THE EFFECTS OF EXTENSIVE SINGLE TASK AND DUAL TASK TRAINING ON THE NEURAL BASES OF VISUAL OBJECT CATEGORIZATION: ESCAPING THE FRONTAL BOTTLENECK

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By

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ABSTRACT

Perceptual learning of visual categorization has been described as a two-stage model, wherein the tuning of representations in visual areas is sharpened to the physical attributes of the stimuli and dorsolateral prefrontal areas develop task-dependent category tuning. Studies have also shown that the lateral prefrontal cortex is the source of a decisional bottleneck, limited to serial task processing, which implies a serious limitation to multitasking. However, some studies have shown the ability to multitask despite this bottleneck. Here we tested the hypothesis that extensive experience with a categorization task in single task (Study 1) and dual task (Study 2) scenarios leads to a shift in the task circuitry out of the frontal bottleneck to more posterior brain regions, accompanied by a concomitant decrease in dual task interference. We used a mobile app to attain >30,000 training trials per participant. We then assessed training related changes in the underlying neural circuitry using both fMRI and EEG rapid adaptation (RA) techniques, and changes in task automaticity using traditional lab-based behavioral testing. In Study 1, EEG-RA showed that extensive single task categorization training led to a categorical signal arising ~100ms earlier compared to initial training and MRI-RA showed numerous categorical clusters outside of the frontal bottleneck, including in left posterior parietal cortex (PPC) and ventral occipitotemporal cortex. As predicted, this posterior shift in the
underlying task circuitry was accompanied by a decreased dual task interference effect. In Study 2, after extensive dual task categorization training MRI-RA revealed categorical clusters in bilateral PPC alone. The EEG-RA results were in good agreement, revealing only one posterior categorical cluster at around 250ms. A comparison of the single task and dual task trained participants revealed a behavioral double dissociation whereby the single task trained subjects where more efficient at processing the category of single stimuli, but the dual task trained subjects showed less dual task interference on categorization. Overall, extensive training in both single and dual task conditions lead to posterior shifts in the underlying categorization circuitry and, with that, improved dual tasking abilities.
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1. INTRODUCTION

Object categorization is a foundational cognitive process that is essential in our everyday lives. Throughout the day we are constantly making categorical decisions from the food we choose to eat (“is this peach ripe or rotten?”), to assessments about mood from a friend’s face (“is this person happy or sad?”), to which car to get into for your ride home (“is this car a Honda Civic with license plate number ABC1234?”). Some of the category decisions we make throughout the day are mediated by conscious effortful processing, but a vast majority happen automatically. Furthermore, new categories can be learned and through practice categorization can be converted from effortful to effortless, with the ability to be done in parallel with another attention-demanding task. As already noted by William James (1890), “actions originally prompted by conscious intelligence may grow so automatic by dint of habit as to be apparently unconsciously performed. Standing, walking, buttoning and unbuttoning, piano-playing, talking, even saying one's prayers, may be done when the mind is absorbed in other things.” The neural basis for the automatization of object categorization and the implications for the resulting ability to multitask are not well known. In today’s world, with it’s increasing pressure to process and interact with multiple streams of information at once, understanding the brain’s ability to automate processes and multitask is more important than ever. The studies described here investigate the neural underpinnings and behavioral changes that result from extensive categorization training (>30,000 trials) in both single task and dual task scenarios and are aimed at testing the hypothesis that extensive training leads to categorization task circuitry, specifically the mapping of the stimulus to a semantic label,
outside of prefrontal cortex (PFC) freeing the categorization decision from the “frontal bottleneck”.

1.1 The Neural Mechanisms Underlying the Learning of Visual Categorization

Computational models of cognitive functions provide an invaluable framework for formulating new hypotheses, as well as integrating and interpreting data across multiple modalities, from single unit recordings to imaging of whole brain networks with fMRI and EEG, and all the way on to behavior. This approach has proven particularly fruitful in the area of visual object recognition and categorization, i.e., the mapping of sensory stimuli to semantic labels (Ashby, Ennis, & Spiering, 2007; Ashby & Maddox, 2011; Riesenhuber & Poggio, 2000). Visual image categorization is mediated by the ventral stream, a simple to complex processing hierarchy that builds up object-level representations from simple features (oriented edges represented in V1, to intermediate-level features in V2/V4, and culminating in whole-object tuned neurons in inferotemporal cortex (IT), in the monkey, or its homologue, the lateral occipital complex (LOC) in the human (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). The Riesenhuber and Poggio (2000) model predicts that neurons in IT/LOC should come to acquire sharper tuning with a concomitant higher degree of selectivity for the trained stimuli, without an explicit representation of category, and that such neurons provide a computationally efficient representation for downstream neurons to learn different tasks. Monkey studies (Freedman, Riesenhuber, Poggio, & Miller, 2003; H. Op de Beeck, Wagemans, & Vogels, 2001; Thomas, Van Hulle, & Vogels, 2001), as well as human fMRI rapid adaptation (fMRI-RA) studies (Gillebert, Op de Beeck, Panis, & Wagemans, 2009; Jiang
et al., 2007; van der Linden, van Turennout, & Indefrey, 2010) have provided support for this two-stage model of perceptual category learning (Ashby & Lee, 1991; Nosofsky, 1986; Panis, Vangeneugden, Op de Beeck, & Wagemans, 2008; Riesenhuber & Poggio, 2000; Thomas et al., 2001) by showing that while categorization training appeared to sharpen the selectivity of neurons in IT/LOC for the trained stimuli (Freedman et al., 2003; Freedman, Riesenhuber, Poggio, & Miller, 2006; Gillebert et al., 2009; Jiang et al., 2007; van der Linden et al., 2010), these neurons appeared to represent physical shape similarity only rather than category membership, and it was in PFC that neurons emerged that were selective for the categorization task (Freedman, Riesenhuber, Poggio, & Miller, 2001; Jiang et al., 2007).

Current theory posits that learning different categorization tasks on the same stimuli (e.g., “sports car” vs. “sedan” or “American car” vs. “European car”) leads to the development of separate groups of neurons in PFC selective for these different tasks, all receiving input from a common representation selective for stimulus shape (Riesenhuber & Poggio, 2000). The activation of these task modules is subject to cognitive control mechanisms (Miller & Cohen, 2001) to ensure activation of the appropriate task circuits and suppression of inappropriate ones. Support for this model comes from recordings of lateral PFC neural activity while monkeys switched between categorizing the same image set along two different category schemes with orthogonal boundaries which found that each category scheme was largely represented by independent PFC neuronal populations and that activity reflecting a category distinction was suppressed when that category was irrelevant (Roy, Riesenhuber, Poggio, & Miller, 2010). Similarly, in a human fMRI study
activation of a category-selective ROI was suppressed when the subject was performing a different task on the same stimuli (Jiang et al., 2007). Thus, the cognitive control system serves to reduce interference between competing task representations and goals by only permitting one task circuit to be active at a particular time. Indeed, a pair of human fMRI studies has elegantly shown regions in the PFC that are unable to process two decision-making operations simultaneously (Dux et al., 2009; Dux, Ivanoff, Asplund, & Marois, 2006).

1.2 The Prefrontal Response Bottleneck

The inability of prefrontal cortex to support more than one task at a time (Dux et al., 2009, 2006) has been postulated to underlie the behavioral “bottleneck” (Pashler, 1994) often found in situations in which subjects are asked to perform two attention-demanding tasks at the same time (“dual tasking”, DT, see next section). Performance on the combined task is poorer than when performing either task independently indicating the presence of the “bottleneck”. This theory of a “central bottleneck” or “response selection bottleneck” posits that certain central operations – including response selection but also decision-making and memory retrieval – cannot be performed in parallel (Levy, Pashler, & Boer, 2006). Indeed, it was found that an area at the inferior frontal junction (IFJ) in posterior lateral PFC, previously shown to be critical for cognitive control, showed response characteristics compatible with this response-selection bottleneck, in that response selection for the second task would be postponed until completion of response selection for the first task (Dux et al., 2006). This delay in processing gives rise to the “psychological refractory period”, referring to the period over which the reaction time to
task 2 is slowed. Thus, this theory argues that dual-tasking depends on a lateral frontal network to control switching from one task to the next (Goodwin, Blackman, Sakellaridi, & Chafee, 2012; Hartley, Jonides, & Sylvester, 2011), and that it is this switching that creates the bottleneck.

1.3 Improving Dual Tasking Abilities: Circumventing the Bottleneck

Whether the response selection bottleneck can be circumvented, resulting in the ability to perform a task in parallel with another, attention-demanding task (commonly taken to be the defining characteristic of task automaticity (Helie, Waldschmidt, & Ashby, 2010; Schneider & Shiffrin, 1977)), has been the subject of intense debate (see, e.g., (Greenwald, 2005)). A number of studies have demonstrated that training in at least some DT scenarios can lead to task automaticity, as defined by the disappearance of DT costs. For instance, Schumacher and colleagues found that after five practice sessions on a simultaneous presentation (0ms stimulus onset asynchrony, SOA) DT scenario involving an audio-vocal and a visual-motor task, dual-tasking costs were negligible, i.e., there was no significant difference in execution speed for the two tasks whether they were executed together or separately (Schumacher et al., 2001). Similarly, others studies have shown that DT practice could eliminate the bottleneck in simultaneous presentation paradigms and those with varying SOA and lead to automatic execution of one or both tasks (Hazeltine, Teague, & Ivry, 2002; Ruthruff, Hazeltine, & Remington, 2006). Likewise, Hommel (1998) showed that stimulus-response translation could occur in parallel in a number of different tasks. These and similar findings of automaticity (Greenwald, 1972; Lien, McCann, Ruthruff, & Proctor, 2005) have led to theories that some tasks can be
processed in parallel without DT costs as they can be processed by a “privileged loop” (Mcleod & Posner, 1984) that bypasses the central response selection bottleneck. Thus, these theories argue for a qualitative change in the neural substrate mediating the execution of highly practiced tasks.

1.3.1 Visual Dual Task Paradigms: A Testbed for Automaticity and Parallel Task Execution

The domain of visual perception is well suited to investigate parallel processing in the brain, as the technique of visual masking affords an opportunity to enforce that the perceptual information relevant for the two tasks is indeed processed concurrently, which is difficult if not impossible to enforce when using unmasked presentation – in particular in multimodal paradigms commonly used in dual-tasking studies (Dux et al., 2009, 2006; Kamienkowski & Sigman, 2008; Ruthruff, Van Selst, Johnston, & Remington, 2006; Schumacher et al., 2001) that combine, e.g., a visual and an auditory task. Moreover, it has been shown that subjects are better able to perform target detection in concurrent streams if targets are in different sensory modalities than when they are in the same, e.g., visual, modality (Duncan, Martens, & Ward, 1997). Thus, the concurrent masked presentation of two visual tasks appears best suited to maximally tax the prefrontal bottleneck, as it requires the parallelization of the categorization, i.e., the stimulus-label mapping. Indeed, it has been shown that there is usually interference if subjects are asked to perform two visual tasks in parallel (Braun, 1994; Lee, Koch, & Braun, 1999). Nevertheless, it has been shown that some complex visual tasks can be performed in parallel with another, attention-demanding task. For instance, subjects can perform
animal detection in natural scenes concurrently with attention-demanding tasks such as rotated letter discrimination or bisected disk color judgments (Fei-Fei, VanRullen, Koch, & Perona, 2005; Li, VanRullen, Koch, & Perona, 2002). However, it is still unclear why some complex visual tasks can be performed concurrently with attention-demanding tasks while others cannot. It has been suggested (VanRullen, Reddy, & Koch, 2004) that an object category can be processed in parallel if there exists a neuronal population selective to this category. In contrast, our data suggest that the presence of a neural representation selective for the target objects is not sufficient for parallel processing. Rather, we propose that a shift of task circuitry outside the prefrontal bottleneck is the crucial enabling step for automaticity as assessed by dual tasking.

1.4 A Theory of Task Automaticity: Escaping the Bottleneck by Offloading

Stimulus-to-Label Decisions to Parietal Cortex, Label-to-Response Mapping to Premotor Cortex

In contrast to the behavioral results arguing for a qualitative shift of the underlying neural processing for automatic tasks, several prior neuroimaging studies of automaticity (Poldrack et al., 2005; Wu, Kansaku, & Hallett, 2004) (in which subjects were trained on a specific task until it could be performed in addition to another, attention-demanding task) have only identified widespread response decreases across cortex, but little evidence for response increases outside the prefrontal bottleneck that could account for the subjects’ ability to perform tasks automatically. This creates the puzzle of how mere response decreases can account for the qualitatively new ability to perform the task in parallel (see (Mazzoni, 2008))?
A possible interpretation of the null result in the aforementioned studies might be lack of sensitivity, or the problem that constant activation levels might mask underlying changes in neuronal selectivity (see section 1.5 below). A more positive answer comes from a recent study (Helie, Roeder, & Ashby, 2010) which provided evidence that extended practice of a perceptual classification task caused a shift of cortical activation from lateral PFC toward posterior cortical regions, in particular premotor cortex (PMC). These results are compatible with a monkey electrophysiology study (Muhammad, Wallis, & Miller, 2006) that showed that after extensive practice on a rule-based task (“same” vs. “different”), neurons in PMC appeared to encode the task and responses earlier than in PFC. Yet, a more recent study (Cromer, Roy, Buschman, & Miller, 2011), in which monkeys had to execute a perceptual match-to-category task on stimuli similar to the morphed car categories described in section 2.2.3, revealed a more complex picture: In that study, PMC neurons were found again to encode match/non-match activity similar to the earlier study (Muhammad et al., 2006). Crucially, however, PMC neurons were found to show little selectivity for the perceptual categories (Cromer et al., 2011), suggesting that the mapping of stimuli to labels, i.e., the actual categorization, occurred somewhere else. This result is compatible with a recent behavioral study that showed that category learning appears to be mediated by separate stimulus-to-label and label-to-response associations (Maddox, Glass, O’Brien, Filoteo, & Ashby, 2010). Taken together, these fMRI, electrophysiological and behavioral data thus suggest the hypothesis that PMC implements the mapping of decisions (for instance, category labeling) to responses, in situations where there is a fixed label-response link, but raise the crucial question where
in the brain the mapping of stimuli to labels could be computed for highly familiar tasks not subject to the prefrontal bottleneck. A requirement for a candidate region is that it, similar to PMC, would need to be connected to the PFC to permit efficient transfer of task circuits. One such candidate region is parietal cortex (Cavada & Goldman-Rakic, 1989; Petrides & Pandya, 1984). Intriguingly, a number of human studies, using fMRI (Rivera, Reiss, Eckert, & Menon, 2005; Sakai et al., 1998) and ERP (Staines, Padilla, & Knight, 2002) have reported that extensive task practice appears to shift task-related activations from frontal to parietal regions. Such a role of parietal cortex as driving the execution of highly familiar tasks is also supported by a number of monkey studies that have broadened the role of parietal cortex, in particular of the lateral intraparietal area (LIP, the monkey homolog of human intraparietal sulcus, IPS (Culham & Kanwisher, 2001; Orban et al., 2006)), in decision-making: While it has long been well established that LIP neurons are modulated by spatial attention and eye movements, and can encode decision-related signals preparatory to a motor response (Gold & Shadlen, 2001), more recent results have shown that LIP neurons can represent decisions independently of how they are reported (Bennur & Gold, 2011). Other studies have shown that LIP neurons can also encode abstract perceptual category memberships (for motion (Freedman & Assad, 2006) and shape (Fitzgerald, Freedman, & Assad, 2011) categories) not linked to specific motor responses. Most relevant for this proposal, a study (Swaminathan & Freedman, 2012), recording from both PFC and LIP while monkeys were performing a perceptual categorization task (the same motion categorization task as in (Freedman & Assad, 2006)), found category signals in both LIP and PFC. However, category signals were stronger, more reliable and had a shorter latency in LIP compared to PFC. As the
monkeys were well familiar with the categorization task, these data are compatible with the hypothesis that, with practice, task execution moves from prefrontal to parietal circuits. *Taken together, these data suggest the hypotheses that task automaticity is associated with a shift of task circuitry computing the stimulus-label link from lateral PFC to posterior parietal cortex. In cases where there is a fixed link between label and behavioral response, this mapping would be computed in PMC, based on inputs from regions in parietal cortex computing the response-independent stimulus-label association.*

### 1.5 Using Rapid Adaptation Imaging Techniques to Measure Category Learning

**Induced Changes in Neural Selectivity**

A significant amount of research activity has focused on elucidating the neural bases of human task learning (Kelly & Garavan, 2005). Functional magnetic resonance imaging (fMRI) studies of learning typically compare blood oxygenation level dependent (BOLD)-contrast responses before and after training and have shown mixed results. Previous studies have found that perceptual and category learning can induce fMRI signal response increases (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; H. P. Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Pollmann & Maertens, 2005), decreases (Helie, Roeder, et al., 2010; Reber, Stark, & Squire, 1998) or both (Aizenstein et al., 2000; Kourtzi, Betts, Sarkheil, & Welchman, 2005; Little, Shin, Sisco, & Thulborn, 2006). This may be explained by the fact that increases in neuronal selectivity, a key component in many models of perceptual learning (Lu & Dosher, 2004), leads to neurons that respond to fewer stimuli (Freedman et al., 2006; Rainer & Miller, 2000). An increase
in selectivity without a change in the number of neurons in an area tuned to a stimulus of interest would lead to a decrease in average response, but training may also increase the number of neurons selective to a stimulus of interest in an area and an increase in the average response could be seen. A method known as fMRI-rapid adaptation (fMRI-RA) has been shown to be able to directly test the selectivity of a certain area for a stimulus feature of interest (Grill-Spector, Henson, & Martin, 2006), making it an incredibly useful approach for studying perceptual learning (see below).

