


# Task learning is subserved by a domain-general brain network

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One of the most important human faculties is the ability to acquire not just new memories but the capacity to perform entirely new tasks. However, little is known about the brain mechanisms underlying the learning of novel tasks. Specifically, it is unclear to what extent learning of different tasks depends on domain-general and/or domain-specific brain mechanisms. Here human subjects ( $n = 45$ ) learned to perform 6 new tasks while undergoing functional MRI. The different tasks required the engagement of perceptual, motor, and various cognitive processes related to attention, expectation, speed-accuracy tradeoff, and metacognition. We found that a bilateral frontoparietal network was more active during the initial compared with the later stages of task learning, and that this effect was stronger for task variants requiring more new learning. Critically, the same frontoparietal network was engaged by all 6 tasks, demonstrating its domain generality. Finally, although task learning decreased the overall activity in the frontoparietal network, it increased the connectivity strength between the different nodes of that network. These results demonstrate the existence of a domain-general brain network whose activity and connectivity reflect learning for a variety of new tasks, and thus may underlie the human capacity for acquiring new abilities.

**Key words:** domain-general learning; task learning; fMRI; functional network; inferior frontal gyrus.

## Introduction

Humans have the remarkable ability to learn completely new skills. Learning is most vigorous in childhood when people master various skills such as reading, writing, arithmetic, sports, and self-control (Piaget 1970). Yet, neurologically healthy humans never lose their ability to acquire new skills, and adults routinely learn new languages, sports, job skills, and social habits. However, it remains unclear what brain mechanisms underlie our ability to learn such a diverse range of new skills. Specifically, a central problem is the extent to which learning across a variety of domains relies on common neural mechanisms vs. domain-specific mechanisms that are different for each task.

Previous research has focused primarily on the neural correlates of learning specific stimuli. For example, studies investigating perceptual learning typically compare brain activity associated with highly trained vs. untrained sensory stimuli (Rainer et al. 2004; Yang and Maunsell 2004; Antzoulatos and Miller 2011), studies on motor learning compare familiar and novel movements (Grafton et al. 2002; Houweling et al. 2008; Bassett et al. 2015; Musall et al. 2019), studies on classical and operant conditioning compare rewarded and unrewarded stimuli (Shuler and Bear 2006; Serences 2008; Summerfield and Koechlin 2010; Baeuchl et al. 2020), and studies on repetition suppression compare repeated and non-repeated stimulus presentations (Henson et al. 2000; Wig et al. 2005). In all of these cases, what is being investigated is

how a learned stimulus or action differs from a novel stimulus or action. The same limitation also applies to other common designs, such as to studies that compare stimulus-evoked brain activity before and after learning (Serences et al. 2009; Deuker et al. 2013; Utzerath et al. 2017; Peter et al. 2021; Stauch et al. 2021). However, despite the tremendous progress made with these approaches, this line of research tells us very little about the brain mechanisms that underlie our ability to learn a new task rather than a new stimulus.

Not surprisingly, previous research focusing on comparing learned vs. novel stimuli has mostly found that domain-specific mechanisms underlie each area of learning. After extensive training, visual stimuli are processed differently in the visual cortex (Rainer et al. 2004; Shuler and Bear 2006; Serences 2008; Serences et al. 2009; Deuker et al. 2013; Utzerath et al. 2017), motor actions are generated differently in the motor cortex (Grafton et al. 2002; Houweling et al. 2008; Bassett et al. 2015; Musall et al. 2019), and rewarded stimuli are processed differently in reward circuits of the brain (Shuler and Bear 2006; Serences 2008; Summerfield and Koechlin 2010; Baeuchl et al. 2020). Based on this research, it is perhaps natural to hypothesize that the ability to learn completely novel tasks that rely on different perceptual, motor, and cognitive processes would rely on domain-specific brain areas. However, an alternative possibility is that learning novel tasks depends on domain-general mechanisms and that

domain-specific brain areas become important primarily when learning specific stimuli, but not the structure associated with a new task.

Several studies have investigated task learning for tasks that rely on the same underlying processes. For example, one approach introduced by Cole et al. (2010) involves constructing 64 different tasks specified using combinations of judging 1 of 4 sensory properties (green/loud/soft/sweet), applying 1 of 4 logic operations (same/just one/second/not second), and executing 1 of 4 motor responses (left/right index/middle finger). Thus, the instructions for 1 of the 64 tasks would be “If the answer to ‘Is it GREEN?’ is the SAME for both words, press your LEFT INDEX finger”. The task consists of observing 2 words (e.g. “gecko” and “leaf”) and making an appropriate response. Several other designs for novel task learning use simpler task structures that consist of learning different stimulus–response pairings and implementing them either immediately (Ruge and Wolfensteller 2010; Hartstra et al. 2011) or after a delay (Meiran et al. 2015a, 2015b). These studies generally found that novel task variants engaged frontal and parietal regions more strongly than previously practiced variants. However, in all of these studies, the different tasks are always specific instances of the same overall task structure that engages the same set of cognitive processes and is likely to activate the same brain areas. Indeed, these studies did not include tasks that are known to depend on different brain areas. As such, it remains unknown whether learning tasks that engage different cognitive processes and brain areas relies on a common set of domain-general regions or different sets of domain-specific regions.

Here we adjudicated between these 2 possibilities. Human subjects ( $n = 45$ ) learned to perform 6 new tasks that rely on perception, motor, or various cognitive processes (attention, expectation, speed-accuracy tradeoff (SAT), and metacognition). These tasks are known to activate dissociable areas in the visual cortex (Heeger 1999; Grill-Spector and Malach 2004), motor cortex (Laut Ebbesen and Brecht 2017; Svoboda and Li 2018), intraparietal sulcus (IPS) (Corbetta and Shulman 2002; Rahnev et al. 2012), dorsolateral prefrontal cortex (Rahnev et al. 2011a), supplementary motor area (Forstmann et al. 2008; Spieser et al. 2017), and anterior prefrontal cortex (Rahnev et al. 2016; Shekhar and Rahnev 2018; Yeon et al. 2020), respectively. As such, they allow us to directly test the hypotheses that task learning depends on a common set of domain-general regions vs. different sets of domain-specific regions. Subjects were first introduced to each new task inside an MRI scanner, which allowed us to examine their brain activity during the process of learning each new task. Each task had 3 variants that differed in several dimensions, while remaining within the same task domain. Importantly, each variant consisted of 2 blocks, and we compared the brain activity during the first block when substantial new task learning is necessary to the second block when relatively less new task learning is taking place. We observed that a domain-general frontoparietal network subserved learning across all 6 tasks. This network showed higher activity during the initial stages of learning and stronger connectivity in the later stages of learning. Little domain-specific activity was observed. These results demonstrate the existence of a domain-general network that underlies task learning.

## Methods

### Subjects

Forty-eight subjects participated in the study. Data from 3 subjects were excluded due to data saving errors. All analyses

were conducted on the remaining 45 subjects (25 females, age =  $23.2 \pm 8.28$  years, mean  $\pm$  SD). All subjects had normal or corrected-to-normal vision, were right-handed, and had no history of neurological disorders. The subjects were screened for MRI safety and provided informed consent. Subjects were paid \$15 per hour for their participation and were not rewarded based on their task performance. The study was approved by the local review board.

