

CHAPTER 37

Brain Changes in the Development of Expertise: Neuroanatomical and Neurophysiological Evidence about Skill-Based Adaptations

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Introduction

As humans acquire skills there are dramatic changes in brain activity that complement the profound changes in processing speed and effort seen in behavioral data. These changes involve learning, developing new representations, strategy shifts, and use of wider cues and approaches. Experts differ from novices in terms of their knowledge, effort, recognition, analysis, strategy, memory use, and monitoring (e.g., see Chi, Chapter 2; Feltovich, Prietula, & Ericsson, Chapter 4). In the last decade there have been major advances in our ability to noninvasively track human brain activity. There are now over a hundred experiments tracking learning or expert performance. Patterns are beginning to emerge that show that learning and skilled performance produce changes in brain activation – and different types of changes – depending on the brain structure and the nature of the skill being learned.

In this chapter we will review the changes that occur in the brain as skill is acquired. We will detail the anatomy and processes

involved. We will provide a brief summary of the methods employed. We will review the nature of learning of skills, resource utilization, and performance of experts. The reader who wishes to learn more details regarding these methods might examine a current introductory chapter (Schneider & Chein, 2003) or current textbooks of cognitive neuroscience (Gazzaniga, Ivry, & Mangun, 2002), brain imaging (Jezzard, Mathews, & Smith, 2001), and cognitive neuroscience modeling (O'Reilly & Munakata, 2000).

An Example of Changes in Brain Activation during One Hour of Skill Acquisition

It is important to realize that most of the issues involved in behavioral skill development are associated with changes in brain activity. Our brains are always active as we perform any task and even when we are at rest. Any change in human behavior, such as skill acquisition, must have some physical cause that involves either a *functional* change in the brain activation or a *structural* change in the size of brain tissue.

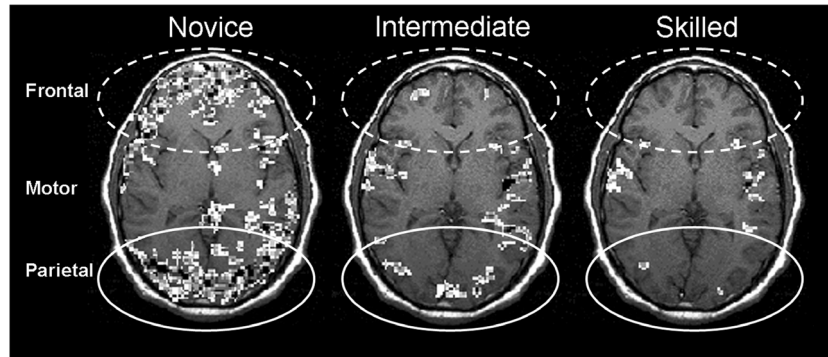


Figure 37.1. Activation of the brain, as a function of practice, in three periods of learning a motor tracking task. This is a maximum projection image with white areas showing the activation of any cortical area either above or below the illustrated brain slice. The image is an axial (aerial) view of the head where the top of the image corresponds to the front (nose) of the head and the bottom corresponds to the back of the head. The frontal areas (dashed ellipse) and parietal attention control areas (solid ellipse) show dramatic reductions in activation. The motor areas (middle of images) shows fairly preserved activation.

The understanding of brain mechanisms is synergistic with the understanding of the behavioral mechanisms. Let us illustrate with an example of how skill changes behavior and brains. Through the functional magnetic resonance imaging (fMRI) technique we can collect brain data and relate that to the behavioral changes observed both in the brain scanner and as a consequence of prior behavioral training. With fMRI we can compare activation across conditions with millimeter spatial resolution and one second temporal resolution.

Figure 37.1 provides a series of activation patterns that shows how brain activity changes as a skill is acquired relative to initial untrained performance. The brain activity changes dramatically over the course of sixty minutes of practicing a simple tracking task. With this task, learning occurs rapidly enough to see changes in brain activation within one scanning session. In the first twenty minutes of task performance many areas of the brain are active. With every ten minutes of practice, brain activation decreases, ultimately reducing by 85% over the course of the first hour.

Subject behavioral performance improves with reductions in tracking error, faster responding with less tracking delay, and as the session continues, tracking becomes less

effortful. As the behavioral changes occur, there are also quantitative and qualitative changes in the cortical activity.

The predominant change is a reduction of brain activation, but changes differ substantially across areas. There is a near drop out of activity in the frontal (anterior) parts of the brain that are involved in task control and working memory (solid ellipses). There are substantial reductions in the posterior part of the brain (parietal cortex) related to attentional control (dashed ellipses). The motor (center region) and perceptual areas (not visible in the brain slice) are involved in making responses and detecting stimuli respectively, and they will remain active because they are necessary for task performance during novice and skilled performance.

One must be cautious about overinterpreting dramatic imaging data, especially with regards to training and brain plasticity (see Poldrack, 2000, for a detailed explanation). When comparing across individuals or time, differences in brain activity can occur for many reasons. Imaging takes a snapshot at a particular point in time. It is difficult to determine if any contrast is stable or due to differences ranging from genetics, experience, strategy, motivation, or changes in baseline.¹

There are a variety of patterns of change in activation seen in skill acquisition experiments depending on the nature of the task, practice levels, task difficulty, and nature of control conditions (see Kelly & Garavan, 2005, for a recent review). The patterns include: brain activity decreases in the control network (see next paragraph), maintenance of activity in the perceptual and motor areas, and occasionally increases of brain activity or shifts in activity to new regions. Throughout the chapter we will review examples of changes in brain function (that is, changes in the activity patterns), and we will relate these patterns to the task parameters, behavioral responses, and level of experience in performing the task.

The most common pattern is **reduced control network activation with maintained perceptual motor activity** (note Kelly & Garavan, 2005, refer to this a “processing efficiency change”). The control network is a group of brain areas that are believed to work together to scaffold learning when performing a new task. This network (see “Network of Specialized Processing Regions”) comprises a set of discrete cortical areas controlling goal processing, attention, and decision making. One would expect to see those (learning-related) areas active early in practice and then decrease activity, possibly even dropping out, as skill is acquired. This is the expected pattern for perceptual motor tasks, where stimulus properties and (motor) response properties remain consistent or unvarying throughout performance (see “Controlled and Automatic Processing during Learning” section). A second pattern is one of **increased cortical tissue devoted to the task after very long periods of training** (e.g., expanded hippocampus for taxi drivers). And a third pattern is **functional reorganization**. As the term implies, there is a reorganization of active brain areas; that is, different brain areas are active in different stages of learning. The engagement and disengagement of brain regions reflects the fact that unique regions are involved in the various types of processing. As a skill is acquired, different strategies are used, and therefore new areas become active to perform the underlying processing (e.g., in mir-

ror reading, early practice involves mental rotation of the letters, and late performance involves recognition of the rotated word and recall of the meaning without slow algorithmic rotation).

Overview of Brain Anatomy and Functional Change

To understand the changes of the brain with skill acquisition it is useful to take a structural/functional view of the brain. We will provide a short overview of the architecture of the brain (i.e., the structure or anatomy) that will illustrate the hierarchical nature of perceptual processing by reviewing the visual system (specifically the occipitotemporal pathway), and comment about brain misconceptions.

The Bare Basics of the Cerebrum

The cerebrum of the brain is divided into five lobes; occipital, parietal, temporal, insular, and frontal. Generally speaking,² the function of each lobe is the following:

1. The occipital lobe is involved in visual processing.
2. The parietal lobe participates in visual processing by coding spatial information, and it is involved in attentional control and somatosensory processing (bodily sensation).
3. The temporal lobe also contributes to visual processing at the level of object formation (and face processing) and is involved in coding auditory and verbal information and memory storage.
4. The insular lobe is involved in emotional processing, taste, and learning.
5. The frontal lobe is involved in executive function, reasoning, effort and emotional coding, conceptual information and rules, motor control, speech, and smell.

Network of Specialized Processing Regions

The brain is a network of hierarchically organized specialized modules. If one moves a

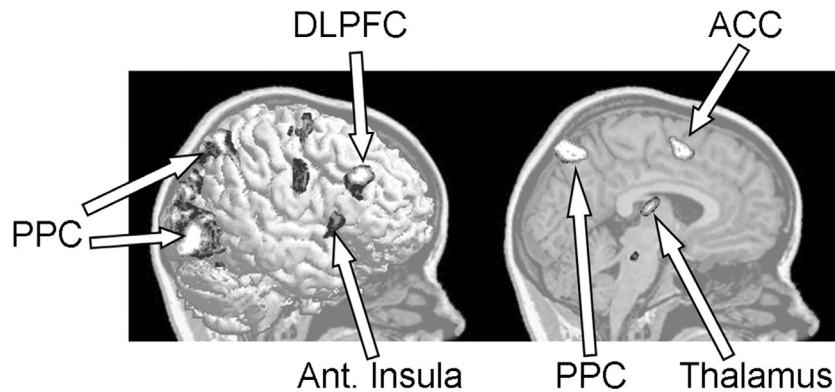


Figure 37.2. Major parts of the Control Network supporting skill acquisition and cognitive control. These areas include dorsolateral prefrontal cortex (DLPFC), anterior cingulate/pre-supplementary motor areas (ACC), posterior parietal cortex (PPC), anterior insula, and thalamus. These areas appear to be domain general and decrease in activation as automaticity develops.

centimeter in the brain, typically the tissue does something distinctively different than the neighboring region.