Measuring neural selectivity with non-invasive imaging techniques poses a real difficulty. The BOLD signal response from an fMRI voxel containing hundreds of thousands of neurons could be of equal amplitude if the given voxel is populated by broadly tuned neurons that are all responding at a low level or populated by selectively tuned neurons that are responding much more sparsely but at a much higher level. FMRI adaptation techniques can be used to circumvent fMRIs limited spatial resolution (Grill-Spector et al., 1999) and probe selectivity at the sub-voxel level (Grill-Spector & Malach, 2001; Krekelberg, Boynton, & van Wezel, 2006). These adaptation techniques were motivated by monkey electrophysiology recordings in IT showing that when the presentation of a given stimulus is repeated the neuronal response to the second presentation is adapted, i.e. diminished compared to the first (Miller & Desimone, 1994; Miller, Li, & Desimone, 1991). In agreement with more recent monkey electrophysiology (De Baene & Vogels, 2010), fMRI-RA studies have shown that the amount of adaptation is strongly dependent on the feature similarities between a pair of sequentially presented stimuli, with the greatest adaptation occurring for a repeat of the same stimulus (Fang,
Murray, & He, 2007; Gilaie-Dotan & Malach, 2007; Jiang et al., 2006, 2007; Murray & Wojciulik, 2004; Panis et al., 2008).

EEG has the benefit of much higher temporal resolution than fMRI hemodynamic measurements since it is a direct measure of neural activity, but EEG is measuring average signal over a much broader neuronal population than what is inside a fMRI voxel making it hard to determine the selectivity from tradition measures like ERP amplitude. Although the rapid adaptation technique has been used more often in fMRI, it has also been leveraged in the realms of EEG and MEG to measure adaptation effects on amplitudes of specific components, for example the N170 in face processing (Harris & Nakayama, 2007; Kovács, Zimmer, Harza, & Vidnyánszky, 2007). Particularly relevant to this current project, M/EEG-RA has been used to study changes in shape and category selectivity during perceptual category learning (Kietzmann, Ehinger, Porada, Engel, & König, 2016; Scholl, Jiang, Martin, & Riesenhuber, 2014). The combination of fMRI-RA and EEG-RA experiments in the studies presented here provides a powerful approach to assessing the spatial and temporal characteristics of category selective neuronal responses.

In order to fully leverage the strengths of RA approaches it is necessary to have a set of stimuli that varies the feature of interest in a controlled manner. For the studies described here the features of interest are stimulus category and shape. Controlling for shape differences within versus across categories in natural stimuli is very difficult if not impossible (but see (Gotts, Milleville, Bellgowan, & Martin, 2011) for one approach).
One solution to this shape similarity within category problem that has been successfully used in monkey electrophysiology studies of shape and category representations is to use morphed stimulus spaces (Freedman et al., 2001, 2003, 2006; H. Op de Beeck et al., 2001). This approach has also been applied to a number of RA studies of human category learning (Gillebert et al., 2009; Jiang et al., 2007; Scholl et al., 2014; van der Linden et al., 2010). In particular, the following studies leveraged the car morphed stimulus space created with morphing software (Shelton, 2000) (see section 2.2.3) that previous training studies from our lab have successfully used in both fMRI-RA (Jiang et al., 2007) and EEG-RA (Scholl et al., 2014) paradigms to explore the neural basis of categorization after the category boundary is initially learned.

1.6 Behavioral Measures of Automaticity

It is almost ubiquitous in training studies that practice on a cognitive task leads to improvement in accuracy and decreases in response time (RT), but at what point can a cognitive process be called automatic? Many studies define it with respect to those very improvements in behavior, concluding that automaticity has been reached once participants have trained beyond point that increases in accuracy and decreases in RT asymptote (Ashby, Turner, & Horvitz, 2010; Helie, Roeder, et al., 2010). Another popular criteria proposed by Schneider & Shiffrin, (1977) is that a process is automatic when it is efficient with respect to the amount of attention it requires and can, therefore, successfully be executed in parallel with another attention-demanding task. However, Moors & De Houwer (2006) argue that automaticity is a continuum and should not be treated as a binary classification based on just one criterion. They propose a feature-based
approach where different aspects of automaticity are tested for the cognitive process of interest. The features they propose include efficient (with respect to attention), unconsciously processed, fast, and a set of features related to goal-independent processing. Here we adopted this approach to assess the automaticity of stimulus-to-label mapping of trained car stimuli. We used a dual task paradigm to test efficiency, a masked priming paradigm to test unconscious processing, and used RT in general across tasks as a proxy for the fast processing feature. This approach is in good agreement with the conclusion from Helie, Waldschmidt, et al. (2010), that there are multiple potential systems underlying categorization that will show different aspects of automaticity at different points along the training time course. In the studies that follow we investigated the relationship between these features of automaticity and the neural correlates of visual categorization observed in our EEG-RA and MRI-RA measures after extensive training in single and dual task scenarios.

1.7 Outline of the to be Discussed Studies

Chapter 1: Categorization before and after extensive single task categorization training.

• Pre-extensive single task training (after ~6,000 trials) EEG and fMRI rapid adaptation measurements taken after initial training (this time point roughly matched the previous work in the lab (Jiang et al., 2007; Scholl et al., 2014).

• Post-extensive single task training (>30,000 single task training trials) EEG and fMRI RA data collected to measure the shift in time and space in the underlying neural circuitry.

• Measures of automaticity at both the “Pre” and “Post” time points.
Chapter 2: Categorization after extensive dual task categorization training.

- Post-extensive dual task training (>30,000 dual task training trials) EEG and fMRI RA data collected.
- Measurements of automaticity at equivalent time points as above (after ~6,000 trials and after >30,000 trials).

Chapter 3: Comparison of single task and dual task categorization training.

- MRI-RA: dual vs. single pre, dual vs. single post.
- Behavior comparisons for measures of automaticity.
2. SINGLE TASK EXTENSIVE CATEGORIZATION TRAINING

2.1 Introduction

Categorization is a foundational cognitive process that much of our higher cognition is based on. In our day-to-day lives we are constantly categorizing, and in most cases it is automatically done on familiar categories (Ashby & Maddox, 2011). However new categories can be learned, as well, and category decisions are not carried out automatically early on in the learning. Despite the fact that the automatic categorization of highly familiar objects is undoubtedly more prevalent in our daily lives as adults, the initial phase of training is more studied than extensive training because, first and foremost, the initial phase is far easier to study (Ashby & Maddox, 2011). Typical human training paradigms on cognitive tasks are brief, consisting of only a few hours of training, and, therefore, likely missing the full extent of practice related changes (Kelly & Garavan, 2005).

One example of a more extensive categorization training study (>10,000 trials, over 20 sessions) showed evidence that the striatum is important for learning at the very beginning, followed by a fairly quick transition to prefrontal cortex (PFC), but by late in extensive training the premotor cortex (PMC) was the most closely associated with performance (Helie, Roeder, et al., 2010). This finding is consistent with the theory that the striatum trains the PFC during the early phase of task learning (Antzoulatos & Miller, 2014; Ashby et al., 2007; Pasupathy & Miller, 2005). Further converging results from monkey electrophysiology studies, where the amount of training is often substantially
longer, showed that after over a year of training on a same/different task, the PMC encoded the task and response information before PFC (Muhammad et al., 2006). However, follow-up work by that same group showed that the PMC lacked any category information about the stimuli on which the same/different decision was being made (Cromer et al., 2011), suggesting that the actual categorization, the mapping of labels to the stimulus, occurs somewhere else. In support of this idea, human behavioral results have shown that category learning is mediated by forming separate stimulus-to-label and label-to-response associations (Maddox et al., 2010). Taken together these findings support the idea that after extensive training the PMC computes the label-to-response mapping. However, the question remains, where is the stimulus-to-label mapping computed?

Imaging studies that perform sufficient category training to achieve automaticity are rare (Kelly & Garavan, 2005). However, as previously mentioned, monkey electrophysiology studies are often done while the monkeys perform extensively practiced tasks. Therefore, we look to categorization studies in that literature. It has long been known that the posterior parietal cortex (PPC), in particular the lateral intraparietal area (LIP, monkey homologue of the human intraparietal sulcus IPS (Culham & Kanwisher, 2001; Orban et al., 2006)), represents decision-related signals in preparation for motor movements (Gold & Shadlen, 2001). It has more recently been shown that LIP neurons can represent decisions independently of the motor response (Bennur & Gold, 2011). Furthermore, LIP neurons can encode abstract category membership determined by motion (Freedman & Assad, 2006) or shape (Fitzgerald et al., 2011) features, also independently of motor
response. Most pertinent to the current study, Swaminathan & Freedman (2012) recorded from LIP and PFC using the same motion-based categories as (Freedman & Assad, 2006), and found that, while populations of neurons in both areas encoded category membership, the category signal in LIP was more robust and at a shorter latency than the category signal in PFC. This provides evidence that, with extensive training, the PPC can lead prefrontal cortex in representing category decisions, at least in monkeys, making it a candidate for the locus of the stimulus-to-label mapping outside of the frontal bottleneck. Interestingly, some fMRI studies in humans have demonstrated a shift in activity from PFC to parietal with training in areas as diverse as visuomotor sequence learning (Sakai et al., 1998) and arithmetic (Rivera et al., 2005).

In this study we tested the hypotheses that task automaticity is associated with a shift in the task circuitry computing the stimulus-label link from lateral PFC to PPC by extensively training participants (>30,000 trials) on a morphed stimulus space that the lab has previously used (Jiang et al., 2007; Scholl et al., 2014), and imaging them using both EEG-RA and fMRI-RA at a “Pre” time point, after initially learning the categories (a similar amount of training compared to our previous studies (Jiang et al., 2007; Scholl et al., 2014)) and a “Post” time point after completing the extensive training protocol. Support for the stimulus-to-label computation initially taking place in PFC was seen in the EEG-RA “Pre” data where the earliest categorical signals began after ~250ms over left frontal channels, in agreement with the previous findings from Scholl et al. (2014). The fMRI-RA “Pre” data provided converging evidence, showing only one categorical cluster in the left middle frontal gyrus (MFG). Support for the shift to parietal areas after
extensive training was seen in the EEG-RA “post” data with a shift of the earliest categorical signal to a more posterior scalp topography ~150ms, and in the fMRI-RA “Post” data where, among other areas, categorical clusters in the left superior parietal lobule (SPL) and left inferior parietal lobule (IPL) were found.

2.2 Methods

2.2.1 Study Overview

This study was divided into six phases (Figure 1: Single task extensive training study overview. A): (1) initial training, (2) pre-extensive practice imaging, (3) pre-extensive practice behavioral testing, (4) extensive practice, (5) post-extensive practice imaging, and (6) post-extensive practice behavioral testing. In phase 1, participants came into lab for consenting and a baseline shape discrimination testing session and then learned pseudoword labels for morphed car images, completing ~6000 trials in one week. In phase 2, participants completed EEG and fMRI Rapid Adaptation sessions (separately, order counterbalanced across participants) with a same/different category task. In phase 3, subjects completed a five-session behavioral battery designed to measure markers of extensive practice. In phase 4, participants practiced the label training extensively, completing one round of training (~6,000 trials) per week for four weeks, and coming into lab for a single testing session between each round of training. In total, participants completed ~30,000 trials of single task car label training. In phases 5 and 6, participants repeated imaging and behavioral tests from phases 2 and 3.
2.2.2 Participants

Thirty-two subjects enrolled in the study, two failed to meet training criteria (see Section 2.2.5 below), one was excluded because of excessive motion in the pre-extensive training MRI scan, one was excluded because of the pharmaceutical exclusion criteria, and fourteen dropped out over the course of training. Fourteen (ten female, mean age = 23.37 years, range = 18-29 years) normal right-handed members of the Georgetown University community completed the training. Three participants were excluded from the analysis because of low performance after initial training on the MRI and EEG task (accuracy two standard deviations below the mean), resulting in a sample of eleven participants (eight female, mean age = 23.4 years, range = 18-29 years). The Georgetown University Institutional Review Board approved experimental procedures, and written informed consent was obtained from all participants before the experiment.

2.2.3 Stimuli

Participants were trained to visually categorize gray-scale car image stimuli generated by a morphing algorithm capable of finely and parametrically manipulating stimulus shape (Shelton, 2000). The algorithm finds corresponding points between car prototypes and computes their differences as vectors. Morphs of two or more prototypes are then computed by adding linear combinations of these difference vectors to a given prototype.
As in our previous studies (Jiang et al., 2007; Scholl et al., 2014), we used this algorithm to generate a large continuous set of images from four car prototypes. The four prototype stimuli were chosen from an initial set of fifteen based on a previous pilot experiment that showed that these four prototypes were of comparable perceptual dissimilarity. Two of the prototypes were assigned to category A and the other two prototypes were assigned to category B, and the categories were given the pseudoword labels “SOVOR” and “ZUPUD” (Scholl et al., 2014). By combining different amounts of the four car prototypes we could generate thousands of unique images, continuously vary stimulus shape, and precisely define category boundaries (Figure 2: Morphed car stimuli.). The category of each stimulus was defined by whichever category prototypes contributed more (>50%) to a given morph (Freedman et al., 2003; Jiang et al., 2007; Scholl et al., 2014). Thus, pairs of stimuli could be physically similar yet situated on opposite sides of the category boundary, as well as physically dissimilar but in the same category. This careful control of physical similarity within and across categories allowed us to disambiguate the neural signals related to category membership from neural signals related to stimulus shape (see Sections 2.3.2 and 2.3.3).
Images composed of blends of three or four prototypes were used for label training and symmetrically spanned a four-dimensional prototype morph space excluding a corridor of distances less than 5% from the category boundary, and the orthogonal hyper-planes in the four-dimensional space. Subsets of these three or four prototype morphs were used in some of the other in lab behavioral tests (see below). The morphing of two prototypes allows us to create a “morph line” by parametrically varying the shape from one prototype to the other over a set of equally spaced discrete jumps in shape space (Figure 2). This allows us to refer to an absolute location on a morph line from car A to car B in terms of a percentage. For example the 35% location along a morph line from car A to car B would be made up of 65% car A and 35% car B. This also allows us to refer to the
morph distance between two stimuli on a morph line in terms of a percent difference, e.g. cars at 40% and 60% absolute location along a morph line are 20% morph distance apart. Given the four prototypes that make up our stimulus space, two for each category, there are six morph lines with four crossing the category boundary and two that are within category. For the most part we will be looking at the four cross-category morph lines and for consistency we will set the convention that the cross-category morph lines go from SOVOR to ZUPUD.