### Tasks

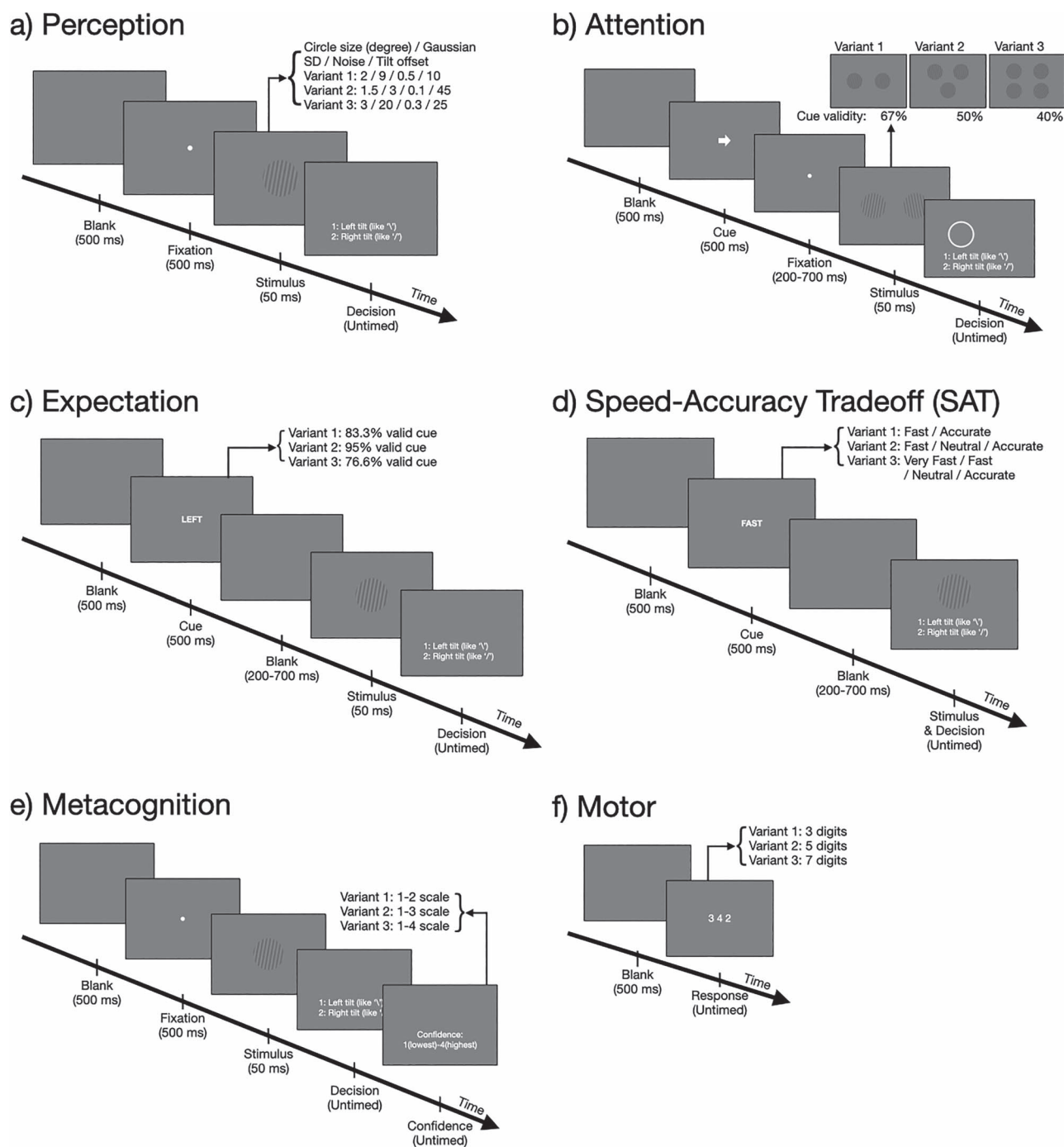
Subjects performed 6 different tasks that required the engagement of perception, various cognitive (attention, expectation, SAT, and metacognition), or motor processes (Fig. 1). The perception task was always learned first, followed by the 4 cognitive tasks in a randomized order, and the motor task that always came last. Each task had 3 variants that were presented in the same order across subjects (see below). Each task variant consisted of 2 identical blocks of 30 trials (for a total of 60 trials per variant for each task). Subjects encountered each task inside the scanner for the first time and received brief on-screen instructions at the beginning of each task, as well as before the start of each new variant. Subjects were allowed unlimited time to read and process the instructions and had a 9.5-s break between the 2 blocks of a single task variant. Subjects gave their responses through an MRI-compatible button box with their right hand. All 6 tasks were completed in a single session, and subjects took 61 min on average to complete all 6 tasks (Min = 52.34 min, Max = 75.96 min).

### Perception task

The perception task required subjects to engage in challenging perceptual discrimination without the need to employ higher cognitive processes. Subjects indicated the orientation of a grating that could be tilted either counterclockwise (“left”) or clockwise (“right”) of vertical (Fig. 1a). Each trial started with a blank screen (500 ms), followed by a white fixation point (500 ms), the grating (50 ms), and an untimed response period. The grating stimuli for the 3 task variants differed in their size (2°, 1.5°, and 3° in diameter), noise level (50, 10, and 30%), spatial frequency of the grating (9, 3, and 20 cycles per degree), and offset from vertical (10°, 45°, and 25°). The contrast of the grating was initially set to 10% in the beginning of each task variant and was then continuously adjusted using 2-down-1-up staircase method (step size = 2% contrast) with the lowest possible contrast set to 2%. The stimuli for the 4 cognitive tasks were identical to the stimulus in variant 3 of the perception task, but with a fixed contrast equal to the mean contrast values of all trials in Block 2 of variant 3.

### Attention task

The attention task required subjects to engage in the deployment of endogenous spatial attention (Carrasco 2011; Chun et al. 2010; Petersen and Posner 2012; Rahnev et al. 2011b). Subjects saw between 2 and 4 gratings positioned 5° from the center of the screen and equally spaced from each other. On each trial, one of the gratings was post-cued and the task was to indicate the orientation of the post-cued grating (Fig. 1b). A trial consisted of a blank screen (500 ms), followed by a pre-cue (an arrow) that pointed to the likely location of the post-cued stimulus (500 ms). After a fixation screen of variable duration (200–700 ms), the gratings were presented (50 ms), and finally a post-cue appeared indicating which grating subjects should respond to. Subjects had unlimited amount of time to indicate the orientation (left or right) of the post-cued grating. The 3 variants differed in the number of



**Fig. 1. Tasks.** Subjects completed a perception task, followed by 4 cognitive tasks (requiring attention, expectation, speed-accuracy tradeoff, and metacognition) in a randomized order, and a motor task that always came last. Each task had 3 variants shown on the top-right of each panel. (a) In the perception task, subjects judged the orientation (left vs. right) of a grating. The 3 variants manipulated the size, noise level, contrast level, and orientation of the grating. The same parameters of the last variant were used for generating the stimuli in all cognitive tasks (the only exception is that the attention task used higher contrast). (b) In the attention task, a pre-cue indicated the location that subjects should attend to. Subjects reported the stimulus orientation at a post-cued location. The 3 variants differed in the number of gratings presented and corresponding pre-cue validity. (c) In the expectation task, a cue indicated the likely orientation of the upcoming stimulus. The 3 variants differed in the predictiveness of the cue. (d) In the speed-accuracy tradeoff task, a cue indicated the speed with which subjects should make the orientation discrimination response. The 3 variants differed in the number of speed stress levels. (e) In the metacognition task, subjects provided a confidence rating regarding the accuracy of their decision. The 3 variants differed in the confidence scale used. (f) In the motor task, subjects typed as quickly as possible the digits (chosen among the digits 1 to 4) presented on the screen using a button box. The 3 variants differed in the number of digits shown.

gratings presented (2, 3, or 4) as well as the predictiveness of the pre-cue (67, 50, and 40%), which was chosen such that the cued location was always 2 times more likely to be post-cued than the remaining locations.

