

Research Report

Neuroimaging studies of practice-related change: fMRI and meta-analytic evidence of a domain-general control network for learning

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Abstract

Functional magnetic resonance imaging and a meta-analysis of prior neuroimaging studies were used to characterize cortical changes resulting from extensive practice and to evaluate a dual-processing account of the neural mechanisms underlying human learning. Three core predictions of the dual processing theory are evaluated: 1) that practice elicits generalized reductions in regional activity by reducing the load on the cognitive control mechanisms that scaffold early learning; 2) that these control mechanisms are domain-general; and 3) that no separate processing pathway emerges as skill develops. To evaluate these predictions, a meta-analysis of prior neuroimaging studies and a within-subjects fMRI experiment contrasting unpracticed to practiced performance in a paired-associate task were conducted. The principal effect of practice was found to be a reduction in the extent and magnitude of activity in a cortical network spanning bilateral dorsal prefrontal, left ventral prefrontal, medial frontal (anterior cingulate), left insular, bilateral parietal, and occipito-temporal (fusiform) areas. These activity reductions are shown to occur in common regions across prior neuroimaging studies and for both verbal and nonverbal paired-associate learning in the present fMRI experiment. The implicated network of brain regions is interpreted as a domain-general system engaged specifically to support novice, but not practiced, performance.

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1. Introduction

Among the most profound characteristics of human performance are the dramatic changes in processing speed, accuracy, and effort that arise through practice [55,62]. Prior neuroimaging research has shown that these behavioral benefits of practice may coincide with broad changes in the functional neuroanatomy of task performance [48,50,52]. While neuroimaging evidence can provide leverage in understanding how and why these changes occur, studies

of practice-related change are relatively scarce in the extant literature and have not been previously considered as a unified corpus of data. Moreover, aside from a concentration of work in the area of motor learning, existing neuroimaging research on the effects of practice comprises a disjointed literature, spanning a diverse range of experimental paradigms and producing results that appear to vary substantially from study to study. For example, whether practice leads to increased activation, decreased activation, or both appears at first glance to be highly dependent on the particular paradigm employed. Using a quantitative meta-analytic approach, the present work demonstrates that, despite apparent variability, there is a meaningful pattern of agreement across studies. Specifically, consistency across

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studies is revealed as a network of distributed brain areas that reliably exhibit decreased activity following practice in disparate task contexts. We interpret the evidence from this meta-analysis through a dual-process theory of human performance [55] and apply the results to establish a priori anatomical predictions for an empirical fMRI investigation of the effects of practice in a paired-associate learning task.

Prior research has shown that, when tasks involve consistent input to output mappings, repeated utilization of these mappings through task practice can lead to substantially improved performance of the task, with both an increase in response accuracy and a speeding of response times [57]. We argue that practice-related reductions observed with neuroimaging often reflect changes in the demand placed on central cognitive resources as this more efficient mode of performance is realized. Such “resource-based” changes are the hallmark of the dual-processing framework adopted by several theories of human learning to explain the effects of task practice [1,27,55,57]. In this framework, a set of central resources mediating *controlled* processing is assumed to play a critical role in scaffolding novice performance, but to become less essential as skilled, *automatic*, processing emerges [57]. Controlled processing is typified by the slow, serial, and effortful behavior found in novice performance, while automatic processing is typified by the fast, parallel, and low-effort behavior exhibited in skilled performance.

The emergence of automatic processing with practice seems to rely on the formation of local associations (via synaptic modifications) in brain regions that process information specific to the practiced task (i.e., domain-specific processing regions). Such associative mechanisms are assumed by almost all modern theories of learning [2,7,13]. However, an additional and fundamental assumption of the dual-processing framework is that early learning also requires the support of a control processing system that can regulate local associative learning. This control system is thought to be structured from a set of interacting domain-general processing centers that deploy working memory, attentional selection, performance monitoring, and information gating mechanisms in order to mediate learning. Accordingly, learning is regarded as the product of combined contributions from domain-specific (local associative mechanisms) and domain-general (the control system) processes. In the present work, we focus on the role of the domain-general control system in learning and assess two core predictions derived from the dual-processing view: (1) *that activity in control processing regions should decrease (or drop out) with practice as the control resources they provide are released*; and (2) *that control processing regions are domain-general and should thus be recruited to support initial task performance regardless of the task or material type being learned*.

The two predictions laid out above are general to the dual-processing view and are computationally validated in

a hybrid connectionist/control architecture (CAP2) developed upon the basic dual-processing framework [55]. The CAP2 model provides a detailing of the control system’s organization and yields a computationally explicit account of the mechanisms that mediate the transition from controlled to automatic processing. The model also affords a third prediction regarding the functional anatomy of controlled and automatic processing. Specifically, the model predicts (3) *that skilled performance should not engage new regions but should activate a subset of those areas engaged by early learning*.

The dual-processing theory (and its predictions) may have certain limitations in scope that should be considered before we embark on an examination of the neuroimaging evidence. One important assumption of the theory is that only tasks involving reliable mappings from task/contextual inputs (e.g., the stimuli) to corresponding outputs (e.g., the responses) can yield automated performance and thus disencumber the control system. Accordingly, practice-related changes are anticipated only for tasks involving such consistent input–output relationships. In addition, the theory has little to say about changes that emerge with practice in tasks that encourage subjects to shift their cognitive strategies as learning proceeds. In such cases of “process shifting,” alternative cortical representations associated with the novel strategy may be engaged (see, e.g., [49]), thereby inducing unanticipated changes in the demand placed on control processing resources (e.g., by engaging previously learned representations) that are difficult to track. The theory is also under-specified with regard to the mechanisms of cortical recruitment, which may lead to the observation of cortically localized practice-related increases [38]. Thus, while the present work focuses on the basis of practice-related activity *decreases*, we caution the reader not to infer that the emergence of practice-related *increases* is necessarily problematic for the theory since such increases may have alternative explanations not within the theory’s scope. Still, the theory is falsifiable. For example, a finding wherein practice in a consistently mapped task produced reliable behavioral benefits, but no concomitant reductions in regional activity (i.e., no significant clusters of activation following conventional image thresholding procedures), would present a strong challenge to the proposed view. Additional skepticism would be merited if these reductions failed to emerge in reliable regions across studies or failed to present themselves in brain areas thought to mediate control (e.g., prefrontal and parietal association cortices).

The dual-processing theory may also be under-specified in certain cases of implicit learning, wherein the subject has no explicit intent to learn or to improve performance (e.g., implicit learning of perceptual patterns). Such cases of implicit learning can involve limited opportunity for the subject to monitor and adjust control, and it is therefore difficult to speculate how practice with these tasks will

influence the engagement of control mechanisms. While the reader might thus be tempted to assume that the theory makes limited contact with findings from the motor or perceptual learning literatures, we believe that the same central control mechanisms are utilized even in these contexts, provided that learning is *intentional*. Accordingly, while it is to be expected that the unique processing demands of a given task will illicit “domain-specific” activations, the explicit prediction of the dual-processing theory is that additional *domain-general* processes will also be engaged (prediction 2). Domain-general processing centers can thus be operationally defined as the brain regions that exhibit activity change coincident with practice over a wide range of tasks.

2. Meta-analysis of prior neuroimaging studies

Practice-dependent changes have been studied with neuroimaging in a variety of tasks, including verbal learning [3,41,52], mirror reading [40,50], working memory [9,30,35], object naming [68], artificial grammar learning [28], abstract design learning [48], face learning [72], and motor learning [31,36,37,39,58] paradigms. Interpretation in most of these studies has focused on explaining the observed changes in brain activity with respect to the particular task being practiced and tested. That is, each study was intended to delineate the effects of practice in a given task domain. Based on the dual-processing theory, however, it is expected that practice-related *decreases* should be present whenever the duration of task practice is sufficient to (at least partially) disengage control resources and that these decreases should be spatially consistent (i.e., found in the same areas) across studies. To determine whether these expectations are met in the extant literature, we conducted a meta-analysis using a quantitative technique described in Chein et al. [18], see also [66].

2.1. Meta-analysis methods

Studies examining the effects of learning, training, or practice on hemodynamic activation (PET or fMRI) were gathered by computerized search using available psychological (PsychInfo) and medical (Medline) databases. The searches included studies published through December, 2003.