The brain has many **domain specific representational areas** connected in a quasi-hierarchical fashion. There are an estimated 500–1000 specialized processing regions (Worden & Schneider, 1995). A complex process such as visual processing occurs in over thirty distinguishable processing regions (Felleman & Van Essen, 1991), including those for detecting lines, colors, shapes, structure (e.g., houses, faces), motion, and spatial relationships. These representation areas appear to be quasi hierarchically connected. There are reciprocal connections between these regions, allowing information flow to be both bottom-up and top-down. Information is coded in the pattern of activity, with any one region encoding many exemplars and types of stimuli (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). These representation areas include input (visual, audition, somatosensory, gustatory) and output motor areas. These areas can be mapped with nearly millimeter precision showing *retinotopic* (a retinal [eye] based coordinate map in visual [occipital] cortex), *tonotopic* (a map of acoustical frequencies in auditory [temporal] cortex), *somatotopic* (a map of bodily sensation in associative [parietal] cortex), and *motor* (map of muscle control of the body). As

information processing flows to higher levels, its spatial localization reduces and object specialization increases (e.g., moving from lines covering 0.1° visual area in V1 [the initial visual processing region located in the occipital lobe] to faces of individuals anywhere in the visual field in the fusiform cortex [a later visual processing region located in the temporal lobe]).

The brain contains a small number of **domain general control areas** that appear to be involved in many tasks and that modulate cortical activity (see Schneider & Chein, 2003, for details). There is initial evidence to suggest some specialization of function within the different areas. However, these areas work as a tightly coupled unit (e.g., typical correlations between activation in respective areas range from 0.8–0.95). The major areas are listed below, and a subset is shown in Figure 37.2:

- attentional control – posterior parietal cortex (PPC)
- process monitoring, decision making, conflict management – anterior cingulate cortex/pre-supplementary motor area (ACC/pre SMA)
- goal processing and tasks switching – dorsolateral prefrontal cortex (DLPFC)
- emotional processing – amygdala
- episodic coding of association – parahippocampus and hippocampus

- smooth sequential processing – cerebellum
- reinforcement and motor control – basal ganglia

The existence of a *single domain general control architecture*, controlling a large number of *domain specific representation regions*, has strong implications regarding the understanding of skill acquisition and performance. Activation of the control network might differ between tasks and cause conflict when two tasks are performed simultaneously (e.g., the perceptual detection of a novel line angle and completion of a sentence in a language task might conflict if both tasks need activation of domain general comparison operations). Competing activation in the specific representational areas would be a problem only if two tasks utilized the same modality-specific region. For example, two tasks involving motion judgments would interfere with each other, causing performance to deteriorate, but a consistent³ motion detection task and an auditory frequency detection task could be performed concurrently.

MISCONCEPTIONS ABOUT THE BRAIN AND EXPERTISE

There are three common misconceptions/myths about the brain that are worth refuting before proceeding in the review:

Misconception 1 – More Brain Implies Better Performance. This is perhaps best illustrated by the popular myth that most people “use only 10% of their brain” (see Beyerstein, 1999) and, by implication, that “using more would be better.” The brain has many specialized areas, and for any specific task only a small subset is active. This is analogous to muscles. At any one point in time only a small subset of muscles are active in a normal person. In fact, if most of the muscles were active (as in generalized dystonia), a person would be out of control. If much of the brain is active (as in a severe epileptic seizure), one is completely dysfunctional. Another similarity to muscles is that in some cases more is better but often it is not (e.g., a skilled skier makes very small focused muscle changes to control direction relative to the novice who

makes frequent erratic changes in muscle tone). In learning to row, training results in a decrease in muscle activation, and coherence increases as stroke rate and power increase (Lay et al., 2002). In the brain, having many areas process an input reduces the availability of those areas to process other stimuli. For example, early mirror reading involves large areas of visual representation to encode the visual input, rotate the individual letters, reassemble the rotated letters, and then recognize the word. However, after practice a small area can recognize the rotated string directly as a visual object (e.g., “αλΟΙ”) and map it to its meaning, leaving large areas of the visual system available for other tasks.

Misconception 2 – Plasticity Is Limited in Adulthood. There is substantial evidence of changes in connection strength and neuron size for adult subjects. The elderly can learn skills (see Krampe & Charness, Chapter 40), and there is substantial evidence that normal elderly still have cortical plasticity (Buonomano & Merzenich, 1998) and exhibit substantial changes in activation with practice (Karni et al., 1998; Kolb & Whishaw, 2003). Cognitive (i.e., dual-task) training has been demonstrated to increase plasticity in the prefrontal brain regions that exhibit the greatest atrophy in aging population (Erickson et al., 2005c).

Misconception 3 – Left/Right Brain Specialization Is a Major Factor in Learning and Performance. It is true that the brain has specialization (e.g., language tends to be more left dominant). However, most functions appear both on the left and right side of the brain. The brain is far more specialized from front to back (e.g., emotion [front], motor, somatosensory [middle], spatial, visual [back]). The key benefit from brain mapping is not simple location (e.g., left/right or anterior/posterior). Rather, it is the understanding of the hierarchical stages of each of the representation systems and how those interact with executive, emotional, and memory processing that elucidates brain function. Practice will cause changes in the brain areas dedicated to the processing of *what* is specifically practiced (see also Ericsson, Chapter 38). People *do* vary in language

and holistic processing, and there is left/right laterality of that processing, but there is little special status for the global feature of being on the left or right.

Next we will preview the six patterns of learning-related brain changes that will be elaborated further in the chapter.

THEMES IN LEARNING LITERATURE, BRAIN PROCESSING, AND BRAIN STRUCTURE

There are six themes evident in the learning literature (Kelly & Garavan, 2005; Poldrack, 2000; Schneider & Chein, 2003; see also Feltovich et al., Chapter 4). First, **learning is localized and very specialized**, with different portions of the brain showing dynamic change and location change depending on the task. Second, in general, **learning and processing occur in the same cortical locations**. Third, **learning can produce both increases and decreases in the areas of activation**, influencing both the richness of the representation and the efficiency of processing. Fourth, **in some tasks there is a reorganization of the task that involves different brain regions when alternate strategies⁴ are used** (e.g., shifting from performing a math algorithm to using recall to produce an answer). Fifth, **behaviorally relevant objects and other stimuli are uniquely processed by experts** (i.e., faces for everyone, birds for bird watchers, ballet movements for professional ballet dancers). Sixth, **learning can produce detectable morphological changes** such that extended training can enlarge the amount of grey matter dedicated to processing the type of information that has been trained. The remainder of the chapter will illustrate these themes in three major sections. Section one, "Controlled and Automatic Processing during Learning," will introduce the reader to the dual processing account of skill acquisition by briefly reviewing the longstanding behavioral effects and the theory's recent extension into characterizing the underlying neural substrates. Themes 1 and 2 will be illustrated in cognitive laboratory tasks that involve several sessions of training. Section two, "Practice Effects on Brain Activa-

tion in Working Memory Tasks and Dual-Tasks," will extend Section one into working memory and dual-task paradigms. Themes 1–4 will be illustrated in cognitive and motor laboratory tasks that involve a range of training from minutes to sessions. Finally, Section three, "Perceptual-Motor Learning and Expertise," will review visual processing, motor learning, kinematics, navigation, reading, and music training. Themes 4–6 will be illustrated primarily through the study of real-world skills that develop over many years of practice. The themes will be stressed throughout the text; however, we recommend that the reader briefly review them (see above) before proceeding.

Controlled and Automatic Processing during Learning

Skill acquisition involves creating representations and altering control routines. In this section we will focus on the control routines. Skill acquisition involves priority learning, learning to code stimuli according to their importance (see Feltovich, Prietula, & Ericsson, Chapter 4, on "Expertise Involves Selective Access of Relevant Information"). Through this learning, critical stimuli (determined by learned priority) ultimately transmit information to stimulus processing regions and trigger control area responses. For example, in the cocktail party effect, hearing one's name in a nearby conversation can draw attention despite competing background noise and focused attention on the current conversation. This is because one's name has become a high priority stimulus that one learns to automatically orient towards over time. (See Proctor & Vu, Chapter 15; Ericsson, Chapter 38, on traditional models of skill acquisition, such as Fitts & Posner, 1967).

Many of the practice effects of learning can be interpreted within the traditionally behavioral framework of automatic processing and controlled processing (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Feltovich et al., Chapter 4, on "Expertise

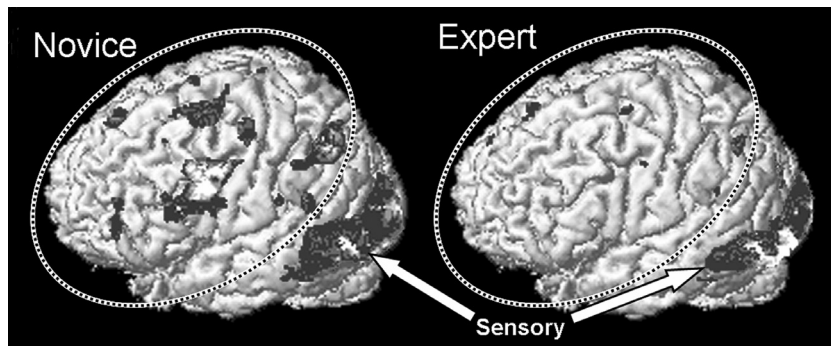


Figure 37.3. Activation early and late in a consistent search task. The dark areas (and dark areas with bright centers) illustrate regions that are active. The ellipses highlight the frontal and parietal areas. There is a substantial reduction in activation in these areas as skill is acquired and more automatic processing develops. The visual areas (lower right parts of the images) show continued activation early and late in practice with the sensory processing continuing even while controlled processing decreases.