### Expectation task

The expectation task required subjects to engage in the integration of non-perceptual knowledge (in the form of a prior) and perceptual information (Bang and Rahnev 2017; Rahnev et al. 2011a;

Summerfield and De Lange 2014; Turk-Browne et al. 2010). Subjects made a perceptual decision combining the information of a predictive cue with the perceptual information from the actual stimulus (Fig. 1c). Each trial began with a blank screen (500 ms), followed by the predictive cue consisting of the words “LEFT” or “RIGHT” shown at the center of the screen (500 ms). After a blank screen of variable duration (200–700 ms), the grating was presented (50 ms) and was followed by an untimed response period. The 3 variants differed in the predictiveness of the cue, which was set to 83.3, 95, and 76.6%, respectively. Subjects were fully informed about the cue predictiveness and encouraged to take the information into account when making their perceptual decision.

### SAT task

The SAT task required subjects to flexibly adjust the speed of their responses (Giordano et al. 2009; Steinhauser and Yeung 2012; Drugowitsch et al. 2015). Subjects made a perceptual decision that emphasized speed vs. accuracy to a different degree in accordance with a preceding cue (Fig. 1d). The 3 variants differed in the number of possible instructions of the cue (variant 1: Fast/Accurate; variant 2: Fast/Neutral/Accurate; variant 3: Very fast/Fast/Neutral/Accurate). Each trial began with a blank screen (500 ms), followed by a cue that presented an instruction word at the center of the screen (500 ms). After a blank screen of variable duration (200–700 ms), the grating was presented and remained on the screen until subjects provided their response.

### Metacognition task

The metacognition task required subjects to engage in evaluating their confidence level about the previously made perceptual decision (Fleming and Dolan 2012; Yeon et al. 2020; Rahnev 2021). After making a perceptual decision, subjects rated how confident they were about the decision they just made (Fig. 1e). Each trial began with a blank screen (500 ms), followed by a fixation screen (500 ms). After a short presentation of a grating stimulus (50 ms), subjects sequentially indicated their perceptual decision and then provided their confidence level (both untimed). The 3 variants differed in the granularity of the rating scale (2, 3, and 4 points) with later variants requiring increasingly more granular confidence responses.

### Motor task

The motor task required subjects to perform a sequence of simple button presses that required minimal involvement of higher cognitive functions (Grafton et al. 2002; Debas et al. 2010; Doyon et al. 2018). Subjects were asked to press buttons corresponding to the digits presented on the screen (Fig. 1f). Each trial began with a blank screen (500 ms), followed by a stimulus presentation screen. The variants differed the number of digits presented on the screen (3, 5, and 7 digits). Numbers between 1 and 4 were used to generate a series of digits. Subjects used the index, middle, ring, and little fingers of their right hand to press buttons associated with the numbers 1–4, respectively. Subjects were instructed to perform the button presses as fast and accurately as possible.

### Image acquisition and preprocessing

The MRI data were collected on a 3 T MRI system (Trio Tim, Siemens) using a 12-channel head coil. Anatomical images were acquired using T1-weighted magnetization-prepared rapid acquisition gradient-echo (MPRAGE) sequences (TR = 2300 ms; TE = 2.98 ms; 160 slices; FoV = 256 mm; flip angle = 9°; voxel size = 1.0 × 1.0 × 1.0 mm<sup>3</sup>). Functional images were acquired using T2\*-weighted gradient echo-planar imaging (EPI) sequences

(TR = 2000 ms; TE = 24 ms; 37 slices; FoV = 224 mm; flip angle = 60°; voxel size = 3.5 × 3.5 × 4.2 mm<sup>3</sup>). After subjects were positioned inside the MRI scanner, functional images were acquired continuously in a single run, during which subjects read the instructions for and performed all 6 tasks. The anatomical images were collected at the end of the experiment.

We used SPM12 (Wellcome Department of Imaging Neuroscience, London, United Kingdom) for data preprocessing and analysis. Functional images were first converted from DICOM to NIFTI. Converted images were then de-spiked for the signal above 2.5 SD with an upper bound of 4 SD. De-spiked images then slice-time corrected in descending order, realigned within individual subject's functional images, and coregistered the mean functional image to the subject's anatomical T1 image. Individual subject's anatomical T1 image was segmented to separate gray matter, white matter, Cerebrospinal fluid (CSF) and bone, soft tissue, and air and background. Functional, anatomical, and segmented images were then all normalized to the Montreal Neurological Institute space template (MNI152). Finally, functional images were smoothed with 6-mm full-width-half-maximum (FWHM) Gaussian kernels.

### Data analysis

#### Behavioral analyses

We computed task accuracy and reaction time (RT) for each block of each task variant. For the perception and the 4 cognitive tasks, task accuracy was computed based on whether subjects correctly identified the grating orientation. For the motor task, a response was only considered correct if all digits were entered correctly. The RT for the motor task was computed as the time from digit presentation until the final digit was entered. We excluded outlier RT values that lie  $\pm 3$  SD of all RTs for a given task variants. We examined differences in RT between Blocks 1 and 2 within each variant using one-sample t-tests, and compared these differences across task variants using paired-sample t-tests. To investigate the learning effect in task accuracy, we averaged task performance block-wise and z-scored the accuracy within each task for individual subjects. We then examined differences in task accuracy between Blocks 1 and 2 within each variant using one-sample t-tests, as well as compared these differences across the 3 variants using paired-sample t-tests. We excluded the perception task in this analysis because the task used a staircase method to continuously adjust the difficulty of the task (Supplementary Fig. 5). Additional analyses for the 4 cognitive tasks, intended to confirm that each task was completed appropriately, are described in Supplementary Figs. 1–4.

#### General linear model (GLM) analyses of the fMRI data

To reveal the brain regions that reflect task learning, we compared the blood-oxygenation level-dependent (BOLD) signal between Blocks 1 and 2 of each task variant. We first defined GLM regressors for Block 1 (all tasks and variants together), Block 2 (all tasks and variants together), the rest period between Blocks 1 and 2, and the instructions period that occurred for every new task and variant. The contrast Block 1 > Block 2 from this GLM was used to identify the brain areas that reflect task learning. In addition, we created 2 more GLMs where the periods for Blocks 1 and 2 were defined separately for each task, or separately for each task variant. The contrast Block 1 > Block 2 from these GLMs was used to examine how the brain activations differed across tasks and task variants. All GLMs included 6 regressors related to head movement (3 translation and 3 rotation regressors), 4 tissue regressors (white matter, CSF and bone, soft tissues, and air and background), and a constant term. Unless otherwise specified,



analyses were performed using familywise error (FWE) corrected  $P < 0.05$  and a cluster size of at least 150 voxels.

## ROI analyses

To examine the domain generality of the brain regions that reflect task learning, we followed the following procedure. For a given task, we examined the contrast Block 1 > Block 2 using the data from the remaining 5 tasks. We then identified each of the 5 regions-of-interest (ROIs) (bilateral inferior frontal gyrus (IFG), bilateral IPS, and left cerebellum) based on the activations obtained using the data from these 5 tasks. This procedure avoided “double-dipping” where the same data are used both to define an ROI and examine its associated activations (Kriegeskorte et al. 2009). Finally, we tested whether activity in these ROIs was stronger for Block 1 than Block 2 in the original task, with the same procedure repeated for each of the 6 tasks. We also examined whether we would observe significantly different activation pattern of the brain outside of the ROIs for individual tasks. To quantify activated regions in the brain besides the ROIs, we first set the  $P$ -value threshold so that half of voxels in the ROIs are activated for each task, and then calculated the proportion of activated voxels outside of the ROIs. Standard error for proportions is calculated using the following formula:

$$SE = \sqrt{p(1-p)/n}$$

where  $p$  is the proportion of the activated voxels and  $n$  is the number of voxels in the ROIs.