Some of the in lab behavioral experiments used stimuli from the training (masked priming, see Section 2.2.7), and some used stimuli from the two prototype morph lines (dual task categorization testing, see Section 2.2.6). In order to reduce the repetitions of the exact same car stimuli we created a set of jittered morph line stimuli that were centered at various positions along the cross category morph lines, but then up to 10% of the other two prototypes were added in equal parts so that the relative position along the original morph line and distance to the boundary were maintained. Categorization testing (see Section 2.2.5) and both the EEG (Section 2.2.8) and fMRI (Section 2.2.9) experiments used these jittered morph line stimuli.

2.2.4 Training

Participants completed category label training remotely with a mobile application on Android, Windows or Mac that recorded data in a MySQL database on a local webserver. The application was powered by Mono, an open source programming language developed by Xamarin. Unity 4.1.5f1 was used as the framework for deployment.
As in Scholl et al. (2014) participants learned to categorize the novel car stimuli into two categories labeled “SOVOR” and “ZUPUD.” A single training trial consisted of a test stimulus presented for 400ms, followed by a 300ms mask, followed by the two category labels positioned on the left and right sides of the screen (Figure 3B). Participants had up to 3000ms to indicate the correct label of the test stimulus with the left or right arrow key, and they were instructed to respond as fast as possible without making mistakes. Incorrect responses elicited auditory feedback along with a display containing the correct label adjacent to the test stimulus that participants viewed as long as desired. The grayscale car images were presented on a white background for training. Training images varied in size (between 200 and 320 pixels wide) and had different resolutions to prevent participants from focusing on local cues and to discourage a strategy based on latching on to individual local image differences.

Each round of training was broken down into 30 levels and accuracy of at least 90% had to be achieved to pass a level. The difficulty of the categorization task increased with level by introducing morphs with increasingly greater contributions from the non-dominant category until participants could reliably (accuracy > 90%) identify the
category membership of 200 randomly chosen images composed of up to 45% of the other category after the first round of training. Left/right locations of the labels were swapped by level to avoid spatial associations with the category labels. Each round of app training was roughly equivalent to the complete training protocol in Scholl et al. (2014). Each round was also similar to Jiang et al. (2007) with the difference being that category labels were not assigned in that study; instead, category groupings were learned using a two-alternative forced choice task. In order to study the effects of extensive training on visual categorization, we had participants complete five rounds of the app training. Each round of training took approximately 3 hours to complete on average, had to be finished in less than 2 weeks, and contained at least 6,000 trials (more if subjects had to repeat a level) resulting in a minimum of 30,000 trials in aggregate over the course of training.

2.2.5 Categorization Testing

Following the completion of the first round of app training, participants were tested on their categorization performance in the lab. Trial timing and presentation arrangement were the same as during training but differed in that no feedback was provided, the grayscale car images were presented on a neutral gray background for testing instead of a white background, and stimulus presentation was controlled by the Psychtoolbox package in Matlab (Brainard, 1997). As in Scholl et al. (2014) and Jiang et al. (2007) the stimuli used for testing were based on morphs of two prototypes belonging to different categories and were, therefore, distinct from the stimuli used for training, which were based on morphs of three to four prototypes, thus testing participants’ ability to generalize. For
category label testing 21 positions at 5% increments along each of the four distinct cross-category morph lines were used as the anchoring locations, and ten repetitions of each stimulus were presented in randomized order with 1-10%, in steps of 1%, combined contribution of the other two prototypes added (See jittered stimuli above). In order to identify the position of each participants’ learned category boundary along each cross-category morph line, categorization performance was fit on an individual participant basis for each morph line with a sigmoid function \( f(x) \), with \( x \) being the morph position along the morph line from SOVOR to ZUPUD (0 to %100), and parameters for the location of the category boundary (\( \beta \)), the rate of the change across the boundary (\( t \)), and the upper (\( a \)) and lower (\( c \)) limits of performance, as in Scholl et al. (2014) and Jiang et al. (2007):

\[
f(x) = \frac{a}{1 + e^{-(\beta-x)/t}} + c
\]

The parameter estimate for the category boundary location on each line was used to determine if a participant had learned the category well enough to move on to the first imaging time point and subsequent extensive training phase. Given that the imaging phase requires categorizing stimuli at 35% and 65% along the morph line (see Section 2.2.8 and Figure 5), the advancement criterion for the category boundary location was conservatively set at 40%<\( \beta <60\% \) for each cross category morph line.

2.2.6 Dual Task Training/Testing

The participants performed a dual task car categorization test after the first round of app training and again after all five rounds of app training in order to test the hypothesis that extensive categorization training leads to a decrease in the amount of attention needed for categorization, as evidenced by an increase in categorization performance in the presence
of another attention-demanding task after extensive training (Fei-Fei et al., 2005; Li et al., 2002). After the first round of app training, in order to acclimate participants to the difficulty of having to respond to two simultaneously presented stimuli without training them on car categorization dual tasking directly, participants were first trained on five sessions of an animal/no-animal dual task paradigm similar to (Fei-Fei et al., 2005; Li et al., 2002) (Figure 4). The training task was made up of three block types: 1) peripheral-only, where participants had to indicate which side of a vertically bisected disk was red (the other side was green), a task that has been shown to remain attention-demanding even after extensive practice (Fei-Fei et al., 2005; Li et al., 2002), 2) central-only, where participants had to decide if a natural scene flashed at fixation contained an animal or not, and 3) dual, where both stimuli appeared simultaneously and subjects had to respond to both. On peripheral-only trials a 33ms cue indicated the position of the disk, which could be anywhere along an invisible circle of radius 6 degrees of visual angle centered at fixation, followed by another 33ms of fixation, then the disk stimuli came on for 33ms, which was masked after a stimulus onset asynchrony (SOA) of variable length depending on performance. On the central-only trials initial fixation was followed by a natural scene image, which might or might not contain an animal, for 33ms, followed by a mask after a performance-dependent variable SOA. The natural scenes were randomly selected on each trial from a set of 500 scenes with animals and 500 scenes without animals. The dual trials combined the peripheral- and central-only tasks, with the natural scene and the disk appearing simultaneously. For all trial types the masks remained on the screen until the participant keyed in their response. Participants responded to the central task with the “S” key for animal and “D” key for no-animal with their left hand and the arrow keys for
the direction the red side of the disk was facing with their left hand, and were instructed to respond to the peripheral stimulus first on the dual trials. Each training session was made up of six groupings of each of the three block types, each consisting of 45 trials. The order that the six block groupings were presented was counterbalanced across the run such that each of the six possible permutations of the ordering of the three block types happened once. On each trial, the correct responses (left/right for the disk, animal/no-animal for the natural scene) were equally likely and trial order was randomized. Feedback tones were provided after each trial, a shorter 100ms lower 800hz tone indicated a correct response and a longer 500ms higher 1200hz tone indicated an incorrect response. On dual trials the feedback for the peripheral task came first, followed by the feedback for the central task. Percent accuracy was reported to the participant after each block. The initial values of the SOA between the stimulus and the mask were set to 150ms for the peripheral task and 100ms for the central task. After each grouping of the three block types the SOA for a given task was decreased by 33.3ms if the accuracy exceeded 85% for that task in the single or dual task condition, and the SOA was increased by 16.7ms for a given task if the accuracy was below 70% for that task in the single or dual task condition. At the end of five runs of training on the animal/no-animal dual task paradigm over five separate sessions, the central task was replaced with a SOVOR/ZUPUD decision task for car dual task testing. The car stimuli were taken from the two prototype morph lines, in 5% increments with the positions around the category boundary (45%, 50% and 55%) left out. The SOAs from the end of each participant’s dual task training were used for testing and, aside from there being no feedback and 36 trials a block for 30 blocks instead of 45 trials a block for 18 blocks, all other aspects of
the paradigm remained the same. After completing the rest of the five rounds of car categorization training on the app, participants completed one refresher round of animal no-animal dual task training, and then were tested on the car dual task paradigm again using the same SOAs.

![Figure 4: Dual task paradigms. A) Animal/No-animal dual task training. B) Sovor/Zupud dual task car categorization testing.](image)

### 2.2.7 Masked Priming

To study whether categorization training led to automatic unconscious processing of the category membership of a stimulus we tested 8 of the 11 participants on a masked priming paradigm. We ran masked priming after each round of training, for a total of five sessions. The trial timing and structure was adapted from successful masked priming experiments in the word processing literature (Malone, Glezer, Kim, Jiang, &
Riesenhuber, 2016; Quinn & Kinoshita, 2008). A trial began with a high contrast forward mask for 500ms, followed by a prime car stimulus presented for 66.7ms, and then a target car was presented immediately after and remained on the screen until a subject made a response or 2000ms elapsed. Novel forward masks were created for each trial to prevent any learning of the statistics of the mask by generating a rectangle of random noise, from a uniform distribution over the interval 0 to 1, that was large enough to cover the prime, then spatially smoothing the noise pattern with a uniform filter and assigning a pixel value of black to any location with a value of less than 0.5 and a pixel value of white to any location greater than or equal to 0.5. The prime and target images were pulled from 200 near prototype images (50 for each of the four prototypes) taken from the first level of training, which were therefore relatively easy for participants to categorize. The target was slightly larger than the prime to ensure effective backward masking. Participants were instructed to categorize the image on the screen as a SOVOR or not a SOVOR, in agreement with the category-A/not category-A type decisions from (Malone et al., 2016; Quinn & Kinoshita, 2008), with “1” or “2”, respectively, on the keyboard number pad. The masked priming experiment was broken into 8 blocks, with each block containing three repetitions of the 16 (4x4) possible prime/target near-prototype pairs, resulting in 48 trials per block and 384 trials total. There were three distinct trial types: 1) “Same” trials contained the same near-prototype for the prime and the target (96 trials). 2) “Congruent” trials contained a prime from the same category as the target, but near the other prototype (96 trials). 3) “Incongruent” trials contained a prime from near one of the two prototypes from the opposite category as the target (192 trials). These trials types allow us to look at simple shape priming (“Same” RT < “Congruent” RT, “Same” RT < “Incongruent” RT),
and, of particular interest, category priming (“Congruent” RT < “Incongruent” RT) with the difference in shape controlled for since all four prototypes were equally dissimilar. Finally, to test if the prime was truly not accessible to consciousness, we tested the visibility of the prime at the end of the study, after all five masked priming testing sessions were complete, by having the subjects run two blocks of the same task but this time informing them of the presence of the prime and asking them to report if the prime was a SOVOR or not a SOVOR to the best of their abilities.

2.2.8 EEG Rapid Adaptation (EEG-RA)

In order to study changes in the time course of the neural processes underlying categorization caused by extensive training, participants were run on an EEG-RA paradigm after the initial round of training, and again after all five rounds of training. During the EEG-RA experiment, participants performed a same/different category task on sequentially presented pairs of stimuli, as in our previous studies (Jiang et al., 2007; Scholl et al., 2014) (Figure 5). The pairs were chosen from the cross category morph lines, jittered around the 5%, 35%, 65% and 95% positions, and the stimuli pairs were always from the same morph line. The gray-scale car images were presented on a neutral gray background. There were four trial types: 1) M0, where the same car was presented twice, 2) M3-within (hereafter shortened to M3w), where the two cars were 30% different but from the same category, 3) M3-between (hereafter shortened to M3b), where the two cars were 30% different and from different categories, and 4) M6, where the cars were 60% different and therefore necessarily from different categories. The M0, M3w, M3b, and M6 conditions occurred with equal probability and in randomized order.
Participants responded with their right index or middle finger to indicate whether the pair of images belonged to the same, or different, categories, with the response mapping counterbalanced across subject. The timing for each trial was 500ms fixation, blank screen for 500–1000ms, stimulus 1 for 200ms, blank for 200ms, stimulus 2 for 200ms, blank until participant response or 2300ms had passed (Figure 5). Participants completed eight EEG runs per session. The odd runs consisting of 192 trials containing pairs of stimuli from the cross category morph lines for a total of 768 cross category trials per participant (192 per condition). The even numbered runs contained 96 trials focused on the within category morph lines and are not considered further in this study.

Figure 5: Same/different task for EEG and fMRI rapid adaptation. A) Trial timing. B) Example stimulus pairings. M0 could be any of the cars repeated.

Electrophysiological Recordings. Scalp voltages were measured using an Electrical Geodesics (EGI, Eugene, OR) 128-channel Hydrocel geodesic sensor net and Net Amps
300 amplifier. Incoming data were digitally low-pass filtered at 200 Hz and sampled at 500 Hz using common mode rejection with vertex reference. Impedances were set below 40 kΩ before recording began and maintained below this threshold throughout the recording session with an impedance check during each break between blocks.

**EEG Data Analysis.** Our analysis pipeline largely follows the pipeline described in Scholl et al. (2014). Data processing and statistical analyses were performed using EEGLAB (Delorme & Makeig, 2004), FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), and custom scripts in Matlab. Data were high-pass filtered at 1 Hz and low-pass filtered at 30 Hz using two-way least squares FIR filtering in EEGLAB, epoched on the interval −600ms to 800ms relative to Stimulus 2 onset for ERP. Trials containing artifacts or blinks were rejected if the recorded signal changed more than 75µV within a trial on any channel from -200ms to 400ms, and baselined on the interval −200ms to 0ms relative to stimulus 2 onset to compare responses to the second stimulus across conditions. Bad channels were identified by visual inspection and replaced by the average of their neighbors through interpolation (Oostenveld et al., 2011). Based on our interest in the parietal cortex as a possible location of categorical signal we rereferenced the data to the average voltage across all channels in order to better detect changes on central electrodes. Analyses focused on correct trials only.

EEG signals were analyzed for stimulus selectivity using cluster-based permutation testing (Maris & Oostenveld, 2007). This approach permits the consideration of all the EEG data without imposing a priori constraints regarding which channels and time points
reflect experimental manipulations while controlling for multiple comparisons. The space–time clusters were identified by subjecting every channel/time-point response pair from the two to-be-compared conditions to a paired two-tailed t-test to identify points where the responses differed at $p < \alpha_{\text{thresh}}$ before correcting for multiple comparisons. These points were then grouped into space–time clusters based on both temporal and spatial adjacency. Two points were considered temporally adjacent if they occurred at subsequent time points; spatial neighbors were constrained by triangulation, resulting in an average of 7.5 neighbors per channel (minimum 5, maximum 10 neighbors). For each cluster, a single statistic was extracted based on the sum of all t-values in the cluster. The significance of each cluster was computed by recalculating each cluster statistic for $10^3$ random partitions of the trial conditions. The overall significance of each cluster was calculated using the proportion of permutations for which the resulting cluster statistic was greater than the statistic calculated with the correct labels, resulting in a probability measure controlled for Type I error (Maris & Oostenveld, 2007).