A subset of the identified studies was compiled on the basis of five additional inclusion criteria. First, it was required that each experiment submitted to the meta-analysis involves a contrast between initial performance of a task and performance of the same task after at least 10 min of practice (more limited practice is unlikely to substantially affect demand on central resources). Second, experiments with explicitly variable input–output mappings (e.g., [30]) were excluded. Third, only experiments

in which subjects made an explicit attempt to acquire new information or skill were included since implicit learning conditions may not engage control mechanisms. Fourth, the set of studies was further limited to those using healthy adult subject populations. Finally, inclusion in the meta-analysis required that the imaging results from the experiment be reported in the stereotaxic space of Talairach and Tournoux [64] or in a coordinate system that could be easily converted to this space (e.g., the Montreal Neurological Institute template). In total, 29 studies passed the inclusion requirements (listed in Appendix A). It should be noted that, due to the limited number of existing imaging studies examining practice-related effects, obtaining a sufficient corpus of data for the meta-analysis necessitated that the inclusion criteria be somewhat lenient and that certain relevant task factors be only partially controlled. For example, studies involving longer periods of practice would have been preferred since automaticity takes many repetitions to fully develop. It would also have been desirable to apply more stringent control over the “consistency” of task mappings. However, to amass a large enough corpus, we included in the analysis some tasks with only limited aspects of consistency (e.g., consistency between the condition cues and the subsequent response requirements). Our inability to strictly control these task factors was a partial motivation for seeking corroboration of the meta-analytic results through the empirical investigation detailed in the latter part of this paper.

To conduct the meta-analysis, stereotaxic coordinates reported from each study were modeled as Gaussian spheres (3-dimensional Gaussian distributions with a spread of 15 mm FWHM \cong a 6.4 mm standard deviation) in a cubic grid which represented the stereotaxic space (in 1 mm^3 voxels). These Gaussian spheres, which can be understood as probability estimates of the actual locations of each reported activation, were then aggregated (summed) across studies to produce a map indicating the degree of cross-study convergence [18]. The resulting “meta-image” was then thresholded (intensity and spatial contiguity) to reveal only the most consistently observed regions of practice-related activity change. The “convergence threshold” was established based on random permutation simulations. Specifically, in each of 1000 simulations, the coordinate locations for each of the points entered into the initial meta-analysis were set to random values falling within the brain space of the stereotaxic grid and were submitted to the Gaussian estimation and aggregation process. The convergence threshold was then established as the intensity value at which a cluster larger than 100 mm^3 appeared in fewer than 5% of the simulated random meta-images. Stereotaxic coordinates associated with practice-related decreases, and those associated with practice-related increases, were analyzed separately to produce two separate convergence maps. The results from the meta-analysis are summarized in Table 1 and Fig. 1.

Table 1
Regions of convergence in meta-analysis of prior neuroimaging studies

Practice-related decreases	BA	x	y	z
R precentral g	6	25	-3	53
R superior parietal	7	11	-61	51
Medial frontal (pre-SMA)	6	-3	11	49
R inferior parietal	40	37	-57	44
L inferior parietal	40	-31	-57	39
Anterior cingulate	32	-1	26	32
R inferior parietal	40	52	-29	25
R middle frontal g	46	38	28	25
L middle frontal g	46, 45	-38	26	20
R cuneus/mid. occip. g	18	19	-90	2
L middle occip. g	18	-25	-88	4
R anterior insula	13	36	20	2
L cerebellum		-24	-65	-23
R cerebellum		26	-54	-27
<i>Practice-related increases</i>				
Paracentral L	31	-3	-10	48
Precuneus	7	2	-69	36
R cuneus	30	6	-70	10
L lingual g	18	-3	-83	-3

2.2. Practice-related decreases

Although studies in unique task domains reveal areas of task-dependent cortical specificity, the analysis shows that there is a notable degree of convergence in the brain

regions showing practice-related decreases across studies. Specifically, the meta-analysis indicates a broadly distributed network of regions including lateral prefrontal, medial frontal (pre-SMA and anterior cingulate), posterior parietal, occipito-temporal, and cerebellar areas in which practice-related decreases are reported consistently, regardless of the task being performed. The existence of these regions, which show common practice-related decreases, lends support to our first two predictions and provides an initial characterization of the neural substrates for a putative *domain-general control system*. The regions implicated in this system are spatially consistent with those known to participate in “attentional control” [46].

2.3. Practice-related increases

Unlike the broadly distributed network of regions showing decreases across studies, practice-related increases were found to converge only in a limited set of regions confined to the medial wall of the cerebral hemispheres. We note that these convergent areas of increase are comparatively reduced in number and distribution to those areas showing decreases with practice. Moreover, these “increasing” brain regions are among those known to become deactivated during task performance when compared to a low-level baseline condition [63]. Thus,

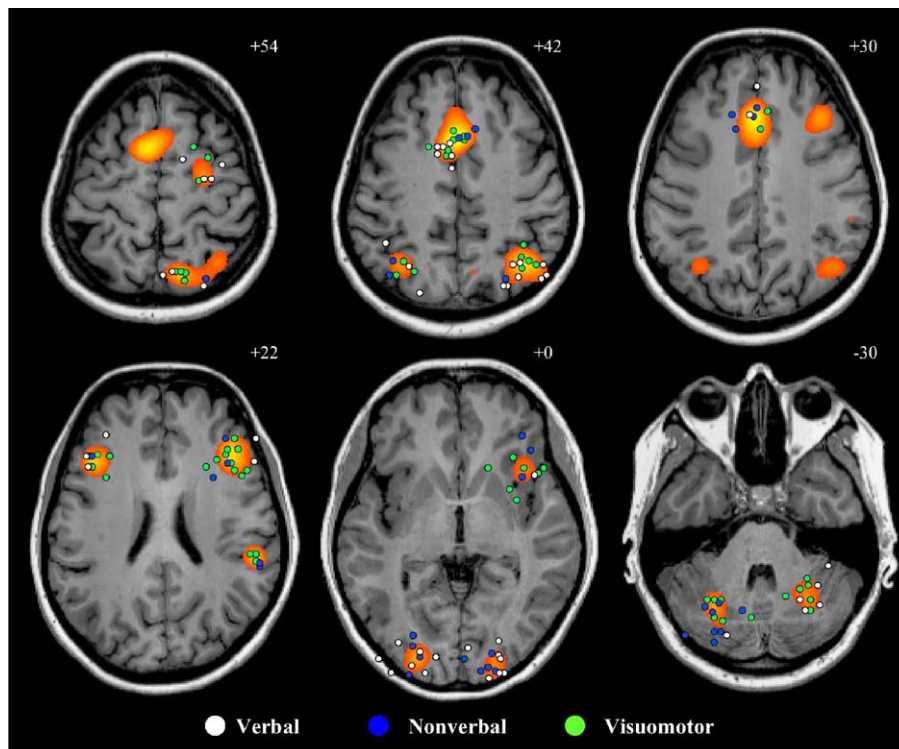


Fig. 1. Foci of convergence and stereotaxic coordinates from prior neuroimaging studies of practice-related change. “Active” regions in the meta-image indicate foci where practice-related decreases were found consistently across studies. Talairach coordinates [64] located within 20 mm of the peak convergence point for each active region are also plotted onto the meta-image (projected to the slice closest to the peak of convergence). To illustrate the domain generality of these regions, plotted coordinates are categorized and colored according to different task types: non-motor verbal (white), non-motor nonverbal (blue), or motor/visuomotor (green).

apparent practice-dependent increases may actually reflect reduced *deactivation* rather than increased activation. Interpreting the function of these regions is therefore somewhat problematic [43,49]. Despite showing less anatomical consistency, a generality that seems worthy of mention is that “true” practice-related increases (i.e., reported as increased relative to both novice performance and low-level control conditions) tend to occur in primary and secondary representational cortices (e.g., early visual regions, motor cortex). That is, in contrast to practice-related decreases, which are observed principally in association areas, practice-related increases are most typically reported in the brain regions where one might expect task-specific representations to be formed and maintained. These areas of increase thus lack spatial consistency over studies using a diverse set of tasks (because they are specific to the particular input and output characteristics of the task employed by a given study) and, accordingly, fail to emerge as convergent areas in the meta-analysis.