Involves Automated Basic Strokes”), with recent extensions to cortical processing (Schneider & Chein, 2003, CAP₂ model). Novice performance is assumed to involve high-effort use of the **domain general network** of control processing through attentional routines. The same pieces of brain tissue perform key tasks such as attention, comparison, and decision across different representation modalities (e.g., visual, auditory or motor). **Controlled processing** typically occurs in novel or varied tasks (see “varied mapping” in next paragraph) when one must compare stimuli and release responses based on information stored in working memory. **Automatic processing** typically occurs for well-practiced, consistent tasks where the responses can occur with little effort. These are representation-specific operations (e.g., the visual mapping “ $\alpha\lambda\sigma\Gamma$ ” to “love” will not transfer to the reversed phonemes [sounds] of the word “love”).

The classic example of a controlled process is visual search of a varied set of objects (see Schneider & Shiffrin, 1977). For example, in a category search task subjects respond if a word is a member of a category (e.g., respond to animal or vehicle). If the memory set alters from trial to trial and there is a *varied mapping* (VM) (e.g., responding to animals on some trial and ignoring vehicles,

and other trials the opposite) the reaction times are over 200ms per comparison (Fisk & Schneider, 1983). In contrast if the categories are *consistently mapped* (CM) (e.g., always responding to animals and ignoring vehicles), reaction time is uninfluenced by the number of categories compared (e.g., slope 1ms) once there is extensive practice. The *novice* search task (both CM and VM) involves goal processing, memory, attention, decision making parts of the control network, representation patterns of the visual input, and memory of the targets. The *practiced* CM search task involves automatic processing in which modules transmit representations to the next stage without involvement of the control network (Figure 37.3).

Controlled and automatic processing show dramatically different and complementary processing benefits and disadvantages (see Schneider & Chein, 2003). Controlled processing has the characteristics that allow rapid acquisition, easy alteration of process,⁵ and modification of memory, but it is a slow, serial, high-effort mode of processing that deteriorates under high workload and stressors (e.g., sleep deprivation, stress, and alcohol). Automatic processing has the complementary weakness and strengths. Automatic processing shows slow acquisition over hundreds of trials, is difficult

to alter, does not modify memory, is fast and parallel, is low effort, and is robust to high workload and stressors. The CAP2 model (for an in-depth coverage of the model, we refer the reader to Schneider & Chein, 2003) provides a connectionist implementation of controlled and automatic processing and interprets interactions in the control and data network and likely brain areas involved in each function. The transition from controlled to automatic processing occurs in this model as the data modules become capable of transmitting their output without mediation by the control system.

From a neural perspective, the development of automatic processing should result, with practice, in reductions in the same regions that support controlled processing (Chein & Schneider, in press; Schneider & Detweiler, 1988; Kelly & Garavan, 2005; Jansma et al., 2001; Schneider & Chein, 2003). To determine if a *specific group of brain areas* are commonly modulated as a function of practice, a meta-analysis of brain-imaging studies that utilized practice was performed (Chein & Schneider, in press; Schneider & Chein, 2003). Study selection was restricted to *consistent* tasks in which novice performance was contrasted to practiced (i.e., minimum of ten minutes) performance of an explicitly acquired skill. The meta-analysis revealed activity in a reliable network (that we refer to as the “control network”) of brain regions. This putative control network includes lateral frontal, medial frontal, posterior parietal cortices, and the thalamus. According to the theory, such a network should be engaged in novel learning situations and should reduce activity or “drop-out” as a function of extensive consistent practice.

Automatic processing occurs as the control-network regions are released, *leaving task-specific processing regions engaged* to support task performance (Chein & Schneider, in press; Schneider & Chein, 2003; see also, Feltovich et al., Chapter 4 on “Expertise is Limited in its Scope and Elite Performance does not Transfer”). Two fMRI studies have varied consistency of learned associations and demonstrated that

consistency and practice can modulate cortical activity (Chein & Schneider, in press; Jansma, Ramsey, Slagter, & Kahn, 2001) when acquiring skilled performance. Jansma et al. (2001) trained a working-memory consonant item-recognition task under consistent (i.e., target and distractor items are always from distinct sets) and variable conditions (i.e., targets and distractor sets are redefined on every trial by selection from a common pool of items) and found that practice produced reductions in activity only for the consistent task.

The control network appears to be domain general. In a study by Chein, McHugo, and Schneider (in prep), early in practice both an auditory task and a visual spatial task had activated a network of common areas in frontal, cingulate and parietal cortex. In addition there were task specific areas (occipital cortex for the visuospatial task and temporal lobe for the auditory task) that were unique to the type of task being performed. In both tasks, with consistent practice the control network dropped out. It is important to note that at the millimeter level of cortical tissue, *very different tasks activated the same cortical control areas* to provide scaffolding to perform and learn the task. The same tissue (i.e., the control network brain regions) was controlling different representation areas, each of which was later able to perform its task automatically.

A separate study, a paired-associate task in which all training was kept consistent, demonstrated engagement of the same network and subsequent practice-related reductions for both verbal and non-verbal (i.e., novel shapes that are difficult to assign verbal labels) associates (Chein & Schneider, in press).

In varied mapping tasks, activation resembled initial, untrained levels, both early and late in practice (Chein, McHugo, & Schneider, in prep). There was no evidence of practice-related increases of activation or reorganization. These studies demonstrate that consistent practice, but not variable practice, results in processing efficiency or activity reduction, in the same regions that support untrained performance.

Furthermore, task-specific processing regions continue to activate without regard to consistency of practice.

In summary, the shift from controlled to automatic processing can occur on a relatively short time scale.⁶ The changes in behavioral performance (i.e., increases in accuracy and/or decreases in reaction time) are associated with underlying changes in brain processing (i.e., decreases in brain regions responsible for learning and control). This shift only occurs through practice of consistent tasks. Furthermore, brain regions involved in motor and perceptual processing remain active even with practice, as ongoing processing in these areas is necessary for task performance. Finally, automated consistent tasks show no evidence of functional reorganization or practice-related activation increases in the control network regions.

The next section will explore practice effects in working memory and dual-task paradigms. In these studies, practice-related activation increases, practice-related activation decreases, and as well as practice-related activation increases and decreases are reported. Although the controlled and automatic processing perspective focuses on practice-related brain-activation decreases, practice-related activation maintenance as well as practice-related activation reorganization are consistent with the theory in cases of variable tasks that require manipulation of working memory (Jansma et al., 2001; Schneider & Chein, 2003).

Practice Effects on Brain Activation in Working Memory Tasks and Dual-Tasks

In this section we will look at practice effects in cognitive tasks that employ online-learning or working memory and tasks that involve learning to process multiple sub-tasks concurrently, that is, dual-task learning. Although these studies were not designed to investigate automatic processing shifts (see prior section), parallels can be made in terms of behavioral improvement and

neural response. Furthermore, these tasks were trained under a range of practice, both “briefly” (i.e., for 30 minutes) and “extensively” (i.e., several weeks), and produced similar results.

BASIC WORKING MEMORY (WM) OVERVIEW

The working memory model is composed of three major parts, an executive control system and two slave processing systems, one involved in visuospatial information and the other involved in phonological information (Baddeley & Hitch, 1974). Distinct from both short-term and long-term memory, this system is involved in processing and maintaining information over brief delays and in manipulating information. WM tasks have three phases, encoding of stimuli, delay (where no stimulus is present and the associated codes must be maintained and/or manipulated), and retrieval (of codes or transformed codes) to enable responding.

PRACTICE AND WORKING MEMORY

Working memory tasks have been frequently studied using behavioral measures and in brain imaging (Baddeley, 2003; Cabeza & Nyberg, 2000), but only recently have studies investigated the impact of training in these tasks. Imaging studies have reported practice-related increases and decreases in neural activity, as well as shifts in activation location (for review, see Kelly & Garavan, 2005; Poldrack, 2000). Increases may result from strengthening of existing activation or from spatial expansion. Decreases in activity, conversely, may reflect the reduction in the strength of existing activation or a reduction in spatial extent. Whereas increases are believed to reflect the buildup of cortical representations, decreases are believed to result from greater neural efficiency, where only a subset of the initial neurons continue to respond to a particular stimulus or support the performance of a particular task. A shift in the location of activity reflects a reorganization of regions used to support performance. The reorganization may reflect a shift in processing or strategy usage as a result of practice. The level of practice, the

period of imaging in proportion to practice amount, the task domain, and task characteristics (such as stimulus-response relationships) influence the dynamics of activation. The majority of experiments involving practice of cognitive tasks report practice-related decreases or reorganization, while motor learning tasks (see motor learning section) tend to report practice-related increases (see below).

Garavan, Ross, Li, and Stein (2000) varied the amount of practice for participants in a visuospatial delayed-match-to-sample task (dot location). Prefrontal and parietal areas, typically implicated in working-memory function (Cabeza & Nyberg, 2000; Carpenter, Just, & Reichle, 2000), were activated during the initial performance of this task. Brain imaging after both brief and extended practice (80 vs. 880 trials; Garavan et al. 2000) showed reduced activation in these regions. Performance after practice was not associated with increased activation in any other regions, which suggests *processing efficiency* as the source of the reduction as opposed to a *functional reorganization*, where practiced task performance would be supported by regions differing from unpracticed performance. Similar findings were obtained by Landau, Schumacher, Garavan, Druzgal, and D'Esposito (2004), who found that the initial activity in frontal, temporal, parietal, and occipital cortex during a face working-memory⁷ task was reduced with practice. The reductions occurred within a single brain-imaging session subsequent to only thirty minutes of behavioral training, which demonstrated that the decreased magnitude of activation can occur rapidly. Other investigators have found initial increases in activation with subsequent reductions after extended training. Hempel et al. (2004) trained participants on a verbal n-back task twice daily for two weeks. At two weeks, performance improvements accompanied increases in right superior parietal lobe and right intraparietal sulcus, followed by stable performance and activation decreases after four weeks of practice.