The primary contrast of interest was M6>M0. Given that M0 trials contain stimuli pairs that are matched for shape and category membership both the neuronal populations tuned to stimulus shape, as well as those that are tuned to stimulus category should show an adapted response to the second stimulus. On the other hand, the M6 trials contain stimulus pairs that are different in shape and are from different categories, so the second stimulus should not elicit an adapted response from shape tuned or category tuned neuronal populations. Therefore, the contrast of M6>M0 identifies space-time clusters that are selective for either aspect of the stimulus, shape or category. By identifying these
clusters using just the M6 and M0 trials, the M3w and M3b trials are separate data that can be used as an independent testing set to determine the nature of the selectivity of the identified cluster. Given that the stimulus pairs from the two M3 conditions are equivalent in shape difference, a shape selective cluster will respond with an equivalent amount of adaptation for the second stimulus in both M3 conditions, likely somewhere between the M0 and M6 conditions. On the contrary, given that the M3 conditions diverge with respect to the category relationship between stimulus pairs, a category selective cluster will have an adapted response to M3w but not for M3b so the response to the second stimulus in M3b will be greater than that of M3w. We would also expect similar responses between the M0 and M3w condition, as well as the M6 and M3b condition in a category selective cluster. There is one other potential response profile we might expect, one that mirrors condition difficulty. Since the M3b condition by design always contains two near boundary stimuli it is the hardest condition. At the other end of the spectrum, the M0 condition is the easiest since it is easy to tell that the same car belongs to the same category. The M3w and M6 conditions fall somewhere in between since they always contain one difficult to categorize near-boundary stimulus and one easy to categorize near prototype stimulus, so a task difficulty tuned cluster would show a response profile like this: M0<M3w=M6<M3b. Secondary contrasts: M3b>M3w and M6+M3b>M0+M3w (different category>same category) were also used in order to better understand the spatial and temporal extend of the category selective signal.

In order to identify the earliest clusters showing a categorical response, as measured by adaptation in the ERP amplitude evoked by the second car stimulus, we performed a
cluster search over all 128 channels using a time window of 50ms to 350ms with respect to stimulus 2. This time window was selected based on a priori hypotheses: 1) 50ms was used as the beginning of the time window because it takes that long for information to reach primary visual cortex (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001) and this is the latency of the earliest visual evoked ERP component, the C1, (Jeffreys & J. G. Axford, 1972). 2) 350ms was used as the end of the time window because previous work from our lab showed category related signal starting just after 200ms and that by 350ms the signal began to reflect condition difficulty (Scholl et al., 2014). Therefore, the initial stimulus to category mapping should definitely occur during this time window for the pre-extensive training EEG session and if anything the stimulus to category mapping should occur faster after extensive training.

2.2.9 FMRI Rapid Adaptation (fMRI-RA)

Participants also took part in an fMRI-RA experiment following their first round of training to assess the brain areas underlying categorization after initial learning of the categorization task (similar amount of training to Jiang et al. (2007)), and then again after the completion of all five rounds of training, to test the hypothesis that the neural circuitry for categorization shifts posteriorly after extensive practice.

Participants performed the same task in the MRI scanner as they did in the EEG experiment. In the fMRI-RA paradigm, two cars were displayed sequentially (200ms each with a 200ms blank screen in-between) at the center of the screen, followed by a 3480ms blank screen during each trial. In these scans, participants needed to judge
whether the two cars belonged to the same or different categories by pressing one of the two buttons held in their right hand with either their index finger or middle finger. No feedback was provided to participants. The relationship between the same/different answers and index/middle finger responses was counterbalanced across participants, matching the EEG paradigm. MRI images from four scans were collected. Each scan lasted 538.56 s and had two 10.2 s fixation periods, one at the beginning and the other at the end. Between the two fixation periods, a total of 127 trials were presented to participants at a rate of one every 4.08 s. For each run, the data from the first two trials were discarded, and analyses were performed on the data of the other 125 trials—25 each of five different conditions. There were the same four conditions defined by the change of shape and category between the two cars as in the EEG-RA paradigm: M0, same category and same shape; M3w, same category and 30% shape change; M3b, different category and 30% shape change; M6, different category and 60% shape change; plus a null trials condition where two fixation crosses were flashed instead of the car stimuli and no motor response was made (Figure 5). Trial order was randomized and counterbalanced using M sequences (Buračas & Boynton, 2002).

**FMRI Data Acquisition.** All fMRI data were acquired at Georgetown University’s Center for Functional and Molecular Imaging using an echo-planar imaging (EPI) sequence on a 3.0 Tesla Siemens Trio scanner with a twelve-channel head coil (flip angle=90°, TR=2.04s, TE=30ms, FOV=205, 64x64 matrix). For both functional localizer scans and ER runs, 44 interleaved axial slices (thickness = 3.2 mm, no gap; in-plane resolution = 3.2 x 3.2 mm²) were acquired. At the end of the session, three-dimensional
T1-weighted MPRAGE images (resolution 1 x 1 x 1 mm$^3$) were acquired for each subject.

**FMRI Data Analysis.** All preprocessing and most statistical analyses were done using the software package SPM12 and its toolboxes. The acquired images were temporally corrected to the middle slice, then spatially realigned, unwarped, resliced to 2 x 2 x 2 mm$^3$, normalized to a standard MNI reference brain using each subjects’ own anatomical scan, and smoothed with an isotropic 6 mm Gaussian kernel.

We conducted whole-brain analyses on data from each time point (pre- and post-extensive training) by modeling the first-level fMRI responses with a design matrix comprising the onset of each trial types (M0, M3w, M3b, M6, and null/fixation-only trials) and movement parameters as regressors using a standard canonical hemodynamic response function (HRF). The parameter estimates of the HRF for each regressor were calculated for each voxel, and then the contrasts of interest at the single-subject/time point level were computed and entered into second-level models in SPM12 (participants as random effects) with additional smoothing with an isotropic 6 mm Gaussian kernel. As with the EEG-RA analysis, M6>M0 was the primary contrast for identifying stimulus selective clusters of voxels. The percent signal change for all conditions was then extracted using the MarsBar toolbox for SPM, and the responses from the two independent M3 conditions were used to differentiate shape-selective clusters from category-selective clusters. M6M3b>M0M3w (Diff.>Same) and M3b>M3w, were again used as secondary contrasts. For all whole-brain analyses, a threshold of p < 0.001
(uncorrected) with at least 10 contiguous voxels was used unless otherwise mentioned.

2.3 Results

Figure 6: Post-single task training categorization testing results.
A) An example individual participant's fitted data. B) Averaged raw data for the group.
2.3.1 Categorization Training and Testing

The goal of this study was to assess changes in the neural substrates underlying a categorization task from when it is first well learned to when it is extensively practiced and more automatic, as assessed by the features discussed in Section 1.6. In order to be sure that the category boundary was well learned after the initial round of training, participants were tested on their categorization performance along the four cross-category morph lines and sigmoidal functions were fit to estimate the location of each participant’s learned category boundary for each of the four morph lines (see Section 2.2.5). Participants whose learned category boundaries were more than 10% morph distance away from the true boundary location of 50% on any of the four morph lines did not advance to the first imaging session. Figure 6A shows the performance and example fits for each of the four morph lines for a representative participant. The x-axis shows the location of the stimulus along the morph line form SOVOR to ZUPUD in percent contribution from the ZUPUD prototype and the y-axis on the left indicates how often the participant labeled the stimuli a SOVOR. The y-axis on the left indicates the mean reaction time (RT) in ms, note the increased reaction time (RT) for category decisions near the boundary indicating a more difficult decision for near-boundary stimuli. A well-learned category boundary would be evident as a sharp drop-off of SOVOR responses near the true category boundary at 50%. This example participant showed learned category boundaries located between 40% and 60% for all morph lines as required. Figure 6B shows the average group data for categorization for each line in the subjects that advanced to the imaging sessions.
To examine the effect of extensive training on categorization behavior we first analyzed the behavioral data from the training app. Looking at a one-way repeated measures ANOVA with training round as the within-subject factor and mean accuracy as the dependent variable, there was a significant effect of training round \( (F=7.3718, \ p=0.003) \), but when the initial round of training was removed and the ANOVA was done over the final four extensive training rounds there no longer was a significant effect \( (F=1.000, \ p=0.410) \). Therefore, mean accuracy increases between the initial round of training and the beginning of extensive training in round two, but then immediately asymptotes (Figure 7A). In contrast, the same ANOVAs, but with mean RT as the dependent variable, showed a significant effect of training round when all five rounds were included \( (F=13.7407, \ p=1.256*10^{-6}) \) as well as when analyzing just the four extensive training rounds \( (F=15.4523, \ p=8.278*10^{-6}) \). Therefore, RTs continued to decrease with extensive training (Figure 7B) while performance remained stable. The decrease in RT without a tradeoff in accuracy is evidence of an increase in the processing speed of the categorization process, one of the features of task automaticity (Moors & De Houwer,
Next we look to the EEG and fMRI data to examine the changes in the neural processing underlying categorization that leads to this increased efficiency.

### 2.3.2 EEG Rapid Adaptation (EEG-RA)

To assess the time course of neural processing underlying categorization after the car categories were first well learned, and how that time course changes with extensive categorization experience, participants were run on an EEG-RA paradigm after the first round of training and again after all five rounds were complete. The task required participants to decide if sequentially presented car stimuli were from the same category or different categories. There were four trial conditions that varied shape and category differences as follows: M0 trials were the same stimulus twice so shape and category were the same, M3w trials contained pairs from the same category but 30% apart on a given morph line, M3b were also 30% apart on a given morph line but on different sides of the category boundary, and M6 which had pairs that were 60% different in shape along a given morph line and therefore always from different categories. This design allows us to identify space-time clusters in EEG sensor space that show adapted responses in ERP amplitude to the second stimulus in the pair that follow either a shape selective profile (M0\(<\)M3w=M3b\(<\)M6) or a category selective profile (M0=M3w\(<\)M3b=M6).
Same/different category task behavior. The M3b condition was expected to be the most difficult because it requires correctly identifying two stimuli that are close to the boundary. M3w and M6 always contained at least one near boundary stimulus so they were expected to be of intermediate difficulty. The M0 condition could be repeated stimuli from any of the four morph line locations, but due to the fact that it is the same stimulus it should be fairly obvious it is in the same category, so we expect this condition to be the easiest. This expected difficulty profile was seen for both the pre-extensive training (“pre”) and post-extensive training (“post”) time points in both the accuracy and RT behavioral measures (Figure 8), in agreement with our previous studies (Jiang et al., 2007; Scholl et al., 2014). Similar to the categorization training data, the accuracies did not differ between the “pre” and “post” EEG sessions (p=0.1316, paired t-test), but the RTs significantly decreased (p=0.002, paired t-test). This decreased RT without a tradeoff
in accuracy provides further support that category information is processed more efficiently after extensive training.

**Figure 9:** Pre-extensive single task training EEG-RA, M6>M0 - time-lapsed scalp topography of the anterior cluster.
Channels that were part of the cluster at any point during a given time widow are marked in black.

**EEG-RA pre-extensive training.** The M6>M0 contrast was used to identify all stimulus selective space-time clusters over the 50ms to 350ms time window relative to post-stimulus 2 onset in the “pre” EEG data, and then the two M3 conditions, which were not involved in defining the clusters, were used to determine what aspect of the stimulus the cluster was selective for, shape or category. The M6>M0 contrast identified a large frontal cluster (Figure 9, cluster-level p=0.001) that spans from 158ms to the end of the search window at 350ms. The scalp topography of the clusters starts over central
electrodes at 158ms and expands radially, before shifting leftward and eventually to bilateral frontal channels. The comparison between the M3 conditions is significant (p=0.022, paired t-test) offering support for categorical selectivity within this space-time cluster, and all other pairwise comparisons between conditions significant as well. Given how spread out in time this cluster is, it is more than likely picking up on numerous aspects of the underlying categorization process. Two other more temporally focal clusters that this contrast identified over posterior channels shed further light on the time course of categorization. There is a significant (Figure 10B, cluster-level p=0.038) posterior cluster spanning a time window, 284ms-350ms, that overlaps with the end of the significant anterior cluster, that also shows a significantly higher mean ERP amplitude for the M3b condition compared to the M3w condition (p=0.02, paired t-test). There is another cluster over a highly overlapping set of electrodes but overlapping with part of the earlier portion, 188ms-228ms, of the significant anterior cluster, though it is only bordering on significance (Figure 10A, cluster-level p=0.074). Although this earlier posterior cluster shows a somewhat similar response profile to the later posterior cluster, there is not a significant difference between the M3w and M3b conditions (p=0.17, paired t-test) supporting more of a shape-selective response for this earlier cluster.
Figure 10: Pre-extensive single task training EEG-RA, M6>M0 - posterior clusters.
The top left subplots in these figures show the channels involved in the cluster highlighted in white overlaid on top of a topological plot of the difference signal determined by the contrast, in this case it is M0 – M6. The top right subplots show the average ERP amplitude over every significant channel/time-point pairing in the cluster for each condition. The ERP trace in the bottom subplot is the average ERP over all channels involved in the cluster at any time point, with the time cluster time window highlighted. The significance is demarcated as follows: *=p<0.05, +=p<0.01, **=p<0.005, +++=p<0.001, ++++=p<0.0005.

The M6+M3b>M0+M3w secondary contrast revealed qualitatively similar results, showing the same three clusters (See Appendix Figure 32). The large anterior and the later posterior clusters showed significantly higher responses for M3b compare to M3w, but the earlier posterior cluster, which was significant for this contrast (cluster level p=0.045), again, did not show a significant difference between the M3 conditions.

The M3b>M3w secondary contrast revealed a more focused anterior cluster (cluster-level p=0.042) spanning a tighter time window, 254ms-350ms, and showing a more left lateralized scalp topography paired with a very categorical response profile (Figure 11A), and a posterior, slightly right lateralized, cluster (cluster-level p=0.028) over a very similar time window, 270ms-350ms that also shows categorical response characteristics (Figure 11B).
Figure 11: Pre-extensive single task training EEG-RA, M3b>M3w.

*=p<0.05, +=p<0.01, **=p<0.005, +++=p<0.001, ++++=p<0.0005.

The M3b>M3w contrast, and the left lateralized to frontal spread of the anterior cluster
beginning around 230ms in the anterior clusters defined by the M6>M0 and M6+M3b>M0+M3w contrasts are in good agreement with previous work from our lab using the same paradigm in subjects with roughly equivalent amounts of training that showed a left anterior category signal beginning just after 200ms and spreading anteriorly and bilaterally over the course of the next ~150ms (Scholl et al., 2014). From the Scholl et al. (2014) study we would expect the 170ms-200ms window to be shape selective. Increasing the cluster identification threshold from the $\alpha_{\text{thresh}} = 0.05$ used above to stricter $\alpha_{\text{thresh}} = 0.01$ for the M6>M0 contrast, isolated the earlier (164ms-232ms) central part of large anterior cluster (cluster-level p=0.008) and revealed it to be shape selective. At this tighter cluster identification threshold the early (192ms-220ms) posterior cluster was significant (cluster-level p=0.039) and shows the same roughly shape selective profile.

Taken together, the EEG results from this section support the same two stage model argued for in Scholl et al. (2014), where early posterior shape selectivity, putatively corresponding to shape selective responses along the ventral visual hierarchy, send feed-forward information to left frontal categorization task circuitry.

**EEG-RA post-extensive training.** Looking at the M6>M0 contrast for the “post” EEG data also revealed a rather temporally expansive anterior cluster (Figure 12A, cluster-level p=0.001) over left frontal channels stretching from 110ms to the end of the search window at 350ms. This cluster is focused over a slightly smaller region of the scalp topography compared to the large anterior cluster from the “pre” time point, but it starts
almost a full 50ms earlier. As with the large anterior cluster in the “pre” time point, the M3b mean ERP amplitude in greater than the M3w mean amplitude (p=0.014, paired t-test), and all other pairwise comparisons were also significant again. Also similar to the “pre” time point there were again two posterior clusters, though they were both shifted earlier in time and showed slightly different scalp topographies with respect to the later and earlier posterior clusters from the “pre” time point. The later 266ms to 350ms posterior cluster was only trending toward significance at the cluster level (p=0.068, Figure 12C), but showed a nicely categorical response profile (M6=M3b>M0=M3w, Figure 12C). The earlier cluster (154ms-238ms) was also only trending towards significance (cluster-level p=0.060), but unlike the earlier posterior cluster from the “pre” time point this cluster showed a categorical response profile with a significant difference between the M3 conditions (Figure 12B, p=0.042, paired t-test).