## Functional connectivity analyses

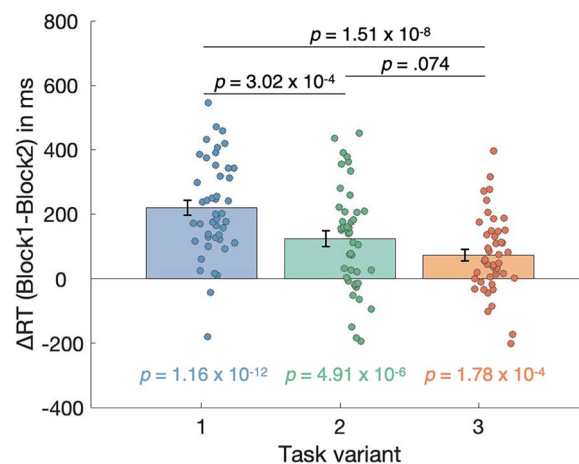
Our main analyses revealed that bilateral IFG, bilateral IPS, and left cerebellum reflect task learning, but could not uncover whether task learning affected the communication between these regions. To address this question, we defined these clusters as ROIs, and then extracted and normalized the time-series data from the preprocessed functional images for each ROI. We regressed out the mean gray matter, mean white matter, and mean CSF signals from the time-series for each ROI (Ciric et al. 2017; Lydon-Staley et al. 2019). We also removed any individual volumes with framewise displacement greater than 0.3 mm, to minimize artifacts related to in-scanner head motion (Jenkinson et al. 2002; Power et al. 2012). Lastly, we filtered the residual signal with a second-order Butterworth filter between 0.01 and 0.1 Hz. Finally, we computed the strength of the functional connectivity between each pair of the 5 ROIs separately for Blocks 1 and 2 by taking the Pearson correlation between each pair of ROIs' volume-by-volume time series. To statistically compare the correlation values between Blocks 1 and 2, we  $z$ -transformed the  $r$ -values and conducted paired-sample  $t$ -tests on the  $z$ -values. All average  $r$ -values reported in the main text and Fig. 7 were obtained by averaging the  $z$ -values and then transforming the average  $z$ -value back into an  $r$ -value.

## Data and code

Data and analysis code are available at <https://osf.io/knzj6>. In addition, all group-level fMRI T-maps are available at <https://neurovault.org/collections/FYJMWHCU>.

## Results

We investigated whether the neural substrates underlying the learning of new tasks is domain-general or domain-specific. Subjects performed 1 perceptual, 4 cognitive, and 1 motor task while



**Fig. 2. RT difference between Blocks 1 and 2 for each task variant.** We computed the RT difference between Blocks 1 and 2 for each of the 3 task variants across all 6 tasks. The  $P$ -values below the plots show the results of one-sample  $t$ -tests comparing the RT difference for each of the 3 task variants against zero. The  $P$ -values above the plots show the results of paired  $t$ -tests comparing the RT differences between different task variants. The results suggest that learning was greatest for the first task variant but remained significant for the second and third variants. Each dot represents the average RT across all 6 tasks for a single subject. Error bars indicate standard error of the mean (SEM).

we collected fMRI data (Fig. 1). The perception task was always performed first, the motor task was always performed last, and the remaining tasks were performed in randomized order. To avoid the introduction of new perceptual learning with each task, the cognitive tasks used the same grating stimuli from the perception task. Each task consisted of 3 variants to ensure the need for constant learning of new task features. Each variant included 2 blocks of 30 trials with the first block naturally requiring more novel learning than the second block.

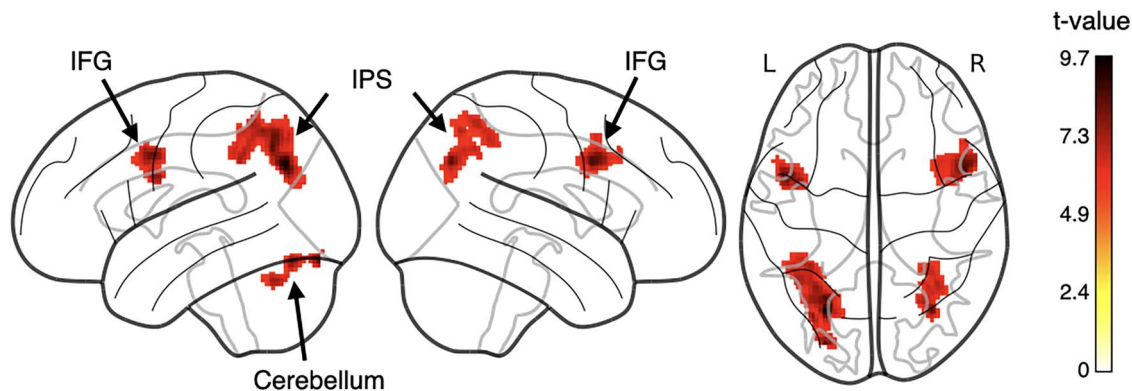
## Behavioral effects

We first confirmed that subjects performed all behavioral tasks as instructed. We observed adequate performance across all tasks (accuracy = 70.6, 59.3, 77, 77.7, 69.7, and 85.9% for the perception, attention, expectation, SAT, metacognition, and motor tasks, respectively). In addition, we confirmed that subjects were more accurate for valid cues in the attention task (Supplementary Fig. 1), preferentially chose the expected stimulus in the expectation task (Supplementary Fig. 2), followed the speed/accuracy instructions in the SAT task (Supplementary Fig. 3), and exhibited higher accuracy for trials with higher confidence in the metacognition task (Supplementary Fig. 4).

We then examined whether there was behavioral evidence for a learning effect when comparing Blocks 1 and 2 of each task variant. We found that subjects exhibited substantially reduced RTs for Block 2 compared with Block 1. This effect was most pronounced for the first task variant (RT difference = 220 ms;  $t(44) = 9.82$ ,  $P = 1.16 \times 10^{-12}$ ; Fig. 2) but was also present for the second (RT difference = 124 ms;  $t(44) = 5.20$ ,  $P = 4.91 \times 10^{-6}$ ) and third (RT difference = 74 ms;  $t(44) = 4.09$ ,  $P = 1.78 \times 10^{-4}$ ) task variants. Moreover, RT difference between Blocks 1 and 2 was larger for the first variant compared with both the second ( $t(44) = 3.92$ ,  $P = 3.02 \times 10^{-4}$ ) and the third ( $t(44) = 6.92$ ,  $P = 1.51 \times 10^{-8}$ ) variants. The RT difference between the second and the third variants was only marginally significant ( $t(44) = 1.84$ ,  $P = 0.074$ ). We also examined task accuracy of the 3 variants. We found a small but significant difference between Blocks 1 and 2 for variant 1

**Table 1. Localization of activations for the contrast Block 1 > Block 2.** Coordinates correspond to the standard MNI brain.

	Side	Coordinates			Voxel size	Peak level	
		(x, y, z)				t-value	P-value
IPS	L	-24	-68	32	1083	9.71	$8.27 \times 10^{-13}$
	R	32	-68	34	494	8.33	$6.72 \times 10^{-11}$
IFG	L	-46	4	38	329	8.23	$9.33 \times 10^{-11}$
	R	50	8	34	431	8.62	$2.63 \times 10^{-11}$
Cerebellum	L	-26	-86	-28	198	8.24	$9.29 \times 10^{-11}$



**Fig. 3. Task learning is reflected in frontal, parietal, and cerebellar regions.** Brain regions with greater activation for Block 1 compared with Block 2 across all 6 tasks. Five clusters emerged in bilateral IFG, bilateral IPS, and left cerebellum ( $P < 0.05$  FWE corrected, cluster size  $\geq 150$ ). Darker shade (red) in the figure indicates higher t-values.

( $t(44) = 2.249$ ,  $P = 0.029$ ), but not for variant 2 ( $t(44) = 2.003$ ,  $P = 0.051$ ) or variant 3 ( $t(44) = 0.293$ ,  $P = 0.771$ ; [Supplementary Fig. 5](#)). These results provide strong evidence for behavioral learning in all 3 task variants, with the learning being greatest in the first variant.

