dewald, Sinnett, & Doumas, 2011; Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d; Lin, Pype, Murray, & Boynton, 2010; Swallow & Jiang, 2010, 2011). TIL has been studied in detail in the case of low-level perceptual learning (A. Seitz & Watanabe, 2005; A. R. Seitz & Watanabe, 2009), and more recently for perceptual memories with the study of a fast form of TIL (Cohen Hoffing & Seitz, 2015; Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d). According to these studies, learning and memory are superior for stimuli that are presented with important events whether or not these stimuli have been deemed 'relevant' to task goals or whether subjects are even aware of the presence. Thus, TIL, and selection of information, and subsequent learning, occurs at times of behavioral relevance (A. R. Seitz & Watanabe, 2009). The mechanism of TIL has been attributed to reinforcement learning (A. Seitz & Watanabe, 2005; A. R. Seitz & Watanabe, 2009), with neurochemical systems such as norepinephrine releasing at times of behavioral relevance and acting as a learning signal, subsequently leading to learning of task-irrelevant stimuli.

One important question that arises, is how different types of behaviorally relevant stimuli influence learning, and specifically TIL. In the memory literature, studies indicate

that emotion-laden information influences memory (Mather & Sutherland, 2011) but the results are mixed as to whether emotion content enhances or impairs memory. While some of this discrepancy can be explained by differences in paradigms (Chiu, Dolcos, Gonsalves, & Cohen, 2013), few studies have addressed the individual contributions of arousal (how exciting or calming) and valence (how pleasant or unpleasant; (Russell, 1980)). Some studies looking at valance have indicated better memorization for information associated with positive stimuli compared to information associated with negative information (Guillet & Arndt, 2009; Okada et al., 2011; Zimmerman & Kelley, 2010). Other studies have also found impaired memorization with negatively valanced stimuli (Bisby & Burgess, 2014). As proposed by Murray et al. (2013), this could indicate that the learning benefit may depend on the valence of the information to be remembered. This valence-dependent effect on memorization is consistent with the hypothesis that negative valence leads individuals to focus attention on local details (Easterbrook, 1959) whereas positive valence leads to a broadening of attention (Fredrickson & Branigan, 2005; Gasper & Clore, 2002; Rowe, Hirsh, & Anderson, 2007; Srivastava & Srinivasan, 2010). In typical TIL experiments, learning is induced using neutral targets, such as squares or letters, but have not yet looked at the impact of emotion stimuli.

In the present study we investigate the influence of emotion stimuli on TIL. TIL is sensitive to attentional manipulations (Choi, Seitz, & Watanabe, 2009; Leclercq & Seitz, 2012d) and is thus a good paradigm for understanding the influence of emotion stimuli on attention and subsequent learning. Specifically, if positive emotions broaden attention, then TIL should be enhanced with the temporally-paired image, whereas learning should be

impaired for images paired with a negative emotion target. In Experiment 1 we first investigate the influence of emotions on TIL and confirm the hypothesis that positive emotion stimuli lead to a broadening of attention, but we did not confirm the hypothesis that negative emotion stimuli lead to a narrowing of attention. In Experiment 2 we run a replication and add a recognition test of the centrally presented emotion targets to test whether negative emotion stimuli lead to the narrowing of attention. We hypothesize that if negative emotion stimuli lead to a narrowing of attention than participants should show improved recognition on the added recognition test. To further shed light on the role of reinforcement systems in the influence of emotion stimuli on TIL we collect pupil data, which has been used as an indirect measure of reinforcement system activity. We hypothesize the different patterns of TIL induced by emotion stimuli will be accompanied by distinct patterns of pupil size fluctuations.

EXPERIMENT 1

Participants

Thirty-seven participants (Age, $M = 26.51 \pm 2.24$; Females, $n = 20$) gave informed consent to participate in this experiment, which was approved by the University of California, Riverside. All participants reported normal or corrected-to-normal visual acuity and received course credit and financial compensation for the one-hour session. Participants were excluded ($n = 10$) either because they had more false-positives than hits on the Image Recognition Task (six subjects), because of their poor overall performance on image recognition (three subjects with less than 10% accuracy) or because they failed to respond

on the majority of trials (one subject with response rate of less than 34% on the target detection task).

Apparatus and Stimuli

An Apple Mac Mini running MATLAB (MathWorks, Natick, MA) and Psychtoolbox Version 3 (Brainard, 1997; Pelli, 1997) was used for stimulus generation and experiment control. Stimuli were presented on a 22" CRT monitor with resolution of 1600 x 1200 resolution and a refresh rate of 100 Hz. Participants sat with their eyes approximately 60 cm from the screen. The backgrounds of all displays were a mid-gray. Display items consisted of 216, 700 x 700 pixel (18.3 degrees of visual angle), photographs depicting natural or urban scenes from eight distinct categories (i.e., mountains, cityscapes, etc.). These images were obtained from the LabelMe Natural and Urban Scenes database (Oliva & Torralba, 2001) at 250 x 250 pixels of resolution, then up-sampled to 700 x 700 pixels of resolution. Target faces were created to convey three different valanced emotions: positive, negative and neutral. distractor face was a made with mixed elements of the target faces. (**Figure 3.1**).

Procedure

Participants viewed a rapid serial visual presentation (RSVP) of images. Each image was presented 133ms, followed by a blank ISI of 367ms for an SOA of 500ms.

Face Detection Task – In the middle of each image a cartoon face was presented. This cartoon face could be a distractor face or a target face. Three types of target faces were used: happy, threat and neutral (**Figure 3.1**). The cartoon face had the same onset and offset time as the image with which it was paired. The RSVP stream consisted of 480 trials, with the presentation of 9 images per trial. In each trial, one image was paired with a target cartoon face (each type of target cartoon face was presented in one third of the trials); the other 8 images were paired with a distractor cartoon face. Participants were unaware of the start and ending of each trial. The target cartoon face could appear in position 2 to 7. Thus, the minimal interval between two targets was 3 images and the maximal interval was 13 images. Of the 216 photographs depicting natural or urban scenes used in this experiment, 8 were paired with the happy cartoon face, 8 with the threat cartoon face, 8 with the neutral cartoon face and the remained 192 photographs were paired with the distractor cartoon face. Each image was presented 20 times during the all experiments. Image assignment to target and distractor pairing was random for each participant. Participants were asked to press the 'Left Arrow key' as quickly as possible whenever they saw a target cartoon face (happy, threat or neutral) and to make no response when a distractor cartoon face appeared. Participants were instructed to memorize all of the images presented during the experiment for a later recognition test. Each participant was presented 480 trials, in 20 blocks of 24 trials. Blocks were separated by brief breaks.

Image Recognition Task – Following the presentation of the stream of images, participants performed an image recognition task. 64 images were presented to the participants: All 24

target paired images (8 images per emotion target), 8 images paired with the distractor and 32 new images never presented in the experiment. Each image was presented until a response was made. For each image, participants were asked to report whether the image was present in the previous streams of images.

Results

To replicate previous findings of TIL on accuracy we compared performance on the Image Recognition Task between distractor- and target-paired images, where a benefit of targets is an indicator of task-irrelevant learning (TIL). Results indicate that target accuracy (M=64.41 ± 1.82%) was significantly higher than distractor accuracy (M = 43.98 ± 4.74%, t(26)=3.95, p = 0.001). This result replicates previous findings of increased accuracy for images paired with detected targets, and thus TIL.

To follow up on the effect of emotion targets on TIL we take the difference of distractor and target-paired image accuracy (**Figure 3.2**). A one-way repeated measures ANOVA indicates a significant difference between the three types of emotion targets (Positive, Negative, Neutral; F(2,52) = 5.00, p = 0.01). Follow-up paired t-tests indicate positive emotion TIL (M = 22.68 ± 6.00%) was significantly greater than negative (t(26) = 3.14, p = 0.004) and neutral emotion TIL (t(26) = 2.02, p = 0.054), but negative emotion TIL (M = 12.04 ± 6.49%) was no different than neutral emotion TIL (M = 14.81 ± 6.47%; t(26) =-0.88, p = 0.39).

Discussion

In this experiment we tested the influence of emotion stimuli on task-irrelevant learning (TIL). The results support the hypothesis that positive stimuli lead to a broadening of attention as indicated by an increase in TIL for positive emotion targets compared to neutral emotion TIL. Our hypothesis that negative targets would lead to a narrowing of attention was not supported by the results which showed no difference in negative compared with neutral emotion target TIL. Because the neutral targets also lead to TIL it's possible that the learning effects are obscured due to learning induced by a target. In Experiment 2, we follow up by testing the hypothesis that negative targets lead to a narrowing of attention by adding a face recognition test where participants are asked to recognize faces. To further shed light on the role of reinforcement systems in the influence of emotion stimuli on TIL we collect pupil data, which has been used as an indirect measure of reinforcement system activity.

EXPERIMENT 2

Here we follow up on results from Experiment 1, which showed that positive emotion targets lead to a broadening of attention, as indicated by enhanced TIL for positive compared to negative images. We also test the hypothesis that attention is reoriented to local details in negative emotion conditions by testing recognition of the target faces. We hypothesize that if negative emotions lead to reorientation of attention to local details than negative faces will show enhanced recognition compared to neutral images. Furthermore,

we use pupillometry to gain insight into how reinforcement systems influence attention and learning.

Pupil size has been used extensively for decades as a window into the mind, as pupil size is under the control of the sympathetic and parasympathetic nervous systems (Steinhauer, Siegle, Condray, & Pless, 2004). For example, pupil size has been reliably used as a biomarker of a variety of cognitive processes such as arousal (Beatty, 1982), emotion (Bradley, Miccoli, Escrig, & Lang, 2008), and learning (Cohen Hoffing & Seitz, 2015; Nassar et al., 2012). For example, research has suggested that neuromodulators like norepinephrine are involved in phasic responses of the pupil while acetylcholine may be more involved in driving tonic responses of the pupil (Aston-Jones, 2005; Cohen Hoffing & Seitz, 2015; Yu & Dayan, 2005). Similar studies have found correlations with pupil size changes and learning rate ((Nassar et al., 2012); (Silvetti, Seurinck, van Bochove, & Verguts, 2013) as well as pupil size and increased task performance (Murphy, Robertson, Balsters, & O'connell, 2011). These data provide evidence that pupil dynamics are related to learning and are consistent with the hypothesized role of neurochemical activity in driving pupil size dynamics and learning. Here we explore the hypothesis that the differences in TIL as induced by emotion stimuli will be accompanied by independent pupil dynamics.

Methods

Participants

Thirty-three participants (M= 20.81 ± 4.07; Females, n = 19) gave informed consent to participate in this experiment, which was approved by the University of California, Riverside. All participants reported normal or corrected-to-normal visual acuity and received course credit and financial compensation for the 1.5-hour session.

Apparatus and Stimuli

An Apple Mac Mini running MATLAB (MathWorks, Natick, MA) and Psychtoolbox Version 3 (Brainard, 1997; Pelli, 1997) was used for stimulus generation and experiment control. Stimuli were presented on a 22" CRT monitor with resolution of 1600 x 1200 resolution and a refresh rate of 100 Hz. The backgrounds of all displays were a mid-gray. Display items consisted of 216, 700 x 700 pixel (18.3 degrees of visual angle), photographs depicting natural or urban scenes from eight distinct categories (i.e., mountains, cityscapes, etc.). These images were obtained from the LabelMe Natural and Urban Scenes database (Oliva & Torralba, 2001) at 250 x 250 pixels of resolution, then up-sampled to 700 x 700 pixels of resolution. Target faces were created to convey three different valanced emotions: positive, negative and neutral. In order to probe learning of the target faces, a surprise memory task was conducted at the end of the experiment. Eight different faces per emotion were created by varying three parameters: face color (pink or orange), face shape (round or oval) and hair color (yellow or red). Finally, a dot was added on each face in one of 6 locations (**Figure 3.3**). Participants sat with their eyes approximately 57cm from the screen

using the Eyelink 1000 tower-mount, which was used to track eye movement and pupil-size fluctuations of the right eye during every 10ms screen refresh. The eye tracker measured pupil diameter with a resolution of 0.2% of diameter, corresponding to a resolution of 0.01 mm for a 5 mm pupil, and has a spatial resolution of <0.01° RMS (Ltd).

Procedure

Eight images were presented for 133ms each, followed by a blank inter-stimulus interval of 667ms for a SOA of 800ms.

Calibration and eye tracking – At the start of the experiment, a randomized target 12-point calibration and validation routine was performed using the EyeLink 1000 software to calibrate gaze and ensure accuracy of pupil dynamic readings. Each trial only began after the participant fixated on the central cross for 450ms. Fixation was followed by a rapid sequence of 8 full-field images.

Face Detection Task – In the middle of each image either a target or distractor face was presented. The face had the same onset and offset time as the image with which it was paired. The experiment consisted in 240 trials, with the presentation of 8 images per trial. In each trial, one image was paired with a target face while the other 7 images were paired with the distractor cartoon face with similar face color, face shape, and hair color to the target face. The target face could appear in position 2 to 6. Each emotion was presented in one third of the trials. Thus, each target face was presented 10 times for total of 80 trials

per valanced target face. Participants had the dual task of detecting the target face and memorizing the image for the recognition task at the end of each trial. In the face detection task, participants pressed the 'Left Arrow key' as quickly as possible whenever they saw a target face (happy, threat or neutral) and made no response when a distractor face appeared. Each participant was tested for a total of 240 trials, in 10 blocks of 24 trials. Blocks were separated by brief breaks.

Image Recognition Task – Following each trial, subjects were presented with a test image and were asked to report (by pressing the up-arrow or down-arrow key) whether the test image had appeared in the previous stream of images. The test image was presented for 3,000ms or until subjects' response. On 50% of the trials (120 trials), the test image was an image presented in position 2-6 of the RSVP sequence. The target-paired images were tested on 45 of trials (15 trials for each valanced face). Images presented in the position just after the target were tested 24 times (8 per valance). Images presented two positions after the target were tested 9 times, and images presented three positions after the target were tested 6 times. The other positions were tested on the remaining trials to ensure that there was no positional relationship between target presentation and test image presentation. On the other 50% of the trials, the test image was drawn from the set of images not presented on that trial. Of note, the target in the face detection task did not predict which image would be tested in the image recognition task, and thus any benefit in processing of the image was task irrelevant in regard to the detection task.