For the secondary contrasts of interest, the M6+M3b>M0+M3w comparison an anterior cluster that was more focused in time, 142ms-280ms, than the M6>M0 anterior cluster, and had a categorical response profile (Figure 13B, cluster-level p=0.005). The early (150ms-226ms, Figure 13C) and late (276ms-350ms, not shown) posterior clusters were only trending towards significance for this contrast, as well, cluster level p= 0.099 and p=0.066, respectively, but both clusters showed categorical response profiles.
Figure 12: Post-extensive single task training EEG-RA, M6>M0.

*=p<0.05, ++=p<0.01, **=p<0.005, +++=p<0.001, ****=p<0.0005.

For the M3b>M3w contrast, none of the clusters survived cluster level correction, but the two that were the closest were a pair of clusters, one over anterior channels (cluster-level p=0.118, not pictured) and one over posterior channels (cluster-level p=0.193, not pictured) showing categorical response profiles over 166ms-236ms and 164ms-224ms time windows, respectively.

These results support a shift in time for the onset of category signal from ~250ms at the pre time point to almost 100ms earlier. There is also a shift in the scalp topography of the earliest category signal to a more posterior distribution of channels. The fMRI sections below are better suited to address the spatial location of the brain areas involved in the
categorization task, but these results already provide support for the broader hypothesis that stimulus to category mapping is shifted out of frontal areas with extensive training.

Figure 13: Post-extensive single task training EEG-RA, M6+M3b>M0+M3w.
* = p<0.05, ++ = p<0.01, ** = p<0.005, +++ = p<0.001.

2.3.3 FMRI Rapid Adaptation (fMRI-RA)

In order to assess the brain areas underlying the categorization process when it is first well learned and how it changes with extensive experience, participants were run on a fMRI-RA paradigm at the same time points as the above EEG-RA, “pre” and “post” extensive training time points. The EEG-RA and fMRI-RA sessions were conducted in separate sessions with the order counterbalanced across participants. The in scanner behavioral task matched the EEG-RA task, in order to provide complimentary spatial information to
the temporal information gleaned from the previously discussed EEG experiment. The behavioral results again showed the predicted pattern of task difficulty across conditions in both the accuracy and RT measures. The same pattern of decreased RT with no change in accuracy is also seen again from the pre-extensive training scan to the post-extensive training scan (Appendix Figure 34).

**MRI-RA pre-extensive training.** First, general task activation was examined to get an idea of the brain regions that are involved in the same/different category task using the contrasting task>fixation, voxel level threshold p<0.001, cluster level FWE p<0.05. Task trials included all experimental conditions: M0, M3w, M3b and M6, and fixation trials included only the null trials. This contrast revealed a network of areas consistent with what would be expected for a visual categorization task with a right-handed button press response: bilateral ventral visual areas, left primary sensorimotor cortex, left premotor cortex, left supplementary motor area, bilateral cerebellum with more activation on the right, bilateral inferior parietal cortex, left superior parietal cortex, bilateral basal ganglia, thalamus and some brain stem (Figure 14). Although this contrast can point to what areas are involved and educated guesses about what sub-components of the task are being executed where based on previous literature can be made, this type of measurement cannot be used to determine what brain areas are selective for aspects of the stimulus such as category membership. As discussed in the Section 1.5, this is where the rapid adaptation approach is used to assess the selectivity of the sub-voxel neuronal population by leveraging their adapted responses to repeated features that population is tuned too.
The rapid adaptation concept is the same here as it was in the EEG section above, except that due to the much slower temporal dynamics of the evoked changes in the BOLD (blood oxygenation level dependent) signal our fMRI-RA analysis models each trial as a single event and we compare the summated BOLD response to the pair of cars, as opposed focusing on the response to the second stimulus which was possible in the EEG experiment due to the much greater temporal resolution with that imaging modality.

As with the EEG-RA results, the M6>M0 contrast (p<0.001, uncorrected) for the “pre” time point was used to identify clusters of voxels that are selective to the car stimuli, and then the separate set of M3w and M3b trials were used to determine which aspect of the car stimuli, shape, category or categorization difficulty, each cluster of voxels is selective
for. The M6>M0 contrast selected a number of clusters in ventral visual, parietal, and frontal cortices. However, none showed categorical response profiles. There were clusters in frontal and parietal areas that had significantly higher BOLD responses to M3b compared to M3w, but the M3w response amplitudes were greater than the M0 response amplitudes and equivalent to the M6 response amplitudes and the M3b amplitudes were greater than the M6 amplitudes, consistent with a response profile that mirrored condition difficulty. As expected from Jiang et al. (2007) and traditional two stage models of perceptual categorization in general, this contrast also revealed shape selective clusters in ventral visual areas, namely bilaterally in both the posterior fusiform and lateral occipital portions of the lateral occipital complex (LOC) (Kourtzi & Kanwisher, 2001) (Appendix Figure 35).

Since the primary contrast did not reveal any category selective clusters in the pre-extensive training fMRI data, the next step was to probe for category selective clusters directly using the M6+M3b>M0+M3w contrast. Again, there were no clusters with categorical response profiles using the a p<0.001, cluster extent > 10 voxels threshold, so the threshold was dropped to p<0.005 revealing a categorical cluster in the left middle frontal gyrus, BA 10, located at MNI coordinates [-42 56 16] (Figure 15). Lastly, the M3b>M3w contrast results in very sparsely significant statistical maps, and what few small clusters there were showed condition difficulty tuned response profiles. The results here point to a categorical cluster in the left frontal cortex. Although the stats are not very robust, the idea of a left frontal cluster is further supported by our EEG-RA clustering
analysis that points to a categorical signal beginning over left frontal channels starting around 250ms post stimulus 2.

![Figure 15: Pre-extensive single task training fMRI-RA, M6+M3b>M0+M3w - categorical response in left MFG.](image)

p<0.005, k>10

- p < 0.1
+ p < 0.05
+ p < 0.01

After a similar amount of training on the same car categories in the Jiang at al. (2007) paper, a right frontal category selective cluster was present. Though the Jiang et al. (2007) paper was very similar to what was done here, there are distinctions between that study and the present pre-extensive training fMRI-RA experiment. One difference is that the stimulus presentation time was shortened from 300ms for each car with a 400ms blank in between to 200ms per car with a 200ms blank in between to exactly match the timing used in the EEG-RA paradigm. A more substantial difference is the car categories were learned in a completely non-verbal 2AFC match-to-sample style paradigm in the
Jiang et al. (2007) paper, but here pseudoword labels were added to the car categories, to match the Scholl et al. (2014) EEG-RA study, and subjects learned the cars by viewing a single car stimulus and choosing the appropriate label. Similar to our current EEG-RA findings, the previous Scholl et al. (2014) study also found evidence of a categorical signal starting over left frontal electrodes slightly after 200ms. Given the left lateralization of language, it is certainly feasible that the addition of labels to the car categorization training would shift the frontal circuitry underlying for categorization after first learning the task from the right to the left side.

**MRI-RA post-extensive training.** In the post-extensive training scan the task>fixation (voxel-level threshold p<0.001, cluster-level FWE<0.05) revealed a similar network of areas as was seen in the “pre” scan, but with more extensive voxel coverage in a number of areas including right inferior parietal cortex, bilateral cerebellum and other subcortical regions in the thalamus and basal ganglia. The differences mentioned here are a qualitative observation and the direct comparison of the “pre” and “post” scans will be addressed below.
Figure 16: Post-extensive single task training fMRI-RA, M6>M0 - category selective cluster in the left inferior parietal lobule (IPL).
Cluster is defined on the M6>M0 contrast on the post data and shows a categorical response profile. Looking at the response profile for the same cluster in the “Pre” scan (lower left) showed no difference between the M3 conditions and is therefore more like a shape selective profile. P-value demarcations: *=p<0.05, ++=p<0.01, **=p<0.005, +++=p<0.001, =*=p<0.0005.

The primary contrast of interest, M6>M0 p<0.001 uncorrected, identified a number of categorical clusters in the “post” fMRI-RA data. In agreement with the parietal shift hypothesis, two clusters in the left parietal cortex showed a categorical response profile. One of the clusters is in inferior parietal lobule (IPL), with a peak at [-30 -46 50] in MNI coordinates, and showed a significantly higher % BOLD signal change for the M3b condition compared to the M3w condition (p=8.0*10^-4, two-tailed paired t-test), Figure 16. The other cluster is in superior parietal lobule (SPL), with a peak location at [-20 -72 56] MNI coordinates, and showed a difference between M3w and M3b trending toward statistical significance (p=0.078, paired t-test), Figure 17. In addition to the parietal clusters, a left cerebellum cluster [-12 -82 -30], located in the medial parts of crus 1 and 2, also showed a categorical response profile with a significantly higher BOLD response.
to M3b compared to M3w. Lastly, a right striatal cluster showed a response profile that looked nicely categorical, though the comparison between the M3 conditions does not quite reach significance (p=0.13).

Figure 17: Post-extensive single task training fMRI-RA, M6>M0 - category selective cluster in the left superior parietal lobule (SPL).

P-value demarcations: \( \approx p<0.1, *=p<0.05, **=p<0.01, ***=p<0.005, +++=p<0.001, ++++=p<0.0005 \)

Using the secondary M6+M3b>M0+M3w, p<0.001 uncorrected, contrast to directly probe for category selective clusters revealed a similar cluster with a categorical response in the left SPL, with a slightly more posterior MNI peak location, [-16 -82 54]. The IPL cluster from the M6>M0 contrast was part of a larger cluster with a difficulty tuned response profile in this contrast, MNI peak location [-30 -46 50]. A categorical left medial cerebellum cluster was also present again with this contrast, peak location [-4 -76 -26]. For the right striatum, this direct test for category selectivity revealed a more focal cluster in the head of the caudate that was very categorical. This direct contrast of same
vs. different category also revealed an unexpected category selective cluster in left ventral occipitotemporal (vOT) cortex MNI peak location [-48 -64 -26] were there was a shape selective response in the “Pre” scan, Figure 18. There were also two categorical clusters in right premotor cortex (PMC), MNI peak locations [-34 0 68] and [-34 -8 32], that were not present in the previous M6>M0 contrast. Finally, the M3b>M3w, p<0.001, secondary contrast revealed only task difficulty tuned clusters.

Figure 18: Post-extensive single task training fMRI-RA, M6+M3b>M0+M3w - category selective cluster in the left ventral occipitotemporal (vOT) cortex.
The direct contrast for category selectivity, i.e. “different category” > “same category”, revealed a categorical response profile in a vOT cluster in the post-extensive training scan. This cluster had shown a shape selective response before extensive training.

MRI-RA “pre” versus “post” results. To assess the changes from pre-extensive training to post-extensive training directly, we first compared general task activation (task trials > null trials) between “pre” and “post”. Each participants first level contrast maps of task-null were entered into a paired second level analysis contrasting “pre” and “post”
time points. The contrast of pre>post, p<0.005 uncorrected, only revealed very few significant clusters, namely just a small cluster in the right cerebellum and another small cluster in the left thalamus. The contrast of post>pre, on the other hand, revealed bilateral areas in the IPL and anterior portions of the anterior temporal lobe Figure 19. However, some of these significant comparisons may arise from decreased negative activation in these regions going from “pre” to “post”, which are hard to interpret. For instance greater automaticity may lead to less suppression of task irrelevant activity such as that arising from the default mode network (Raichle et al., 2001). However, bilateral early visual areas in left and right lingual gyrus, with respective peak MNI coordinates [-10 -94 -16] and [4 -84 -12], and right anterior hippocampus/amygdala, peak coordinates [16 -4 -14] did show increased activation from pre to post that appears to be driven by increases in the post time point.
Figure 19: Regions of increased task activation after extensive training.
A paired second level analysis comparing task activation (task>fixation) for post-extensive training vs. pre-extensive training (Post>Pre) revealed increased task activation in areas including anterior temporal lobe (p<0.005, uncorrected).

Next, we looked at changes in category selectivity from “Pre” to “Post”. Leveraging the RA approach, we conducted a second level within subjects comparison of the change in the categorical contrast M6+M3b>M3b+M0 from pre to post (p<0.005, unc.). Interestingly, areas along the inferior temporal lobes came up as more categorical post. Figure 20, looks at the overlap between the areas that come up for the contrast mentioned above (in red) and the areas that come up for the M6+M3b>M0+M3w contrast p<0.005 at the post time point (in blue). In addition to the left vOT area we have already discussed, there is another more anterior ROI. Its response profile is shown at the bottom of Figure 20. Although the negative response profile is hard to interpret, the temporal lobe is an intriguing alternative/complement to our posterior parietal hypothesis given the findings
of category specific neuronal responses in medial temporal lobe with human intracranial recordings in epilepsy (Kreiman, Koch, & Fried, 2000; Quian Quiroga, Reddy, Kreiman, Koch, & Fried, 2005), and the important role the anterior temporal lobe has been proposed to play in semantics (Patterson, Nestor, & Rogers, 2007).

Figure 20: Temporal lobe areas showed increased levels of adaptation for same category stimuli post-extensive training.
2.3.4 Behavioral Evidence for Increased Automaticity with Extensive Training

Dual Tasking.

In order to test whether extensive categorization training reduced the amount of attention necessary for categorization, participants were tested on a dual task paradigm in which they had to perform car categorization in the presence of another, attention-demanding task. The decrement in categorization accuracy in the dual task condition compared to categorization in the single task condition has been interpreted as an indicator of the amount of attention required for the categorization task (Fei-Fei et al., 2005; Li et al., 2002).

In our study, participants were trained on five sessions of the animal/no-animal dual task paradigm following the initial round of car categorization app training, and then tested on SOVOR/ZUPUD dual tasking using the final SOAs from dual task training (see Section 2.2.6). After extensive car categorization training was completed, participants ran one session of the animal/no-animal DT training as a refresher and then ran the SOVOR/ZUPUD dual task testing session again using the same SOAs as the previous pre-extensive training car dual task testing session. The comparison of interest was the categorization accuracy in the dual task condition normalized by the categorization accuracy in the single task categorization blocks pre-extensive training versus post-extensive training. The hypothesis was that extensive training decreases the amount of attention necessary for the categorization task resulting in increased categorization accuracy under dual-task conditions, when attention resources are limited. As hypothesized, significant improvement in the normalized dual task categorization
accuracy with extensive training was seen (p=0.014, one-tailed paired t-test for “Post”>”Pre”), though not to the level of no dual task interference because the categorization performance was still significantly lower in the dual condition compared to the single task condition (paired t-test, p=1.059∗10⁻²⁰), as is readily apparent in Figure 21 showing the normalized dual task categorization performance well below 1. It is also worth noting that dual task performance on the peripheral disk task did not improve after extensive car categorization training, a paired t-test on the normalized dual task disk performance pre vs. post was not significant (p=0.9795).

Figure 21: Extensive single task training improves dual task performance.
Participants carried out a car categorization task by itself, an attention-demanding disk identification task in the periphery by itself or both tasks simultaneously. In the figure above the y-axis depicts the accuracy on the disk task in the dual scenario divided by the accuracy on the disk task by itself. The x-axis is the accuracy on the car categorization task in the dual scenario divided by the accuracy on the car categorization task by itself. The absence of a dual task interference effect on a task is when the performances are equivalent in the dual and single conditions and therefore the measure above would be one. Extensive single task training on car categorization leads to decreased dual task interference when performing the car categorization task at the same time as another attention-demanding task.
One concern is that this improvement in the car categorization task is due to a test/re-test effect and not the result of extensive single task categorization training. We therefore analyzed the animal/no-animal normalized dual task performance in the last training session before each testing session, which matched the testing sessions in all aspects except there was no intervening extensive training on the central animal/no-animal scene categorization task. One subject was not run on the post extensive training animal/no-animal dual task refresher, but for the remaining ten subjects there was no improvement in normalized animal/no-animal dual task categorization performance (one-tailed paired t-test of post>pre, N.S., p=0.1697), supporting the idea that the improved car categorization dual tasking ability was not due to a test-retest effect.