Not all studies report practice-related activation reductions in working memory tasks. Olesen, Westerberg, and Klingberg (2004) trained subjects in a visuospatial span task and monitored this activation in fMRI on five occasions, once per week. The increases found in frontal and parietal regions were interpreted as evidence of cortical plasticity occurring on a slower time scale through extensive training, akin to the "slow learning" changes reported in the motor-learning literature (Karni et al., 1995). Additionally, the experimental training resulted in improved performance on several untrained neuropsychological tests (i.e., spatial tasks, including the Raven's Progressive Matrices, a task that involves reasoning). Olesen et al. (2004) suggest that extended WM training may improve processing capacity, which is necessary for high-level performance on a neuropsychological test battery.

Olesen et al. (2004) and Klingberg et al. (2002) used adaptive training (tasks in which difficulty is adjusted for individual performance) over a longer time scale. The increases in neural activity reported by Olesen may reflect this continual increase in task difficulty, the extensive amount of training conducted relative to other studies, and/or the specifics of the task. Extensive training alone is not likely to account for the increases. At four weeks, Hempel et al. (2004) report *decreases* in n-back training, whereas Karni et al. (1995) report *increases* in activity in finger opposition sequence performance. The increases are consistent with other studies of sequence learning (Karni et al., 1995; Hazeltine, Grafton, & Ivry 1997; Honda et al., 1998), suggesting a distinction between practice on motor and cognitive tasks.

Most of the reviewed studies report decreased working memory activation with task practice, whether the experiment employed "short" training regimens thirty minutes, "long" training regimens (weeks), or both. One study of visuospatial span (Olesen et al., 2004) did find practice related increases with long training; however, although the task is a working memory

task, it is also a sequence task (in which participants had to perform both forward and backward sequences), and the neural response was similar to sequence learning paradigms (which typically contrast new [or transformed] and old sequences [Hazeltine et al., 1997; Honda et al., 1998]) and the finger opposition paradigm [Karni et al., 1995]; see the motor learning section). This suggests a distinction between motor and cognitive tasks in which motor task practice leads to functional increases of activation, whereas cognitive task practice leads to functional decreases reflecting neural efficiency. Cognitive task decreases of activation are not restricted to working memory tasks per se; decreases were also found in the studies of automatic and controlled processing.

DUAL-TASK METHODOLOGY

An important aspect of skilled performance is the ability to perform multiple tasks at one time. Dual-task performance is an area of interest because of its potential to inform understanding of attention limitations, learning, and executive processing, both through behavioral investigations and more recently in brain-imaging studies. Dual-tasks paradigms employ the performance of two or more tasks in close temporal proximity (see Meyer & Kieras, 1997; Pashler, 1994; Schneider & Detweiler, 1988). Simultaneous performance that is untrained typically results in decreases in accuracy and increases in reaction time relative to isolated task performance. Although all dual-tasks report this concurrent performance cost at some point in training, a distinction is made between dual-tasks that employ *short, variable time lags* (i.e., interstimulus interval, ISI) between component tasks, known as psychological refractory periods (PRP; short ISI < 300 msec), and those dual-tasks that use relatively *longer, fixed time lags* (typically > 1 second). In PRP tasks, reaction time increases for the second task response in the short-lag condition, relative to the long-lag condition, because short ISIs force the performer to use overlapping task processing,⁸ which is a limited resource (that is, for short

ISI RT₂ > long ISI RT₂). PRP tasks are also typically given response priorities because one task is designated as the primary task while the other is designated the secondary task. The PRP effect is immutable with practice unless performers are allowed to respond without regard to task designation (remove the primary and secondary task-response designation). Non-PRP dual-tasks (ISI > 1 second) do not have immutable concurrent performance costs because practice results in the speeding of processing so that the performer can learn to respond to each task quickly in isolation, as long as there are no structural limitations (such as having only one response finger) (see Meyer & Kieras, 1997).

There are a variety of patterns of activation seen when contrasting single- and dual-task conditions. This is not surprising when one considers the range of paradigms that are referred to as dual-tasks. A dual-task can be composed of subtasks that involve *concurrent* component tasks (such as PRP tasks) or temporally *separated* component tasks. The subtasks are sometimes "simple" tasks, such as detection or discrimination, or more "complex" tasks, such as spatial rotation or reading comprehension.

Generally speaking, dual-tasking typically involves more effort and time sharing than the single task performance. And motivation and practice history (both single- and dual-task) must be considered when comparing single- and dual-task performance. All of these factors must be interpreted with caution when reviewing dual-task effects in a behavioral study, and the issues are further complicated in a brain-imaging study. For example, in fMRI, threshold selection can cause an area to appear active only under dual-task performance, when in fact it is active, but to a lesser extent, under single-task conditions. In addition, a region that is below threshold because of lack of statistical power may in fact be above threshold due to greater demand for the region in a dual-task setting. Alternatively, time sharing *between two areas* while dual-tasking can result in an area that was active in a single task to drop below threshold during dual-task

performance. Typically, however, areas engaged in single tasks are still active in dual-tasks, with equal or greater activity in dual-task conditions.

An early dual-task study by D'Esposito, Detre, Alsop, and Shin (1995) found that concurrent performance of two non-working memory tasks engaged dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC), though these areas were not active during component-task performance. Increasing the difficulty in one of the component tasks (spatial rotation) did not result in activity increases in either of these areas. Together these patterns were interpreted as evidence of DLPFC and ACC as candidate areas for task coordination, an executive function.

Since this study, dual-task specific prefrontal activity has been a contested issue. Adcock et al. (2000) used the same task as D'Esposito et al. (1995), auditory semantic categorization and spatial rotation, to serve as a replication and added another task, face matching, to further test the concept of domain general dual-task specific processing. Both the replication dual-task pair and the new dual-task pair activated prefrontal areas; however, component tasks also engaged these areas to a lesser extent when performed in isolation. The contradictory finding (regarding component-task prefrontal activity) with the original study may be the result of insufficient power or threshold selection (Bunge et al., 2000) such that the prefrontal activity appeared dual-task specific in the D'Esposito study. Furthermore, these purported dual-task areas (DLPFC and ACC) are very commonly reported in single-task experiments (see Cabeza & Nyberg, 2000), and multiple researchers, using a variety of tasks, have not found dual-task specific areas (Adcock, Constable, Gore, & Goldman-Rakic, 2000; Bunge, Klingberg, Jacobsen, & Gabrieli, 2000; Erickson et al., 2005c), though dual-task performance can result in the further activation of areas involved in single-task processing. Alternatively, it has been suggested that concurrent performance may result in the modulation of single-task brain regions (Adcock et al.,

2000; Bunge et al., 2000; Erickson et al., 2005c).

Dual-task performance, however, does not always result in brain activity increases. When component tasks compete for the same processing resources, concurrent activation of the same tissue can result in dual-task reductions (Bunge et al., 2000; Just, et al., 2001; Klingberg, 1998). Klingberg (1998) found that auditory and visual working memory tasks activate overlapping areas in prefrontal, cingulate, and inferior parietal cortex that are not sensory modality specific. Furthermore, concurrent performance results in a lesser activation in the face of increasing working memory demand. (Jaeggi, et al. (2003) found similar DLPFC and inferior frontal increases in both single-task and dual-task performance when load was parametrically varied in two n-back task. However, the increase in activation as a consequence of load was less for the dual-task compared to the summed single-task activation. This also suggests that concurrent performance does not necessarily require specific dual-task processing regions.

Recent imaging studies suggest that dual-task specific processing occurs when tasks involve interfering processing (Herath, Klingberg, Young, Amunts, & Roland, 2001; Jiang, 2004; Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Stelzel, Schumacher, Schubert, & D'Esposito, 2005; Szameitat, Schubert, Muller, & von Cramon, 2002); Szameitat, Lepsien, von Cramon, Sterr, & Schubert, 2005). These tasks employ the psychological refractory period paradigm in which a short ISI⁹ results in longer response times for the secondary task.¹⁰ Activation of inferior frontal regions were found when concurrent-task performance resulted in interference (i.e., ISI > 300 msec). Interference in these studies was attributed to different sources (motor effector, Herath et al., 2001; perceptual attention [when attending to the periphery of both tasks], Jiang, 2004; central processing, Szameitat, Schubert et al., 2002); Szameitat, Lepsien et al., 2005; stimulus-response modality incompatibility, Stelzel et al., 2005). Herath et al. 2001) found

inferior frontal gyrus (IFG) only when there was a concurrent performance cost (i.e., only during the shorter ISI). However, recent work by Erickson et al. (2005c) suggests that right IFG activity is not specific to dual-task interference but alternatively is associated with preparing to make multiple responses (whether in the context of a single or dual-task) and not actual coordinated performance. This area was engaged by *single-task performance* when comparing mixed single-task trials (i.e., interspersed with dual-task trials) to pure single-task trials (i.e., exclusively single-task trials) in a mixed event related design.¹¹ Furthermore, this area was *not engaged* by dual-task performance, suggesting that the area is sensitive to “*preparing to perform multiple tasks*” as opposed to the actual performance of multiple tasks.

Two of the studies employing psychological refractory period paradigm (Herath et al., 2001; Szameitat et al., 2002) found dual-task specific prefrontal activity that was *spatially distinct* from the component-task activity, which also activated prefrontal regions. The inconsistent dual-task specific prefrontal activation may potentially be attributable to whether concurrent performance results in a performance deficit and to the level of component task complexity. Although differences in task complexity and performance appear to factor into prefrontal activity, the extent of the impact is a matter of speculation. Further research is necessary to elucidate the role of prefrontal cortex in task coordination and interference.