Face Recognition Task – At the end of the 240 trials, a surprise recognition task was administered. This task consisted of 96 trials. At each trial, two faces were presented to the subjects, one to the left and one to the right of the fixation point. One of the faces was one used during the experiment, while the other was the same but with the black spot located at the symmetric position (**Figure 3.4**). On each trial, subjects were asked to report (by pressing the right-arrow or left-arrow key) which face was presented in the experiment. Each face used in the experiment was presented four times.

Data Analysis

For behavioral analysis participants were excluded if target detection task accuracy was below 70% (n=3). To ensure that our analysis reflected the influence of the target we only analyzed trials in which the target was successfully detected. For the analysis of pupil dynamics seven participants were excluded due to experimenter errors leaving a total of 26 participants. Pupil diameter was normalized by dividing each data point by each subjects' pupil-size session mean. Pre-trial intervals were not used as a baseline because they were contaminated by the Image Recognition Task. Analysis of pupil-size only examined Target and Distractor trials. Distractor trials that only had tested trials before target presentation were used. To analyze effects of target and distractors on pupil size fluctuations we extracted pupil data so that it was time-locked to the onset of the presentation of one image before the tested image. Blinks were interpolated and smoothed using the algorithm developed in Siegle, Steinhauer, Stenger, Konecky, and Carter (2003). Based off of previous research we quantified two pupillometric measures which might reflect distinct

neurochemical systems (Cohen Hoffing & Seitz, 2015): pupil size change and pupil size baseline. Pupil size change is defined by taking 50ms window around the max value from 150 to 230ms and subtracting a 50ms window around the min value after target presentation from 100 to 172ms. Pupil size baseline is defined by taking 50ms window around the min value from 172 to 258ms. The selection of time windows was based on visual inspection of individual participants. Error bars reflect standard error of the mean. Reported p-values from t-tests reflect two-tailed tests.

Results

To replicate previous findings of TIL on accuracy we compared performance on the Image Recognition Task between distractor- and target-paired images. Accuracy results indicate a significant effect of Trial Type (Targets vs. Distractors; $F(1,32)=4.26$, $p=0.047$) with target-paired images (M= 58.03 ± 3.13%) showing increased accuracy compared to distractor-paired images (M= 54.82 ± 3.1%), suggesting that we replicated the TIL effect found in Experiment 1. To further test the effect of emotion targets on TIL, and whether we also replicate findings from Experiment 1 we compared TIL by emotion (**Figure 3.5**). Results indicate a trending effect of Emotion Type ($F(2,64)=2.21$, $p=0.12$) with paired t-tests indicating significant increase in accuracy for negative TIL (M= 6.91 ± 1.93%) compared with positive TIL (M= 0.24 ± 2.79%; $t(32) = 1.88$, $p = 0.07$) and trending when compared with neutral TIL (M= 2.30 ± 2.46%; $t(32) = 1.51$, $p = 0.14$). No significant difference between positive and neutral TIL ($t(32) = -0.66$, $p = 0.52$). This result indicates that we replicated findings of TIL, but were unable to replicate findings of increased TIL

induced by positive emotion targets. While the pattern of TIL is different in Experiment 2, we also note that there are significant differences in baseline accuracy between the two experiments with Experiment 1 showing overall increased accuracy in the image recognition task (M= 64.41 ± 1.82%) compared to Experiment 2 (M= 54.43 ± 3.44%). The accuracy difference between Experiment 1 and 2 was significant, (t(58)=2.14, p = 0.04) suggesting that the pattern of TIL in Experiment 2 might arise from methodological differences. Overall, these results indicate that negative targets lead to a broadening of attention as indicated by an increased image recognition accuracy, however we can't make any strong conclusions because the difference between positive, negative and neutral targets was trending.

Previous research shows that TIL is moderated by sex (Leclercq & Seitz, 2012c). To ensure that TIL isn't present in the neutral and positive emotion targets, as was predicted, we investigated whether TIL is moderated by sex. Results looking at the difference of target and distractor accuracy indicate no significant main effect of Sex (Female, Male; F(1,31) = 0.79, p=0.38), Emotion Type (Positive, Negative, Neutral; F(2,62) = 2.15, p = 0.12) or interaction (F(2,62) = 0.25, p = 0.78). This result suggests that both males and females showed TIL, but also that neither sex showed a benefit of positive emotion targets.

To test the hypothesis that negative emotions lead to a narrowing of attention, we looked at how emotion targets influenced performance on the face recognition task (**Figure 3.6**). Because accuracy was at a chance performance we focused on RT from correct trials. Reaction time results indicate a trending main effect of Emotion Type (F(2,64)=2.462,

p=0.093) with positive targets leading to faster responses ($M_{positive}$ = 1,414 ± 58ms, $M_{neutral}$ = 1507 ± 71ms) compared to the neutral emotion targets (t(32) = -2.00,p = 0.05) but no difference between the negative ($M_{negative}$ = 1454 ± 67ms) and positive emotion targets (t(32) = -1.30, p = 0.20). No significant accuracy difference between emotion type was found (F(2,64) = 0.26, p = 0.77). Overall, these results indicate that positive targets lead to a narrowing of attention as indicated by a faster RT, however we can't make any strong conclusions because the difference between negative, positive and neutral face recognition was trending.

Pupillometry

A key question in this experiment is whether pupillometry can shed light on the behavioral results of increased accuracy for negative target-paired images and faster reaction time for positive face recognition. To investigate this, we compared the time course of pupil dilations and constrictions (**Figure 3.7A**) for each emotion target type (Positive, Negative and Neutral) by trial type (Target, Distractor) using pupil size change and pupil size baseline.

Pupil size change results (**Figure 3.7B**) indicate a significant main effect of trial type (F(1,25) = 30.48, p < 0.001) with a larger pupil size change for targets (M= 10.98 ± 0.69%) compared with distractors (M= 7.52 ± 0.67%). A significant main effect of emotion type (F(2,50)=4.40, p = 0.017) is driven by a larger pupil size change for positive (M=9.54 ± 0.75%) and negative targets (M= 9.66 ± 0.81%) than for neutral targets (M= 8.54 ± 0.79%). No significant interaction was found (F(2,50)=1.318, p = 0.28). Follow-up paired

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t-tests comparing pupil size change between emotion type indicate a significant difference between negative and neutral (t(25)= 2.85, p = 0.008), and positive and neutral (t(25) = 2.08, p = 0.05), but no significant difference between negative and positive pupil size change (t(25) = 0.34, p = 0.73). Pupil size baseline results indicate no significant difference between trial type (F(1,25)=2.08, p=0.16), emotion type (F(2,50)=0.55, p = 0.58), or interaction (F(2,50)=0.10, p = 0.90; **Figure 3.7C**). These results replicate previous findings of increased pupil size change for targets compared with distractors. Additionally, in line with results indicating that emotions lead to increased arousal, we find increased report findings of increased pupil size change for emotion targets compared with neutral targets. Here we find no difference between negative and positive pupil size change or baseline indicating that pupil measures do not only reflect mechanisms underlying TIL, per se.

To ensure that incorrect trials aren't obfuscating pupillometric differences we followed up by comparing correct and incorrect target trials (**Figure 3.8A**). One participant was excluded from this analysis because they had no incorrect target trials. Pupil size change results indicate a significant effect of Emotion Type (F(2,24) = 6.07, p = 0.005) indicating the same pattern as found before with increased pupil size change for emotion targets compared with neutral targets (**Figure 3.8B**). No significant effect of Target Accuracy (Correct, Incorrect; F(2,24) = 1.7, p = 0.20) or interaction (F(2,24) = 0.98, p = 0.38) was found. Pupil size baseline results indicate no significant difference between Target Accuracy (F(2,24) = 0.56, p = 0.46), Emotion Type (F(2,24)=0.95,p=0.40) or interaction (F(2,24) = 1.22, p = 0.31; **Figure 3.8C**). These results indicate that pupil size changes induced by targets occurred regardless of subsequent image accuracy and that

emotion targets led to increased pupil size change compared to neutral emotion targets. These results further suggest that pupil measures do not only reflect underlying TIL.

Post-Target Behavioral Effects

Previous research has indicated that images following targets also receive behavioral benefits from target processing (Cohen Hoffing). In the current data set we followed up on these effects by investigating performance changes to images that followed the target. First, we looked at how emotional targets affect subsequent recognition. Next, we looked at the benefit of target processing on image recognition in relation to the target position.

To look at the effect of emotion targets on subsequent recognition we compared accuracy of tested images that came before versus after the target (**Figure 3.9**). Results indicate a main effect of Target Relation (Before, After; $F(1,32) = 25.41$, $p < 0.001$) with tested images after the target showing an increase in accuracy (M= 54.85 $\pm$ 3.41%) compared with tested images before the target (M= 49.18 $\pm$ 3.96%). No significant effect of Emotion Type ($F(2,64) = 0.16$, $p = 0.85$) or interaction was found ($F(2,64) = 0.881$, $p = 0.42$). To follow up on whether this effect can be explained by pupil size metrics, we compared pupil size change and pupil size baseline on tested images that were positioned before and after target presentation. Pupil size change results indicate a trending non-significant main effect of Target Relation ($F(1,25) = 3.35$, $p = 0.08$), and non-significant effect of Emotion Type ($F(2,50) = 0.24$, $p = 0.79$) and interaction. The trending effect was driven by a significantly larger pupil size change ($t(25)= 1.76$, $p = 0.09$) for images presented after a target (M= 7.52 $\pm$ 0.66) compared to before the target (M= 6.62 $\pm$ 0.64%).

Pupil size baseline results indicate a non-significant effect of Target Relation ($F_{(2,50)}$ = 1.71, p = 0.20), Emotion Type ($F_{(2,50)}$ = 0.28, p = 0.76), and interaction ($F_{(2,46)}$ = 0.12, p = 0.89). While non-significant, we numerically found a difference in baseline pupil size after the target (M= 96.33 ± 0.90) compared to before (M= 94.60 ± 0.74).

To look at the effect of target on tested image position we looked at the accuracy of

tested images that were one, two, and three images after target presentation (**Figure 3.10**). Results indicate no significant effect of Position ($F_{(1,32)}$ = 0.866, p = 0.43). Overall, we find that the presentation of a target leads to a temporary shift in pupil size change and pupil size baseline that accompanies an increase in accuracy. However, because effects are non-significant we cannot make any strong conclusions.

Discussion

In Experiment 2 we followed up on the results of Experiment 1 by attempting to replicate an increased task-irrelevant learning (TIL) for positive but not negative or neutral emotion targets. We additionally investigated whether negative emotion targets led to a processing benefit for target recognition compared with positive and neutral emotion targets. Additionally, pupil size dynamics were measured to shed light on the neurochemical processes involved in the benefits of emotion stimuli to learning found in experiment 1. Behaviorally, Experiment 2 results failed to replicate the effects seen in Experiment 1 and instead showed the opposite pattern of TIL with negative emotion targets showing TIL, while positive and negative emotion targets did not induce TIL. Results from the face

recognition task indicate a benefit of positive target processing compared to neutral and negative emotion target processing as indicated by a reduced reaction time for recognizing positive emotion faces. Together, results from Experiment 2 support the hypothesis that negative emotion targets lead to a broadening of attention while positive emotion targets lead to a narrowing of attention. However, due to the aforementioned effects showing trending significance we are unable to make strong conclusions.

Pupillometry results replicated previous findings of increased pupil size change for targets compared to distractors. We report the novel finding in TIL of an increase in pupil size change for emotional targets compared with the neutral target, however pupillometry measures were unable to dissociate the accuracy differences found between valence of emotion of increased recognition for negative target-paired images and decreased reaction time for recognizing positive targets. We also looked at effects of targets on image recognition by comparing recognition of images presented before a target compared to after a target. Results indicate that there is increased accuracy for images tested after the target compared to before the target. Furthermore, non-significant trends indicate that this increase in post-target accuracy is accompanied by an increase in pupil size change and pupil size baseline suggesting an overall increase in arousal.

General Discussion

In this study we investigated how emotions, which have been found to influence memory formation, affect task-irrelevant learning (TIL). Previous research suggests negative emotions lead to a narrowing of attention while positive emotions leading to a broadening

of attention (Easterbrook, 1959; Fredrickson & Branigan, 2005). We hypothesized that if positive emotions lead to a broadening of attention than there should be an increase in TIL as indicated by an increase in accuracy for images paired with positive emotional targets. Conversely, if there is a narrowing of attention from negative emotions than there should be a decrease in TIL. In Experiment 1 results indicated an increase in TIL in positive emotion targets, which supports the hypothesis that positive emotions lead to a broadening of attention. While we hypothesized that negative emotion targets would lead to a decrease in TIL due to a narrowing of attention, our results did not support this hypothesis.

To follow up on these results we added a face recognition task that would assess learning of the targets themselves as the lack of a reduced TIL effect for negative targets may have been due to an overall increase in TIL that is typically induced by targets. Thus, if a narrowing of attention as induced by negative emotional targets does occur, there should be a benefit to negative emotion target recognition. Results did not support this hypothesis and indicated the opposite pattern of results from Experiment 1, as such we did not combine results across experiments.

This pattern of results may have been due to differences in the paradigm of Experiment 2 that inadvertently increased difficulty, as evidenced by the overall decrease in accuracy compared to Experiment 1. First, the inter-stimulus interval was extended to accommodate the longer time course of the pupillary response, which may have resulted in taxing the memory systems more. Second, the addition of the eye tracking component itself may have increased difficulty as participants were required to maintain gaze on the central cross at the beginning of each trial to proceed. However, these two reasons are not

likely to be the primary cause of a decrease in accuracy because previous experiments using a similar paradigm have used longer ISIs without a substantial decrease in accuracy (Cohen Hoffing & Seitz, 2015). Lastly, in Experiment 1 the stream of images was continuous with the image recognition test at the end of image stimulation. In contrast, in Experiment 2 the image recognition test was presented after every trial. This repeated testing in combination with the fact that images in Experiment 2 were also presented in other trials, but not necessarily tested each trial, could have caused memory interference. This memory interference may have resulted in the observed near chance accuracy.

All together, these methodology changes could likely lead to differences in attentional demands which TIL has been shown to be sensitive too (Leclercq & Seitz, 2012b, 2012d). Nonetheless, these changes do not necessarily explain our results which indicate TIL induced by negative emotion targets. In fact, our results also show a decrease in reaction time for recognition of positive emotion targets suggesting that negative emotional targets led to a broadening of attention, while positive emotion targets led a narrowing of attention. These results are in line with findings from the dot-probe task literature where attentional biases to positive stimuli are found (van Rooijen, Ploeger, & Kret, 2017). These findings have been suggested that positive stimuli attract attention, because they act as a positive reinforcer related to pro-sociality and may indicate desirable environmental conditions (van Rooijen et al., 2017). Though, the question remains as to why we see the opposite pattern of TIL in Experiment 2. We address this below, with evidence from pupillometry.