### Task learning is reflected in frontal, parietal, and cerebellar activation increases

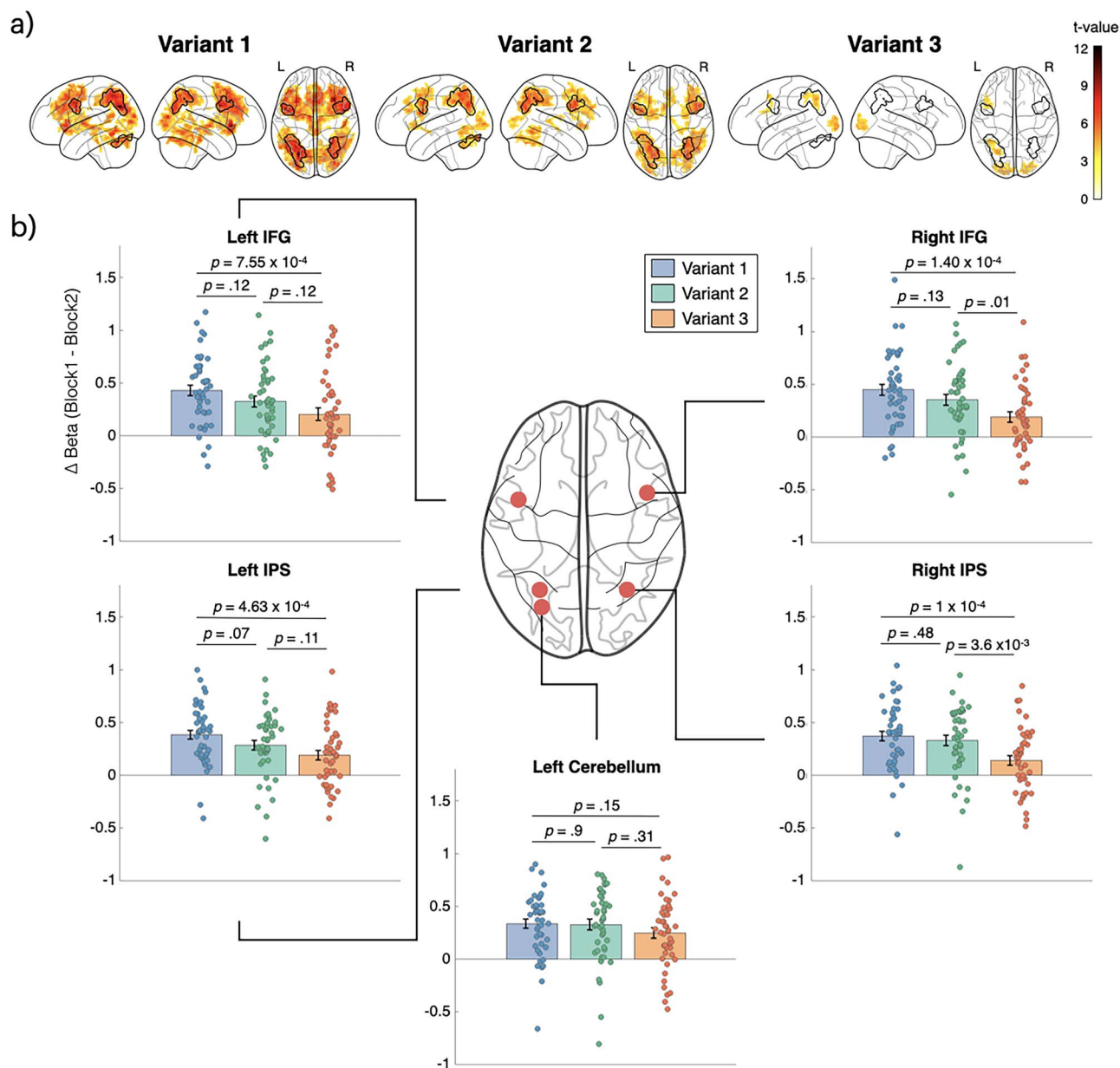
The behavioral analyses confirmed that substantial task learning took place during Block 1 (as reflected by the faster RTs on Block 2 compared with Block 1). Therefore, we investigated the neural correlates of task learning by determining the brain areas that show larger activations for Block 1 than Block 2. We applied FWE correction at  $P < 0.05$  and searched for clusters of at least 150 voxels (see [Supplementary Fig. 6](#) for a map including clusters of any size). The results showed bilateral activation in the IFG, bilateral activation in the IPS, and left cerebellum activation ([Fig. 3](#), [Table 1](#)). No voxels survived the same threshold for the opposite comparison (Block 2 > Block 1).

The behavioral results demonstrated that learning was greatest for the first variant of each task and then monotonically decreased for the second and third variants ([Fig. 2](#)). Therefore, we examined whether the difference in activation between Blocks 1 and 2 in these 5 clusters also peaked for the first variant and decreased for later variants. Qualitatively, the comparison of Blocks 1 and 2 produced large swaths of activity in the first variant, less activity in the second variant, and even less activity in the third variant ([Fig. 4a](#)). We quantified this effect by examining the activations for each task variant specifically for the 5 regions from [Fig. 3](#), which we defined as ROIs. We found that all 4 frontoparietal ROIs showed a monotonic decrease in activation difference between Blocks 1 and 2 ( $P < 0.001$  for all pairwise comparisons between variant 1 and variant 3; [Fig. 4b](#)). While the cerebellar ROI also showed a pattern of monotonic decreases,

none of the pairwise comparisons between the 3 variants were significant (all  $P$ 's > 0.1). Thus, even though the bilateral IFG and IPS ROIs were defined using a contrast that was independent of variant order, each of them showed a neural effect that mimicked the corresponding behavioral learning effect. An exploratory analysis also revealed a significantly positive correlation for the first variant only between (i) the RT difference between Blocks 1 and 2 averaged across 6 tasks and (ii) the brain activation difference between Blocks 1 and 2 averaged across 6 tasks and all 5 ROIs ([Supplementary Fig. 7](#)), though such across-subject brain-behavior correlations should be interpreted with caution ([Marek et al. 2022](#)). Overall, these results strongly suggest that learning of these tasks is reflected in the activity in bilateral IFG, bilateral IPS, and, to a lesser extent, in left cerebellum.

### Task learning effects in frontal, parietal, and cerebellar regions are domain-general

The results above clearly demonstrate that the frontal, parietal, and cerebellar brain regions reflect task learning, but do not clarify whether these regions are domain-general. Specifically, it is possible that each task exhibits strong domain-specific effects that are obscured by examining all tasks together. To explore this possibility, we examined the contrast between Blocks 1 and 2 separately for each of the 6 tasks. Previous imaging studies have demonstrated that visual perception tasks activate the visual cortex ([Heeger 1999](#); [Grill-Spector and Malach 2004](#)), that top-down attention tasks activate the dorsal attention network ([Corbetta and Shulman 2002](#); [Rahnev et al. 2012](#)), that expectation tasks activate the dorsolateral prefrontal cortex, IPS, and medial temporal cortex ([Rahnev et al. 2011a](#)), that speed-accuracy tradeoff tasks activate the supplementary motor area ([Forstmann et al. 2008](#); [Spieser et al. 2017](#)), that metacognitive tasks activate the anterior prefrontal cortex, dorsolateral prefrontal cortex, and anterior