DUAL-TASK PRACTICE EFFECTS

Few studies have investigated the effects of practice on dual-task related neural activity (Erickson et al., 2005a; Erickson et al., 2005b; Hill & Schneider, 2005). Erickson et al. (2005a) found that untrained dual-task performance engaged the same areas as the component tasks (letter and color discrimination), but to a greater extent. This study is consistent with those that do not report specific prefrontal dual-task processing regions (Adcock et al., 2000; Bunge et al., 2000). After extensive dual- and

single-task training outside of the scanner, most regions decreased in activity except for dorsolateral prefrontal cortex. An increase in left DLPFC was associated with mixed single-task (single-task trials interspersed with dual-task trials) performance for participants that received behavioral training.¹² Bi-lateral DLPFC activity was found for the dual-task condition. These areas were not significantly active at session one. Erickson et al. (2005b) regard the training increase as a shift in processing, where DLPFC begins to support task coordination as a result of training.

Hill and Schneider (2005) found widespread decreases in activity as a result of training an object-word visual search dual-task and a pattern-letter visual search dual-task. These decreases included prefrontal areas, and no areas were found to increase activity with training, suggesting processing efficiency of performance. The training decreases were predicted based on prior work (Chein, McHugo & Schneider, in prep; Chein & Schneider (in press); Schneider & Chein, 2003) demonstrating practice-related reductions when developing automatic processing for consistent tasks (see “Controlled and Automatic Processing during Learning” section).

Differences in activation dynamics between the studies potentially reflect differences in task design and training history. Hill and Schneider (2005) extensively trained *all single-tasks* prior to any scanning, effectively scanning changes related to naïve versus experienced dual-task performance (participants were unpracticed on dual-task performance at scan one). Conversely, scan sessions of Erickson et al. (2005a) reflect untrained task performance (both single and dual-task) compared to trained task performance. The difference in the direction of DLPFC may reflect different assessment points of learning. In addition, the Erickson et al. (2005a, 2005b) dual-task involved simultaneous concurrent letter and color discrimination (ISI = 0), where the Hill and Schneider (2005) dual-task involved continuous rapid visual search (nine search locations changing five times per second);

however, simultaneous targets did not occur in this design (targets could appear at any time during the minute search window as long as it occurred at least two seconds after the prior target). Although participants were instructed to give equal task priority in both studies, Erickson et al. (2005c) subject's tended to respond to the color discrimination task first. PRP interference occurs when one task is instructed to be given response priority or if this strategy is employed by the performer (Meyer & Kieras, 1997). The DLPFC activity may reflect interference related to strategy choice of responding in a fixed order.

In summary, dual-tasks that use a psychological refractory period design elicit inferior frontal activation under conditions of high interference, when the ISI is short. The neural effect of practice on these designs is an unexplored area; however, since practice does not attenuate behavioral interference, inferior frontal cortex would likely maintain activation with training. Dual-tasks with longer, fixed ISI (non-PRP tasks) generally do not report dual-task specific prefrontal (or otherwise) activity, suggesting no general locus for task coordination, an executive process. These tasks tend to have complex subtasks, and therefore it may be difficult to find particular areas engaged in task coordination processing. Dual-tasks that contrast the effects of practice have generally found decreases for initial-task-engaged brain regions; however, one study reports a DLPFC increase. Practice must be employed in more studies to determine the conditions under which practice-related increases would arise. For a discussion of skilled individuals engaging in high-level "real-word" multiple-task environments (such as pilots), see Durso and Dattel (Chapter 20).

Previous sections have looked at performance and brain changes in laboratory cognitive tasks under conditions of short to moderate amounts of training. The final sections will look at performance and brain changes that occur over longer amounts of practice for basic perceptual and motor skills. Examples are face processing, which

is developed normally through experience, and music skill, which occurs through intentional training.

Perceptual-Motor Learning and Expertise

Much of human skill acquisition and expertise involve perceptual-motor learning (see Chapter 29 on perceptual-motor expertise by Rosenbaum, Augustyn, Cohen, & Jax). Learning can occur at many levels within the processing hierarchy, depending on the nature of the task. In the case of vision, training has resulted in improved ability to perform discrimination in various tasks (texture segregation, motion discrimination, line orientation, etc.). In some cases, such as line orientation, learning of the trained orientation is specific to the trained location. The failure to transfer learning to other locations argues that the learning occurs early in the processing stream (that is, V_1 , the locus of initial visual processing in occipital cortex) where receptive fields are small, tightly tuned to a specific orientation, and topographically organized. This is remarkable because early visual processing regions were traditionally considered fixed in the adult brain. The specificity of learning (i.e., does training transfer to untrained location, quadrant, or eye) has demonstrated that perceptual learning can occur at different levels of the processing hierarchy. The specificity effects, however, have not always been consistent (i.e., sometimes transfer occurs and other times it does not), even when training the same type of perceptual task. Note, in a hierarchy of areas, learning can occur at multiple potential levels that show differential transfer (e.g., attend to the lower left oriented line or an oriented line anywhere in the visual field).

The nature of attention and task difficulty can influence the specificity of what is learned in a discrimination task. According to Reverse Hierarchy Theory (Ahissar & Hochstein, 2004), difficult tasks (short vs. long ISI and/or fine vs. course line discrimination) are learned with a high degree of

specificity According to this view, learning is driven by attention, with learning occurring first at the top of the processing hierarchy, then proceeding to the lower levels. Skill on a specific discrimination task also constrains learning such that the performers have improved their signal-to-noise ratio at the lower processing levels and can perform difficult discriminations. Less-skilled performers have poor signal-to-noise ratios at low levels and use high-level representation, providing more generalization and perhaps faster learning, but without the very high levels of performance. Note, in a hierarchical attention network (see Olshausen, Anderson, & Van Essen, 1993), proficiency allows the performer to determine the optimal level of processing given the difficulty of the discrimination.

Learning to perceive phonemes, faces, chess patterns, music, or radiology images all involve multi-level perceptual learning. A simple illustration is the inability even to find word boundaries in a spoken language that is unfamiliar. With experience, phonemes, words, and phrases become units of processing (see Feltovich et al., Chapter 4, "Expertise Involves Larger Cognitive Units"). Imaging data show changes in cortical processing at multiple levels of processing as perceptual discrimination improves (Karni & Sagi, 1991).

In the following we will see how high-level visual areas represent and process objects in the temporal lobe and other brain regions. Visual processing begins in occipital cortex in the back of the brain. As we move forward into the temporal cortex, neurons become responsive to larger receptive fields and more complex configurations of stimuli. Along this pathway, perceptual discrimination develops into object-based representation (that is, entities with specific meaning) through *reciprocal* interactions between high-level and low-level processing regions.

Face Processing

Humans are required to process faces on a daily basis, and it has been suggested they develop greater expertise in this pro-

cessing than in any other domain (Haxby, Hoffman, & Gobbini, 2000). Neuroimaging studies implicate a visual area in the right mid-fusiform gyrus (though sometimes bilateral) that increases its activity when faces are detected (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). This area has been termed the Fusiform Face Area (FFA) because although it is responsive to other objects, it is most responsive to faces (Kanwisher et al., 1997; Haxby et al., 2000). Imaging studies have demonstrated this greater response to faces, without regard to format (photos and line drawing) and without regard to familiarity (i.e., not more responsive to famous faces) (Gorno-Tempini & Price, 2001; Gorno-Tempini et al., 1998). FFA activation is greater for faces than for hands, animals, objects, and scenes (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 2000; Ishai et al., 1999; Kanwisher et al., 1997; Kanwisher, Tong, & Nakayama, 1998; Yovel & Kanwisher, 2004). Imagined faces also elicit activation in this area (Kanwisher & O'Craven, 2000). It is undisputed that right FFA responds greatest to faces; however, it has been suggested that this area is not specifically modulated for face processing per se, but for processing visual items for which an individual has developed high levels of expertise and familiarity that can be categorized on the individual level¹³ (Tarr & Gauthier, 2000; Feltovich et al., Chapter 4, "Expertises Is Limited in its Scope"). Support for this argument comes from fMRI studies that demonstrate an FFA response to items that are learned at high levels of expertise, such as cars, birds, and "greebles," artificial animal-like stimuli (Gauthier & Tarr, 1997; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier & Tarr, 2002). All of these items are visual, classifiable at the individual level (like faces), and only elicit FFA responses in an individual who has developed expertise for these items.

The FFA response to non-face objects has sparked a debate as to whether this area is a module for face detection (Kanwisher, 2000; Kanwisher et al., 1997;

Kanwisher et al., 1998; Yovel & Kanwisher, 2004), an area of visual expertise (Gauthier & Tarr, 1997; Gauthier et al., 2000; Tarr & Gauthier, 2000), or one area in a network of regions responsible for the distributed-representation of faces and other learned objects. The distributed-representation view claims that all objects produce a pattern of activation across a series of visual areas that codes the learned category (Haxby et al., 2000; Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001). The intricacies of this debate are beyond the scope of this chapter, but as a consequence they have produced evidence that humans process all faces as members of an expert class of objects¹⁴ in a small localized area of cortex (e.g., the faces areas in cortex represent less than 1% of the brain). The processing is not unique to one stimulus class but to a range of related stimuli (e.g., faces and other objects).