Pupillometry results indicate that we did replicate previous findings of TIL of overall benefit for targets compared with distractors accompanied by an increased pupil size for targets compared with distractors (Cohen Hoffing & Seitz, 2015). However, the increase in TIL for experiment 2 was driven by negative targets, which were not accompanied by differences in pupil measures for negative and positive targets. Instead, we find that both positive and negative emotion targets show an increased pupil size change compared to neutral emotion targets. Previously, we had suggested that the increase in pupil size is reflective of neurochemical processes involved in TIL. Here, we find that even without showing TIL we find an increase in pupil size induced by target presentation. One possible interpretation is that pupillometry does not, in fact, reflect the neurochemical processes involved in TIL.

An alternative explanation is that pupil size does indeed reflect TIL but to the extent that TIL is driven by arousal effects and not effects of valance. Pupil size has been extensively studied in context of arousal manipulations (Beatty, 1982; Bradley et al., 2008; Cohen Hoffing & Seitz, 2015; Steinhauer et al., 2004; Wierda, van Rijn, Taatgen, & Martens, 2012) such as arousal induced by uncertainty and difficulty load (Beatty, 1982; Nassar et al., 2012). Previous research conducted in our lab has also indicated that TIL and pupil size changes are sensitive to arousal manipulations using surprising noises (Cohen Hoffing & Seitz, 2015); see experiment 2). Here, our results suggest that pupil size may be sensitive to arousal but not valance as indicated by no difference between the emotion conditions. Thus, arousal effects due to methodological differences in Experiment 1 and 2

may account for differences in TIL and pupil size dynamics. However, this remains speculative as arousal was not explicitly manipulated in our experiment.

A model proposed by (Seitz & Dinse, 2007) further support the explanation that increased difficulty interfered with learning and the lack of detecting pupil size differences between valance. In their model they suggest that there exists a learning threshold that must be passed to select what sensory input should be learned. Other processes such as neuromodulatory activity and attention alter the sensory input and push it past the learning threshold. Thus, in Experiment 2 pupil size measures do reflect reinforcement learning but that learning differences, as induced by the effect of reinforcement systems, might not have been sufficient to be picked up by pupil size measures.

Another possibility for not finding pupil size differences between valanced stimuli, is that averaging across trials obfuscates any pupil size differences. As such, more advanced statistical techniques may be needed to make use of trial-by-trial data. One candidate technique is signal detection analysis that is frequently applied in studies using electroencephalography and function magnetic resonance imaging. For example, time-frequency analysis can be applied to trial-by-trial data to extract oscillatory patterns of different frequencies (i.e delta, alpha, theta, etc.; Cohen, 2014). In context of pupillometry, this analysis technique might better be able to identify phasic and tonic fluctuations contributing to behavior. For example, in our results we find phasic responses to targets related to increased accuracy, as well as find a baseline shift in pupil size measures after target presentation related to increased accuracy for all images occurring after the target.

Altogether, these results suggest that differences between Experiment 1 and 2 may have contributed to overall increase in difficulty, leading to a change in overall levels of arousal or and decrease in learning signals, which together, may account for the discrepancies in TIL. The perception-reinforcement-action process framework suggests that discrepancies between Experiment 1 and 2 could be due to a difference in the relative activation of multiple reinforcement systems. For example, it is possible that emotion targets, such as the ones used here activate different reinforcement systems than those involved in TIL. Research suggests that emotion content is processed by different reinforcement systems involving the orbitofrontal cortex (Ochsner & Gross, 2014), while TIL implicates reinforcement systems involving norepinephrine (A. R. Seitz & Watanabe, 2009). Supporting this conjecture, Experiment 1 results indicate that TIL is induced regardless of target emotion type which is in line with the literature that shows many types of target stimuli induce TIL such as arrows, numbers, letters, shapes and sounds (Cohen Hoffing & Seitz, 2015; Leclercq & Seitz, 2012a, 2012b, 2012c, 2012d; A. R. Seitz & Watanabe, 2009). However, experiment 2 did not show similar patterns of TIL, suggesting other factors at play in TIL. Overall, our results fail to show a consistent effect of emotion targets on TIL. These inconsistencies indicate that TIL is sensitive to the influence of multiple reinforcement systems indicating that TIL paradigms along with pupillometry can be a rich methodology for understanding learning, but to understand these inconsistencies further research is needed.

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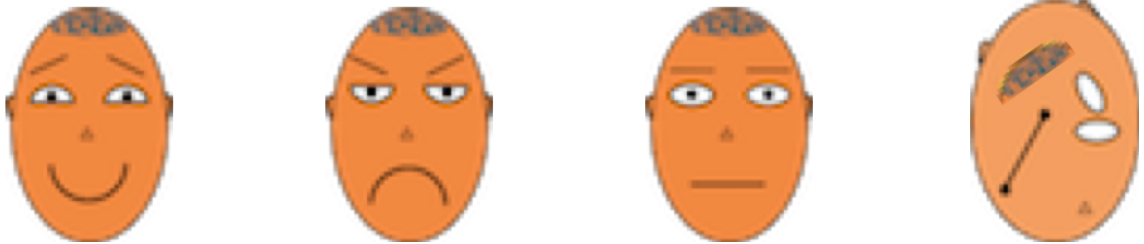
Figures

Figure 2.1: Participants were instructed to respond to target faces and not respond during distractor faces (far right). Cartoon faces were either positive, negative, or neutral.
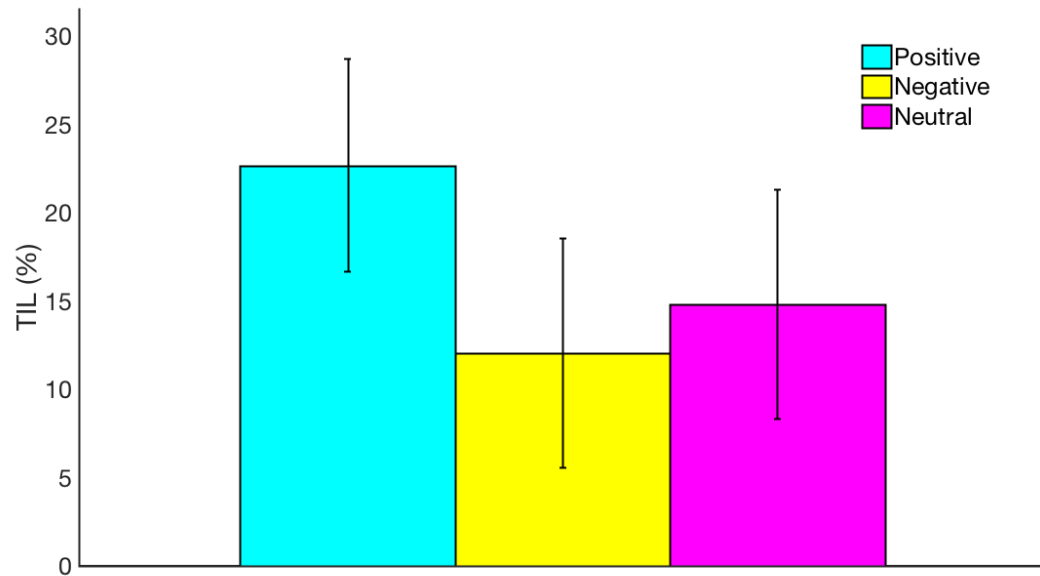
Figure 2.2: Image recognition task accuracy indicates task-irrelevant learning (TIL) for all target stimuli but an increase in task-irrelevant learning for positive compared to negative and neutral emotion targets suggesting that positive emotion targets lead to a broadening of attention. Error bars reflect standard error of the mean.

Figure 2.3: Cartoon faces used in Experiment 2 were altered for later testing on the face recognition task. Faces could vary by hair color, face color, face shape and spot position.