3. Empirical fMRI investigation

While the meta-analysis lends preliminary support to at least the first two predictions and is useful in forming expectations regarding the anatomical loci of common practice-related effects, meta-analytic evidence is by its very nature indirect and affords limited control over relevant factors. We thus set out to obtain direct empirical evidence by conducting an fMRI study contrasting, within subjects, the performance of a paired-associate task (PAT) with low-imagability words (verbal domain) and low-verbalizability shapes (nonverbal domain). Importantly, such empirical investigation allowed experimental control over degree of practice, task consistency, thresholding and analytic methods, and statistical power. The PAT was expected to engage central control operations in order to coordinate the formation of associations between arbitrarily paired items. While a stronger test of the domain-generality hypothesis might cross not only material type, but also task type (i.e., might involve some other tasks), the duration of testing required to obtain sufficient within-subject data sampling prevented the addition of other tasks to the design. However, we note that the basic associative mechanisms that subserve learning in the paired-associate task are believed to be the fundamental building blocks for the learning of most complex tasks and skills [6].

4. Material and methods

4.1. Subjects

Ten right-handed adults (five females; mean age 21.3 years), all native speakers of English, participated in the

study. Subjects were recruited from the undergraduate and graduate student populations at the University of Pittsburgh and gave informed written consent.

4.2. Stimuli

Paired-associate testing was conducted with materials from verbal and nonverbal domains. In order to establish a clear domain separation between the two material types, we selected nonverbal stimuli that would explicitly limit consequent verbal processing and verbal stimuli that would explicitly limit consequent visuo-spatial processing. The nonverbal stimuli were abstract two-dimensional shapes [4] that are highly resistant to verbal labels (Fig. 2A), as confirmed by norming and pilot testing (see below). Shape stimuli selected based on the norming procedure were formed into six sets with five pairs each for testing.

The verbal stimuli were common English words with high written frequency (greater than 20 occurrences per million) [29] that received low-imagability ratings in prior norming studies [20]. Groups of five words sharing word-initial phonemes were used as either cue or response items to compose six sets of five word pairs (Fig. 2B). Phonemic similarity was used to roughly equate difficulty in the verbal and nonverbal versions of the task.

To insure dissociation of the verbal and nonverbal stimulus domains, two important measures were taken. First, a separate norming study (run in two groups of 20 subjects) was conducted on the “nonverbal” stimuli. For each of 130 abstract shape stimuli generated for potential use in the study, participants were asked to view the shape for 5 s, rate its verbalizability on a continuous line scale, and tag items to which they could assign a reliable verbal label within the allotted time. Items receiving an average verbalizability rating over 5% on the continuous scale, or tagged by more than 10% of the participants, were discarded. In an additional pilot study (18 subjects), we examined paired-associate learning under “verbal” (articulatory suppression) and “nonverbal” (spatial finger tapping) forms of dual-task interference. The expected dissociation of verbal and nonverbal processing was evidenced by a significant impairment of verbal, but not nonverbal, paired-associate learning under articulatory suppression and a significant impairment of nonverbal, but not verbal, paired-associate learning under concurrent spatial tapping (significant interactions were found for both accuracy, $F(2,17) = 6.09$, $P = 0.024$, and reaction time, $F(2,17) = 6.29$, $P = 0.023$, measures).

4.3. Procedure

The PAT was performed in two training sessions and an fMRI scanning session. The experimental paradigm used in training and scanning was implemented using the E-prime experiment suite (Psychology Software Tools, Pittsburgh). To establish the contrast between novice and skilled

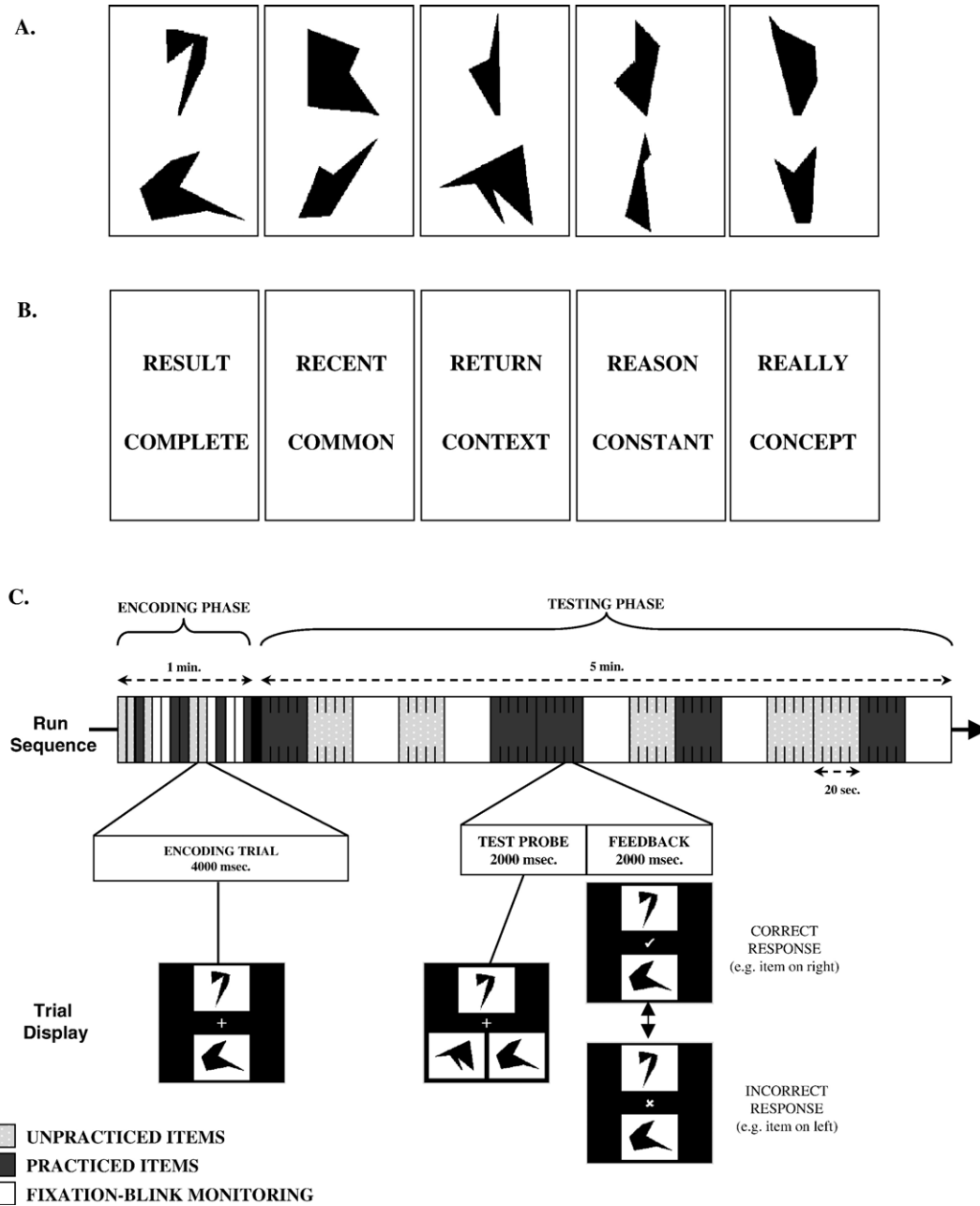


Fig. 2. Sample sets of the (A) abstract polygonal shapes and (B) low-imagability words used for paired-associate testing. (C) Schematic diagram of the sequencing of the components of a run. Each run began with an encoding phase in which each pair (unpracticed or practiced) was viewed once for 4 s. The ensuing testing phase was comprised of 20-s blocks (unpracticed item testing—light gray, practiced item testing—dark gray, fixation-blink monitoring—white). Testing blocks consisted of five trials in which each of the pairs from a given set was probed, and feedback was given.