**Masked Priming.** Participants were run on a masked priming paradigm, based on Quinn and Kinoshita (2008) to probe the unconscious processing aspect of automaticity (see Section 2.2.7). There were three conditions: 1) “Same”, where the prime was from the same category and had the same dominant prototype as the target, 2) “Congruent”, where the prime was from the same category but had a different dominant prototype, and 3) “Incongruent” where the prime and the target were from different categories. Comparing the “Congruent” and “Incongruent” conditions allowed us to measure the priming effect of category with shape differences controlled, while the comparison of “Same” versus “Congruent” allowed us to measure the shape effects on priming with category membership controlled.
A 3x2 repeated measures ANOVA, with condition ("Same", "Congruent", "Incongruent") and time point (Pre- vs. Post-extensive training) as within-subject factors, was carried out for both the mean accuracy as well as the median RT on correct trials. For the 3x2 ANOVA with mean accuracy as the dependent variable, the main effect of condition was significant (Greenhouse-Geisser corrected, F=7.899, p=0.017), but the main effect of session (F=1.090, p=0.327) and the interaction effect (F=1.212, p=0.324) were not. Planned comparisons testing for category priming (one-tailed paired t-test of “Congruent” accuracy > “Incongruent” accuracy) and shape priming (one-tailed paired t-test of “Same” accuracy > “Congruent” accuracy) were carried out for both time points. At the “pre” time point, there was a trend toward a category priming effect on accuracy (T=1.894, p=0.05), and no significant shape priming. At the “post” time point, there was a significant category priming effect (T=3.36, p=0.006), but again no pure shape priming effect.

For the 3x2 ANOVA with median RT as the dependent variable, the main effect of condition was significant (F=9.514, p=0.002), and the main effect of session was also significant (F=12.942, p=0.007), but the interaction effect (F=2.228, p=0.140) was not. Planned comparisons testing for category priming (one-tailed paired t-test of “Congruent” RT < “Incongruent” RT) and shape priming (one-tailed paired t-test of “Same” RT < “Congruent” RT) were carried out for both time points. At the “pre” time point, there was a category priming effect on RT (T=2.296, p=0.028), and there was also a highly significant shape priming effect (T=3.147, p=0.008). At the post time point,
there was again a significant category priming effect on RT (T=3.33, p=0.007), but no longer any additional shape priming effect.

The lack of a difference between the “Same” and “Congruent” conditions on accuracy is not surprising because the prime stimulus in both cases causes no interference at the response level. Additionally, the categorization decision was intentionally made to be fairly easy by using car stimuli chosen from the first level of training, which sampled the stimulus space quite close to the dominant prototype, and accuracy was near ceiling. Therefore, the RT measure is probably more sensitive as is often the case in priming experiments.

In summary, the category priming effect becomes more significant after extensive training and the difference between “Same” and “Congruent” is no longer significant. However, a direct comparison of the size of the category priming effect between pre and post does not show a significant difference (p=0.415, paired t-test). The lack of a significant difference in category priming from pre to post may be because we are looking for a change in a priming effect that is already a small, tens of milliseconds at most, and we only have 8 participants who ran this paradigm. It is interesting to note that there are already some category priming effects at the “Pre” time point, suggesting that some aspects of automaticity are already coming online after the first training session.
2.4 Discussion

The EEG and fMRI results shown above support the hypothesis that extensive training leads to a shift in the neural circuitry underlying visual object categorization (stimulus-to-label mapping) from PFC when the category is first learned to posterior areas after extensive training. This posterior shift is accompanied by more automatic processing as evidenced by significantly faster RTs without and decrement in accuracy, a significant decrease in dual task interference, and increased priming effects.

2.4.1 Post-Extensive Training Posterior Category Signal

The EEG-RA study shows a sizeable shortening of the latency of categorical adaptation effects post stimulus 2, with onsets occurring roughly 100ms earlier, accompanied by a posterior shift in their scalp topography. These results clearly support a posterior shift of the initial categorization decision out of PFC – but to where? The fMRI-RA results seem to offer two candidate regions, namely the left SPL and the left vOT. For starters, the present data shows more robust support for the left SPL cluster because it was identified by the primary M6>M0 contrast and was shown to be categorical with the independent M3 comparison, whereas the left vOT cluster only came up for the direct category contrast M6+M3b>M0+M3w. However, this alone might not be enough reason to dismiss the vOT cluster, since it was also identified in the M6>M0 comparison, just as part of a larger cluster that showed a shape selective response.

An EEG source estimation analysis is ongoing to provide an estimation of the neural source of the signal from the time window of the first significant EEG cluster in the
“Post” data. In the meantime, it is helpful to consider the extant literature. From the monkey electrophysiology literature, the SPL cluster as the source of the early category selectivity following extensive training appears as the more likely option, considering the studies that motivated the parietal hypothesis in the first place (Bennur & Gold, 2011; Fitzgerald et al., 2011; Freedman & Assad, 2006; Swaminathan & Freedman, 2012). On the other hand, the categorical vOT region does not fit well with the previous monkey electrophysiology literature, where extensive recordings have been done in IT that consistently showed shape selective responses without a representation of category (Freedman & Assad, 2006; Freedman et al., 2003; H. Op de Beeck et al., 2001). However, a very recent training study using a similar design to this one but for MEG-RA reports category adaptation effects arising as early as 110ms post stimulus 2 localized to OT cortex after ~16,000 training trials (Kietzmann et al., 2016). However, this study showed repetition enhancement for this early category selectivity, which raises issues of interpretation. An additional issue is that the RA measure in this study was based on a template of activation to the first stimulus in the adaptation pair from a pre-training session, which was then used to measure RA at the various time points throughout training. The assumption that the same template is appropriate throughout training assumes no training effects and is therefore invalid. However, after the repetition enhancement effect at 110ms, the next earliest effect in their post-extensive training data is repetition suppression effect around 170ms post stimulus 2, in the same temporal window as our earliest categorical cluster post-extensive training. Unfortunately, that study does not show any localization data for that time window, but the scalp topography they show fits with a left posterior neural source.
2.4.2 Categorical Responses in Motor Areas in the “Post” fMRI-RA Data

In the fMRI-RA data for the “Post” time point, the right head of the caudate, the right cerebellum and the left premotor cortex (PMC) show categorical response profiles as well. The subjects are performing a same/different task in the scanner not categorization of a single car as in training, so they are performing a new superordinate task that requires car categorization as a subcomponent. The learning of motor response portion of the in scanner task is, therefore, still in the early training stages. This set of areas is consistent with the motor output areas one would expect to see while a new task is being learned. The caudate nucleus has been associated with the early stages of task learning in monkey electrophysiology (Miyachi, Hikosaka, & Lu, 2002; Pasupathy & Miller, 2005) and fMRI (Boettiger & D’Esposito, 2005; Helie, Roeder, et al., 2010), as well as computational work (Ashby et al., 2007). The cerebellum has also been implicated in the initial phases of motor learning (Balsters & Ramnani, 2011; Shadmehr & Holcomb, 1997; Ungerleider, Doyon, & Karni, 2002). These two subcortical structures are key structures in two parallel loops that interact with cortex, including PMC, and underlie motor learning (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Ashby et al. (2007) makes the theoretical prediction that over time, in categorization tasks with static response mapping, the striatal-cortical loop would train direct cortico-cortical connection between association areas and PMC. This leads to the prediction that extensive practice with the same/different task would lead to a decrease in the relevance of the subcortical circuits as the PMC becomes the primary locus of label-to-stimulus mapping, and in fact a monkey electrophysiology study recording from PMC, PFC, and striatum while
monkeys performed a similar “same” or “different” judgment, which they had trained on for over a year, showed that PMC leads PFC and striatum (Muhammad et al., 2006).

Therefore, the complete loop for our same/different categorization task might look as follows: Stimulus 1 is categorized in SPL or vOT and is stored in the frontoparietal working memory network. Then Car two is categorized in SPL or vOT and compared in working memory and the same/difference label is produced, causing the activation in the network of ROIs that show a task difficulty profile. 3) The appropriate same/different motor response is processed by parallel striatum/PMC and cerebellum/PMC loops. In order to assess this hypothesis, we are currently working on a new whole brain effective connectivity analysis with Gustavo Deco’s group in Barcelona (Gilson, Moreno-Bote, Ponce-Alvarez, Ritter, & Deco, 2016). Preliminary findings support a reduced engagement of prefrontal areas during categorization comparing the “pre” and “post” time points.
3. DUAL TASK EXTENSIVE CATEGORIZATION TRAINING

3.1 Introduction

The recent proliferation of technologies permitting constant engagement in our culture has made multitasking increasingly prevalent, as is evident in new policy challenges as people’s attempts at multitasking exceed their cognitive capabilities, such as when texting while driving. Dual task performance is also one of the most widely used tests of automaticity in cognitive neuroscience (Helie, Waldschmidt, et al., 2010; Shiffrin & Schneider, 1977), where it is interpreted as a measure of the efficiency of the process being tested with regards to the amount of attention the process requires (Moors & De Houwer, 2006). However, the neural bases of automaticity and multitasking are still poorly understood, leading to substantial disagreement about the brain’s multitasking capabilities (See Main Introduction, Section 1.3).

In the single task extensive training study described in chapter 1, there was no direct pressure to offload stimulus-to-label mapping from frontal cortex. In contrast, an attention-demanding bisected disk task (Fei-Fei et al., 2005; Li et al., 2002) was added in the periphery during training in this study in order to tax prefrontal cognitive control circuitry and investigate the effect that added dual task pressure had on learning a novel categorization task through extensive (>30,000 trials) training. We hypothesized that the decreased frontal attention resources available for learning during the dual task training would lead to the development of categorization circuitry outside of the frontal bottleneck.
Recent behavioral work has shown that learning a categorization task is made up of two dissociable subcomponents: 1) stimulus-to-label mapping and 2) label-to-response mapping (Maddox et al., 2010). The case for the label-to-response mapping being computed by the PMC after extensive training has good theoretical (Ashby et al., 2007) and experimental support from human fMRI (Helie, Roeder, et al., 2010) and monkey electrophysiology (Muhammad et al., 2006), but PMC does not appear to be the where the stimulus-to-label mapping is calculated (Cromer et al., 2011). Therefore, in the study described in this chapter we were again interested in the automatization of the stimulus-to-label mapping step of categorization, i.e. the category-decision itself, and not the label-to-response mapping step. 

Therefore we used a visual/visual dual task paradigm with masking to ensure simultaneous processing of the stimulus and focused on categorization accuracy as our performance metric. This approach has been used previously to show that with ten to fifteen hours of training (~12,000 trials) processing of a complex categorization task (animal/no-animal with natural scene images) can be successfully completed without a dual task cost in accuracy (Fei-Fei et al., 2005; Li et al., 2002). We adapted the Li et al paradigm to train subjects on the same morph car categorization task used in the previously described single task extensive training study, as well as the lab’s previous work (Jiang et al., 2007; Scholl et al., 2014), and then imaged participants after extensive dual task categorization training (>30,00 trials) using EEG and fMRI RA.

We were specifically interested in testing the hypothesis that learning a categorization task under dual task pressure would decreased the amount of attention available for the
categorization task, thus increasing the pressure to learn the categorization decision outside of the frontal bottleneck leading to category selectivity in more posterior brain regions. We further hypothesized that the development of posterior categorization circuitry would lead to concomitant improvements in our automaticity measures (normalized dual task performance, and categorical masked priming).

What are the brain regions that are potential candidates for the off loading of categorization circuitry from PFC? Posterior parietal cortex (PPC) is a prime candidate given the monkey electrophysiology results showing that PPC can encode decision signals independently of response (Bennur & Gold, 2011), can encode abstract category information for motion-based (Freedman & Assad, 2006) and shape-based (Fitzgerald et al., 2011) categories and can represent category information earlier and more reliably than PFC (Swaminathan & Freedman, 2012). Another possible location of the categorization circuit is in the temporal lobe given findings of category specific visual responses in human intracranial recordings from the medial temporal lobe (MTL) epilepsy patients (Kreiman et al., 2000; Quian Quiroga et al., 2005) or the anterior temporal lobe (ATL) which has been proposed to be a semantic hub(Patterson et al., 2007). Other studies have pointed to the sensorimotor striatum (Ashby et al., 2010; Miyachi et al., 2002) or PMC (Helie, Roeder, et al., 2010; Muhammad et al., 2006) as important in late stages of task learning and execution, but since we did not have our participants training with a static response mapping these areas were less likely candidates.
Despite the number of potential locations for the stimulus-to-label mapping outside of the frontal bottleneck, our fMRI-RA analysis only found categorical clusters in one location: bilateral PPC clusters and the EEG-RA found only one categorical space-time cluster occurring over posterior/central channels beginning at a latency of ~250ms, supporting the hypothesis that extensive dual task categorization training results in the formation of categorization circuitry in the PPC. Additionally, by the end of training subjects were able to categorize the car stimuli in dual task conditions with no decrease in accuracy, thus meeting one of the predominantly used criteria for automaticity (Shiffrin & Schneider, 1977), supporting our hypothesis of more automatic processing with the formulation of parietal categorization circuitry.

3.2 Methods

3.2.1 Study Overview

This study was divided into five phases (Figure): (1) initial training, (2) pre-extensive practice behavioral testing, (3) extensive practice, (4) post-extensive practice behavioral testing, and (5) post-extensive practice imaging. In phase 1, participants came into lab for consenting and five sessions of dual task training using an animal/no-animal dual task paradigm before they learned to categorize car images in a dual task scenario, completing ~6000 trials in one week. In phase 2, subjects completed a single-session behavioral battery designed to measure markers of extensive practice. In phase 3, subjects practiced the dual task label training extensively, completing one round of training per week for four weeks and coming into lab for one behavioral testing session between every round. As in the single task extensive training study, subjects completed ~30,000 trials of car
label training in total. Equal amounts of practice with the car categorization task allowed for a direct comparison of the effects of single vs. dual task training on the neural circuits underlying the categorization task, which will be discussed in Chapter 4. In phase 4, participants repeated the behavioral tests from phase 2. Finally, in phase 5, participants completed EEG and fMRI Rapid Adaptation sessions (separately, with order counterbalanced across subjects) while performing a same/different category task.

| Phase 1: Initial Training | Phase 2: Behavioral Testing | Phase 3: Extensive Practice | Phase 4: Behavioral Testing | Phase 5: Imaging |

Figure 22: Dual task extensive training study overview.

3.2.2 Participants

41 participants were consented, 3 did not meet inclusion criteria, 12 quit during training, 12 didn’t meet the DT training criterion in phase 1 (see Section 3.2.6), 2 didn’t meet the post-extensive training categorization criterion in phase 4 (see Section 3.2.5) and 12 completed the study. The twelve participants (ten female, mean age = 22.58 years, range = 18-26 years) who completed the study were normal right-handed members of the Georgetown University community. The Georgetown University Institutional Review Board approved experimental procedures, and written informed consent was obtained from all participants before the experiment.

3.2.3 Stimuli

The stimulus space was the same as the stimulus space described for the single task
extensive training study (see Section 2.2.3). The images for 18 of the 30 levels of training were the same as the images from the equivalent level in the previous app. 12 new levels were added, which were made up of 3 repetitions of 4 levels that were each focused around one of the four cross category morph lines. These new levels were added to make it more difficult to pass training without learning all parts of the stimulus space that would ultimately be tested in the fMRI and EEG experiments.

### 3.2.4 Training

Participants completed category label training under dual task conditions remotely with a new 30-level mobile application accessible on Android, Windows or Mac devices. As in the single task overtraining study, the application recorded data in a MySQL database on a local webserver. Like the previous single task app, the application was powered by Mono, an open source programming language developed by Xamarin, and Unity 4.1.5f1 was used as the framework for deployment.