Figure 2.4: Participants were instructed to choose the face presented in the previous streams of images. Each face was the same with the exception of the dot being placed in a symmetric location.
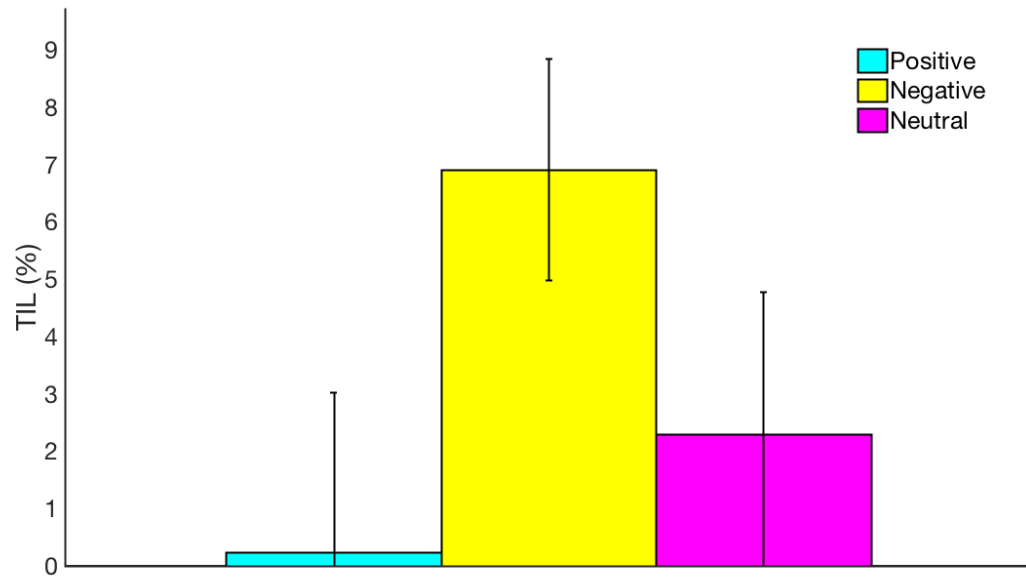
Figure 2.5: Image recognition task accuracy indicates no significant effect of emotion on TIL indicating a failure to replicate results from Experiment 1. This result may be due to an increase in difficulty in Experiment 2. Error bars reflect standard error of the mean.
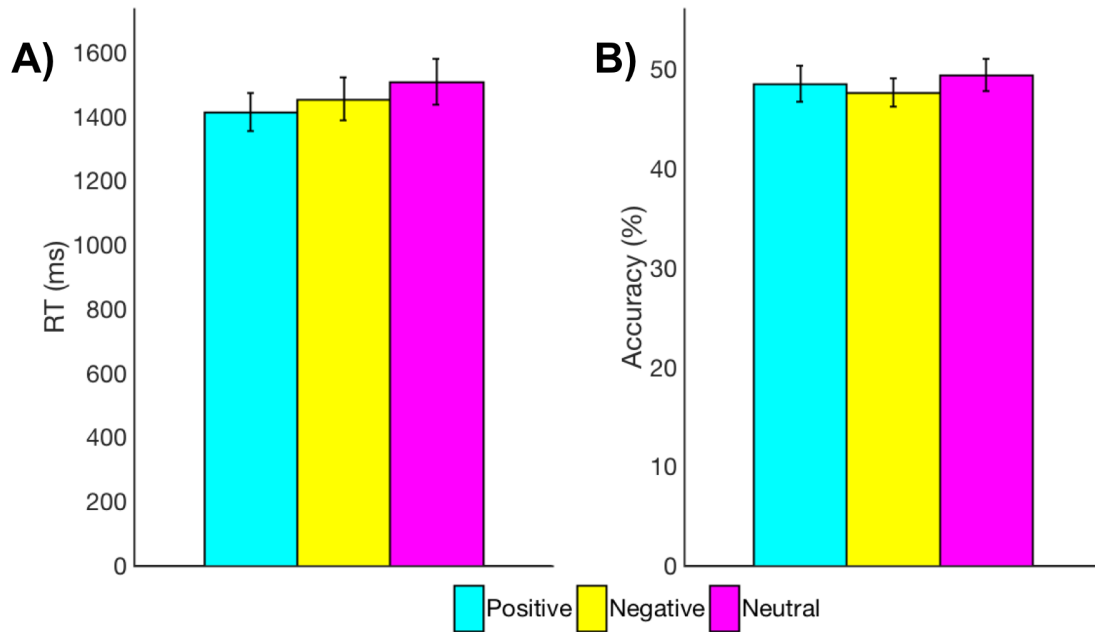
Figure 2.6: Face Recognition Test Performance results indicate that positive targets had faster RT compared to neutral targets but there was no difference between negative and neutral target RT suggesting a narrowing of attention induced by positive targets. No difference in accuracy between emotion type was found. Error bars reflect standard error of the mean.
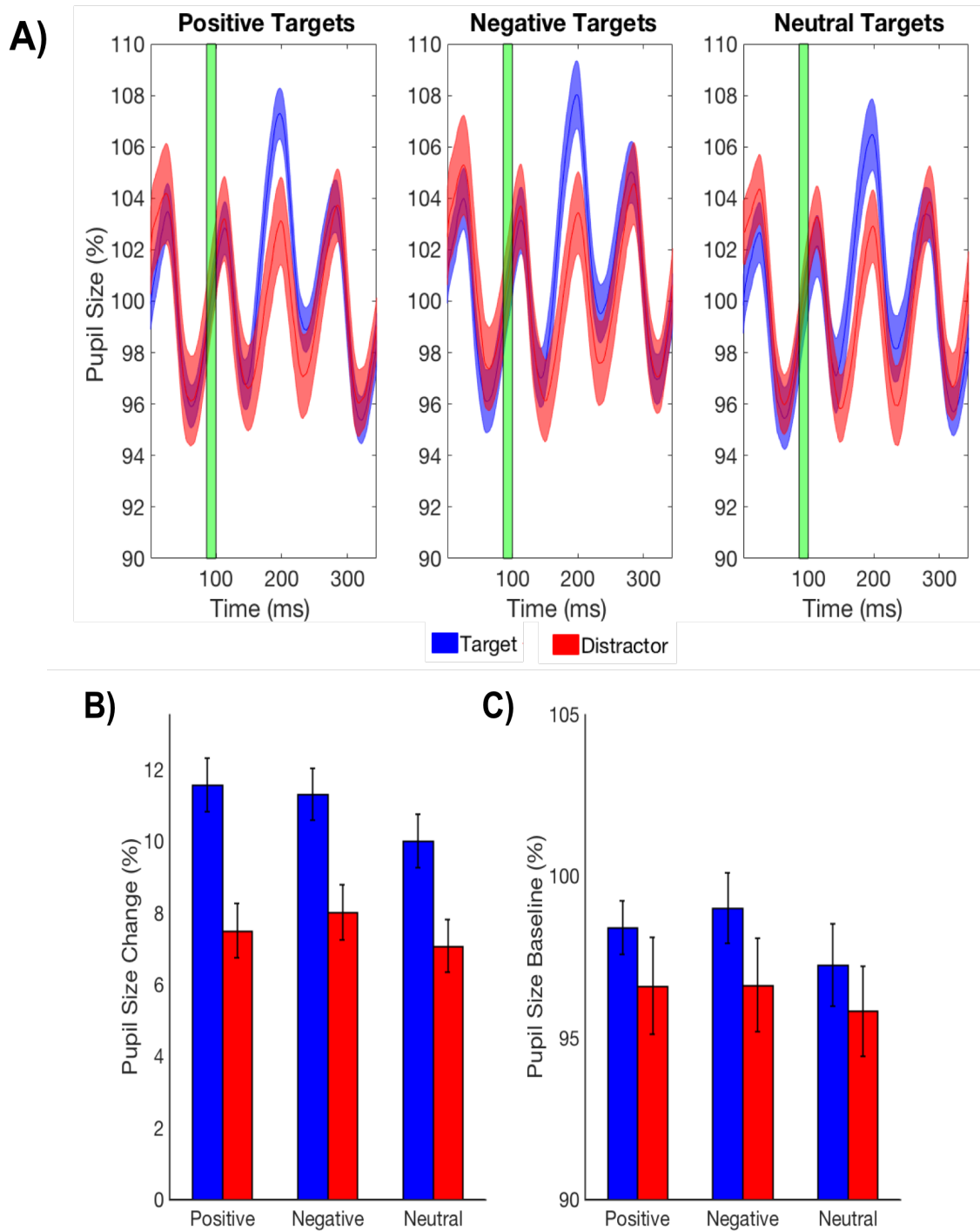
Figure 2.7: Pupil size over time on target and distractor trials (A). Pupil size measures indicate an increased pupil size change from both emotion targets (B) while no difference was found between emotion targets using pupil size baseline (C), suggesting that pupil size may not be sensitive to effects of valence on TIL. Error bars and shading reflect standard error of the mean.
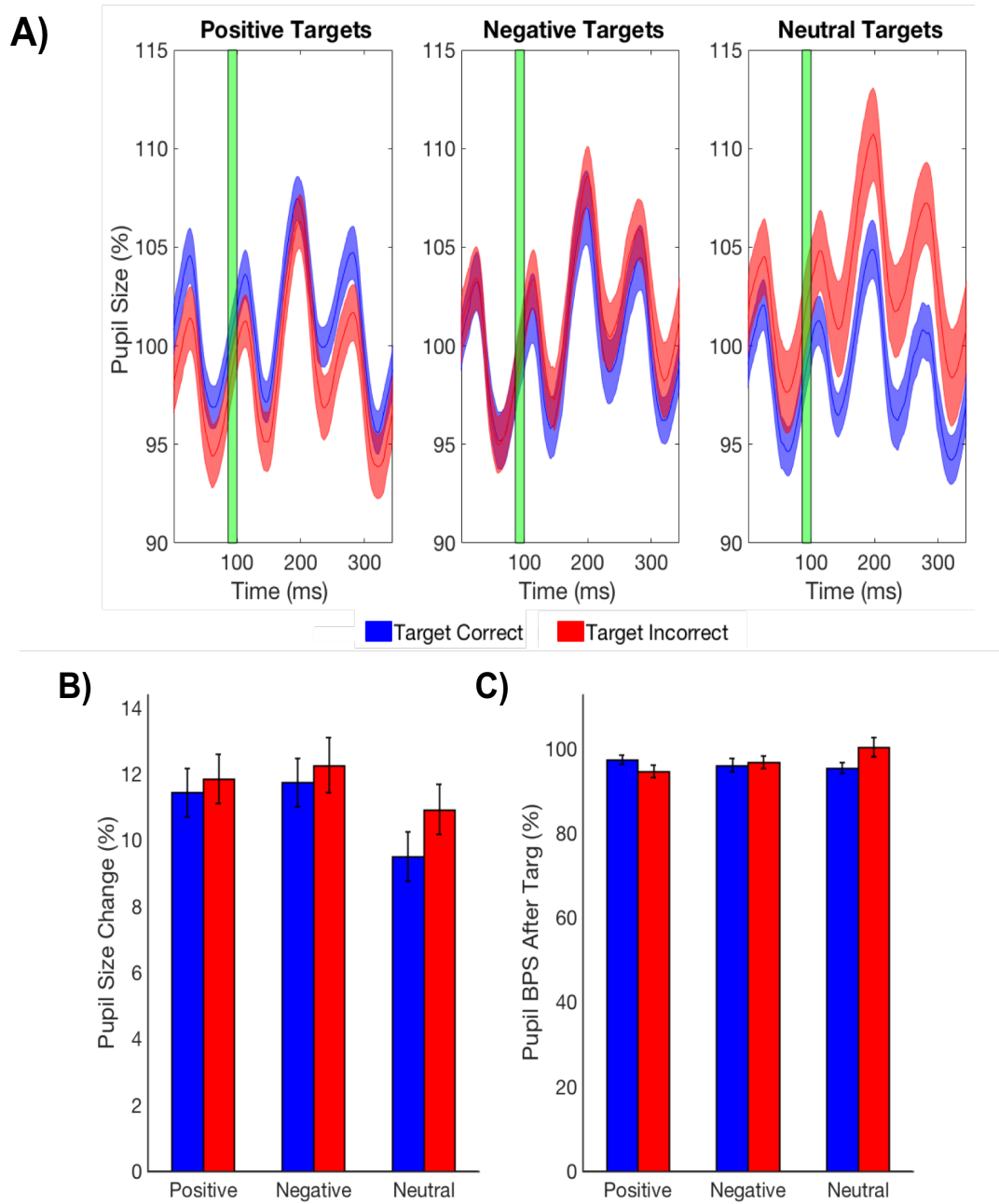
Figure 2.8: Pupil size over time on target correct and incorrect trials (A). Pupil size measures indicate no significant difference in target incorrect and correct pupil size change (B) or baseline (C) suggesting that pupil size may not be sensitive to valence effects on TIL. Error bars and shading reflect standard error of the mean.
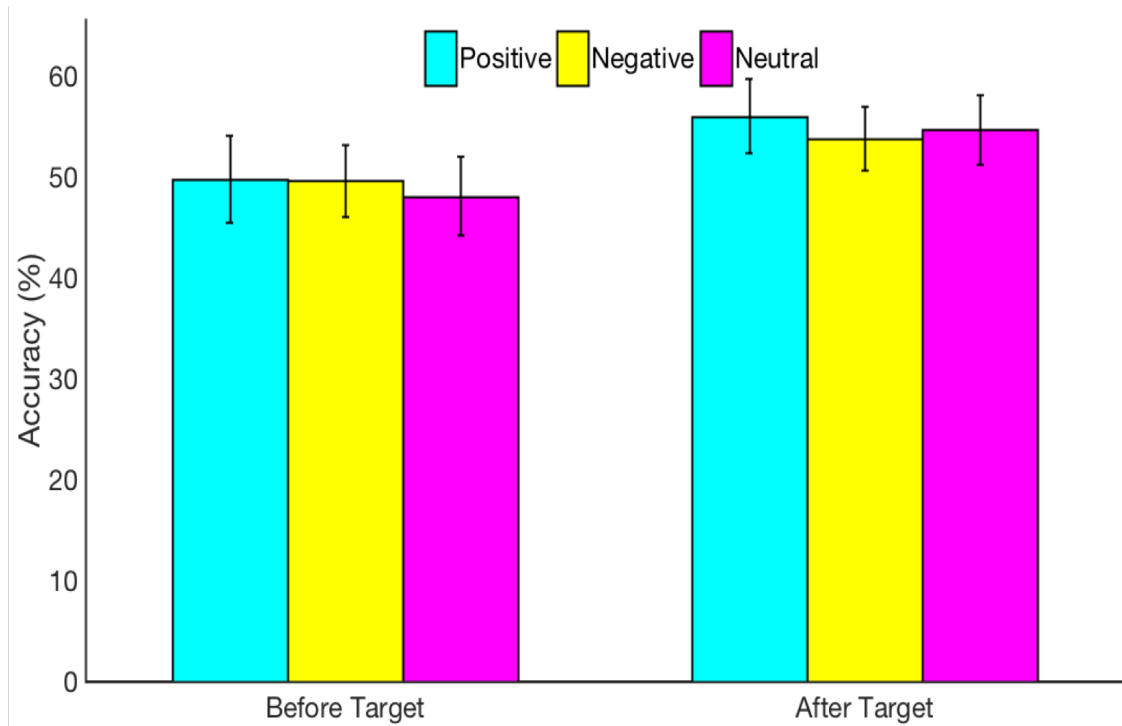
Figure 2.9: Image recognition task accuracy indicates increased accuracy for images tested after compared to before the target but no difference between emotion type was found suggesting an attentional boost for all images post-target presentation. Error bars reflect standard error of the mean.
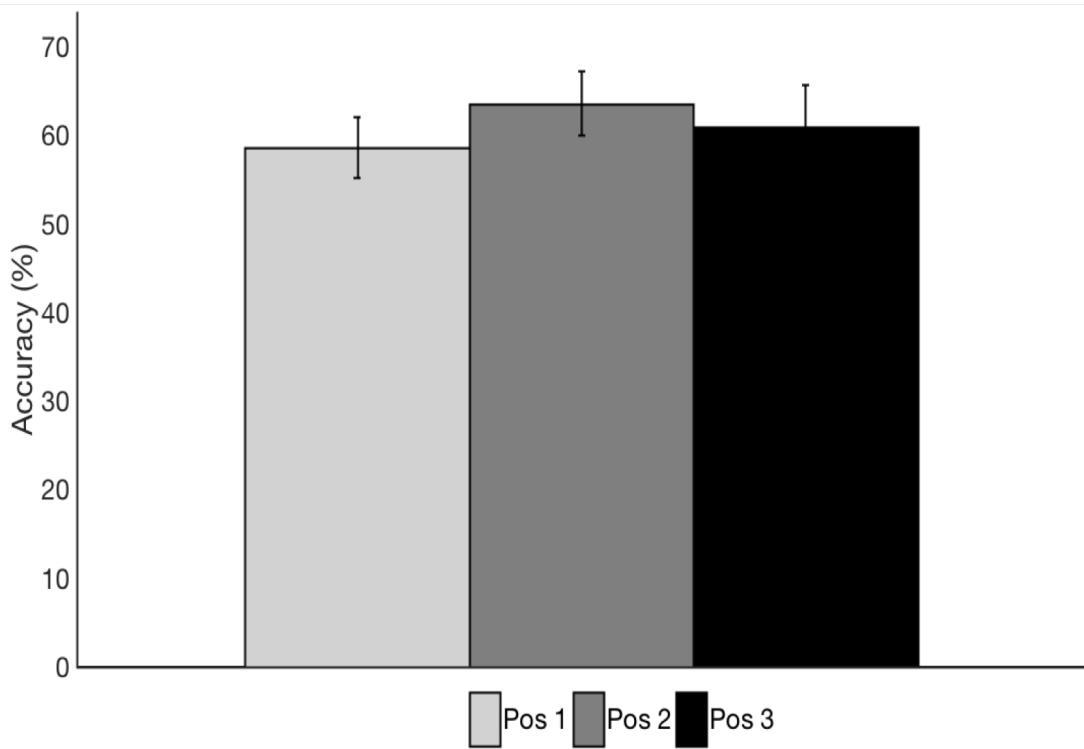
Figure 2.10: No image recognition accuracy differences between positions, in relation to target presentation, were found suggesting an attentional boost for all images post-target presentation.

Chapter 3

This chapter has been previously published as

The Influence of Feedback on Task-Switching Performance: A Drift Diffusion

Modeling Account

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Abstract

Task-switching is an important cognitive skill that facilitates our ability to choose appropriate behavior in a varied and changing environment. Task-switching training studies have sought to improve this ability by practicing switching between multiple tasks. However, an efficacious training paradigm has been difficult to develop in part due to findings that small differences in task parameters influence switching behavior in a non-trivial manner. Here, for the first time we employ the drift diffusion model to understand the influence of feedback on task-switching and investigate how drift diffusion parameters change over the course of task switch training. We trained 316 participants on a simple task where they alternated sorting stimuli by color or by shape. Feedback differed in 6 different ways between subjects groups, ranging from no feedback to a variety of manipulations addressing trial-wise vs block feedback, rewards vs punishments, payment bonuses and different payouts depending upon the trial type (switch/non-switch). While overall performance was found to be affected by feedback, no effect of feedback was found on task-switching learning. DDM revealed that the reductions in RT switch cost over the course of training were driven by a continually decreasing decision boundary. Furthermore, feedback effects on RT switch cost were also driven by differences in decision boundary, but not in drift rate. These results reveal that participants systematically modified their task-switching performance without yielding an overall gain in performance.

Introduction

Task-switching is an important cognitive skill that facilitates our ability to choose appropriate behavior in a varied and changing environment. Task-switching ability changes throughout the lifespan (Cepeda, Kramer, & Gonzalez de Sather, 2001; Davidson, Amso, Anderson, & Diamond, 2006; Huizinga, Dolan, & van der Molen, 2006; Kray & Lindenberger, 2000; Wasylyshyn, Verhaeghen, & Sliwinski, 2011), suggesting that this ability may be malleable. Consistent with this, training studies show that task-switching can, at least in certain circumstances, be improved through training (Karbach & Kray, 2009; Minear & Shah, 2008; Strobach, Liepelt, Schubert, & Kiesel, 2012). These training paradigms are promising as a method to improve task-switching functions but give rise to inconsistent learning outcomes (Karbach & Kray, 2009; Minear & Shah, 2008; Pereg, Shahar, & Meiran, 2013). It is likely that part of these training outcome inconsistencies are due to the use of different task structures and parameters across studies (Vandierendonck, Liefooghe, & Verbruggen, 2010). In task-switching training, different preparatory times (Monsell, 2003), cues (Monsell, 2003) and predictability of the task switch (Minear & Shah, 2008) have been found to influence performance and learning. In the present paper, we add to this literature by examining the influence of feedback on training, which has not been well explored in the context of task-switching.