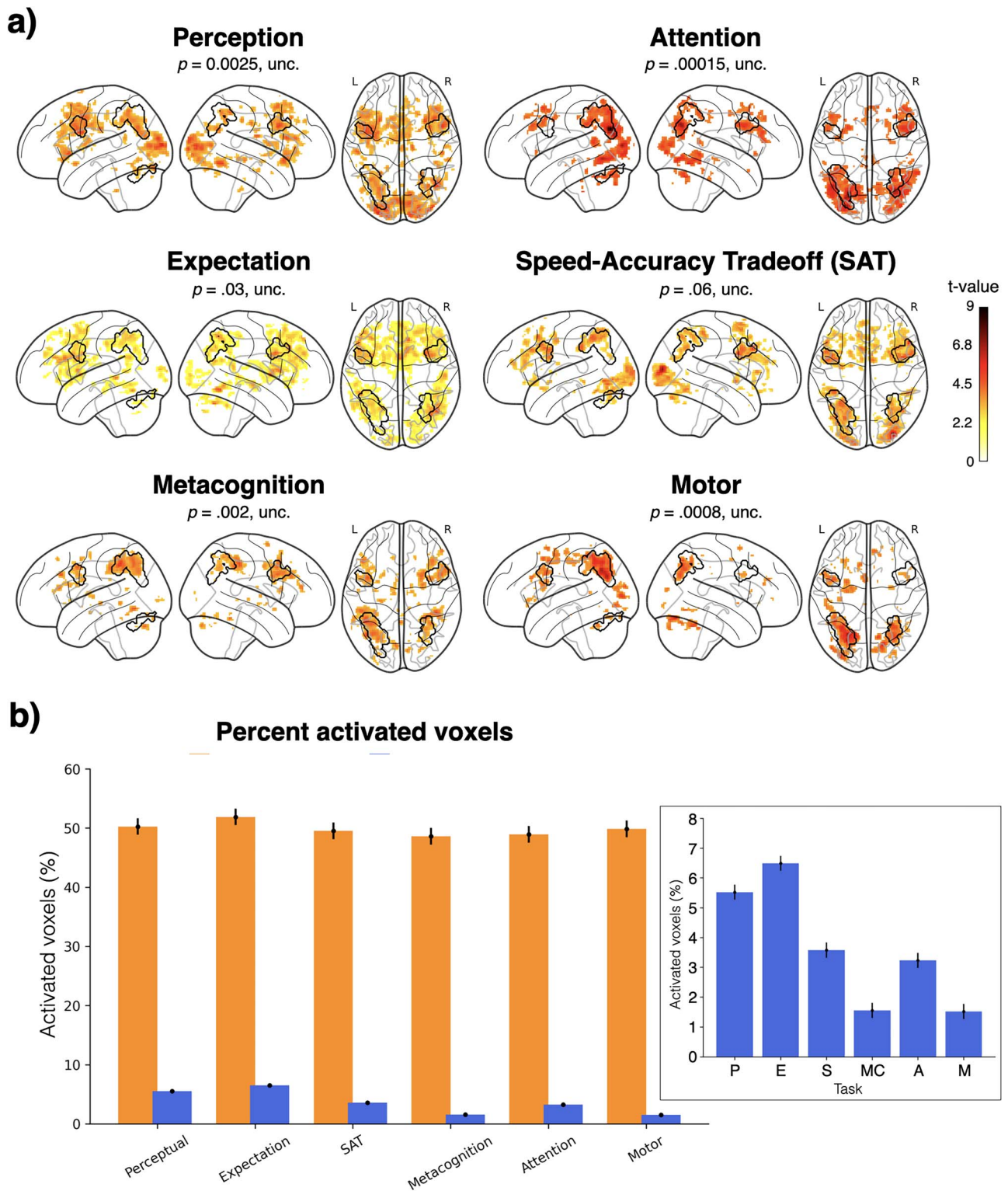
**Fig. 4. Brain activations for each of the 3 task variants.** (a) Brain regions with greater activation for Block 1 compared with Block 2 across all 6 tasks displayed separately for each of the 3 task variants. For display purposes, the figures are thresholded at  $P < 0.001$  uncorrected, cluster size  $\geq 150$ . Brain activations are clearly strongest for the first task variant and weakest for the third. Black borders indicate the 5 regions from Fig. 3, and darker shade (red) indicates higher t-values. (b) Beta values difference between Blocks 1 and 2 for each of the 5 ROIs from Fig. 3. Each ROI shows a decreasing trend such that the activation difference between Blocks 1 and 2 is greatest in the first task variant and smallest in the third, but the comparison is only significant in the 4 frontoparietal regions. Error bars indicate SEM. IFG, inferior frontal gyrus; IPS, intraparietal sulcus.

cingulate (Rahnev et al. 2016; Shekhar and Rahnev 2018; Yeon et al. 2020), and that motor control tasks activate motor and premotor cortices (Laut Ebbesen and Brecht 2017; Svoboda and Li 2018). A domain-specific account of task learning would predict that the same areas involved in the execution of each task would also be activated when learning the corresponding task.

However, we found that the learning-related activations for the individual tasks were remarkably similar. First, a standard analysis where each task activation was thresholded at  $P < 0.001$  uncorrected found that activations for each task overlapped substantially with the across-task results (i.e. the 5 ROIs defined above), with the only exception of a prominent visual cortex activation for the perception task (Supplementary Fig. 8). We further investigated whether we could find any domain-specific

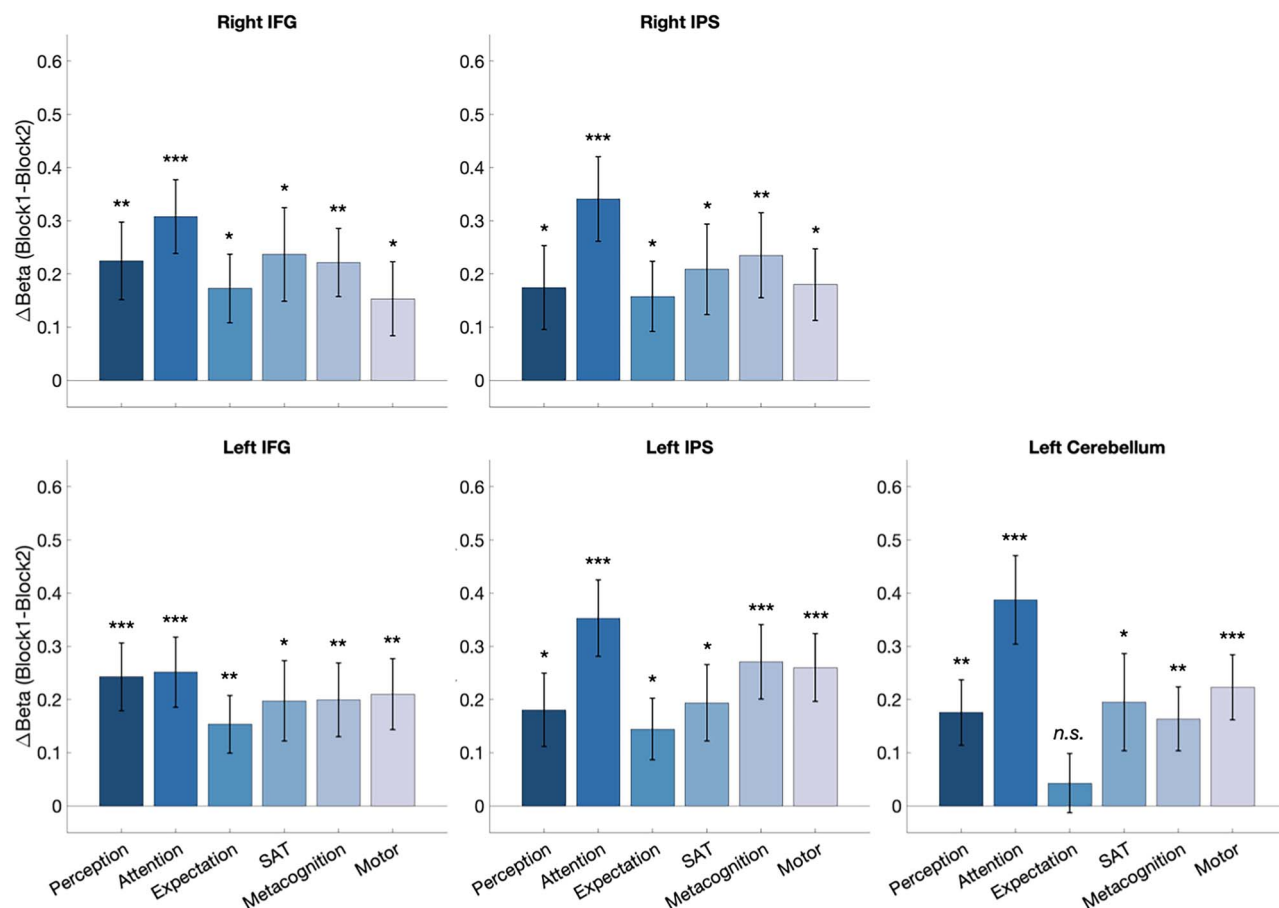
effects by looking into the activation of each variant of each task separately. Similar to the group analysis of each variant (Fig. 4), most tasks showed the strongest activation in the first variant, except for the metacognition and motor tasks, but no domain-specific activations emerged for any of the variants in any of the tasks except for the same visual cortex activation for the perception task (Supplementary Fig. 9). Meanwhile, we could not find any distinctive domain-specific activation across all tasks. However, these analyses led to large differences in the extent of the observed activations, making it difficult to compare the selectivity of the activations across tasks. Therefore, in a separate analysis, we used different thresholds for the activations for each task so that every task activated about half of the voxels in the 5 ROIs (Fig. 5a). Our procedure resulted in the