performance, subjects received 2 h of practice on one set of pairs from each domain prior to scanning. For each subject, one of the six nonverbal stimulus sets and one of the six verbal stimulus sets were randomly chosen for use in training. The sets used in training served as the practiced pairs during scanning. The remaining five sets from each material type were reserved as unpracticed pairs for test during scanning. Over the course of training, each trained stimulus pair was practiced 80 times (by cued recognition, see below) so that these pairs were learned to a very high degree of accuracy. The results from the training sessions

are shown in Fig. 3A. By the end of training, subjects were accurate on approximately 96% of trials and had reduced reaction times by approximately 200 ms relative to novice performance (both accuracy and reaction time measures were asymptotic based on a contrast of performance in the penultimate training block to that in the final training block, $T(9) < 1.0$, $P > 0.05$). As a last stage of training, subjects were asked to briefly perform the PAT under dual-task conditions, with concurrent performance of a fixation-blink monitoring task. The purpose of this dual-task stage of training was to enhance the automatic execution of learned

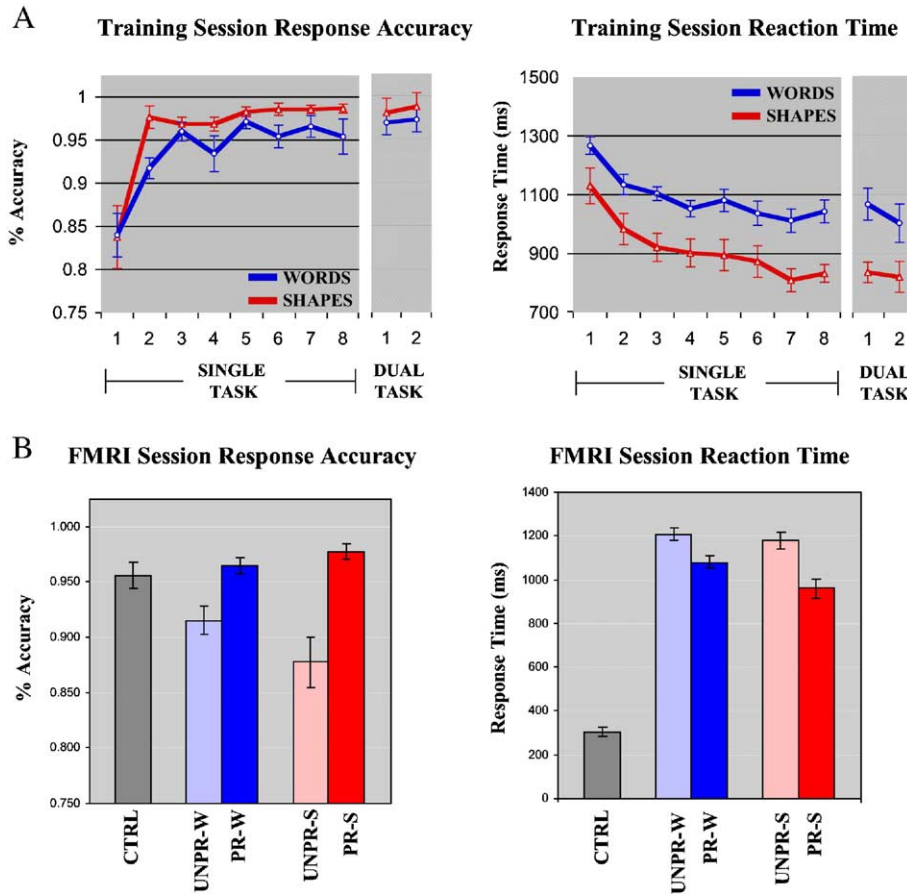


Fig. 3. Average response accuracy and reaction time data collected from (A) single- and dual-task blocks of training with practiced paired-associate sets and (B) the testing phase of the fMRI scanning session. CTRL = fixation-blink monitoring, UNPR-W = unpracticed word pairs, PR-W = practiced word pairs, UNPR-S = unpracticed shape pairs, and PR-S = practiced shape pairs.

associations by encouraging subjects to “let go” of control mechanisms [56]. Subjects performed the dual-task condition only during training and did not encounter this condition while in the scanner.

During both training and scanning, each run of the task consisted of an encoding phase and a testing phase (Fig. 2C). For encoding, subjects passively viewed the paired items that would next be tested. Pairs were presented one at a time for 4 s each. In scanning sessions, the presentation of the five practiced pairs was randomly intermixed with the presentation of five unpracticed pairs. The unpracticed pairs were unique to each run and were thus completely novel at the point at which they were introduced to the experiment.

The ensuing 5-min testing phase was segmented into blocks, lasting 20 s each, during which subjects performed either cued recognition testing with the unpracticed pairs, cued recognition testing with the practiced pairs, or a fixation-blink monitoring control condition. Scanning runs included 5 blocks from each condition, and the block ordering was counterbalanced across runs and subjects. The 20-s blocks of cued recognition testing consisted of five trials, with each pair from the set being tested (unpracticed or practiced) occurring once.

Testing trials began with a probe in which the cue item from a given pair was presented above a fixation cross, with two possible response items presented side by side below the fixation (Fig. 2C). On all trials, one response item in the probe correctly matched the cue item, and the other was a foil (the response item for a different cue from the same set). Subjects were given 2 s to identify the correct match. In the scanner, subjects responded on a 5-button, MRI compatible response collection device (Psychology Software Tools, Pittsburgh) by pressing their right index finger to indicate selection of the item on the left and their right middle finger to indicate selection of the item on the right. The trial concluded with visual feedback in which the correct pairing was displayed together with an indication of response accuracy (the central fixation cross was replaced by a green checkmark if the correct match was selected or by a red “X” if either the foil was selected or no response was given).

During control blocks, subjects attended to a centrally located fixation cross that would blink briefly at unpredictable intervals. Subjects were required to respond with a button press whenever a blink occurred. This “fixation-blink monitoring” task controlled for basic attentional and motor response components of the paired-associate task

blocks while still providing a relatively low-level reference condition.

4.4. fMRI procedure

Subjects were scanned in a 1.5-h session. During scanning, subjects performed separate runs of the PAT using either the verbal or nonverbal materials. The session included five 6-min long runs with each material type. Scanning was conducted on a 1.5-T whole-body GE Signa magnet. To minimize changes in head position across the session, a bite-bar head restraint system was employed. A 36-slice oblique-axial structural series, collected parallel to the AC–PC plane with a standard T1-weighted spin-echo pulse sequence (TE = 12 ms, TR = 500 ms, FOV = 24, slice thickness = 3.8 skip 0), was collected as an “in-plane” anatomical reference. Functional series were acquired in the same plane as the structural series, but with coverage limited to the 26 center slices. Functional images were collected with a T2*-weighted, gradient-echo, two-shot spiral pulse sequence (TE = 35, TR = 2000, FOV = 24, slice-thickness = 3.8 skip 0 mm, flip angle = 70, inplane resolution = 3.75 mm) [44], which provided a full volume functional acquisition once every 4 s.

4.5. fMRI data analysis

Analysis was conducted off-line using the NeuroImaging Software package 3.3 (developed at the University of Pittsburgh and Princeton University) and select utilities from other software packages, with integration provided by Fiswidgets [26]. Images were corrected for subject motion using a 6-parameter rigid-body automated registration algorithm (AIR 3.08) [73] and were submitted to linear detrending. To form a group composite dataset, the structural images collected from each subject were co-registered to a common reference anatomy using a 12-parameter affine transformation algorithm [74]. Functional images were then transformed into the same common space. The statistical map resulting from each subsequent analysis was transformed into stereotaxic space [64] for final reporting.

Analyses of the fMRI data were conducted using voxel-based statistical techniques. Each analysis employed a mixed effects model, wherein subjects were treated as a random factor. In all statistical tests, we used an alpha of 0.05 (uncorrected) and a clustering criterion of five contiguous active voxels. We additionally applied a split-half test–retest criterion to ensure the reliability of our findings. Specifically, the reliability of the result in each voxel was established by conducting the statistical comparisons twice: once using the data collected from the first half of the session for each subject, and then again using the data collected from the second half of the session. Only voxels passing the probability threshold and clustering criterion in both halves of data collection were accepted into the final statistical maps. While somewhat unconventional, the

combination of a relaxed statistical significance criterion along with cluster contiguity thresholding and a secondary reliability check enabled regions exhibiting small but consistent practice-related changes to survive the analysis. Allowing for some simplifying assumptions regarding spatial autocorrelation in the noise structure of the data, it can be estimated that the combined adjustments from clustering and split-half replication criteria resulted in a corrected voxel-wise P value of 0.001.