Feedback on the accuracy and timeliness of one's performance can provide critical information to guide behavior (Yeung, Botvinick, & Cohen, 2004). While the role of external feedback is critical to achieve accurate proficiency in tasks where the correct response can only be learned operantly (such as in the Wisconsin Card Sorting Task),

feedback can be less important in tasks where the participant knows which answers are correct and those which are not (Herzog & Fahle, 1997; Liu, Dosher, & Lu, 2014; Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006). For example, in typical task-switching tasks, participants will know whether their responses are correct or incorrect and thus feedback may be more relevant as a motivational signal rewarding participants for a job well done (Seitz, Kim, & Watanabe, 2007; Seitz & Dinse, 2007). For example, feedback has been used to study motivated decision making by associating different reward values to correct stimulus-response mappings with results suggesting that higher valued responses are related to increases in performance (Botvinick & Braver, 2015). Consistent with this motivational framework, in some cases people show more learning when falsely inflated feedback is provided than when accurate feedback is provided, suggesting models where feedback serves to increase learning rates rather than to supervise learning (Shibata et al. 2011). On the other hand, feedback meant to provide motivation can also impair learning (Katz, Jaeggi, Buschkuehl, Stegman, & Shah, 2014), perhaps due to the distracting role that some feedback can have during task performance. Given these conflicting roles of feedback in the literature, we sought to determine both the extent to which feedback alters performance during task-switching and to understand what components of the decision process are altered.

While multiple studies have looked at which task parameters influence task-switching learning and performance, few have shed light on the changes to decision processes that underlie that learning. With current computational techniques it is possible to model decisional processes during task-switching. In particular, the Drift Diffusion

Model (DDM) (Ratcliff, 1978) decomposes the decision process into different components, addressing biases, information integration rates, and the amount of accumulated information required to make a decision; each component offers insight into changes in the decisional process responsible for differences at the behavioral level. A benefit of the DDM is that it can jointly account for both the reaction time and accuracy distributions providing a more informative description of behavior than summary statistics such as the mean RT. The DDM has been successfully applied to understand processes involved in a variety of two-alternative forced choice tasks, such as recognition memory tasks, lexical decision and visual-scanning tasks (Ratcliff, 1978; Ratcliff & McKoon, 2008; Ratcliff & Rouder, 1998; Strayer & Kramer, 1994).

While some studies have applied the DDM to understand task-switching (Karayanidis et al., 2009; Madden, Bennett, & Song, 2009; Schmitz & Voss, 2012), here, for the first time we employ the DDM to understand the influence of feedback on task-switching and how drift diffusion parameters change over the course of task switch training. To accomplish this, we trained 316 participants on a simple task-switching task where they alternated sorting stimuli by color or by shape. Feedback differed in 6 different ways between subjects ranging from no feedback to a variety of manipulations addressing trial-wise vs block feedback, rewards vs punishments, payment bonuses and different payouts depending upon hard or easy trial types. This way we could look at how different feedback conditions may lead to different patterns of performance change across 10 blocks of training trials. Results showed that the most significant distinction was between the no feedback condition compared to the other feedback conditions, and that while reaction time

and accuracy data provided a pattern of results that was difficult to interpret, the DDM model parsimoniously accounted for the data through differences in both integration rate and decision boundaries.

Materials and Methods

Participants

A total of 316 participants (Female=202; Age:, Mean=19.66, STD=2.84) were recruited to participate in the experiment. All participants had normal or corrected-to-normal visual acuity and received course credit for the 1hr session. All participants gave written informed consent, as approved by the University of California, Riverside Human Research Review Board.

General Procedure and Training Task

Participants trained for one session on a task-switching task. Each session is comprised of 10 training blocks and 4 pre/post blocks (2 pre, 2 post) with 60 trials a block for a total of 840 trials. Participants switched between two tasks categorizing colored shapes. In Task 1 participants categorized images by color (Blue or Green) and in Task 2 stimuli are categorized by shape (Circle or Square). Eight stimuli were randomly chosen from a set of 25 stimuli comprised of multiple exemplars of the rule categories. For example, 5 shades of Blue and Green, and 5 sizes of Circles and Squares were used. Stimuli appeared for 2s or until a response was made. Afterwards, a blank screen was displayed during the randomized inter-trial-interval of 0.5-0.9s. Trials in which a switch occurs are referred to as "switch trials" and trials in which a task repeats are referred to as "non-switch trials".

Switch trials occurred every 4 trials and were cued (i.e. "Rule Change" was displayed) for 1s whereas non-switch trials appeared after the Inter-Trial-Interval (ITI). In the rest of the paper we analyze only training block performance because feedback conditions differed only on these blocks.

Experimental Manipulation on Feedback

Participants were randomly assigned to one of the six training conditions based on subject number. Conditions consisted of No Feedback (NFB, N=51), Accuracy Feedback (AFB, N=53), Difficulty Aware (DFB, N=57), Punishment (PFB, N=55), Monetary Bonus (MFB, N=52), or Block Feedback (BFB, N=48). Each condition only differed on the 10 training blocks. Feedback (if provided) was given in the form of gold coins immediately after a response. Standard correct responses received 1 gold coin, and bonuses are provided based on difficulty and speed in relation to a 600ms response time criterion. The speed criterion was taken from the average reaction time (600ms) from a pilot study of 306 participants. In the NFB condition participants did not receive any feedback. In the AFB condition participants were only given feedback indicating correct or incorrect responses. In the DFB condition, participants received bonuses according to performance during difficult trials as described in the bonus structure above. In the DFB condition, we took into account the fact that responses are slower on switch trials by giving 1 bonus coin if an accurate response is within 20% of the speed criterion on switch trials and 5% of the speed criterion on non-switch trials, and 3 bonus coins if an accurate response is within 5% of the speed criterion on switch trials. In the PFB participants received feedback as described above, however

incorrect or slow responses were punished with a -1 gold coin. The MFB condition was the same as the PFB condition except that participants received .2 cents per coin they won. The BFB condition was the same as the PFB condition except participants received feedback at the end of each block indicating the percent of total coins received.

Data Analysis

Out of 316 participants, 11 were excluded based on a 80% accuracy criterion (**Figure S3.1**). In addition to analyzing mean RT and accuracy across participants we looked at switch cost which is defined as a ratio of switch and non-switch trials to determine relative changes in performance. Defining switch cost as a ratio (as opposed to the difference) better accounts for relative changes from baseline RT (e.g., a 200ms slow down represents a greater change from a 400ms baseline than from a 1200ms baseline). Furthermore, this allows for simpler comparison between switch costs as estimated from RT and estimated from model parameters. Finally, using switch cost differences rather than switch cost ratios produced qualitatively similar results.

Modelling

To better understand how the different feedback conditions influence decision processes we fitted a drift diffusion model (DDM; see **Figure 3.1**) to our data. DDM construes the decision making process as a random walk which can be simulated using the equation:

$$W(t + dt) = W(t) + v \cdot dt + n \,, \qquad\qquad (1)$$

where dt is a time step in simulation, v is the mean drift rate and n is random Gaussian noise. W is a location at any given time between the two boundaries 0 and *a*. The decision is made once either of the boundaries is reached. In our case, reaching 0 corresponds to an incorrect response, while reaching *a* corresponds to a correct response. W(t=0) is a starting point that reflects any bias towards a particular stimulus, but since we fit correct/ incorrect responses no such bias is possible, therefore we fixed the starting point at an equal distance from the two boundaries, that is W(t=0) = *a*/2.

Drift rate (v) reflects the efficiency with which stimulus information is used to select a response; it can be affected by task difficulty, individual differences in intelligence and working memory capacity, as well as motivation, fatigue or inattention (Schmiedek, Oberauer, Wilhelm, Süss, & Wittmann, 2007). In the task-switching paradigm, the drift rate might be affected by the activation of S-R mapping rules (e.g., carry-over effects), task-set biasing, or other factors contributing to task readiness (Schmitz & Voss, 2012).

Decision Boundary (a) is normally regarded as a measure of caution or conservatism: larger values of the boundary result in slower responses but higher accuracy (Schmiedek et al., 2007). In other words, it captures speed-accuracy trade-off effects. Some studies suggest that in a task-switching paradigm, the decision threshold can vary on trial-by-trial basis: caution can be reduced for predictable repeat trials (Schmitz & Voss, 2012) or increased for predictable switch trials (Karayanidis et al., 2009).

Non-decision time (t_0) is thought to reflect the duration of pre-decision processes such as encoding, preparation of the right task set, and motor processes of the response system (Ratcliff & McKoon, 2008). Previous studies have found that, non-decision time

on switch trials was the same as on non-switch trials with a cue-stimulus interval as low as 600ms (Madden et al., 2009). Because we used 1500-1900ms cue-stimulus interval, we assumed the non-decision time to be fixed across switch and non-switch trials.

To fit the DDM we used a hierarchical Bayesian parameter estimation toolbox (Wiecki, Sofer, & Frank, 2013) which enabled us to get more robust fits as it makes use of commonalities among individuals (both individual and group-level parameters are fitted at once, where group-level parameters function as a prior for individual fits). This is especially advantageous in datasets with small number of trials. DDM parameters can be very sensitive to outliers in individual responses, especially when arbitrarily quick responses are made. To account for the fraction of random responses, we assumed a lapse rate of 10% (i.e. drawn from a uniform distribution).

Results

Behavioral data

To understand how the feedback manipulations influenced task performance, we performed a mixed ANOVA on Block X Trial Type X Feedback Condition with subjects as random effects. Examining average task performance showed a main effect of Block on RT ($F_{(9,295)} = 16.87$, $p < 0.001$) and Accuracy ($F_{(9,295)} = 7.94$, $p < 0.001$), indicating a decrease in RT (Block 1: 710ms, Block 10: 659ms) and Accuracy (Block 1: 95.07%, Block 10: 92.64%). The fact that both RT and Accuracy decreased as a function of training block demonstrates a speed-accuracy tradeoff (**Figure 3.2; A, B**). However, a significant interaction for Block X Trial Type for RT ($F_{(9,295)} = 5.61$, $p < 0.001$) but not accuracy ($F_{(9,295)} = 1.68$, $p = 0.088$) suggests that improvements in RT are not solely due to the

speed-accuracy tradeoff (**Figure 3.2 C, D**), which complicates interpretation of the raw behavioral data. To quantify changes in switch cost with time, we performed paired t-tests on changes in switch cost between Blocks 1 and 10, and found a significant decrease in both RT and accuracy (**Figure 3.2E** ; $t(304) = 988.1$, $p < 0.001$; and $t(304) = 606.3$, $p < 0.001$, respectively), with a proportionately greater change in RT than in accuracy, suggesting a reduction in switch costs. Altogether, direct examination of RT and accuracy provide a mixed story: it is unclear whether something other than a speed-accuracy tradeoff, such as learning, is occurring.

We next examined whether the different feedback conditions impacted performance and learning (**Figure 3.3 A, B**). A main effect of Condition ($F(5,299)=3.868$, $p=0.002$) on RT suggests that feedback did influence participants' performance. The two-way interaction between Condition X Block found for RT ($F(45,1475) = 1.67$, $p = 0.004$) but not for accuracy ($F(45,1475) = 1.03$, $p = 0.425$), suggesting that task feedback also had an effect on learning, where with time participants became faster in some of the feedback conditions. The three-way interaction term between Condition X Trial-Type X Block, however, failed to reach significance for either RT ($F(45, 1475) = 1.0$, $p=0.458$) or accuracy ($F(45, 1475) = 0.8$, $p=0.854$), suggesting that different feedback conditions had minimal effect on the change in task switching performance over training. To look at changes in switch cost over the course of training by condition we conducted a one-way ANOVA (**Figure 3.4**) on the change in switch cost between Block 1 and 10 and failed to find a significant difference across conditions in either RT ($F(5,299)=1.41$, $p=0.222$) or Accuracy ($F(5,299)=1.39$, $p=0.229$). These results suggest that while feedback affected

overall task performance and learning, it did not significantly impact changes in switch costs.

Modelling

We used a DDM to investigate what aspects of the decision process are affected by training and feedback and to determine to what extent speed-accuracy tradeoff was driving the observed behavioral effects. We fitted a set of DDMs, each of which differed in what parameters were allowed to vary across blocks and trial types. If conditioning a parameter on trial type or block improves the model fit, it means that that parameter does vary across trial types or blocks, respectively. The set of models were compared based on Deviance Information Criterion (DIC), which is a standard measure for comparing hierarchical models (Wiecki, 2013). In the following, we present only the results for our winning model, which conditions drift rate (v) and decision boundary (a) on trial type and block (see **Supplement Table S3.1** for the alternative models).

First, we looked at the change in parameters on switch and non-switch trials averaged across conditions (**Figure 3.5A,B**). As with the behavioral data, we performed a 3-way mixed ANOVA to determine changes in parameters driving overall performance and switch cost effects. We found that there was a significant main effect of Block with a decrease in both drift rate ($F(9,295) = 53.27$, p <0.001) and decision boundary ($F(9,295)$ = 82.03, p < 0.01). For the drift rate this decrease was significantly different between trial types (Block X Trial Type ($F(45,1475) = 50.57$, p < 0.001) with a greater decrease in switch trials (Block 1: 2.87; Block 10: 2.15) than in non-switch trials (Block 1: 2.58; Block 10:

2.49). The same was true for the decision boundary (Block X Trial type: $F(45,1475) = 62.80$, $p < 0.001$), with a greater decrease in switch (Block 1: 3.22; Block 10: 2.45) than in non-switch trials (Block 1: 2.00; Block 10: 1.75). While a decrease in drift rate alone would result in increased RT and decreased accuracy, a decrease in decision boundary would lead to decreased RT and also decreased accuracy. Taking this into consideration, the results suggest that the observed decrease in RT switch cost over the course of training was solely due to the decrease in decision boundary, with changes in the switch trial parameter driving these improvements. To quantitatively compare the changes in drift rate and decision boundary, we performed a paired t-test on the difference of switch costs between Block 1 and 10, and found that decision boundary decreased significantly more than drift rate ($t(304) = 1378.1$, $p < 0.001$; **Figure 3.5C**).