**Fig. 5. Similar brain correlates of task learning for each of the 6 tasks.** (a) Brain regions with greater activity for Block 1 compared with Block 2 for each task. For each task, we used a different P-value threshold so that about half of the voxels within the 5 ROIs from Fig. 3 were activated. Despite notable variability in the strength of the effects across tasks, a qualitatively similar activity pattern appears across all 6 tasks. No domain-specific activations were found for any of the tasks, with the exception of a prominent visual cortex activation cluster in the perception task. Black borders indicate the 5 regions from Fig. 3, darker shade (red) indicates higher t-values. (b) Percent activated voxels within (orange, or the lighter shade) and outside (blue, or the darker shade) the 5 ROIs in (a). The motor and metacognition tasks had the most selective activations such that they produced the smallest percent of activated voxels outside of the 5 ROIs (1.52 and 1.56%, respectively). Inset shows the percent of activated voxels outside the 5 ROIs for each task with different scale. Labels on x-axis indicate task names (perceptual: P, expectation: E, SAT: S, metacognition: MC, attention: A, and motor: M). Error bars represent standard error.





**Fig. 6. Domain generality of the activations in the frontal, parietal, and cerebellar regions.** To assess the domain generality of the 5 ROIs (left and right IFG, left and right IPS, and left cerebellum), we defined each ROI based on the activations in 5 tasks and examined the activations in the left-out task. Except for the left cerebellum ROI in the expectation task, all ROIs showed a significantly larger activation for Block 1 compared with Block 2 (all  $P$ 's < 0.05). These results establish the domain generality of each of the 5 ROIs by demonstrating that each ROI reflects the learning on all 6 tasks (or 5 tasks in the case of left cerebellum). Error bars indicate SEM.

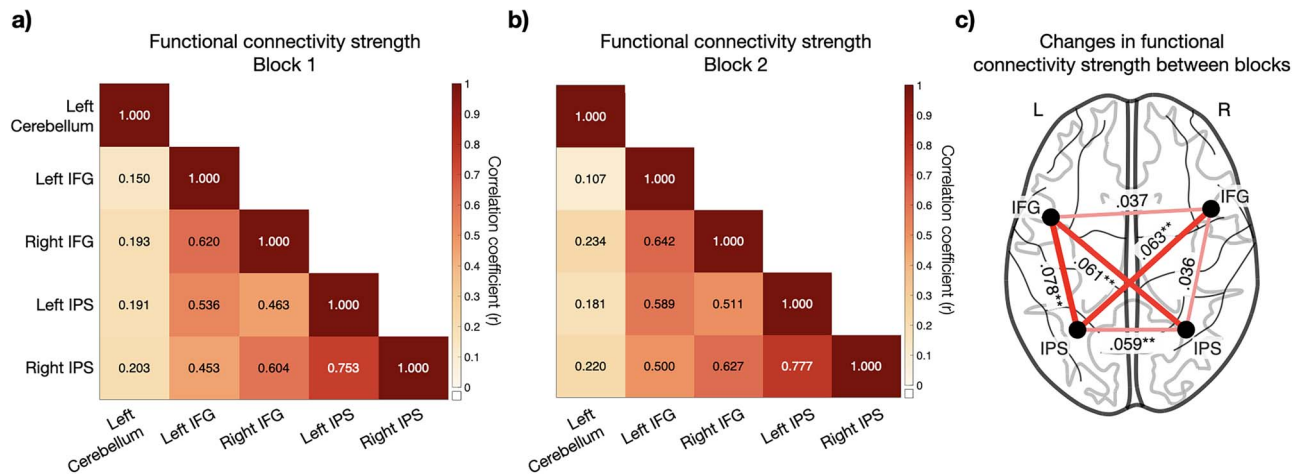
selection of uncorrected  $p$  thresholds of 0.0025, 0.00015, 0.03, 0.06, 0.002, and 0.0008 for the perception, attention, expectation, SAT, metacognition, and motor tasks, respectively, with the percent of activated voxels within the 5 ROIs between 48.6 and 51.9% for all 6 tasks. Critically, the percent of activated voxels outside the 5 ROIs was substantially lower (mean = 3.65%, range = 1.52–6.49%; Fig. 5b). Comparing across tasks, we found that the motor task produced the most selective activations such that the percent of activated voxels outside of the 5 ROIs was smallest ( $P < 2.38 \times 10^{-5}$  for all pairwise comparisons between motor and other tasks except for the comparison with the metacognition task where  $P = 0.91$ ). Given that the motor task has the most unique structure (e.g. all of the other tasks used similar stimuli), these results demonstrate that the finding of domain-general task learning-related activations is not simply due to superficial similarities between the tasks.

These results qualitatively support the existence of a domain-general mechanism for task learning, but do not establish that all 5 ROIs are involved in each of the 6 tasks. To explore this issue, we performed a more direct test of whether each of the 5 areas above (bilateral IFG, bilateral IPS, and left cerebellum) were activated for all or just for a subset of the tasks investigated here. For each task, we defined the 5 regions as ROIs based exclusively on the data from the remaining 5 tasks. For example, the ROIs used for the perceptual task were defined solely based on the attention, expectation, SAT, metacognition, and motor tasks. This procedure

avoided “double-dipping” where the same data are used both to define and test an ROI (Kriegeskorte et al. 2009). We then tested whether activity in these ROIs was stronger for Block 1 than Block 2 in the left-out task. We found that this was the case for 29 of the 30 tests (all  $P$ 's < 0.05), with the only exception being the left cerebellum ROI in the expectation task (Fig. 6). These results confirm that the activity found within the frontal, parietal, and cerebellar ROIs associated with task learning are indeed domain-general and not driven by only a subset of tasks.

### Learning increases functional connectivity between frontoparietal regions

The results above establish that task learning is subserved by domain-general activations in bilateral IFG, bilateral IPS, and left cerebellum. Yet, it is unclear whether these 5 regions form a single network, and whether learning changes the way they communicate with each other. Here we examined these questions by investigating the functional connectivity between all 5 regions separately for Blocks 1 and 2. We found strong functional connectivity within the bilateral frontoparietal regions (all  $r$ -values between 0.453 and 0.777; Fig. 7a, b) but much weaker functional connectivity between the left cerebellar region and the frontoparietal areas (all  $r$ -values between 0.107 and 0.234). In fact, each of the 6 within-frontoparietal network  $r$ -values was significantly higher than each of the 4 cerebellum-to-frontoparietal  $r$ -values for both Blocks 1 and 2 ( $P < 0.00001$  for all 48 tests). Thus, it



**Fig. 7. Functional connectivity for Blocks 1 and 2 between the 5 ROIs.** (a) Average region-to-region functional connectivity for Block 1. (b) Average region-to-region functional connectivity for Block 2. (c) Change in functional connectivity strength between the 2 blocks. Warm colors (or the darker shades) indicate increased connectivity in Block 2 compared with Block 1. Both the thickness of the edges and the numerical values represent the change in connectivity from Block 1 to Block 2. \*\* $P < 0.01$ .

appears that the 4 bilateral frontoparietal regions form a single network that the left cerebellar region is not a part of.