5. Results

5.1. Behavioral results

Data were analyzed for the effects of practice and material type (Fig. 3B). The task was designed so that performance levels would differ significantly between unpracticed and practiced pairs but would be approximately equated across materials. Subject accuracy showed the expected pattern. Specifically, there was a significant main effect of practice [$F(1,9) = 26.39, P < 0.001$], but no main effect of material [$F(1,9) = 0.865, P > 0.05$] or interaction between practice and material [$F(1,9) = 3.16, P > 0.05$]. Planned contrasts showed that the main effect of practice was driven by significant differences between unpracticed and practiced pairs for both the word and shape stimuli [$T(9) > 3.25, P < 0.005$, one-tailed]. Reaction time data also revealed the expected main effect of practice [$F(1,9) = 188.97, P < 0.001$], with post-hoc t tests indicating that reaction times for both word and shape pairs were significantly faster for practiced than unpracticed pairs [$T(9) > 4.29, P < 0.001$, one-tailed]. However, a main effect of material type also approached significance [$F(1,9) = 4.67, P = 0.059$], and there was a significant practice by material interaction [$F(1,9) = 24.93, P < 0.01$]. Further post-hoc tests showed that the source of these additional effects was a significantly faster mean response time for practiced shape pairs relative to practiced word pairs [$T(9) > 3.25, P < 0.005$, one-tailed], but no difference for unpracticed shape pairs versus unpracticed word pairs [$T(9) < 1.83, P > 0.05$].

6. Imaging results

6.1. Practice-dependent activity

An analysis of practice-dependent changes served to test the prediction that activity in control processing regions should decrease, or drop out, with practice (prediction 1). Analysis was conducted using only the test-phase data and ignored the data from the encoding period. A voxel-wise 2×2 ANOVA with level of practice (unpracticed, practiced) and material type (verbal, nonverbal) as within-subjects factors was first conducted to identify regions

sensitive to the manipulation. To characterize the specific effects of practice on regional activity, voxels showing either a main effect of practice or a practice by material interaction were further probed in planned contrasts that compared the fMRI signal collected for unpracticed pairs to that collected for practiced pairs. These contrasts were performed independently for each material type, allowing the determination of whether statistically significant practice-dependent changes were present for both material types, for only one material type, or for neither material type. The comparisons yielded two statistical maps of *practice-dependent change* in the paired-associate task (PAT): 1) unpracticed word PAT vs. practiced word PAT and 2) unpracticed shape PAT vs. practiced shape PAT. Regions in which the fixation control condition produced the highest degree of activation (i.e., where the PAT produced deactivations) were masked out of the resulting maps, and the surviving regions are detailed in Table 2 and Fig. 4. Each map showed many regions exhibiting dependence on

practice. Supporting our first prediction, many of these regions exhibited a decrease in activity over the course of practice (i.e., had significantly greater activity during performance with the unpracticed stimuli as compared to the practiced stimuli). Indeed, the predominant effect of practice was a decrease in activity, with decreases accounting for over 99% of the voxels surpassing the significance threshold for either material type (19 of 21 regions for words; 23 of 25 regions for shapes).

6.2. Domain-generalizability

While regions showing sensitivity to a given material type (i.e., “domain-specific” areas) were observed in the data (as the main effect of material type in the ANOVA described above), we sought to identify regions exhibiting activity consistent with a domain-general role in processing. Specifically, to test the prediction *that control processing regions are domain-general and should thus be recruited to*

Table 2
Local maxima of regions showing practice-dependent changes

	BA	Verbal				Nonverbal			
		x	y	z	P value	x	y	z	P value
<i>Practice-related decreases</i>									
Frontal cortex									
Medial frontal/ant. cingulate	32, 6	−1	19	50	0.005	3	20	48	0.0001
L precentral g	6	−45	9	50	0.0005	−37	−4	58	0.001
R precentral g	6	33	2	62	0.001				
L middle frontal g	9, 46	−40	36	4	0.0005	−43	46	5	0.005
	9					−44	25	39	0.005
R middle frontal g	9	46	31	30	0.05	46	29	36	0.005
L inf. frontal/insula	44, 45	−42	18	20	0.0005	−42	4	34	0.0005
	47, INS	−41	24	−8	0.0001	−31	22	1	0.0005
R inf. frontal/insula	44					47	11	34	0.05
	47, INS	36	29	5	0.05	32	25	2	0.0005
Parietal cortex									
Medial parietal/precuneus	7, 19	−4	−84	40	0.001	−13	−74	42	0.00001
	7					−8	−70	58	0.0005
L posterior parietal/intraparietal	7, 19, 39	−19	−74	26	0.0005	−13	−74	42	0.00001
	40					−29	−57	41	0.00001
R posterior parietal/intraparietal	7, 40, 39, 19	31	−68	37	0.01	18	−73	41	0.00005
Occipito-temporal cortex									
L fusiform/inf. occip.	19, 37	−35	−67	−5	0.0005	−38	−71	−9	0.00005
	19					−16	−51	−9	0.001
L middle temporal	37, 21	−43	−48	−12	0.005				
	21	−50	−39	3	0.0005				
R fusiform	37	44	−50	12	0.05	34	−52	−8	0.005
Occipital cortex									
L lingual g/cuneus	17, 18	−6	−84	8	0.01	−6	−90	−10	0.05
R lingual g	18					15	−82	−17	0.005
L inf. occipital g	18					−28	−85	4	0.00001
R inf./mid. occipital g	18, 19	43	−81	−6	0.005	25	−85	1	0.0005
Subcortical									
Thalamus		−1	−13	15	0.001	−5	−18	15	0.0005
Brain stem		0	−33	0	0.005	9	−25	−5	0.05
<i>Practice-related increases</i>									
Precuneus/posterior cingulate g	7, 31	17	−70	22	0.05	10	−72	25	0.05
Superior parietal lobule	7	21	−58	52	0.05				
Thalamus						23	−15	3	0.05

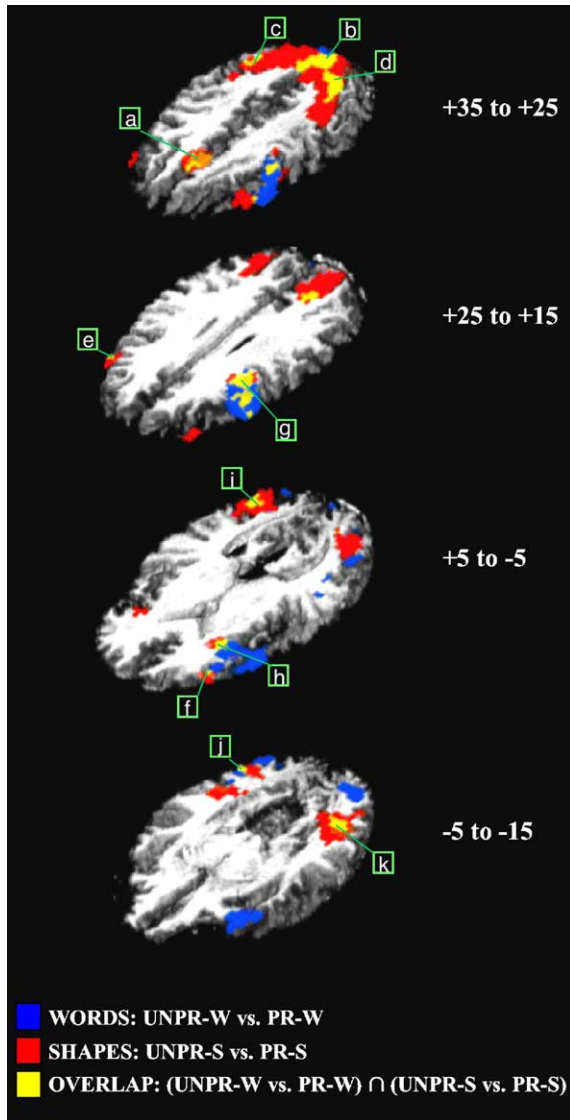


Fig. 4. Regions revealed in the contrasts of unpracticed words with practiced words (blue) and unpracticed shapes with practiced shapes (red). Shown in yellow are regions exhibiting practice-related change for both word and shape pairs. These regions, comprising the proposed domain-general control system, include the (a) anterior cingulate cortex, (b) medial parietal cortex, (c, d) bilateral posterior parietal cortex, (e, f) bilateral middle frontal gyrus (DLPFC), (g) left inferior frontal gyrus (VLPFC), (h) left anterior insular cortex, (i) right middle occipital gyrus, and (j, k) bilateral fusiform gyrus.