FFA appears to activate differently based on experience with different types of faces. Although FFA is not further activated by famous faces (Gorno-Tempini & Price, 2001; Gorno-Tempini et al., 1998), one study found greater FFA activation for most subjects for same-race faces, compared to faces from other races, presumably because of greater experience with same-race faces (Golby, Gabrieli, Chiao, & Eberhardt 2001); for a critique see Phelps, 2001). This processing area is also sensitive to inversion effect, considered a sign of expert-level object processing,¹⁵ an impairment in recognition for upside-down objects (Yin, 1969; Yin, 1970). Brain-imaging studies have found that inverted faces elicit the same or slightly less FFA activation compared to upright faces (Kanwisher et al. 1998); however, inverted faces further activate object-sensitive regions to a greater extent than upright faces, presumably reflecting that they are processed more like objects (Aguirre, Singh, & D'Esposito 1999; Haxby et al., 1999). In other words, object sensitive regions are highly responsive to inverted faces compared to non-inverted faces, and since the same pattern is exhibited for inverted objects compared to non-inverted

objects, one can argue that faces are treated like objects by object-processing regions.

Existence of the specialized area for face processing is also supported from studies of prosopagnosia patients, who have impairment in identifying individuals through facial recognition (Moscovitch, Winocur, & Behrmann, 1997). This disorder occurs both congenitally and as a consequence of stroke. These patients do not have a general problem with (visual) identification, as they can identify and name individual face parts such as noses, and they can identify people through other cues such as voices. Prosopagnosia patients, however, are not impaired in face inversion presumably because they process inverted faces more like objects (Yin, 1970). Since object inversion is specific to objects for which someone has developed expertise, this may reflect a shift in processing once a class of objects is extremely well learned.

Object Processing

In addition to face processing, humans spend a great deal of time processing other types of objects. The ventral occipitico-temporal cortex is activated when viewing pictures of objects, houses, and scenes, compared to textures, noises, or scrambled objects (for a review see Grill-Spector 2003). Many brain-imaging studies have contrasted faces and objects to differentiate processing between these complex visual items (Aguirre et al., 1999; Gauthier et al., 2000; Haxby et al., 2001; Ishai et al., 1999; Malach et al., 1995; McCarthy et al. 1997). There are areas that respond to both parts and whole objects. Object parts elicit responses from object-sensitive regions (Lerner Hendler, Ben-Bashat, Harel, & Malach, 2001), in contrast to the fusiform face area, which is not responsive to face parts. Temporal lobe areas perform object processing. These areas are more sensitive to greater complexity (i.e., these cells are not simple, single feature detectors, they are most responsive to configurations of features; see "Network of Specialized Processing Regions" section) and exhibit some activity to object scrambling,

which has been interpreted as evidence that object representation is based on component features (Grill-Spector et al., 1998; Lerner et al., 2001). Recall that objects are typically learned at the basic level (e.g., chairs, chairs, and more chairs, though there is some amount of individual level categorization – “bar stool” versus “armchair”), whereas faces are identified on a highly individualized level (e.g., Mary, Albert, Samantha, Jennifer, Sue, Jean, and David). Some objects (birds, cars, dogs¹⁶) can support the development of face-like individual level expertise and elicit responses in face-processing regions in individuals who have acquired this expertise through intentional learning; however, most objects are not learned at an expert level, as compared to faces, and are processed differently as such (i.e., object sensitive regions respond to object scrambling, face sensitive regions do not respond to face scrambling).

Experience with objects, however, does impact their processing in other ways. Object recognition in ventral occipitotemporal cortex is *invariant to size* and location (Grill-Spector et al., 1999). Human behavioral work demonstrates that the ability to recognize backwards-masked objects improves with specific practice, and ability transfers when trained objects are *modulated in size* (Furmanski & Engel (2000). Monkey single unit studies (e.g., recording electrical activity from individual units (neurons) to understand neuronal responsiveness)¹⁷ of inferotemporal (IT) neurons have demonstrated that IT neurons develop view-point invariance to objects that *prior to training* were meaningless and unfamiliar (Logothetis, Pauls, & Poggio, 1995). Other studies confirm that IT increases its responsiveness to trained objects (Kobatake, Wang, & Tanaka, 1998) as well as learned patterns (Sakai & Miyashita 1991; 1994).

Recent work implicates these neurons in visual object expertise (i.e., face, acquired bird expertise, etc.; Baker, Behrmann, & Olson, 2002; for comments see Connor, 2002). Baker et al. (2002) performed discrimination training on monkeys to determine if training enhances IT selectivity (i.e.,

tendency to respond to fewer or specifically one thing). Although there was some enhanced selectivity for individual object parts,¹⁸ there was a notable enhancement for “configurations of parts,” that is, whole objects. Importantly, this study showed that the specific enhancement in selectivity for trained objects is not due to differences in the strength of response between trained and untrained stimuli. Selectivity allows objects to be coded at the individual level (see face-processing section, i.e., specific to a particular category example) instead of at the basic level (i.e., at the category level without regard to a specific example). The former is the hallmark of expertise. Typically objects are not coded at this level. For example, an individual without specific experience studying birds should not be able to identify many subtypes relative to an expert. The Baker et al. (2002) result (i.e., a neuron that is selective to an individual item) suggests a mechanism by which bird watchers may develop selectivity as they learn to identify individual types of birds.

Although the temporal lobe is clearly involved in object learning, training influences frontal cortical areas as well. A recent monkey study by Rainer and Miller (2000) showed that training enhances specificity in PF neurons. Though novel objects elicited a greater PF response than familiar objects, with training neural activity became more narrowly tuned for familiar objects in these neurons. Training also results in a PF representation that is robust to the effects of stimulus degradation. In addition, Freedman, Riesenhuber, Poggio, and Miller (2001) demonstrated that PF neurons are important in learning new object categories.

In summary, objects such as faces and other highly behaviorally relevant objects (i.e., relevant for the task at hand, such as birds are behaviorally relevant to bird watchers) receive specialized processing in the visual-processing stream. In the motor sections we will present further examples of how behaviorally relevant movements (i.e., finger movements for violinist) and stimuli (i.e., words for readers) are represented uniquely in the cortex. We will

also see that practice with these items will sometimes result in structural expansions of cortex.

Word Reading

Learning to read is a key skill in our modern society. It involves developing new representations in a variety of cortical areas. Of particular importance is the Visual Word Form Area (VWFA), an area of left fusiform gyrus that appears sensitive to words that are specifically presented visually. The basic findings with regard to this area have been reviewed by McCandliss, Cohen, and Dehaene (2003) and will be summarized below. VWFA is insensitive to visual variation such as changes in case, font, and even location (i.e., no difference in response to left or right hemisphere presented words). It is also insensitive to lexical properties of words such as word frequency, and it even responds to pseudowords as long as these words are well formed according to regularities of the language system. This area is also responsive to non-word objects for which a person has achieved visual expertise such as faces. Therefore VWFA has been suggested as an area specifically implicated in word-form processing as a result of developed expertise in processing behaviorally relevant stimuli. A recent meta-analysis of imaging cross-cultural language processing (Bolger, Perfetti, & Schneider, 2005) provides support by demonstrating that VWFA is consistently activated across word tasks and writing systems (both eastern and western). Furthermore, lesions to the VWFA region have resulted in impairments in recognizing and naming words and pronounceable non-words, but are relatively spared in the identification of digits, objects, and, in some cases, letters themselves. This is a disorder known as pure alexia. Thus, the role of processing visually abstract forms of candidate words has been ascribed to this region (McCarthy & Warrington, 1990; Miozzo & Caramazza, 1998). However, owing to the complex vasculature of the brain, pure alexia stemming from the inferior temporal region rarely ever occurs (Price & Devlin, 2003).

What are the areas that support reading change as a function of proficiency? A cross-sectional fMRI study (subjects ranged in age between six and twenty-two) found a shift in brain regions associated with an implicit word-processing task as reading ability develops (Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003). As reading began to reflect knowledge of abstract word properties (semantics and phonological properties) and was less supported by rote memorization of words based on visual features and context (i.e., "stop" in a stop sign), readers demonstrated increased activation in left middle temporal and inferior frontal gyri and decreases in right inferotemporal regions.

Brain plasticity in the reading circuit can be observed even in adult subjects after short periods of training. In a novel orthography training experiment, Bolger, Schneider, and Perfetti (2005) trained subjects to learn to read eighty words written in Korean script. Pilot studies conducted with training on only sixteen words found increases in cortical activation occur rapidly: a 0.7% increase in BOLD signal from learning trials one through four to trials thirteen through sixteen (Bolger, 2005). After four sessions (twenty words/session) of training, the response in the VWFA increased significantly and with greater learning in a componential (i.e., learning letter-sound correspondences) compared with a holistic (i.e., learning of the whole word) training approach to the material.

How people attend and process stimuli alters what cortical areas show plasticity. Sandak et al. (2004) explored the effects of orthographic, phonological, and semantic pseudowords training on overt naming ability. Orthographic training involved making judgments about consonant and vowel patterns in pseudowords, phonological training involved making rhyme judgments in pseudowords, and semantic training involved learning novel semantic associations to pseudowords. Phonological and semantic training resulted in equivalent (but superior when compared to orthographic training) performance on reading ability. Despite

comparable behavioral performance, phonological and semantic training effects were driven by different neural processes. Phonological training modulates VWFA processing. The reported reduction in activation was interpreted as reflecting efficient processing in this region.

Studies have shown the structural connectivity of white matter fiber tracts to be deficient in poor versus skilled readers (Klingberg et al., 2000). Similarly, functional-connectivity studies of correlated cortical activity have revealed stronger connectivity between angular gyrus with inferior frontal and ventral fusiform regions as a function of reading skill (Horwitz et al., 1998). Pugh et al. (2001) conducted their own functional-connectivity study of the angular gyrus comparing normal to impaired readers. Their findings reveal that in dyslexics connectivity in the angular gyrus region is weak for word and pseudoword reading.