The dual task app was modeled after our dual task car categorization experiment from the single task training study. SOVOR/ZUPUD categorization was the central task and the red/green bisected disk task was the peripheral task, and the presentation timing was the same. The SOAs between the stimuli and their masks were again initialized to 150ms for the peripheral task and 100ms for the central task and increased or decreased in the same performance-dependent manner that was described in the animal/no-animal dual task training from the previous study. Responses were keyed in by pressing buttons on the touch screen or using the keyboard (button “1” or “2” for left and right disk responses,
respectively, and left and right arrow keys for the car task), subjects generally reported using the keyboard. The location, and corresponding arrow key, of the SOVOR/ZUPUD response buttons were switched at every level to avoid learning a fixed motor response for each category. Auditory feedback was provided, and incorrect trials were followed by an option to view the car stimulus with the correct label until the participant initiated the next trial. The first 5 levels in the first round of training were made up of 72 trials each of central only, peripheral only and dual task, grouped into blocks. After that, levels were made up of 200 dual task trials for the remainder of round one of training and for all levels in rounds two through five. The advancement criteria for each level combined central and peripheral task performance in the dual condition as follows:

\[ \frac{1}{3} \text{[central task accuracy]} + \frac{2}{3} \text{[peripheral task accuracy]} > 70\% \]

### 3.2.5 Categorization Testing

The categorization testing paradigm was the same as described in the single task study (see Section 2.2.5). However, it was run following the completion of the first round and the last round of the dual task app training, instead of just after the first round. Given that the time course of learning the car categorization task has not been studied in the dual task scenario, plus the fact that the imaging experiments with same/different task requiring accurate categorization of the 35% and 65% stimuli on the one-to-one morph lines was not until after extensive training, the advancement criteria for the category boundary location, again set at $40\% < \beta < 60\%$ for each morph line, was enforced at the post-extensive training categorization testing time point instead of after one round of
training.

3.2.6 Dual Task Training/Testing

As in the previous study, participants were trained on five runs of the animal/no-animal dual task paradigm before running any car dual tasking, but since the participants in this study would be learning the cars under dual task conditions these five training runs were done before the first round of training. Again, the SOAs were initialized at 100ms for the central task and 150ms for the peripheral task. After each grouping of the three block types the SOA for a given task was decreased by 33.3ms if the accuracy exceeded 85% for that task in the single or dual task condition, and the SOA was increased by 16.7ms for a given task if the accuracy was below 70% for that task in the single or dual task condition (see Section 2.2.6). In order to advance to the first round of training, participants were required to show a decrease from the starting SOAs for both the peripheral disk task and the central animal/no-animal categorization task by the end of 5 rounds, in order to show that they were able to learn the dual task paradigm with an already known category decision (animal/no-animal) before moving on to the more difficult task of learning a new categorization task (SOVOR/ZUPUD) under dual task pressure. In-lab dual task testing with the car stimuli was performed with these participants after every round of training using the SOAs for the central and peripheral task from their last training run.

3.2.7 Masked Priming

Dual task trained subjects were tested on the same masked priming paradigm as the
single task trained subjects after the initial round of training and after the final round of extensive training. As with the single task trained subjects, visibility of the masked prime was tested after the final masked priming testing session.

3.2.8 EEG-RA

All aspects of the experiment: stimuli, task, EEG recording, and data analysis matched the previous aim (see Section 2.2.8) with the exception of the following adjustments:

1. The odd blocks of that focused on the within category morph lines were dropped and the replaced with two more runs of 192 trials on the across category morph lines, this increased the number of trials per session in this analysis to 1152, distributed evenly across M0, M3w, M3b and M6 trials.
2. This increase in number of trials allowed us to be more stringent with our bad trial removal so we expanded the rejection window from -200ms-400ms with respect to stimulus 2 to -400ms-600ms.
3. The cluster searches reported in this section used the same 0-400ms time window as the Scholl et al. (2014) study, as opposed to the hypothesis driven shortened time window of 50ms-350ms used in the single task extensive training data above.
4. This study only includes a post-extensive training EEG-RA session.

3.2.9 fMRI-RA

The fMRI-RA scan and analysis were not changed from what is reported above for the previous study (see Section 2.2.9). However, there is only a post-extensive fMRI-RA
3.3 Results

3.3.1 Dual Task App Training and Categorization Testing

Unlike the single task extensive training study where there was EEG and fMRI data from previous studies from our lab (Jiang et al., 2007; Scholl et al., 2014) so we knew that participants should learn the car categorization task well with one round of training (~6,000 trials), the process of learning the car categorization while dual tasking was new territory. Like the single task training study we tested categorization after one round of app training (Figure 23A), but unlike the previous study subjects were not excluded for having learned boundary fits farther than 10% morph distance away from the true boundary on any of the four morph lines. Instead, subjects advanced to the extensive training round regardless of the location of their learned boundaries. Since we only had post-extensive training EEG-RA and fMRI-RA experiments that required discrimination of cars located at 35% and 65%, we ran a second categorization testing after the full five rounds of extensive training (Figure 23B) and only then did we enforce the learned boundary location within 10% of the true boundary advancement criterion. As is evident from the group average categorization performances depicted in Figure 23, participants had not learned the morph car stimulus space well after just one round of training, but by the end of extensive dual task categorization training the participants had consistently high performance for the near-prototype stimuli and reasonably sharp transitions near the true category boundary.
Figure 23: Categorization testing in dual task trained participants. 
A) After one round of training. B) After all five rounds.

3.3.2 EEG-RA

As with the single task overtraining study, the primary M6>M0 contrast was used to identify space-time clusters that responded selectively to stimulus shape OR stimulus category, and then the comparison between the M3 conditions was used to determine if the cluster was shape (M3b=M3w) or category (M3b>M3w) selective. A single significant cluster (cluster level p=0.004) was identified over central channels starting 242ms after stimulus 2. The comparison between the average ERP amplitude was higher for M3b vs. M3w, indicating category selectivity (Figure 24A). The secondary contrasts revealed categorical clusters over similar sensors and starting just slightly later latencies, 252ms for the M6+M3b>M0+M3w contrast and 264ms for the M3b>M3w contrast.
Figure 24: Post-extensive dual task training EEG-RA, M6>M0.
A) Cluster inclusion threshold of $\alpha < 0.05$. B) Cluster inclusion threshold of $\alpha < 0.01$.

As was done in Scholl et al. (2014), we wanted to see if the category selectivity in this cluster predicted participants’ performance on the same/different task. The logic behind this analysis being that the more categorical the neural response, as measured by the difference in average amplitude between the M3 conditions over the space-time cluster, the better the subject is at discerning the category of the individual stimuli, which should be reflected in better performance on the difficult M3 conditions of the same/different
task. The correlation between the difference in average amplitude and the mean performance on the M3 conditions, did not reach significance (R=-0.330, p=0.322) using the cluster defined by the M6>M0 contrast with a cluster inclusion threshold of alpha<0.05. However, the ERP traces in the middle panel of Figure 24A, show that there are two components contained within the temporal window of this cluster, and, while the earlier part looks nicely categorical, the later part looks like is starting to reflect task difficulty, as was seen in the later part of the signal in Scholl et al. (2014). If the cluster were representing difficulty, then the higher the amplitude for M3b, the most difficult condition, and the lower we would expect performance to be. Increasing the stringency of the cluster inclusion threshold to alpha<0.01 reveals a significant cluster (cluster level p=0.03, Figure 24B) within the latency of just the earlier more categorical peak, 266ms to 304ms. The amplitude difference between the M3 conditions (M3b-M3w) for the more stringently defined cluster significantly correlates with the mean performance on the M3 conditions (Figure 25, R=-0.780 [n.b., the negative correlation is due to the fact that it is a negative component], p=0.005).
Categorical selectivity of the post extensive dual task training posterior EEG cluster predicts mean M3 performance on the same/different task. Categorical selectivity was measured as the amplitude difference between the M3 conditions for the 266ms to 304ms central/posterior cluster, and it predicts mean accuracy in the same/different task on the M3w and M3b conditions, $R=0.78$, $p=0.005$.

3.3.3 fMRI-RA

In order to get an idea of the brain areas that are involved in the task, we began by looking at the task>fixation contrast ($p<0.0001$, cluster level FWE<0.05). Whole brain task activity shows a network of bilateral ventral visual, left posterior parietal (PPC) left sensorimotor, left premotor (PMC), left supplementary motor (SMA), and a substantial amount of bilateral subcortical activation in the basal ganglia, thalamus and cerebellum.

The primary M6>M0 contrast ($p<0.005$, $k>10$) reveals bilateral PPC as the only location with clusters that showed a categorical response profile (Figure 26). The left PPC cluster
was located in the precuneus/superior parietal lobule (SPL) with its peak activation located at MNI coordinates [-26 -64 42] and the right PPC cluster was located in the precuneus with its peak location at MNI coordinated [24 -60 34]. This contrast also revealed shape selective responses in ventral visual areas, as expected, namely in left fusiform, left lateral occipital cortex, and right inferior temporal cortex. The remaining clusters were spread out across frontal and parietal regions and mostly showed response profiles that mirrored condition difficulty. The secondary M6+M3b>M0+M3w contrast showed the same bilateral parietal areas, but no other categorical clusters (Appendix Figure 36).

Figure 26: Post-extensive dual task training MRI-RA, M6>M0 - category selective clusters in bilateral inferior parietal areas.
3.3.4 Behavioral Measures of Automaticity

**Dual tasking.** Participants attained high dual task proficiency as a result of training. This was expected, given that they were extensively trained on the car categorization dual task paradigm (Sagi & Tanne, 1994). Specifically, participants showed improved normalized dual task categorization performance from the first testing session, pre-extensive training, after one round of app training (~6,000 trials) to the last testing session, post-extensive training, after all five rounds of app training (>30,000 trials) (Figure 27, p=0.032, one-tailed paired t-test of “Post”>”Pre”). On the other hand, the normalized dual task performance on the peripheral disk task, which has previously been shown to remain attention demanding with practice (Fei-Fei et al., 2005; Li et al., 2002), did not show improvement from “Pre” to “Post” (p=0.4, one-tailed paired t-test for “Post”>”Pre”). In addition to showing improvement compared to the pre-extensive training time point, the participants showed equivalent accuracy on the car categorization task in the dual and single task conditions (p=0.9285, paired t-test), though it is worth noting that the bisected disk task was not equivalent by the end of extensive training, continuing to show a dual task interference effect (paired t-test of single versus dual peripheral performance, p=3.1*10^-7).
Figure 27: Extensive dual task car categorization training leads to a reduction in dual task interference. After extensive dual task training there is no significant difference between car categorization in the single and dual task scenarios which is reflected by the normalized central task performance ~1 for the post time point.

**Masked priming.** Participants were tested on masked priming (see Section 2.2.7) after the initial round of training, “Pre” and after extensive training, “Post”, to see if there was evidence of unconscious processing, another feature of automaticity (Moors & De Houwer, 2006). A 3x2 repeated measures ANOVA, with condition (“Same”, “Congruent”, “Incongruent”) and time point (Pre- vs. Post-extensive training) as within-subject factors, was carried out for both the mean accuracy as well as the median RT on correct trials. For the 3x2 ANOVA with mean accuracy as the dependent variable, the main effect of condition was significant (F=7.856, p=0.009), but the main effect of session (F=0.535, p=0.48) and the interaction effect (F=1.821, p=0.212) were not. Planned comparisons testing for category priming (one-tailed paired t-test of “Congruent” accuracy > “Incongruent” accuracy) and shape priming (one-tailed paired t-test of
“Same” accuracy > “Congruent” accuracy) were carried out for both time points. At the “pre” time point, there was a category priming effect on accuracy (T=2.004, p=0.035), and no significant shape priming. At the “post” time point, there was a significant category priming effect (T=3.743, p=0.002), but again no pure shape priming effect.

For the 3x2 ANOVA with median RT as the dependent variable, the main effect of condition was significant (F=13.125, p=0.001), and the main effect of session was also significant (F=7.172, p=0.011), but the interaction effect (F=0.057, p=0.945) was not. Planned comparisons testing for category priming (one-tailed paired t-test of “Congruent” RT < “Incongruent” RT) and shape priming (one-tailed paired t-test of “Same” RT < “Congruent” RT) were carried out for both time points. At the “Pre” time point, there was a significant shape priming effect on RT (T=3.199, p=0.012), but there was no category priming effect (T=0.067, p=0.474), and. At the post time point, there was again a significant shape priming effect on RT (T=3.199, p=0.004), but still no category priming effect.

In summary, there was a category priming effect in the accuracy measure at both time points, but no interaction effect with training. Furthermore the RT measure showed only shape priming before and after extensive training, as opposed to the single task trained subjects who showed a category priming effect in the RT measure. The two aims will be compared in Chapter 4.
3.4 Discussion

The fMRI-RA analysis revealed categorical clusters in bilateral posterior parietal category clusters and no where else in the whole brain analysis supporting the hypothesis that extensive dual task category training results in the development of categorization circuitry in posterior regions outside of the frontal bottleneck. The scalp topography of the earliest category cluster in the EEG-RA results are in good agreement with a parietal neural source, but an EEG source estimation analysis is underway to provide more convergent evidence that the EEG-RA and MRI-RA analyses are picking up on the same underlying neural substrates.

Given the purely shape selective responses in the ventral visual areas, the purely task difficulty selective responses in frontal, the neural processing stages underlying our same different task appear to as follows: 1) Stimulus 1 category is calculated in PPC from the stimulus shape information represented in vOT. 2) The result of the first categorization is then stored in frontoparietal working memory network. 3) Stimulus 2 category is calculated in PPC from the shape information in vOT and compared to the category of Stimulus 1 stored in working memory. 4) Same different response is calculated and executed by the motor network. It is worth noting here that unlike the post-extensive training fMRI-RA results, the motor areas do not show categorical responses. The differences between the training paradigms will be discussed more in the next chapter, but two potential reasons for this difference are: 1) the “post” time point in the single task training study was the second time participants completed the EEG-RA and fMRI-RA same/different task (see Section 2.4.2), so the motor response component was not novel
as it is here. 2) The accuracy for the single task trained subjects was higher for the in scanner task (see Chapter 4). As with the previous study, a new effective connectivity whole brain analysis (Gilson et al., 2016) to assess this proposed network is underway in collaboration with Gustavo Deco’s group in Barcelona.

### 3.4.1 Future Analysis to Address Categorization During Dual Tasking

The data discussed here address how categorization is done in single task scenarios after being trained in dual task scenarios but does not tell us what is happening when the brain is actually categorizing in dual task scenarios. To answer this question, fMRI data was collected from these subjects while they were categorizing cars in single and dual task scenarios. MVPA analyses will be carried out to assess where the category information can be read out in dual task scenarios compared to single task scenarios.
4. SINGLE TASK VS. DUAL TASK TRAINING

4.1 Introduction

In order to assess the differences between categorization learned through extensive single task training and categorization learned through extensive dual task training we directly compare the two participant cohorts at both the behavioral and neural level. A clear double dissociation in the behavioral profile is present, whereby the single task trained participants have higher accuracy and lower RT for tasks involving single car categorization and show greater category priming effects, but the dual task trained subjects show less dual task interference. Next we examine the differences in fMRI data to elucidate the brain basis for this behavioral difference. In the discussion we discuss the interpretations and limitations in these comparisons.

4.2 Results

4.2.1 Behavioral Measures of Automaticity

Dual tasking. Comparing across the studies, extensive dual task training confers a clear advantage over extensive single task training for dual task categorization performance (Figure 28). After one round of training the normed dual task categorization performance was already significant (pre time point, p=0.0051, two sample t-test) and the dual task trained participants grew in their advantage with extensive training (post time point, p=2.2851e-04). Additionally, the dual task trained subjects’ performance after one round of training was nearly significantly better than the single task trained subjects’ performance after all of training (p=0.0754). By the end of extensive training the dual
task cohort showed no dual task interference for the central categorization task, whereas the single task trained cohort, despite improvements, still had a very significant dual task interference effect. This is compatible with the idea of training specific improvement that is often observed in perceptual learning (Sagi & Tanne, 1994). It is worth noting that the groups never differed on normalized dual task disk performance, the task subjects were instructed to pay attention to and answer first, despite the fact that the dual task trained subjects had a great deal more exposure to the disk task.