support initial task performance regardless of the task or material type being learned (prediction 2), we conducted a conjunction analysis in which the maps of practice-dependent change from each of the two domains were inspected for anatomical overlap. Consistent with the prediction, we found that several regions showing practice-dependent effects with one material type had a direct counterpart in the test of practice dependence produced with the other material type (Fig. 4, Table 3). The close correspondence between these overlapping regions is further indicated by examination of the (Euclidian) distances between the coordinates of the nearest local maximum in each map

(Table 3, right column). Overlapping regions showing practice-related decreases included medial frontal (BA 32), left inferior frontal (BA 44), bilateral middle frontal (BA 9,46), left anterior insular, bilateral parietal/intraparietal (BA 7,40), medial parietal (BA 7), bilateral fusiform (BA 37), and right inferior occipital (BA 18) regions. Non-overlapping but spatially contiguous decreasing clusters were also found in the thalamus. Only one small region, located in the posterior midline (precuneus/posterior cingulate), exhibited an overlapping increase with practice.

6.3. Task-dependent activity

A further set of analyses was used to identify all brain regions producing activation associated with performance of the PAT (not just those showing practice-related effects). We conducted independent voxel-based *t* tests comparing PAT with each material type (verbal, nonverbal) at each level of practice (unpracticed, practiced) to the fixation-blink monitoring control condition. These four contrasts revealed all regions engaged by the task and provided for an assessment of the hypothesis that skilled performance should not engage new regions, but should activate a subset of those areas engaged by early learning (prediction 3). Overall, regions of activity were similar across material types and across levels of practice (Fig. 5). For the purpose of this assessment, a newly emergent region was operationally defined as a peak activation falling outside of any

Table 3
Regions of overlap in conjunction of practice-dependent changes for words and shapes

	BA	Overlap (center of mass)			Distance between nearest peaks
		x	y	z	
<i>Practice-related decreases</i>					
Medial frontal	32, 6	-2	19	47	4.6
Medial parietal/precuneus	7, 19	0	-80	44	13.6
L posterior parietal/intraparietal	7, 19, 39	-22	-70	43	17.1
R posterior parietal/intraparietal	7, 39, 40	32	-65	36	14.5
L inf. frontal g	44	-40	6	34	19.8
R middle frontal g	9	46	31	30	6.3
L middle frontal g	46	-44	44	7	10.5
L anterior insula	INS	-31	22	5	13.6
L fusiform/inf. occip.	19, 37	-38	-64	-9	6.4
R fusiform	37	46	-55	-12	22.4
R middle occipital g	18	22	-84	-12	19.7
<i>Practice-related increases</i>					
Precuneus/post. cingulate g	7, 31	12	-70	23	7.9

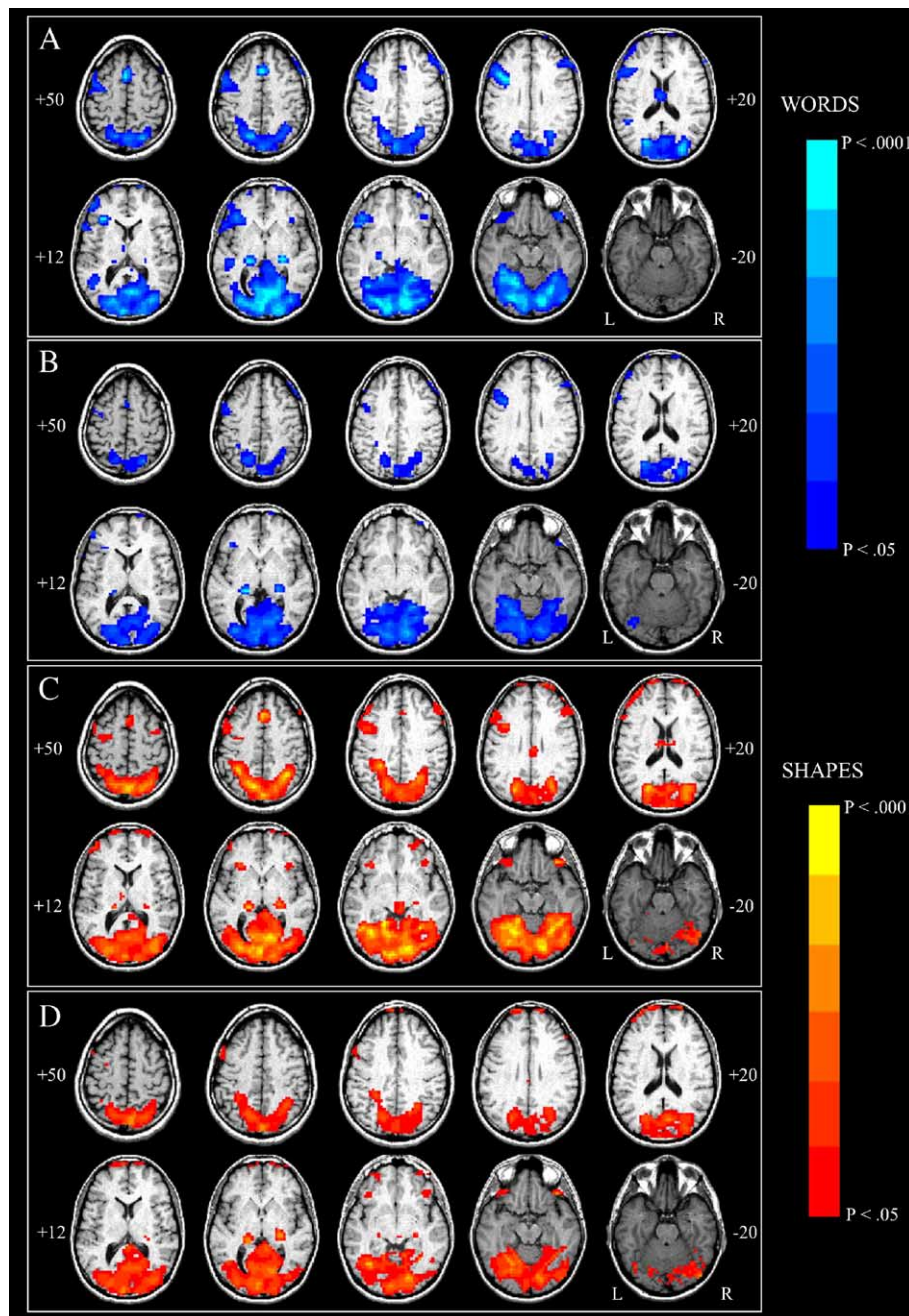


Fig. 5. Regions of activity resulting from the contrasts of (A) unpracticed word pairs versus control, (B) practiced word pairs versus control, (C) unpracticed shape pairs versus control, and (D) practiced shape pairs versus control. Voxels shown surpassed a statistical probability threshold of $P < 0.05$ in the group composite data, comprised a cluster of at least 5 contiguous significant voxels, and replicated in the first and second halves of data collection. The statistical images are shown overlaid onto horizontal sections, at 8 mm increments, from the structural MRI image used for inter-subject registration, which has been warped into stereotaxic space [64]. The numbers to the left and right of each row represent the distance, in millimeters, from the anterior commissure to posterior commissure plane.

previously activated cluster, yet exceeding the statistical criteria. We found no such peak activations in the practiced data and found instead that practiced pairs elicited activity within the same network of brain regions as did unpracticed pairs, with unpracticed pairs producing generally larger and higher magnitude regional activity. That is, for each material type, the voxels engaged by practiced PAT performance were a subset of those engaged by unpracticed PAT performance. This pattern held true even in the limited

set of regions where practice-related increases were observed, with these regions showing statistically significant activations both before and after practice.