The reading literature illustrates some anatomical mechanisms of learning in the brain. Processing is localized and very specialized, with VWFA showing word encoding, learning, and processing occurring in the same area. Learning produces both increases in activation early in practice and decreases as reading becomes more automatic (i.e., if processing rate is controlled). Words are processed in specialized areas by experts, and learning can produce detectable morphological changes. In addition, the training studies show that the nature of the practice (e.g., phonological or semantic encoding) impacts where the plastic change takes place.

Motor Learning

Motor areas can *rapidly* change as a result of skilled movement practice and improved performance. Primary motor cortex or M1 is notable for plastic change with *very extensive experience and practice* (for a review see Sanes & Donoghue, 2000). M1 motor representations are experience dependent and highly modifiable under changing environments. For example, blind individuals with knowledge of Braille have enlarged M1 representation for their (reading) index finger (Pascual-

Leone et al, 1993; Pascual-Leone and Torres, 1993). Perhaps most dramatically, structural damage, such as a facial nerve lesion, resulted in the rat primary motor cortex (M1) shifting representation to a new group of muscles (representing the forelimb) within one to three hours of the insult (Huntley, 1997).

Primary motor cortex learning effects have been investigated extensively with sequence learning paradigms. An early functional magnetic resonance imaging study (Karni et al, 1995) found that M1 modulates its response to trained finger-thumb opposition sequences according to the level of practice. Early in practice, M1 is sensitive to order, initially being more responsive to the first sequence and later being more responsive to the second sequence, within one session of training. Karni has referred to the reversal of order effect as the fast learning phase. However, after four weeks of training M1 is more responsive to the trained sequence, compared to the untrained sequence, regardless of practice order – termed the slow learning phase. In addition to slow and fast learning, M1 is believed to be involved in consolidation or in performance improvements that occur subsequent to practice (Ungerleider, Doyon, & Karni, 2002). The consolidation process is time dependent; disruption of M1 by repetitive Transcranial Magnetic Stimulation (rTMS) immediately after practice diminishes the effects of training (Muellbacher et al., 2002). rTMS of control brain¹⁹ regions and of M1 six hours after training does not mitigate the effects of practice. M1 consolidation effects are evidence that this region is involved in early learning processing; however, consolidation blocking has been found in other regions. This has been regarded as evidence for a distributed network of areas involved in early phases of motor learning, particularly the learning of complex motor skills (Baraduc, Lang, Rothwell, & Wolpert, 2004).

Although brain-imaging work implicates M1 in sequence learning, (Karni et al., 1995), single-unit research suggests that M1 is involved in movement execution but is insensitive to temporal order aspects of skilled movement (Tanji & Shima;

1994). Single-unit recording in the monkey implicates supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA) involvement in sequence learning. Neuron response properties in these regions are sensitive to *particular* trained sequences and rank orders (i.e., “always respond to the second action”); additionally, they are sensitive to movement interval and movement initiation, both with regard to specific movement types and sequence completion (Tanji & Shima, 1994; Shima & Tanji, 2000). The distributions of neural responsiveness for the aforementioned functions vary between SMA and pre-SMA, as does the specific selectivity for each function (for example in the case of rank-order neurons, their response may be exclusive to the second action, or they may respond to both the first and second action but not the third). More pre-SMA neurons (10%) as compared to SMA neurons (2%) respond during the initiation of a new sequence, suggesting a role in the early stages of learning for pre-SMA. Injecting pre-SMA with muscimol to produce a reversible lesion resulted in a disruption of performance (in terms of button press errors) for novel but not learned sequences (Nakamura, Sakai, & Hikosaka 1999). Injection of SMA produced a similar pattern (i.e., disruption occurring only for novel sequence performance); however, this was not a significant effect. Furthermore, in another study, pre-SMA neurons became less active as sequences become automated (Nakamura, Sakai, & Hikosaka 1998). Together these studies provide evidence that pre-SMA is involved in sequence learning.

Body Kinematics

Complex motor actions, such as those involved in dance and martial arts (see Noice and Noice, Chapter 28, are coded differently by an observer, depending on the observer’s own expertise executing the specific movements (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Regions sensitive to motor expertise include bilateral pre-motor cortex and intraparietal sulcus, right superior parietal lobe, and left poste-

rior superior temporal sulcus. These areas respond stronger when an expert observer *views* a movement that was *specifically acquired previously by the observer* (e.g., *seeing a dance move that the observer had learned to perform*). Therefore, the brain is sensitive to complex acquired movement, such that passive viewing of another individual performing behaviorally relevant movement results in specialized processing and representation. Studies of the macaque “mirror” neurons provide a mechanism for this viewer-based processing of relevant movement. Mirror neurons discharge when the monkey performs an action or observes another monkey or human perform this action, hence their name, and have been proposed to exist in humans (Gallese & Goldman, 1998; Rizzolatti et al., 1996). In the monkey these neurons are known to exist in premotor and parietal cortex. According to Calvo-Merino et al. (2005), the human mirror system appears to code for “complete action patterns” that are in an individual’s motor repertoire, as opposed to movements that are highly familiar to the observer. They scanned professional ballet dancers, professional capoeira martial artists, and control subjects with no specific movement expertise as these individuals passively viewed video-taped movements from both disciplines. They were able to demonstrate the mirror system’s expertise specificity, which even distinguishes ballet and capoeira, despite similar kinematics for males. Even though whole movements were somewhat similar (sub-movements can be identical) the expert brain is sensitive enough to discriminate between acquired movements in the studied discipline and similar movements in the non-studied discipline. In other words, if the participant was an expert performer, such as a ballet dancer, their brain had a greater response to viewing ballet movements when compared to viewing capoeira, even though there is similarity in the types of movements being performed in both disciplines (see also, Feltovich et al., Chapter 4, on “Expertise is Limited . . .”). It is important to stress that Calvo-Merino et al. (2005) argue that expertise is operating at the level of being able to

perform the movement and not just being familiar with the movement (i.e., this suggests that there is a difference between the brain of a professional dancer and an avid dance enthusiast) that appears to drive these regions. Female and male ballet dancers code movements differently based on the “gender” of the movement; that is, in classical ballet certain movements are only performed by men, and other movements only by women, but many movements are gender neutral. For example, men never learn to dance “on point,” that is, stand on their toes. Although no dancer can perform all movements, all dancers are highly familiar with viewing all movements through rehearsals, classes, and performances. Left parietal cortex is less responsive in female ballet dancers when they view “male” ballet movements. A skilled movement, in this case gender-matched specific movements, modulate the level of evoked representation by the expert brain. Therefore, the ability and personal experience with performing these specialized movement patterns appear to be critical to the difference in representation of the movements. These results show brain specializations that enable the encoding of observed actions into one’s own action systems in a way that may potentially enable replication of the observed actions.

Automotive Spatial Navigation

Brain areas supporting spatial navigation are sensitive to expertise with regard to function and structure (see Durso & Dattel, Chapter 20). One example of a spatial navigation expert is a taxi driver. These highly skilled individuals have to know large metropolitan areas and how to reach locations in the most efficient manner. London taxi drivers rigorously train, on average for two years, to pass a series of exams about street names and their locations, which is required for their taxi license. Their extensive experience learning navigation has been suggested to produce functional and structural changes (Maguire, Frackowiak, & Frith, 1997; Maguire et al., 2003). Functional MRI revealed increased right posterior hippocampus (RPH) activation with successful recall of routes around

London (Maguire et al., 1997). Grey matter volume in this region (as well as left posterior hippocampus; LPH) was subsequently shown to be greater in the expert (driver) population, compared to a non-expert control group (increase relative to non-drivers: RPH = 1.936%, LPH = 1.506%; Maguire et al., 2000) and another control group ranging in navigational expertise but without specific taxi driving experience (Maguire et al., 2003).²⁰ Posterior right hippocampal grey matter volume is positively correlated with taxi driving experience ($r = 0.6$; $p < 0.05$) in drivers, but there was no associated grey matter relationship in non-drivers. Maguire and colleagues suggest that the structural differences in taxi drivers are based on acquired experience and *not* innate ability that might cause high performers to seek out this profession. Correlation analysis shows that individuals skilled in “wayfinding” (new route development) activated anterior hippocampus during novel routes but activated the head of the right caudate when following well-learned routes (Hartley, Maguire, Spiers, & Burgess, 2003). This distinction is not found in individuals who perform poorly at wayfinding.

Expert drivers use these two areas dependent on the task at hand; the hippocampus is purported to form a modifiable cognitive map supporting new route development, whereas the caudate supports fast, automatic navigation of well-learned routes. Furthermore, these areas have been proposed to support learning in a complimentary fashion (Hartley et al., 2003) in other task domains (classification learning, Poldrack et al., 2001; mirror reading, Poldrack & Gabrieli, 2001). These studies demonstrate that expertise provides the flexibility to choose the optimal strategy for successful completion of a given task (cf. Feltovich, Spiro, & Coulson, 1997). These different strategies rely on different brain structures for their execution.

MUSIC TRAINING

Music expertise is an important topic in skill acquisition (see Lehmann & Gruber, Chapter 26) in which mastery has been

shown to produce changes in brain regions that support both motor and auditory functions. Analogous to the section on ballet dancer expertise (see “Body Kinematics” section), trained musicians code behaviorally relevant movements uniquely in their given discipline. And consistent with the information presented in the motor learning section, we again see that movement practice results in the expansion of motor cortex. This section will briefly review motor related changes. (For extensive reviews, including related changes in the auditory cortex, see Gaser & Schlaug, [2003]; Pertez & Zatorre, [2005].