To determine what effect different feedback conditions had on decision making processes we looked at the effect of condition on the model parameters (**Figure 3.6 A,B,C,D**). We found that task feedback only affected the decision boundary ($F(9, 295)=5.46$, $p<0.001$), but had no effect on the drift rate ($F(9, 295)=0.9$, $p=0.484$). This suggests that the overall variation in RT and accuracy for different task feedback (**Figure 2**) originates from variation in the decision boundary. Furthermore, the interaction between trial type and feedback was significant for decision boundary (Trial Type X Condition: $F(5,299)=3.23$ $p=0.007$), but not drift rate (Trial Type X Condition: $F(5,299)=0.42$, $p=0.834$), indicating that differences in switch cost for different feedback conditions also originated from differences in decision boundary. However, it must be noted that the condition that most differed from the rest was the NFB condition (**Figure 3.6E**). Finally,

a non-significant 3-way interaction between Block, Condition and Trial Type for drift rate (F(45,1475)=1.1, p=0.299) and decision boundary (F(45,1475)=1.25, p=0.123) indicated that feedback did not affect the changes in switch costs during training (**Supplementary Figure S3.2**).

Discussion

In this study we investigated the effects of feedback and training on task-switching performance. Behavioral results showed that both task feedback and training had an effect on task switching performance as reflected by differences in switch costs across feedback conditions and across blocks. We used Drift Diffusion Modelling (DDM) to understand the effects of feedback and training on the underlying decisional processes. DDM results revealed that differences in performance across feedback conditions were driven by differences in decision boundary, but not drift rate. In comparison to when no feedback was given, feedback that motivated faster performance (e.g. Difficulty, Monetary, Punishment and Block FB conditions) led to a decreased decision boundary on switch trials, reflecting speed-accuracy tradeoffs. Furthermore, the effects of training – reduction in RT switch costs – were also found to be driven by the reduction in the decision boundary, while a simultaneous but smaller reduction in drift rate only served to partly counter such effects.

DDM parameter analysis also revealed that participants accumulated information slower and used higher decision boundaries on switch compared to non-switch trials. These findings are in line with the interpretation that drift rates primarily reflect carry-over

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interference from the task on the previous non-switch trial while a larger decision boundary reflects a preparatory response to adapt to more difficult trials (Karayanidis et al., 2009; Schmitz & Voss, 2012). Moreover, the continuous decrease in drift rate and decision boundary was found only on switch trials while it stayed relatively constant on non-switch trials, reflecting that changes in performance over the course of training were due to changes in the decisional process on switch trials. Learning that is reflected in the decrease of decision boundary is consistent with other training studies (Dutilh, Krypotos, & Wagenmakers, 2011; Liu & Watanabe, 2012; Petrov, Van Horn, & Ratcliff, 2011; Zhang & Rowe, 2014). Such decreases have been interpreted as a change in behavior due to complying with speed-accuracy tradeoff instructions. Another possible interpretation of the decreased decision boundary is that it reflects task learning (Dutilh et al., 2011). Zhange & Rowe (2014) found that when an untrained stimulus was tested, decision boundary did not change while drift rate did, suggesting that the decision boundary reflected learning that transferred across tasks.

The decrease in drift rate over the course of training is more difficult to explain in terms of learning. Learning, as studied outside of task-switching research, has typically been shown to be driven by an increase in drift rate rather than a decrease (Dutilh et al., 2011; Liu & Watanabe, 2012; Petrov et al., 2011; Zhang & Rowe, 2014). Thus, one possible explanation for the decrease in drift rate could be fatigue that arises over the course of the task (Schmiedek et al., 2007). However, the largest decrease occurs within the first few blocks with incremental changes thereafter and only on switch trials suggesting that this effect may reflect more meaningful changes in the decision process itself.

In our study, the decrease in decision boundary on switch trials may reflect learning to anticipate when switches would occur and participants choosing increased speed at the expense of accuracy. This learning effect is in line with previous research showing that task switching performance is altered by task predictability. For example, Dreisbach et al. (2002) found that switch cost was increased when a switch was preceded by a 75% valid cue compared to a 100% valid cue (Dreisbach, Haider, & Kluwe, 2002). Minear & Shah (2008) also found that switch costs performance varied with the predictability of the switches.

Adjusting speed-accuracy tradeoff over the course of training also explains why some feedback conditions had an overall decrease in decision boundaries on switch trials. An effect of task learning is evident in the Accuracy and No Feedback conditions where feedback did not motivate optimizing the speed-accuracy trade-off on switch trials compared to non-switch trials. In comparison, the Difficulty, Punishment, Monetary and Block feedback conditions, switch trial performance was rewarded more for correct and faster performance leading to an overall decrease in switch trial decision boundary which explains the overall decrease in RT for these conditions.

Finally, our results are relevant to the task switch training literature in that feedback can be used to successfully motivate behavior that coincides with training goals. To achieve training goals, behavior must change on the relevant task dimension. In the case of task switching training the typical goal is to improve the ability to switch to another task. While results in the present study indicate that feedback is not improving task switching ability, we show that feedback can motivate participants to specifically modify behavior on switch

trials. This result indicates that reward structures, if properly constructed to align with training goals, may be able to modify behavior in a manner consistent and beneficial to training outcomes.

Conclusion

We found that both feedback and training can have significant effects on task-switching performance. We used DDM modeling to account for speed-accuracy trade-offs and, for the first time, to show how decisional processes change over the course of task-switching training. Specifically, we found that participants show a decreased drift rate and increased decision boundary on switch trials compared to non-switch trials, possibly reflecting task set interference and a preparatory response before more difficult trials. Moreover, the change in switch cost over the course of training was driven by a decrease in the decision boundary, reflecting speed-accuracy tradeoffs. Finally, task feedback effects on RT switch cost were also driven by differences in decision boundary, but not drift rate. These results help show that learning is not necessarily best described as improvements of task performance, but instead should be characterized by how participants adapt their behavior to the training procedure that are made most relevant to them by feedback on their performance. Overall, our results suggest that DDM can provide additional insight into feedback and training effects on task-switching performance.