7. Discussion

Results from meta-analysis, and from an fMRI study manipulating degree of practice and material type within-

subjects, indicate that the most consistent effect of practice is a reduction of the extent and magnitude of regional activity. Furthermore, both the meta-analytic and fMRI data show that this diminished activity is reliably present in the same set of brain regions, regardless of the specific task demands. As proposed in the Introduction, these findings can be meaningfully interpreted through the resource-based account embodied in the dual-processing framework, in which learning causes a transition from dependence on controlled processing resources to a state of processing that is independent of these resources.

Based on our meta-analysis of the existing literature, we established a priori predictions regarding the specific regions that would emerge as domain-general control regions in the subsequent empirical investigation. Given the general variability of imaging results, a certain degree of mismatch between the empirical and meta-analytic findings could be expected. Still, consistency in the regions produced by each method was readily evident, as illustrated for example by examination of the spatial conjunction of the meta-analytic and empirical findings. Of the eleven regional clusters found to exhibit domain-general practice-related decreases in the empirical data (resampled in the stereotaxic space), eight included voxels that overlapped with an a priori cluster from the meta-analysis. Overlapping regions included the medial frontal, bilateral middle frontal, left inferior frontal, bilateral posterior parietal, medial parietal, and right middle occipital regions. A ninth region, the left anterior insula, was not overlapping but had a counterpart in nearly the exact coordinates of the contralateral hemisphere. Therefore, of the empirically derived regions, only the bilateral fusiform foci were not predicted a priori. Conversely, only four of the fourteen predicted regions were not activated in the empirical data; these included bilateral cerebellar regions, the right precentral cortex, and a small cluster in the right inferior parietal cortex.

We view the presence of consistent practice-dependent decreases (observed in both meta-analytic and empirical approaches) as a neural signature of attenuated demand on domain-general supervisory (attention, performance monitoring) and working memory resources [15,25]. In line with the interpretation of these areas as a coordinated control network, prior work has shown (through techniques that expose the covariance structure of activity in multiple brain regions, e.g., structural equation modeling) that these same brain regions behave as a dynamically interacting network during learning and initial task execution [9,42].

In the present empirical data, reductions with practice were found to be particularly salient in frontal cortex, where the level of activity in some subregions (e.g., left DLPFC, anterior cingulate) was no longer significantly different after extensive practice from the baseline condition. Similar observations of reduced activity in the frontal cortex have led, in previous studies, to the postulation that practice induces an anterior (frontal) to posterior shift in the functional anatomy of task performance [53,59,72]. We

note, however, that posterior brain regions also show practice-related reductions and that some frontal areas remain strongly active during practiced performance (e.g., left ventral prefrontal with word pairs). It can be inferred from these findings that, while the specific control resources provided by frontal areas may be most fully disengaged following practice, posterior regions also mediate important control mechanisms. That is, control is distributed widely in the neocortex and does not appear to be a strictly frontal function (see below for discussion on the localization of various control operations). Conversely, the persistence of activity in prefrontal subregions following practice is suggestive evidence that at least some of the prefrontal cortex is devoted to representational functions that are not directly associated with cognitive control.

The present fMRI results also provide support for the assumption of the CAP2 dual-processing model that skilled performance relies on the same neural substrates as are engaged for untrained task performance. The notion that there are two *modes* of processing (controlled and automatic) has at times been misinterpreted as implying two separate *pathways* for processing. However, our computational implementation of the dual-processing theory demonstrates that these two processing modes can take place within a system that relies on identical representational structures for both novice and skilled performance. This view is confirmed by the fMRI data, where it is found that skilled performance engages a subset of the regions engaged during novice performance and does not appear to have its own cortical pathway.

While the present results are thus consistent with three predictions derived from the dual-processing framework, a number of alternative interpretations do deserve consideration. As discussed in Poldrack [49], practice-dependent changes in the functional anatomy of task performance can originate from a wide variety of sources. Although reduction of the demands placed on certain cognitive resources may explain the observed decreases in activity, other possible explanations include confounding from performance differences across conditions, changes in synaptic efficacy, repetition priming, and shifts in subject strategy.

Though practice-induced changes in performance (e.g. reduced reaction times, improved accuracy) are the behavioral markers of successful learning, they can be viewed as confounding factors in the present study. That is, one could argue that apparent practice-dependent changes simply result from differences in reaction time or trial accuracy across conditions. Close inspection of the behavioral and imaging data, however, suggests that performance differences alone cannot explain the findings. If activity differences reported in the present study were due solely to confounding from performance disparities, such differences would be expected in any contrast of conditions for which performance differed significantly, but not in contrasts of conditions for which performance was equated. The data do not support this alternative account. For example, a contrast

of the practiced word and practiced shape conditions (for which reaction times differed significantly) produces no regions of activation beyond those present in a contrast of the unpracticed word to unpracticed shape conditions (for which there were no performance differences).

Decreases in regional activity with practice may alternatively be interpreted as a reflection of local changes in synaptic efficacy [32]. Synaptic changes are assumed to affect the strength of local associations by tightening connections between neurons that contribute effectively toward task processing and weakening connections between those that do not. As mentioned in the Introduction, such associative mechanisms are assumed by almost all theories of learning, including the dual-processing view. However, it is also commonly accepted that synaptic modifications occur principally in cortical circuits having receptive field properties enabling the representation of task-specific information [38]. Accordingly, changes associated specifically with synaptic plasticity should occur in brain regions tuned for processing of particular material types (e.g., primary sensory cortices), and not in regions that exhibit practice-dependent decreases across material types. Both empirical and meta-analytic data indicate, however, that decreases occur in common regions despite highly distinct stimulus and task attributes. Thus, the data appear to be insufficiently explained by synaptic mechanisms alone and to be more reasonably addressed in a framework recognizing that a brain region may not itself experience synaptic modifications yet may still exhibit practice-dependent change.

A similar line of argument seems to rule out repetition priming as a general explanation for the observed patterns. Repetition priming, or a decrease in the responsiveness of a given brain region following repeated exposures to a stimulus, is normally found in brain areas responsible for representation of specific attributes of the repeated stimulus [12,14,70]. While the use of stimuli with some common visual attributes may explain decreased activity observed in the ventral visual pathway (see Occipito-temporal cortex section below), distributed decreases observed in common areas for verbal and nonverbal stimuli are not readily explained by task-specific repetition priming effects. In addition, we have recently replicated the present findings in a study using an auditory verbal task, with all but the occipito-temporal regions produced in the present empirical study again showing practice-related decreases (unpublished data).

As alluded to in the Introduction, another way to explain practice-related changes is to assume that they arise from changes in the strategies engaged by subjects over the course of learning. That is, practice-induced changes may reflect a qualitative shift from dependence on one set of cognitive processes (those supporting strategies used in unpracticed performance) to dependence on a different set of cognitive processes (those supporting strategies used in practiced performance). While some prior studies have shown evidence of strategy shifting [50,52,67,71], the telltale signature of such a shift is the

reciprocal decrease of activation in regions supporting the initial strategy and increase of activation in regions supporting the alternative strategy. However, practice in the present study did not cause new areas to emerge and thus does not appear to have promoted the engagement of an alternative performance strategy.

While based on the above arguments we conclude that activity changes in domain-general processing areas are most suitably interpreted as proposed within the dual-processing framework, we must acknowledge that a number of important questions regarding these “domain-general” areas are not fully resolved in the present analysis. One question is whether putative domain-general processing areas may exhibit additional “sensitivity” to particular task types. That is, whether certain control processing areas may be taxed to a greater or lesser extent in particular task domains. Indeed, the present empirical data contains evidence of differential levels of control process engagement across the verbal and nonverbal tasks, and the reasons for these differences are deserving of further empirical consideration. It may additionally be argued that the resolution of fMRI is simply insufficient to identify subregions within “domain-general” areas that are in fact dedicated to processing in specific domains. In that patterns of neuronal connectivity engender preferred input and output pathways, it is certainly the case that, in the limit, there are “domain-specific” cell populations within each region. However, we believe that domain-general areas are imbued with lateral (intra-regional) connections that force these domain-specific sub-populations to compete for representation. Since only a subset of representations can be co-active in this competitive network, it is most appropriate to conceive of these regions as central (domain-general) processing resources.