Increased cortical representation, specific to the muscles engaged in the task at hand, is associated with playing musical instruments. For example, the fingers on the left hand of violinists have reliably larger cortical representation compared to the same hand in non-musicians (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). There are no right-hand differences between musicians and non-musicians, consistent with the fact that the right-hand fingers do not move independently when playing the violin, unlike the left hand. This increased representation reflects cortical reorganization that is more dramatic in individuals who began musical study at an early age. Furthermore, a training study found that both physical and mental piano practice has resulted in increased M1 representation for the trained hand, but only in novice players (Pascual-Leone et al., 1995). Experienced players have already developed M1 representations for relevant movements in their acquired domain.

In addition to increasing M1 representation, music training may influence how digits are represented (Small, Hlustik, Chen, Dick, Gauthier, & Solodkin, 2005). Although thumb movement resulted in a “predictable”²¹ M1 activation for all subjects, non-dominant left-hand individual finger movements were predictable in right M1 for violinist but not non-musicians. Conversely, non-musicians showed the opposite pattern, in which dominant right-hand finger movements were the only ones to produce pre-

dictable left M1 activation. Dominant-hand M1 predictability was not found in the violinist. Musical training did not result in a difference in primary somatosensory cortex for musicians and non-musicians. This preliminary work suggests that the relative distribution of M1 activity for individual digits is sensitive to experience and *typically encodes* individual movements in the *dominant hand* (i.e., the hand with the greater dexterity). However, violin-specific highly individuate finger training impacts the “default state” of M1 encoding (i.e., contralateral²² M1 typically encodes individual movements in the dominant hand), which results in a *predictable* contralateral M1 *encoding the non-dominant left hand* of violins. Presumably this reorganization reflects representation of movement at a task-specific level, modulated by practice. In other words, M1 representation reflects behavioral relevance. The learning is specific (e.g., to the hand and type of motor action).

Finally, in a recent study, music training has been demonstrated to induce structural changes (increased myelination in white matter tracts) in professional pianist (Bengtsson et al., 2005). Several areas show this increased myelination, but most areas correlated with childhood practice (i.e., practice occurring at age sixteen years or younger). Furthermore, practice-related myelination thickening was greater for childhood practice than adulthood practice.

Music training results in structural changes (expansion and increased myelination). Primary and secondary motor areas are considerably less active in professional musicians (Jäncke et al., 2000). This suggests that in terms of functional differences, training produces greater efficiency with regard to processing in experts. Therefore, expertise results in a savings in processing in a music-related motor task.

Other Types of Expertise Discussed in This Handbook

In their chapter on exceptional memory, Wilding and Valentine (Chapter 31) discussed the imaging studies by Maguire

et al. (2003) comparing the world's memory experts' to control participants' brain activation during memorization. They found that the differences in brain activation during different memory tasks could be completely accounted for by the superior strategies that the world experts reported using (similar to taxi drivers; Hartley et al., 2003). The same study did not find any anatomical differences in the brains of the world experts compared to the control participants,²³ which suggests that the difference in memory performance can be explained in terms of acquired skill (Ericsson, 2003; Chapter 13).

Of additional interest, Butterworth (Chapter 32) describes the evidence on brain activation during routine and challenging mathematical calculations. He reviews evidence that fronto-parietal networks support the performance of routine numerical tasks (Pesenti, Thioux, Seron, & De Volder, 2000) with left intraparietal sulcus being specialized for numerical processing (Dehaene, Piazza, Pinel, & Cohen, 2003). The brain of an expert calculator named Gamm is also discussed. Similar to the taxi driver study of Hartley et al. (2003), Pesenti et al. (2001) found that experts use different brain systems to support their calculations and also could exhibit flexibility in strategy choice (supported by different brain regions) to solve their problems.

In summary, in addition to processing efficiency, enriched representations, and structural expansions, experts can flexibly use strategies, by recruiting the associated brain regions, to solve a range of problems, whereas novice performers can not.

Conclusion

The development and execution of skills has profound effects on the nature of brain processing. The brain is a plastic structure that can change the amount of area and the activity of areas as a function of training, effort, and strategy. There are hundreds of specialized areas of the brain. Training has differential effects on the domain

general control areas and the domain specific representational areas. The presence of a single domain general control network that supports novice and variable performance represents a severe resource limit for performing novel or varying tasks and working memory dependent tasks (see also Feltovich et al., Chapter 4, "Expertise is an Adaptation"). This network provides the scaffolding to support new learning and to maintain working memory variables and operations in order to allow varying the nature of the performance and strategy shifts in cognitive processing. In consistent tasks, as processing becomes more automatic, the domain general activity decreases or drops out.

The specific nature of the representational areas suggests that both training and performance will be sensitive to the strategy and nature of the training. What is learned is based on which representational areas are active during training. Typically, as practice develops, activity decreases, and there are rarely new areas that develop in laboratory studies of skill acquisition. This suggests that training causes local changes in the specific representational areas that support skilled performance. In studies of extensive training, there is ample evidence for changes in cognitive processing as well as structural changes in the nervous system.

Brain training has analogies and differences to muscle training. Working a specific brain area can increase the representation space and make processing more focused. If one wants to strengthen a brain area, one needs to attentively activate those areas to alter the neurons in that area. Training of the domain specific areas typically decreases activity as processing gets more focused; however, it can cause increases in some motor tasks as well as some tasks involving exceptional memory. The domain general areas might be analogous to cardiovascular training in muscle training (e.g., training endurance transfers across many sports). However, the specific training (e.g., shooting in basketball and hitting in baseball) is unlikely to activate the same areas or representation and do not lead to transfer.

Cognitive neuroscience is in a synergistic research development with skill-based research. We know that training dramatically effects performance and brain activity. We are now beginning to relate those changes to better understand both the brain and skilled performance.

Footnotes

1. fMRI data is not an absolute value and therefore the signal is always assessed as a percent change relative to a baseline or control condition. One can determine whether a location differs in activation over time (e.g., active when stimulus present but not during resting periods).
2. This is not a comprehensive list of functions. Often performance relies on dynamic interactions among various regions, both within and across lobes. Furthermore, there are regions outside the cerebrum, namely, the brain stem, cerebellum, and spinal cord, that make important contributions to the performance of skills.
3. See "Controlled and Automatic Processing during Learning" section.
4. Evidence will also be presented that experts are more flexible in their strategy utilization.
5. That is, performance characteristics can be flexibly modified on the fly.
6. This shift typically involves no more than several sessions of training for simple cognitive tasks such as visual search paradigms (where one searches for targets in a display containing distractor items), as opposed to several years of training for learning a musical instrument or high-level chess mastery.
7. The task involved recognition of faces presented at encoding after a delay period. Load was varied to compare low-load (one to two faces) with high-load (three to four faces) conditions.
8. This is referred to as processing bottlenecks, which means that a specific process must be performed serially. Serial processing produces interference (increased RT) when in a dual-task environment. The nature of locus of such bottlenecks is a matter of debate (Meyer & Kieras, 1997; Pashler, 1994; Schneider & Detweiler, 1988; Shiffrin, 1988).
9. The paper uses the term "SOA" for stimulus onset asynchrony instead of "ISI" for inter-stimulus interval.
10. Marcantoni et al. (2003) uses another interference paradigm, rapid serial visual presentation (RSVP).
11. Dual task and single tasks were scanned in a mixed event-related design allowing blocks to contain pure (i.e., exclusively) single-task, pure dual-task, and mixtures of single- and dual-task trials. This design allowed the activity associated with individual trial types to be contrasted against any other trial, regardless of block, such that differences in dual-task performance when planning to perform exclusively a dual-task trial versus a mixture of dual- and single-task trials could be addressed.
12. A control group was employed to control for non-training specific effects in dual-task activity.
13. Most objects, such as "tables," are classified at the basic level. Faces are considered relatively unique because they are processed at the individual level, which is with regard to particular examples.
14. The authors are not presenting this information in support of the Gauthier et al. (2000) visual-expertise interpretation. It should be noted that some of these findings have been contested or interpreted as both support for and evidence against this FFA-individual-level-expertise model. The work is mentioned because it pertains to differential processing of expert or experienced-based items.
15. Dog experts, compared to novices for instance, exhibit dog-inversion decrements in identification (Diamond & Carey, 1986).
16. To clarify, being familiar with a few specific types of birds or even an individual bird (i.e., a pet parrot) does not grant this level of expertise. To develop face-like expertise for a non-face object category such as birds, one must become extremely knowledgeable in identifying many bird subtypes. This expertise-based processing would develop only in an avid bird watcher and not the typical individual who can identify a few varieties of birds and/or may own birds as pets.
17. Much of our understanding of the visual system traditionally comes from invasive monkey physiology studies. Since the advent of non-invasive brain imaging techniques, we have been able to confirm that the human

- visual system works in a highly similar way. Single-unit recording studies allow us to determine the response properties of individual neurons; however, because this technique is invasive, it is typically not performed on humans, with the rare exception being patients undergoing neurological surgical procedures.
18. Selectivity enhancement for object parts has been demonstrated also when features are diagnostic (Sigala & Logothetis, 2002).
 19. "Control brain regions" does not refer to the control network, but rather other brain regions serving as experimental controls.
 20. Overall hippocampal size does not differ between drivers and non-drivers, because non-drivers have an increase in anterior hippocampi regions relative to drivers.
 21. A split-half correlation analysis was performed, based on a technique developed by Haxby et. al., (2001), on primary motor and somatosensory cortex (respectively M1 and S1). Digit movement was defined more predictably for a particular region, in this case M1, if the movement-specific activity correlated better with itself across the two halves of the data than with any other digit movement.
 22. In the motor system, the right side of the body is controlled by the left side of the brain and vice versa.
 23. Taxi-drivers do have morphological expansions based on experience, see "Automotive Spatial Navigation" section for an explanation.
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