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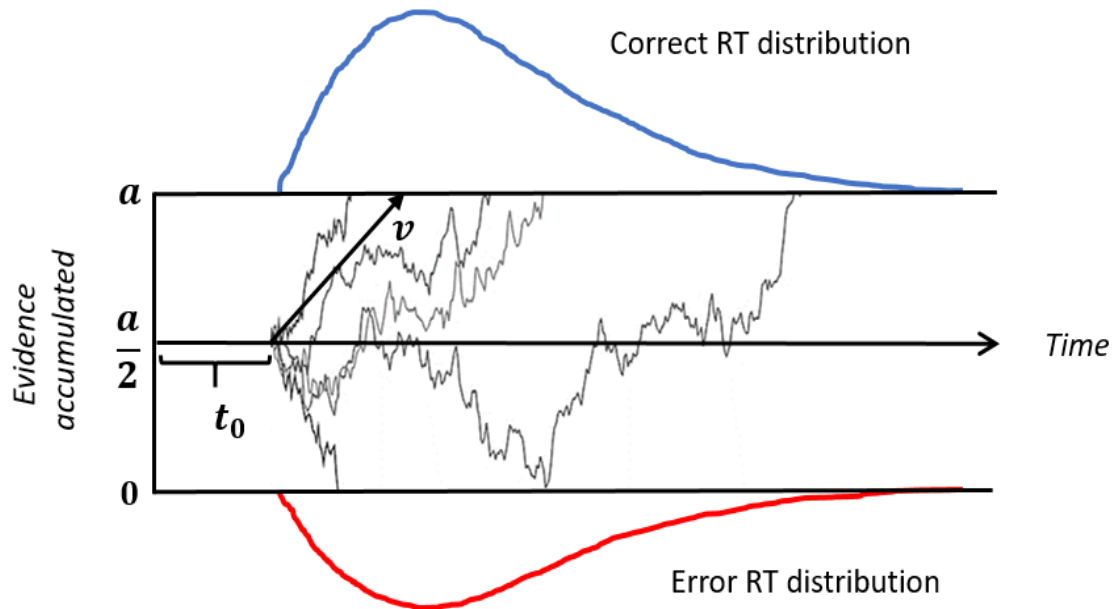
Figure 3.1. illustration of drift-diffusion model. Thin black lines represent trajectories of individual random walks. Each walk captures noisy accumulation of evidence in time on a single trial. The speed of accumulation is determined by the drift-rate (v). A response is initiated when either of the boundaries (a or 0) is reached. The upper (blue) and lower (red) panels represent RT distributions for correct and incorrect responses, respectively. The time gap between the onset of a stimulus and start of the evidence accumulation is non-decision time, denoted by t_0.
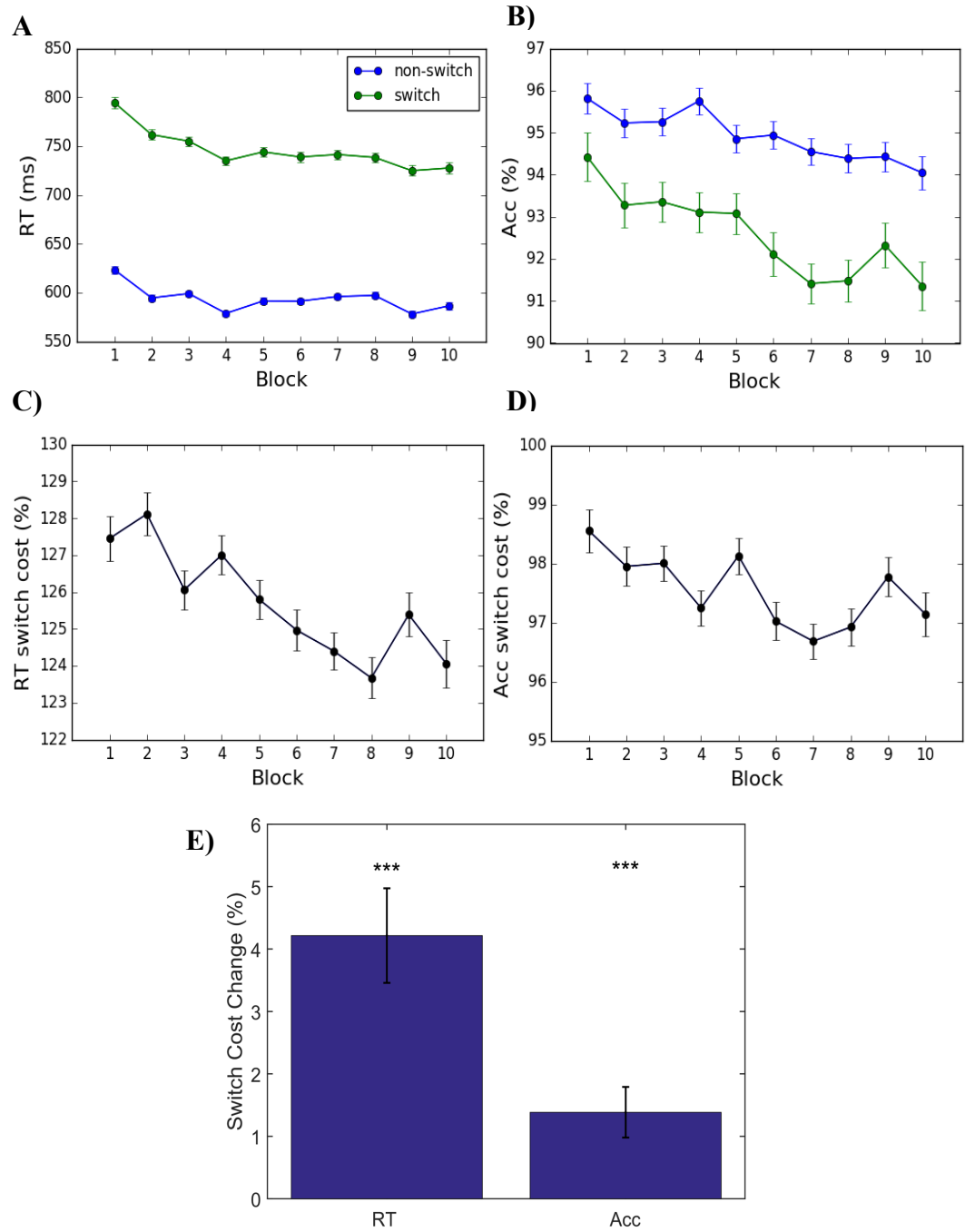
Figure 3.2. A,B: Average reaction time and percent correct by block. Results indicate a decrease in Average RT (top left) and Accuracy (top right) for switch and non-switch trials. C,D: Switch cost is calculated by dividing switch by non-switch performance. A larger decrease in switch trials is reflected in a reduction in switch cost RT and switch cost accuracy. E: Switch cost change is calculated by subtracting Block 10 performance from Block 1. The bar plots indicate that change in RT and accuracy switch costs are significantly greater than 0. Error bars represent within-subject errors.
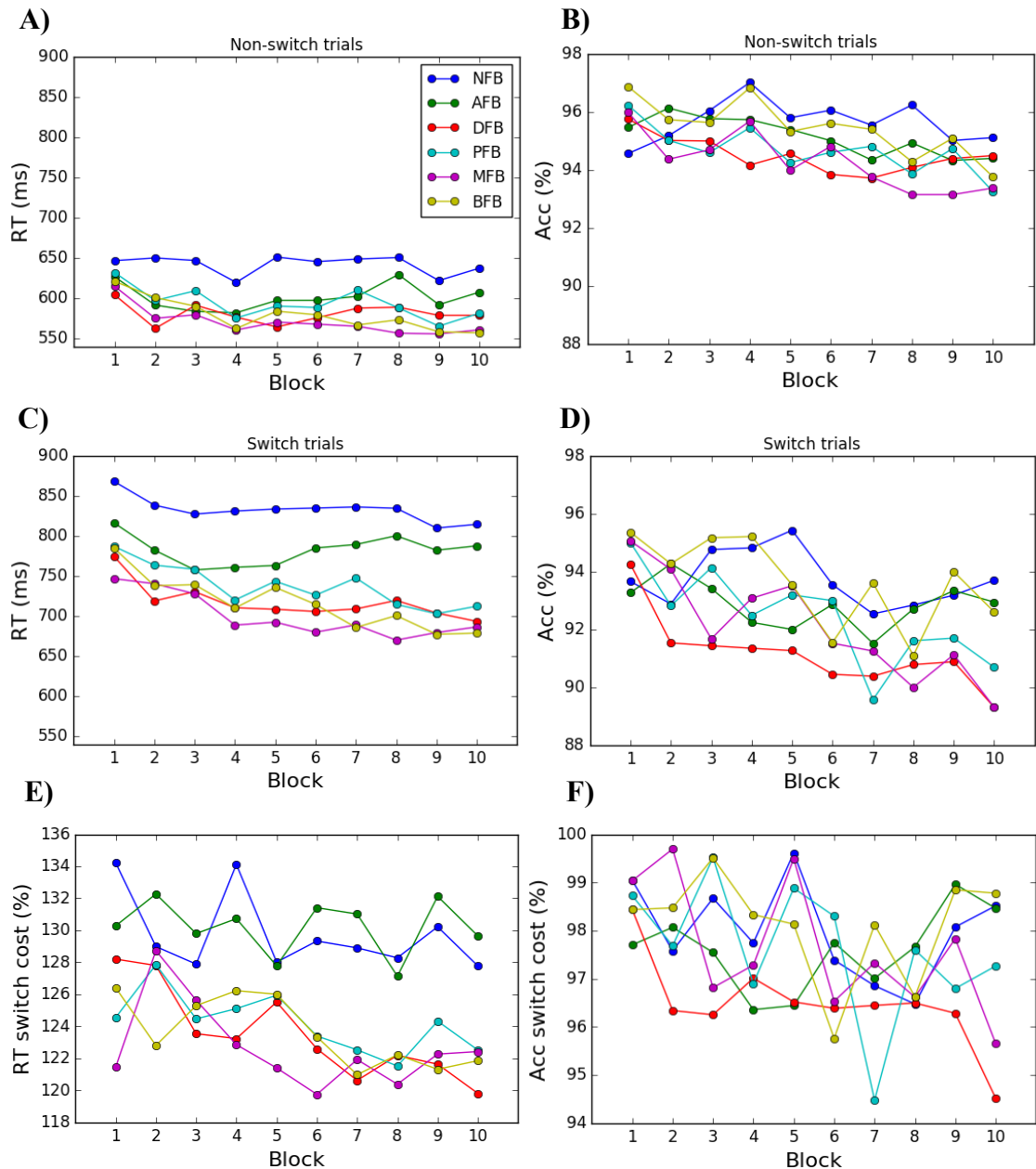
Figure 3.3 A,B: Average reaction times and accuracy (B) for non-switch (A,B) and switch trials (C,D) in each block and corresponding switch costs (E,F). Results indicate that feedback condition influences overall performance in average RT and switch cost RT but not RT switch cost change. Each color corresponds to a different condition (NFB – No feedback, AFB – Accuracy feedback; correct or incorrect feedback, DFB – Difficulty aware feedback; bonus if fast and correct, PFB – Punishment feedback; punishment, -1 coin for incorrect responses, MFB – Monetary Feedback; same as PFB, but each coin is worth 0.2 cents, BFB – Block feedback; same as PFB, but at the end of each block they are given block accuracy performance.
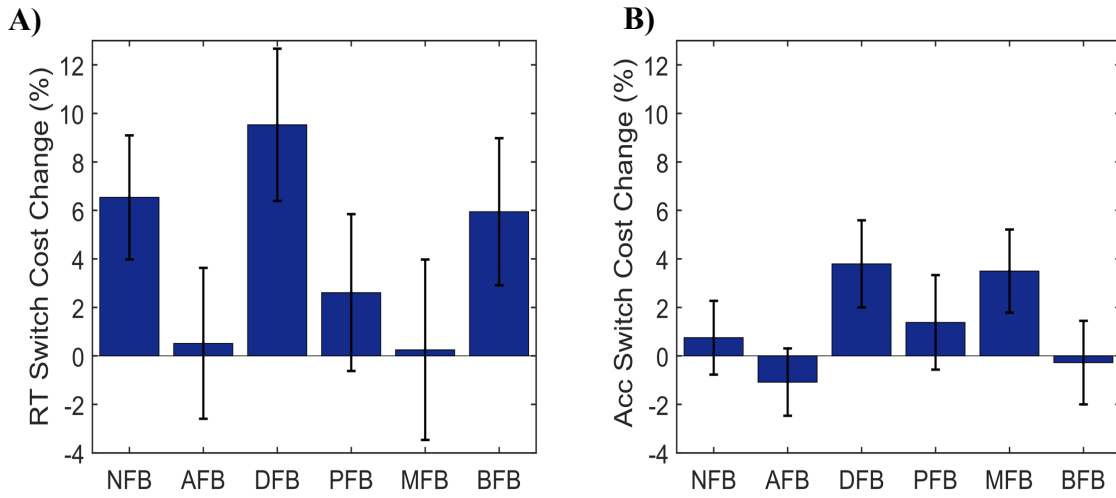
Figure 3.4. Change in Switch Cost from blocks 1-10 for RT and Accuracy by Condition. NFB –No Feedback, AFB- Accuracy Feedback, DFB- Difficulty Aware Feedback, MFB- Monetary Feedback, BFB- Block Feedback. Results indicate no difference between conditions in RT or Accuracy in switch cost change. Error bars represent standard errors
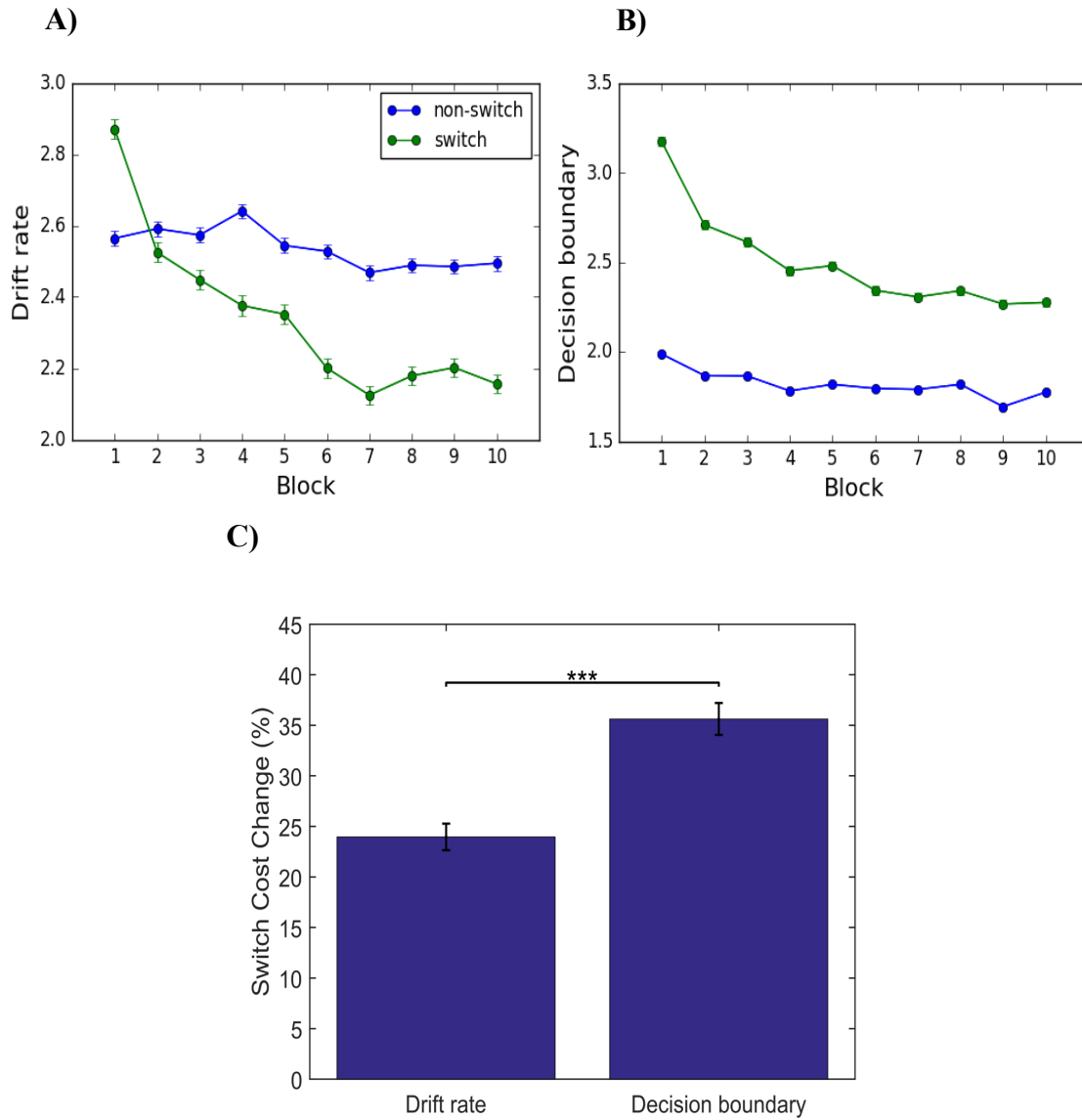
A)

B)

C)

Figure 3.5. Group level parameters for all participants (n=305) for switch trials (green) and non-switch trials (blue). A,B: Results indicate a decrease in drift rate (A) and decision boundary (B). C) A larger change in decision boundary than in drift rate from blocks 1 to 10 indicates that the decrease in RT and Accuracy is driven by a decrease in decision boundary. Error bars represent within-subject errors.
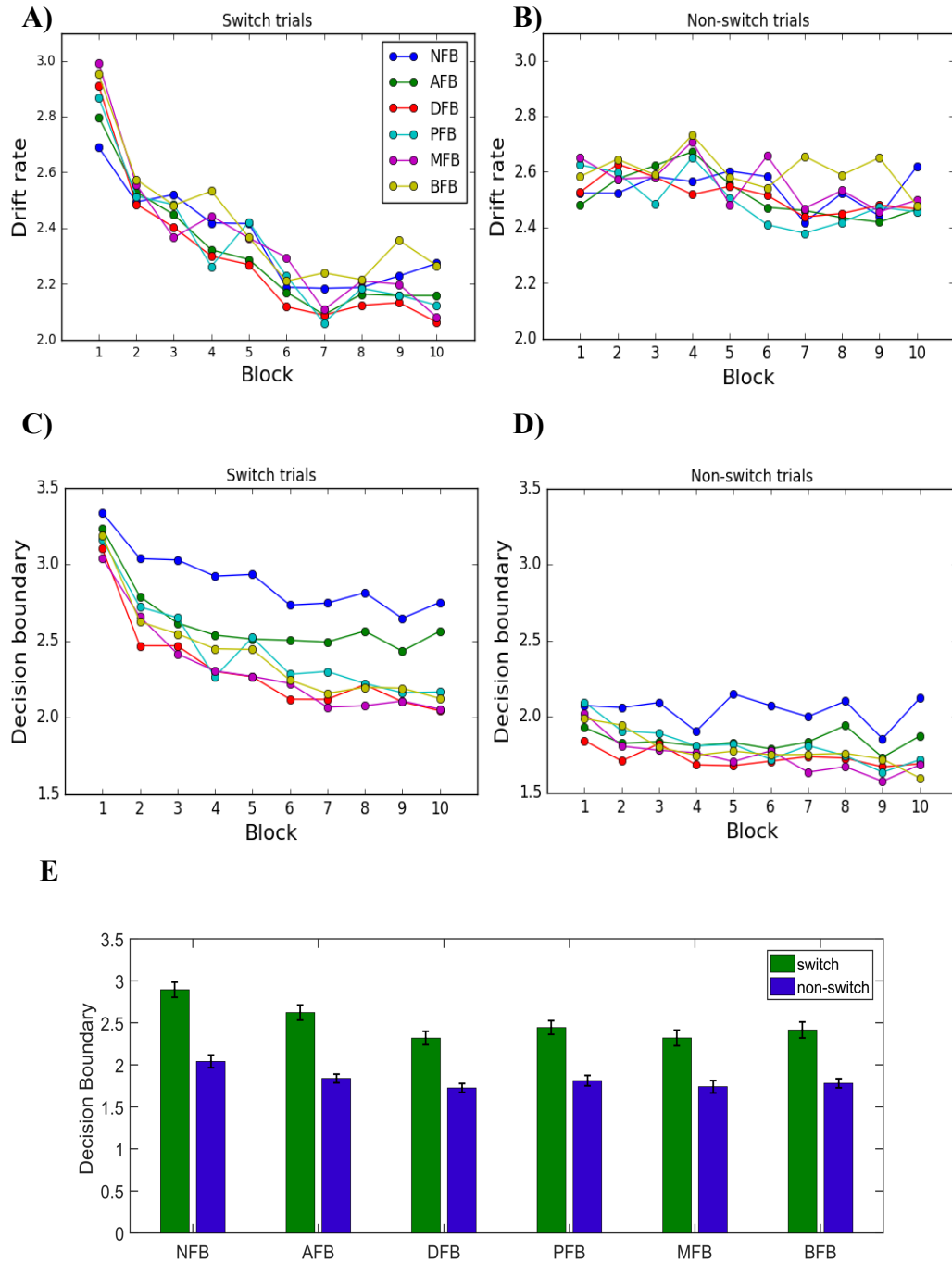
Figure 3.6. A,B,C,D: Group level parameters for each feedback condition for switch trials and non-switch trials, drift rate, decision boundary. Results indicate that behavioral changes by condition are primarily due to differences in decision boundary. E: Decision boundary by condition and trial type. Results indicate an overall decrease in decision boundary as feedback motivates good performance on switch trials, with the decrease being driven by the switch trial boundary. Error bars represent within-subject errors.
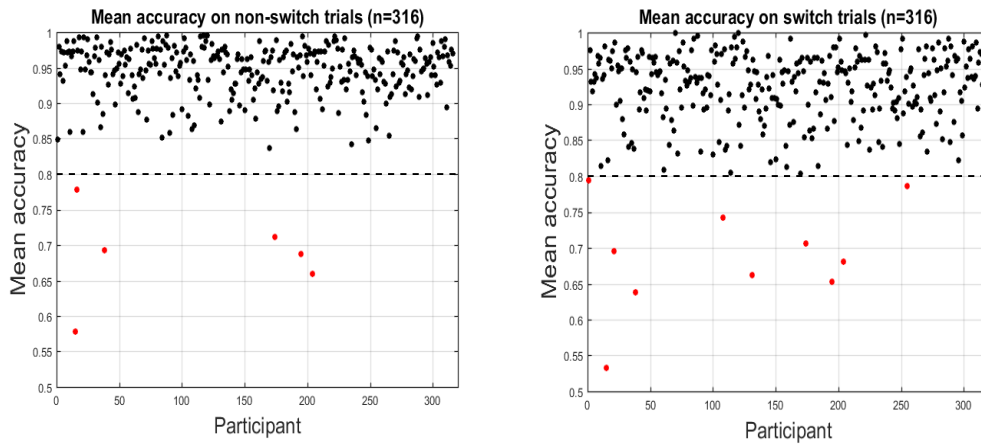
Figure S3.1. Mean accuracy of every individual on switch (right panel) and non-switch (left panel) trials. The dashed line indicates exclusion criterion and red dots are individuals that did not satisfy the criterion. Across the two trial types this resulted in excluding 11 participants.