A further question that has received some attention in recent work [30,34,46] is how patterns of activity are influenced when training is specifically directed at the functions supported by the central control system (as opposed to practice of tasks that initially tax these functions). In two studies [34,46], activation was found to be enhanced within the control system (prefrontal and parietal regions) following several weeks of training on working memory tasks that involved variable task mappings (interchangeable targets and distractors from trial to trial). While these results are generally consistent with the present framework, which anticipates decreased activity specifically when there are consistent input–output task mappings, the opposite finding was reported by Garavan and colleagues [30]. In this latter study, several hours of practice in a variably mapped working memory task yielded significant activity decreases in several of the regions presently implicated in control processing. We have recently completed a complementary study in which subjects practiced for a week on both consistent and variable mapping conditions of a memory search task and found that, although there were some regional reductions for the variable mapping condition (which could not be automated), the consistent mapping

condition produced more substantial and widespread reductions (unpublished data). Thus, the weight of available evidence appears to support the current view, but inconsistent findings suggest a need for further work in this area.

To truly understand the role of the proposed domain-general control network, we must ultimately explain the distribution of function across its constituent brain regions and the precise nature of their interaction. While the design of our experiment affords limited information regarding the specific distribution of function across the network, we can offer some initial speculations based on prior research findings and on the specific conception of control processing in the CAP2 dual-processing architecture.

7.1. Prefrontal cortex

In the CAP2 model, the control system is divided into distinct control processors, each with its own particular function. The prefrontal cortex, which has been previously implicated in goal-based and planning processes (e.g., [60]), is most readily associated with CAP2's "Goal Processor", whose primary function is to guide novice behavior by instantiating the task context (e.g., the instructions) and then structuring the sequential execution of task-relevant operations. Correspondingly, Cohen and colleagues [8,19,45] have argued that the prefrontal cortex, in particular the dorsolateral part, serves to maintain goal-related information that biases subsequent processing according to task demands. By this account, practice-related decreases observed in the DLPFC may occur as practice strengthens the stimulus–response associations between paired items, correct responses are potentiated, and the need for monitoring and biasing from task context (and thus the prefrontal cortex) is reduced.

Common practice-related decreases were also observed in ventrolateral and insular frontal regions. While our modeling work does not address control mechanisms that map readily onto these areas, a number of reasonable interpretations are afforded by the literature. One possibility is that these regions are engaged by verbal mediation or covert verbalizations made by subjects as they encounter novel aspects of the task [69]. Alternatively, these regions may be activated to encode the novelty of information [12,22,65]. From a working memory perspective, the activity in these regions during encoding may reflect material non-specific rehearsal processes to maintain information on-line, while it is being more permanently embedded into long-term memory [10].

7.2. Parietal cortex

The empirically observed domain-general network also included an extensive posterior parietal region (spanning the PPC and IPS) where activity decreased with practice. We believe that this region, which is widely viewed as an attentional center of the brain [21,24,51], subserves a

control process that allocates attention to task-specific information processing regions. In CAP2, such attentional modulation is imposed by an "attention controller" that guides information flow by regulating the output of distributed information processing modules during novice performance. After practice on a task, the demand for attentional control is reduced as associations become strong enough to trigger information flow in the absence of attentional modulation. Such reductions in the demand for attentional control provide a likely account for practice-related decreases in the lateral parietal cortex.

Two separate areas of medial parietal cortex were also found in our empirical work to show common practice-dependent changes across PAT performance with word and shape items. In a more dorsal region, there was a decrease with practice, while a more ventral region was the only area to exhibit a cross-domain increase with practice. Buckner [11] also found two distinct regions in the medial parietal cortex showing opposite patterns of activity (one increase and one decrease) during episodic retrieval. The location of our more dorsal region corresponds very closely to a posterior medial parietal region reported in this earlier study, to which the authors attributed a role in retrieval effort. The observation that this region is more active for unpracticed items (when retrieval is most difficult) than for practiced items (when retrieval is easier) matches well with this retrieval effort hypothesis. Though the function of the more ventral medial parietal region remains less clear, we speculate that the increases in this region observed with practice for both word and shape stimuli may link its activity to retrieval success.

7.3. Anterior cingulate cortex

Practice also led to decreased activation of the anterior cingulate cortex for both verbal and nonverbal paired-associates. We believe that that function of this region corresponds to an "Activity Monitor" in CAP2's control system. The Activity Monitor acts to track and record recent activity levels in task-relevant areas and to establish a decision threshold for identifying strongly activated areas to the goal processor. Indeed, much of the recent literature on cingulate function has emphasized its role in communicating a need for greater cognitive control to other executive brain regions [17]. This view has been applied to explain high levels of activity observed in the ACC when performance is error-prone or when a task produces a high degree of processing conflict [5,16,47]. However, we suggest that activity in the ACC is not sensitive to the presence of conflict or errors per se. Rather, we have argued that activation of the Activity Monitor, and hence the ACC, depends on the duration over which it samples distributions of regional activity in order to establish a decision threshold. The duration of sampling may depend, for example, on the difficulty of comparisons required by the task or on the perceived consequence of speeding response times (see

[61]). Accordingly, this region's decrease in activation with practice may correspond with the decreased sampling time needed to select a decision threshold as familiarity with the correct pairings increases.

7.4. Occipito-temporal cortex

The cortex in the inferior occipital and temporal lobes is generally thought to mediate processes associated with the ventral visual pathway [33]. Accordingly, we suspect that the activity patterns in these regions do not truly reflect components of a domain-general control system (which would presumably mediate non-visual learning as well) but result from the use of visual stimuli (for both materials in our fMRI study and, more generally, across studies included in the meta-analysis). Studies of perceptual priming [54] have shown that these regions often exhibit decreased activity over repeated visual exposure to a given item. Interestingly, both imaging [68] and neurophysiological [23] works have shown that the decreases found along this occipito-temporal pathway with repeated experience may last well beyond the duration typically examined in studies of perceptual priming and may represent lasting changes in the cortical representation of repeated items. Such representational changes are likely reflected in the practice-related decreases observed in occipito-temporal areas following repeated stimulus exposures in the paired-associate learning task.

8. Conclusions

In summary, we have shown that previous neuroimaging studies examining the effects of practice, despite apparent differences, reveal a consistent pattern of regional activity reductions across a distributed cortical network. In an empirical fMRI study, this same network of regions is shown to be engaged during early associative learning for both verbal and nonverbal material types, but disengaged in later performance of the task, once the associations are well-learned. We interpret these practice-related changes as reflections of the waning contributions of a domain-general control system as a task becomes well learned, an interpretation consistent with the central tenets of the dual-processing framework. Our preliminary mapping of regions in this domain-general network to specific components of a dual-processing model offers a foundation for future work seeking to detail the specific processes that take place within this network and the ways in which its subregions interact to support learning.

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Appendix A. List of studies included in the meta-analysis

First author	Year	Task
Andreasen	1995	Recall of narratives
Andreasen	1995b	Recall of word lists
Buchel	1999	Encoding of object–location associations
Doyon	1996	Sequential finger movements
Fletcher	1999	Grammaticality judgments with artificial grammar
Grafton	1992	Pursuit rotor task
Hazeltine	1997	Color-cued keypress sequence
Jansma	2001	Working memory for letters
Jenkins	1994	Trial-and-error keypress sequence
Jueptner	1997	Trial-and-error keypress sequence
Jueptner	1997b	Trial-and-error keypress sequence
Kassubek	2001	Reading of mirror-reversed words
Kopelman	1998	Encoding of word lists
Krebs	1998	Movement of manipulandum under applied forces
Petersson	1997	Recall of abstract designs
Petersson	1999	Recall of abstract designs
Poldrack	1998	Reading of mirror-reversed words
Raichle	1994	Verb generation
Rauch	1995	Location-cued keypress sequence
Sakai	1998	Trial-and-error keypress sequence
Schiltz	1999	Line orientation discrimination
Schiltz	2001	Line orientation discrimination
Toni	1998	Trial-and-error keypress sequence
Van Horn	1998	Maze tracing
van Mier	1998	Maze tracing
van Turenout	2000	Encoding of objects
Weissman	2002	Global/local attention to letter stimuli
Wildgruber	1999	Recall of ordered word lists
Wiser	2000	Recall of faces

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