The dual task study did have an early dual task performance inclusion criterion that the single task study didn’t have, raising the possibility that the differences were due, at least in part, to a selection bias for participants who were naturally good at dual tasking. As a control analysis we compared the performance on the 5th session of the animal/no-animal dual task training paradigm, the last session before the “Pre” car dual task testing experiment. We found no difference in the normalized dual task animal/no-animal performance (p=0.3555, two sample t-test), although there was a slight difference in the normalized dual task disk performance (p=0.0436). It is hard to say if the initial difference in the disk task performance is cause for concern about a potential selection bias when making comparisons between aims, particularly because the disk performance was never different in the car-DT paradigm comparisons, but the fact that there was no difference on the animal/no-animal task is encouraging.
Figure 28: Dual task training confers a clear advantage over single task training for DT performance.

**Masked priming.** Comparing the category priming effects across study (single versus dual) and training time point (pre vs. post) using a 2x2 ANOVA on the difference in accuracy between congruent and incongruent revealed no main effects or interaction effects involving study, but for the same ANOVA with RT difference between congruent and incongruent as the dependent variable there was a significant effect of study (F=5.194, p=0.035), with no interaction with training time point, meaning that single task trained participants showed more category priming as measured by RT effects.

**Same/Different RA task.** Comparing the participants across each group on their performance on the EEG and MRI behavioral task indicates that the dual task trained subjects were not as good at categorizing single cars (Figure 29). Looking at the accuracy
data from both the fMRI-RA sessions and the EEG-RA sessions reveal lower performance between aims for not only the post-extensive training for the dual task (the only imaging time point in that study) and the post-extensive training time point for the single task trained participants (EEG, p=0.0002; MRI, p=3.76*10⁻⁵), but also for the “Post” dual task time point compared to the “Pre” single task time point (EEG, p=0.0012; MRI, p=9.17*10⁻⁶). Further support for this is evident when comparing the group level categorization curves from the categorization test (Figure 6B for single task “pre” compared to Figure 23 for the dual task).

![Figure 29: A comparison of performance on the same/different category task across studies.](image)

“Pre” and “Post” extensive training imaging sessions were run for the single task trained subjects. The dual trained subjects were only imaged after extensive training.

### 4.2.2 fMRI-RA

Next we compare the MRI results for the dual task trained and single task trained subjects. As in the Same/Different behavior section above, we have “Pre” (after one round of training) and “Post” (after all five rounds of training) for the single task trained subjects and just “Post” (after all five rounds of training) for the dual task trained subjects.
First examining the comparison for task activation (cars>fixation), we see that DT trained participants showed greater activation compared to both single task time points (Figure 30, single task “Pre” in red, and single task “Post” in blue) in right motor cortex, right thalamus, and early visual areas. Compared to the single task-“Pre” time point, DT trained participants also engaged the bilateral striatum and angular gyrus more (with the caveat the bilateral angular gyrus was negatively activated for the single task-“Pre” time point). Looking at the opposite comparison, greater task activation for aim2 compare to aim1, the contrasts are not significant. Given that the single task trained subjects had better performance on the in scanner same/different categorization task, the increased activity in the dual task trained group is likely the result of more attention being devoted to the task which is of greater difficulty for them.
Next we examine the differences in adaptation across the aims to determine what areas show a difference in stimulus selectivity across the two training cohorts. Interestingly, the M6>M0 contrast revealed greater selectivity in early visual areas, as well as IT for the single task trained cohort at both time points compared to the dual task trained cohort, with the comparison with the single task “Post” time point showing more extensive significant clusters. Also interestingly, the M3b>M3w and M6+M3b>M0+M3w contrasts also reveal more category selectivity in left IT (Figure 31). Looking for greater adaptation, an therefore greater stimulus selectivity, in the dual task trained cohort compared to the single task trained cohort revealed no differences for the dual task versus single task “Post” time point, but for the dual task greater than single task “Pre” time point comparison the M3b>M3w and M6+M3b>M0+M3w revealed more category
selective adaptation in right motor cortex (ipsilateral to the hand they are responding with).

In summary, the dual task trained subjects showed greater activation in early visual areas compared to both single task trained scanning time points, but these areas were shown to be more stimulus selective with the M6>M0 rapid adaptation contrast in the single task trained cohort at both time points. Taken together these data suggest that the single task trained subjects have sharper tuning to the visual features of the car stimuli and the dual task trained subjects have not encoded the visual features of the car stimuli as well. Unique to the comparison of the dual task trained cohort to the single task trained cohort at the “Pre” time point was increase task activation bilaterally in the striatum, and greater category adaption effects in the right motor area for the dual task trained subjects.
4.3 Discussion

Behaviorally we see a double dissociation whereby dual task trained subjects show less dual task interference for car categorization compared to single task trained subjects, but single task trained subjects show higher accuracy and lower response times for single car categorization tasks.

Interestingly, in the fMRI data we see that the dual task trained participants are showing greater task evoked activity in visual areas, but that these areas are responding less selectively for car stimuli than they are in the single task trained participants. This data
offers an interesting explanation for the dual task subjects lower performance on the single car categorization based behavioral tests, namely, that dual task training results in less sharpening of the tuning for the physical features of the car stimuli in visual areas.

There are some differences between the two studies that we have to take into consideration as we interpret differences in the categorization behavior and the underlying neural activity. The only difference in the stimuli each cohort was trained on was that dual task training included more stimuli close to the one-to-one morph lines to ensure that these participants learned each part of the stimulus space that was relevant for our behavioral and imaging experiments. If anything, this would advantage the dual task trained subjects over the single task trained subjects on our in lab measures of single car categorization.

Another difference is that the dual task training study had an advancement criterion based on the animal/no-animal dual task training that the subjects did before starting training. Given that we have observed a good deal of variability in dual tasking ability, this criterion was instantiated to make sure that we had subjects who had the best chance at being able to learn the cars under dual task conditions, but means that we cannot rule out that the differences, particularly the fMRI results, were not the result of a selection bias. To allay these concerns we examined the difference in performance on the last session of the animal/no animal DT training paradigm and observed not differences between the two groups normalize dual task categorization performance. If the fact that there was a difference in their normalized dual task peripheral disk discrimination performance is
thought to be a concern, we could select for equal performance using this data and see if the currently reported differences change. Given that the disk task did not show a significant difference in the car DT itself, we believe it is unlikely to change the results.

One concern that still needs to be addressed here is that the normalized dual task car categorization performance is measured relative to the single task categorization performance, which we have shown to be lower in the dual task trained cohort. However, looking at just raw DT performance is also not a useable metric because the dual task interference must be defined with respect to the single task baseline performance. One approach to take might be to look at the correlation between the single task categorization performance and the normalized dual task categorization for each training cohort individually and then the two cohorts combined too see if the single task categorization predicts the normalized dual task categorization performance significantly better for the separate cohorts than for the combined.

Other future studies modeling the behavior with drift diffusion models of decision-making (Ratcliff & McKoon, 2008) might prove useful in assessing our hypothesis from the fMRI results that the dual task participants have less selective representations of the physical features of the car stimuli.
5. DISCUSSION

The studies presented here investigated two types of extensive categorization training: single task and dual task, with the purpose of testing the hypothesis that with extended training the stimulus-to-label mapping step moves out of PFC, and free of the serial processing limitation of the central bottleneck. We further hypothesized that this shift would result in a concomitant increase in features of automatic processing such as increased efficiency as evidenced by a reduced dual task cost (Shiffrin & Schneider, 1977) and unconscious processing as assessed by masked priming. In both studies there is strong evidence to support the formation of categorization circuitry outside of PFC, as well as accompanying behavioral changes suggestive of increased automaticity of the categorization process.

5.1 Single Task Extensive Training

In the single task training study EEG-RA at the “Pre” time point showed early shape selective signals over posterior channels that transitioned to category selective responses over left frontal channels at a latency ~250ms, in good agreement with previous findings from Scholl et al., 2014. fMRI-RA at the “Pre” time point provided converging evidence detecting a category selective cluster in left MFG and shape selective clusters in bilateral LOC. Taken together these data support previous findings of a two stage perceptual learning model (Riesenhuber & Poggio, 2000) with shape information represented in ventral visual areas and category decision circuitry in frontal (Freedman et al., 2003; Gillebert et al., 2009; Jiang et al., 2007; Scholl et al., 2014).
The main focus of this study was how extensive single task training would affect the underlying categorization circuitry. The participants went on to complete over 30,000 training trials and then came back for follow up imaging. The EEG-RA at the “Post” time point revealed a sizeable shortening of the latency to the earliest categorical response, by ~100ms, to an onset of ~150ms. This decreased latency of the first category selective clusters was accompanied by a posterior shift of that cluster. This early more posterior category cluster supports our hypothesis of a posterior shift in categorization with extensive training. The fMRI-RA experiment from the “Post” time point showed increased categorical selectivity in left SPL, left vOT, left PMC, right caudate nucleus, and cerebellum. Furthermore, comparison of the change overall change in activation, as well as in adaptation, from pre to post implies that more anterior IT might also be playing a role in representing car categories post training.

The SPL region fits with our PPC hypothesis as the location of the stimulus-to-label computation and is supported by the extant monkey electrophysiology literature (Bennur & Gold, 2011; Fitzgerald et al., 2011; Freedman & Assad, 2006; Swaminathan & Freedman, 2012). The left vOT region does not receive as much support from the monkey literature, but a recent study using and MEG-RA approach to study the effects of extensive training (~16,000 trials) concluded that extensive training shifted the earliest onset on category specific information shifted from a time window starting at 275ms with activity that localized most strongly to the PFC to a much earlier time window beginning at 113ms that localized most strongly to OT. Lastly, the more anterior temporal regions
are also reasonable given the role of the anterior temporal lobe in representing semantic information (Patterson et al., 2007) and the findings from human intracranial recordings of category selective single units in medial temporal lobe structures (Kreiman et al., 2000; Quian Quiroga et al., 2005).

EEG source estimation analysis is underway to help determine the potential neural sources of our early categorical cluster in the “Post” EEG data and see how it fits with the fMRI-RA data, but it remains entirely possible that all of these areas are capable of working together or separately to represent category information in different contexts. An ongoing whole brain connectivity analysis (Gilson et al., 2016) will help elucidate how these areas interact at the network level.

At the behavioral level, support for our hypothesis of increased automaticity with the formation of these posterior categorization circuits was seen in the significant decrease in dual task interference, though it is important to note that it was still present. Evidence of category priming in our masked priming paradigm was already present after the initial round of training, supporting the idea that different features of automaticity can be present at different stages of learning (Helie, Waldschmidt, et al., 2010) and support the approach of assessing automaticity by feature (Moors & De Houwer, 2006).

5.2 Dual Task Extensive Training

In the case of the dual task extensive training study we only assessed the brain basis of categorization after extensive training. The EEG-RA analysis revealed only one
significant cluster over central/posterior channels starting ~250ms after stimulus two onset, and the category selectivity of this cluster, as assessed by the difference in amplitude of the two M3 conditions, and the participants performance on those same M3 conditions are highly correlated. The latency of this cluster seems late compared to the single task trained “Post” time point, but it makes sense with the behavior because these dual tasked trained participants had longer response times on single car categorizations tasks. The fMRI-RA results also only detected categorical response profiles in only one region, bilateral PPC. These data strongly support our hypothesis that extensive dual task training leads to the development of categorization circuitry outside of the prefrontal bottleneck, strongly implicating the PPC as the location where the stimulus-to-label mapping is computed after training. In agreement with our hypothesis about improvements in dual tasking accompanying the development of categorization task circuitry outside of the frontal bottleneck, dual task trained subjects showed significant improvement in their normalized dual task categorization performance without a decrement in their normalized dual task disk task performance, and by the end of training they were able to categorize cars with equal accuracy in the single and dual conditions. Though it must be noted that the peripheral disk task still showed some dual task interference, so there still was some dual task cost.

5.3 How Does the Posterior Categorization Circuitry Arise?

One of the reasons we proposed the PPC in the first place was because its reciprocal connections with PFC (Cavada & Goldman-Rakic, 1989; Petrides & Pandya, 1984) made it an ideal area for the efficient transfer of task circuitry out of frontal cortex. We propose
that initial learning on the car categorization task proceeds in accordance with the traditional two stage perceptual learning model (Riesenhuber & Poggio, 2000) where sharpened visual representations of the stimulus shape are developed in ventral visual areas (Freedman et al., 2003, 2006) and task circuits are built up using those representations in PFC (Freedman et al., 2001; Jiang et al., 2007), with the striatum helping to provide a training signal to cortex (Antzoulatos & Miller, 2014; Ashby et al., 2007; Pasupathy & Miller, 2005). Next comes the transfer of task circuitry back to PPC; after the PFC learns the rule, it sends top down category signal feedback to the PPC, which we know also receives bottom up input from visual areas from its role in calculating bottom up saliency maps. Overtime the category information being fed back from PFC and the visual information being fed forward from the vOT would form a categorical representation in PPC, perhaps with the assistance of corticostriatal loops (Ashby et al., 2007).

5.4 Future Directions

The focus of this study was on the effects of extensive training on categorization, so the imaging time points were set up to best catch the training effects. Now that we have provided support for the existence of these categorization task circuits outside of PFC, the question of “how is the category circuit trained up?” is of great interest. We proposed a theory of how this might occur above. Future studies set up to measure this proposed feedback training signal are required to test our model would be of great interest. For instance, is this feedback reduced when attention on the task is reduced? This might serve as a basis for the differences in the single task and dual task findings above.
Analysis of individual differences in task learning and automaticity would be another important next step in this line of research. In the data set we already have collected we could start investigating some very interesting questions on this front. Do behavioral performance metrics (or in the case of the single task training study neural measures from the “pre” time point as well) from the beginning of training predict neural or behavioral outcomes? For instance, we could look at our priming or dual task data from after one round of training to see who is more automatic in their behavioral profile, and we could then see if their fMRI or EEG signals are more similar to the post extensive training group data that the less automatic participants. It would also be interesting to investigate how more general factors like intelligence modulate category learning (Neubauer, Grabner, Freudenthaler, Beckmann, & Guthke, 2004). As a start, in our current data set participants’ general attention abilities were assessed using the Attention Network Task (Fan, McCandliss, Sommer, Raz, & Posner, 2002) and it would be interesting to see if they had any predictive power for behavioral or neural training outcomes.

5.5 Conclusion

In conclusion, whether it is in dual task or single task scenarios, 30,000+ categorization trials lead to categorization circuitry computing the initial stimulus-to-label mapping outside of PFC. The two types of training resulted in unique neural and behavioral profiles. Single task trained participants showed left lateralized categorization activity in vOT and SPL, whereas the dual task trained subjects showed bilateral parietal category selective clusters. The time course of the emergence of the category selective signal was
also very different, with the single task trained subjects showing categorical signals 100ms earlier than dual task trained subjects. These neural differences go along with a double dissociation in the behavioral profiles of the two cohorts, with the dual task participants showing less dual task interference than the single task trained participants, but showing less category priming and lower accuracy and RT on single car categorization.
6. APPENDIX

Figure 32: Pre-extensive single task training EEG-RA, M6+M3b>M0+M3w – time-lapsed scalp topography of the anterior cluster.

Figure 33: Pre-extensive single task training EEG-RA, M6+M3b>M0+M3w - posterior clusters.
Figure 34: fMRI-RA same/different category behavior before and after single task training.
A) Mean accuracy by condition, "Pre". B) Mean individual median RT by condition, "Pre". C) Mean accuracy by condition, "Post". D) Mean individual median RT by condition, "Post". E) Mean overall accuracy “Pre” vs. “Post”. F) Mean overall individual median RT “Pre” vs. “Post”, p=.002. All error bars show SEM.

Figure 35: Pre-extensive single task training fMRI-RA, M6>M0 - shape selective responses in ventral occipitotemporal (vOT) cortex.
Figure 36: Post-extensive dual task training fMRI-RA, M6+M3b>M0+M3w - category selective clusters in bilateral inferior parietal areas.
7. REFERENCES


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