Model	DIC
DDM_11 (*v,* and *a* depend on *trial type* and *block; t* fixed; *z=0.5*)	**31088**
DDM_25 (*v* depends on *trial type* and *block; a, t* fixed; *z=0.5*)	56681
DDM_24 (*a* depends on *trial type* and *block; v, t* fixed; *z=0.5*)	40582
DDM_21 (*v,* and *a* depend on *trial type* only*; t* fixed; *z=0.5*)	68488
DDM_22 (*v* depends on *trial type* only*; a, t* fixed; *z=0.5*)	77260
DDM_23 (*a* depends on *trial type* only*; v, t* fixed; *z=0.5*)	71611

Figure S3.2. Model evidence for different model assumptions. Lower DIC value indicates a better model. The best model here is DDM_11.
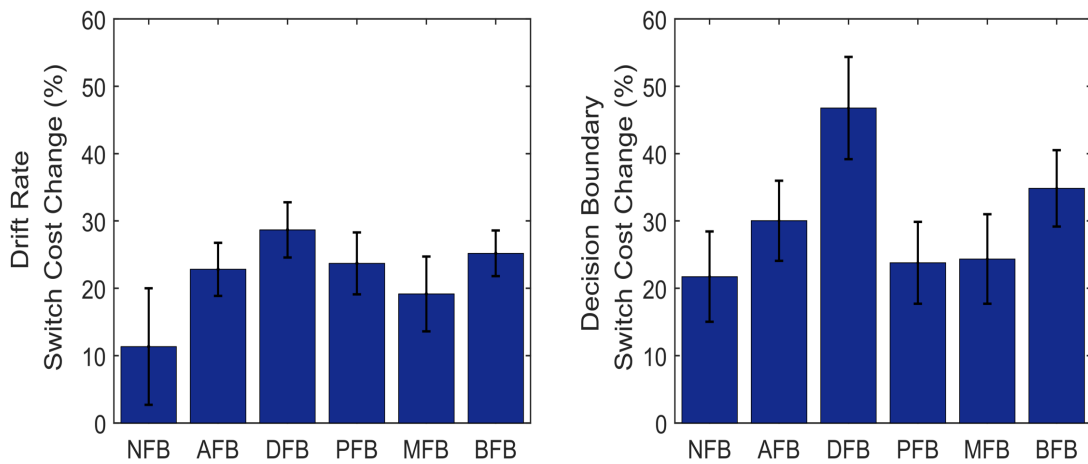
Figure S3.3: Change in switch cost drift rate and decision boundary by condition from block 1 to 10. A one-way ANOVA on the switch cost difference between Block 1 and 10 and found no significant difference between conditions for Drift Rate ($F_{(5,299)}=1.28$, $p=0.27$) and a trending difference in Decision Boundary ($F_{(5,299)}=1.79$, $p=0.12$).

General Discussion

Extant research suggests that learning is the consequence of a number of interacting including reinforcement systems. The overall goal of this dissertation is to further understand how reinforcement systems contribute to learning. This was accomplished by conducting a series of studies investigating how different types of reinforcers activate reinforcement systems and influence subsequent learning. In Chapter 1 we tested the hypothesis that the norepinephrine reinforcement system mediates task-irrelevant learning (TIL), by using pupillometry, which is an indirect measure of norepinephrine activity. Consistent with this hypothesis results indicated that increased recognition accuracy for target-paired images (i.e. TIL) is accompanied by phasic changes in pupil size. In Chapter 2 we studied how TIL is influenced by reinforcement systems underlying emotion processing and find that emotion targets can lead to the enhancement (Experiment 1) or suppression (Experiment 2) of TIL. Furthermore, compared to neutral targets, emotion targets are accompanied by an increased change in pupil size. Together, these results are consistent with the hypothesis that multiple reinforcement systems contribute to TIL, and specifically, that emotion targets activate a distinct reinforcement system than the norepinephrine system. In Chapter 3 we studied how explicit reinforcers (i.e. feedback) influence learning in a task-switching training task. We show that feedback rewarding speeded responses influence behavior to adopt strategies that sacrifice accuracy in favor of speed.

In sum, we find four distinct learning effects from our studies: 1) Learning for stimuli that are task-irrelevant as indicated in Chapter 1 and 2 with increased recognition

accuracy for target-paired images in Chapter 1 and suppression and enhancement of TIL by emotion targets in Chapter 2, 2) Learning for stimuli that are task-relevant as indicated in Chapter 2, with decreased RT for recognition of positive emotion targets, 3) Learning that is temporally proximal to task-relevant events, as indicated in Chapter 1 and 2 with increased recognition accuracy of images that follow target presentation, and 4) Changes in behavioral strategies as indicated in Chapter 3, with changes in the speed-accuracy tradeoff. Below, these results are interpreted in context of the perception-action-reinforcement (PRA) framework, the threshold model of perceptual learning and the attentional gating model of perceptual learning.

A Multiplicity of Mechanisms Underlying Learning

The perceptual learning models account for these learning effects by invoking multiple processes that contribute to the learning such as reinforcement, attentional, and passive learning processes. The PRA framework accounts for the results by invoking multiple reinforcement systems which interact and give rise to actions (i.e. changes in arousal). Below, we discuss results in context of each of the models.

Task-Irrelevant Learning

Results from Chapters 1 and 2 indicating an enhancement of recognition accuracy for images paired with the target, is in line with the hypothesis, as well as the aforementioned models, that reinforcement systems are involved in TIL. Specifically, that reinforcement systems release signals which 'tag' brain states (i.e. the image and target) that are then

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learned. Furthermore, findings of an increased pupil size accompanying TIL is consistent with the hypothesis that the norepinephrine system mediates this reinforcement signal.

Results from Chapter 2, indicating that emotion stimuli moderate TIL, are consistent with the conceptual models which predict that multiple reinforcement systems are involved in learning. Supporting this hypothesis are findings from the dot-probe task literature where attentional biases to positive stimuli are found (van Rooijen, Ploeger, & Kret, 2017). These findings suggest that positive stimuli attract attention, because they act as a positive reward which may reflect desirable environmental conditions (van Rooijen et al., 2017). In line with this hypothesis is research indicating that emotion stimuli activate a reinforcement system involving the orbitofrontal cortex (Ochsner & Gross, 2014), while TIL implicates the reinforcement norepinephrine system (Seitz & Watanabe, 2009).

While the models make clear predictions about the role of reinforcement systems in learning during the presentation of a reinforcer (i.e. target detection), they are less clear about the role of reinforcement systems in learning that happens after the target has disappeared. Below, we discuss the role of attention and arousal mechanisms in learning.

Task-Relevant and Temporally Proximal Learning

Results from Chapter 2, Experiment 2 are consistent with perceptual learning models which suggest attentional systems can influence TIL (Choi, Seitz, & Watanabe, 2009; Leclercq & Seitz, 2012a). In Experiment 2, results indicated that negative emotion targets lead to increased recognition accuracy for paired images, while positive reinforcers led to decreased target recognition speed suggesting that positive reinforcers led to a

narrowing of attention and negative reinforcers led to a broadening of attention. However, in both Chapters 1 and 2 we find that target processing leads to increased recognition accuracy for images following the target, regardless of emotion content. Because no reinforcers are presented in this time period, it is unclear how reinforcement systems play a role. Within context of the perceptual learning models this can be accounted for by invoking attentional mechanisms, such as a temporally extended alerting signal. In context of the PRA model, increased recognition accuracy post-target presentation may be due to sustained phasic activation of the locus coeruleus due to the target. Further research is needed to test these hypotheses.

The main difference between the PRA framework and the perceptual learning models are conceptual. While the perceptual learning models suggest that attentional mechanisms and reinforcement systems might share neuromodulator substrates, such as the norepinephrine system that is found to be commonly involved in reinforcement learning and attention (Aston-Jones, Peterson & Posner 2012), this assumption is built into the PRA framework. The PRA framework conceptualizes changes in arousal, as changes in the action stage that occur due to activation of norepinephrine reinforcement systems. This interpretation is consistent with the model proposed by Aston-Jones (2005). Aston-Jones (2005) proposes that the norepinephrine system has two modes: a phasic mode involved in exploitation of the currently available information and a tonic mode involved in exploration of the environment.

Additionally, changes in tonic mode of the locus coeruleus may account for the failed replication of Chapter 2, Experiment 1 patterns of TIL in Chapter 2, Experiment 2.

This result is likely due to an increase in difficulty due to methodological differences in Experiment 2. A change in difficulty would influence levels of arousal (i.e. tonic mode), as suggested by previous research (Beatty, 1982; Steinhauer et al., 2004), and interact with TIL, thus decreasing the benefits of increased recognition accuracy from phasic activation in favor of task-disengagement behavior elicited by tonic mode activation.

Strategy Learning

Finally, here, the fourth learning effect, where explicit reinforcers influence a change in behavioral strategy, is discussed. In Chapter 3 we find that over the course of task-switching training participants increase response speed at the expense of accuracy. This finding may occur from the formation of expectations of when a switch will occur, as switch trials consistently occurred every four trials. Drift diffusion modeling (DDM) results from our study and others (Cohen Hoffing, Karvelis, Rupprechter, Series, & Seitz, 2018; Karayanidis et al., 2009) further support the formation of expectations by showing that participants can shift decision criterion on a trial-by-trial basis as indicated in a decreased drift rate and increased decision boundary on switch compared to non-switch trials. The formation of expectations underlying the changes in behavioral strategies can partially be accounted for in the perceptual learning models by invoking passive learning mechanisms. For example, statistical learning research suggests that statistical regularities of the task can be picked up and learned (Bays, 2016; Seriès & Seitz, 2013).

One possible alternative mechanism of the change in behavior by feedback is a motivational one. While the role of explicit feedback can be crucial to guide behavior

where the correct response can only be learned operantly (such as in the Wisconsin Card Sorting Task), feedback can be less important in tasks where the participant knows which answers are correct and those which are not (Herzog & Fahle, 1997; Liu, Dosher, & Lu, 2014; A. R. Seitz, Nanez, Holloway, Tsushima, & Watanabe, 2006). The perceptual learning models suggest that this motivational effect may be a learning heuristic used when other learning mechanisms are not yet applied (Seitz, Kim, & Watanabe, 2007; Seitz & Dinse, 2007). Consistent with this hypothesis, in some cases, people show more learning when falsely inflated feedback is provided than when accurate feedback is provided, suggesting feedback can serve to increase learning rates rather than to supervise learning (Shibata, Yamagishi, Ishii, & Kawato, 2009).

Within the PRA framework, this motivational learning heuristic can be accommodated by invoking a reinforcement system, activated by explicit rewards, which gives rise to speeded responses at the action stage. Over the course of training, this reinforcement system contributes more to behavior relative to other reinforcement systems. In sum, passive learning, top-down control and motivational effects of feedback can explain changes in strategy selection. However, a speed-accuracy tradeoff invokes the concept of an optimization process. Extensive research has examined how cognitive systems assign value allowing for the balance of speed with accuracy (Khodadadi, Fakhari, & Busemeyer, 2014; Standage, Wang, Heitz, & Simen, 2015), but value assignment has been understudied in the field of perceptual learning. Below we further discuss the role of valuation in learning.

Towards a More Complete Understanding of Perceptual Learning: The Role of Valuation

Our results suggest there exist multiple reinforcement systems that influence learning. For example, in Chapter 2, emotion stimuli can influence the pattern of TIL, suggesting the involvement of a distinct reinforcement system. How then, is the relative influence of multiple reinforcement systems on learning decided? One possibility, is that the relative activation of reinforcement systems is decided by the relative value assignment to stimuli, where increased value assignment leads to more influence on learning signals and subsequent behavior (Gershman & Daw, 2017; Graybiel, 2008; Montague, King-Casas, & Cohen, 2006). Alternatively, one possibility is that top-down signals regulate the relative influence of reinforcement systems.

The role of top-down signals in directing reinforcement systems is consistent with the Aston-Jones (2005) model, as well as reinforcement learning literature (Gershman & Daw, 2017; Graybiel, 2008; Montague et al., 2006). The Aston-Jones (2005) model suggests the contributions of brain states to goals are evaluated. These states are then balanced to give rise to optimal behavior. In Aston-Jones (2005) a computation of the utility of how current behaviors contribute to goals, facilitate either exploration of the environment or exploitation of the environment. In this model it was hypothesized that the orbitofrontal cortex might serve the role of calculating utility and shift the norepinephrine system between phasic and tonic modes.

In line with this hypothesis, research has indicated the role of valuation in perceptual learning. Zhang and Rowe (2014), using DDM, found that a speed-accuracy

trade-off is involved in perceptual learning. DDM results indicated that speed-accuracy tradeoffs, emphasizing accuracy, occur at the beginning of training, as indicated by an increased drift rate, decision boundary and non-decision time, while perceptual learning effects, of a decreased drift rate and decision boundary, only occurred after training. Overall, these results suggest that evaluative processes play a role in perceptual learning, however more research is needed to understand their role in reinforcement systems.

Conclusion

Overall, our results are consistent with perceptual learning models that suggest that a multiplicity of processes contribute to learning, including reinforcement, attention and valuation systems. Here we further the understanding of the role of reinforcement systems in learning by providing evidence that suggests that pupillometry can be used to understand the role of the norepinephrine reinforcement system in the brain. Furthermore, a novel framework is presented, the perception-reinforcement-action framework, which reconceptualizes the role of reinforcement systems, such that actions (i.e. arousal) arise from activation of reinforcement systems, rather than arising from distinct systems.

A significant challenge for future research will be defining how multiple reinforcement systems interact to influence behavior and learning. Making progress towards developing such a comprehensive model will not only be a boon to further understanding the multiplicity of mechanisms that contribute to learning but can also be applied to create efficacious cognitive training paradigms.

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