Critically, we examined the changes of functional connectivity between Blocks 1 and 2. We found that functional connectivity between the 4 frontoparietal regions was significantly higher in Block 2 (average  $r = 0.618$ ) than Block 1 (average  $r = 0.582$ ;  $t(44) = 3.92$ ,  $P = 3.01 \times 10^{-3}$ ). Furthermore, this difference appeared for all 6 pairs of regions and was significant for 4 of them (Fig. 7c). The only nonsignificant increases between individual regions were right IFG to right IPS (difference in  $r$  values = 0.036,  $t(44) = 1.98$ ,  $P = 0.054$ ) and right IFG to left IFG (difference in  $r$  values = 0.037,  $t(44) = 1.70$ ,  $P = 0.096$ ). Conversely, the connectivity between left cerebellum to the frontoparietal regions showed no change from Block 1 to Block 2 (average difference in  $r$  values = 0.002,  $t(44) = 0.117$ ,  $P = 0.907$ ). Thus, task learning specifically increased the connectivity within the 4 frontoparietal regions, but not between the frontoparietal regions and the cerebellum.

## Discussion

We investigated the extent to which task learning is subserved by domain-general vs. domain-specific neural mechanisms. We found strong evidence for the domain-general account: the same 5 frontal, parietal, and cerebellar regions subserved the learning of 6 tasks that on their own engage different cognitive processes and have different brain substrates. At the same time, virtually no domain-specific regions were found to be involved. Furthermore, task learning increased the functional connectivity between the frontal and parietal areas, suggesting altered communication between these areas. These results demonstrate that unlike the learning of specific stimuli, movements, or rewards, the learning of an entirely new task is domain-general and thus may underlie the human ability for acquiring new abilities.

Most previous research on how humans learn has focused on specific sensory stimuli (Rainer et al. 2004; Yang and Maunsell 2004; Antzoulatos and Miller 2011), motor movements (Grafton et al. 2002; Houweling et al. 2008; Bassett et al. 2015; Musall et al. 2019), and rewards (Shuler and Bear 2006; Serences 2008; Summerfield and Koechlin 2010; Baeuchl et al. 2020). These studies found that each area of learning is subserved by

domain-specific brain areas, making it seem like all learning—including for entirely new tasks—depends on domain-specific regions.

A growing literature has examined the neural correlates of task learning (for reviews, see Cole et al. 2013, 2017 and Meiran et al. 2017). Thus far, this literature has focused on studying different task instances that rely on the same underlying processes. In some studies, each new task involves a different type of stimulus-response mapping (Cohen-Kdoshay and Meiran 2009; Ruge and Wolfensteller 2010; Dumontheil et al. 2011; Hartstra et al. 2011; Meiran et al. 2015a, 2015b; Muhle-Karbe et al. 2017). In other studies, subjects first learn several elementary rules and then perform a variety of tasks where the elementary rules are combined in novel ways (Cocuzza et al. 2020; Cole et al. 2010; Cole et al. 2013b; Stocco et al. 2012). For example, in the classic study by Cole et al. (2010), the tasks that subjects completed differed in the specific instructions but engaged the same underlying cognitive functions (e.g. 2 different tasks may be “If the answer to ‘Is it LOUD?’ is true for the SECOND of two words, press your RIGHT MIDDLE finger” vs. “If the answer to ‘Is it GREEN?’ is the SAME for both words, press your LEFT INDEX finger”). This line of research has identified different frontoparietal areas as critical for implementing a new task instruction. However, the fact that these tasks activate the same brain areas cannot be used to adjudicate whether task learning is domain-general vs. domain-specific. In fact, the differences between the various tasks in prior research are similar to the differences between the 3 variants within each task in the current study.

The current study investigated learning for tasks that are known to rely on different underlying processes. Our 6 tasks required the involvement of perceptual, motor, or various cognitive (attention, expectation, SAT, and metacognition) processes that each depend on different brain areas (Corbetta and Shulman 2002; Forstmann et al. 2008; Grill-Spector and Malach 2004; Heeger 1999; Laut Ebbesen and Brecht 2017; Rahnev et al. 2012, 2016; Rahnev et al. 2011a; Shekhar and Rahnev 2018; Spieser et al. 2017; Svoboda and Li 2018; Yeon et al. 2020). Yet, we found that learning on each of these tasks depends on the same set of regions. It may be argued that our results were driven by the fact that the perceptual and the 4 cognitive tasks were not that different from each other because they all used the same

stimulus. This view would predict that the neural correlates of task learning for those 5 tasks should be relatively similar but the neural correlates of learning the motor task should differ substantially from the rest. However, this is not what we found. In fact, as demonstrated in Fig 5, out of the 6 tasks, the neural correlates of motor task learning were the most similar to the average across all tasks. Therefore, our results are not driven by the similarity in stimulus or task structure in the first 5 tasks. Thus, by providing strong evidence for domain-general substrates among these 6 tasks, our results suggest that learning novel task structures is subserved by a domain-general frontoparietal network consisting of bilateral IFG and bilateral IPS. Future research should expand the current set of tasks to additional domains such as language, theory of mind, working memory, etc. Based on the current results, we would predict that such tasks, when learned inside the scanner, would produce greater activations in the same 5 ROIs during the initial stages of learning.

One open question is what exactly happens in the brain when people learn a new task. We speculate that there are 2 main components of task learning. The first component is the explicit encoding of the task instructions. In the current study, this process likely occurred during the instruction period and the current study was not designed to investigate it. The second component is the fine-tuning of the neural pathways as to be able to perform a new task in the most efficient way possible. What is learned over time by the brain is how to optimize the transformation of the specific input into appropriate output based on the task rules. It is likely that this transformation starts off slow and inefficient, but over the course of several trials, the brain optimizes the relevant pathways for efficiency, accuracy, and speed. For example, a previous study showed several neural effects of practice in a working memory task, with some changes not being captured by behavioral metrics like accuracy or RT (Landau et al. 2004). Our findings suggest that while what is actually learned is specific to the task, a domain-general network becomes active to make such task learning possible.

The frontoparietal areas identified here have partial overlap with several intrinsic brain networks that have been identified with resting fMRI data (Menon and D'Esposito 2021), including the frontoparietal, ventral attention, and dorsal attention networks (Power and Petersen 2013; Vossel et al. 2014; Chand et al. 2017; Ptak et al. 2017). These networks are generally important for goal-oriented, cognitively demanding tasks, as well as for both maintaining and manipulating information (Naghavi and Nyberg 2005; Asplund et al. 2010; Dixon et al. 2018; Causse et al. 2022). Similarly, the areas identified here also have some overlap with the nodes of a network labeled "the multiple demand network" associated with the execution of diverse cognitive operations, which include IPS, inferior frontal sulcus (IFS), pre-SMA, anterior cingulate cortex (ACC), anterior insula, and rostral prefrontal cortex (PFC) (Duncan 2010). Note that the activations here did not include many of the nodes of the multiple demand network (e.g. pre-SMA, ACC, insula, and rostral PFC), that our frontal site (IFG) was posterior and superior to the IFS cluster in Duncan (2010), and that we found a cerebellar activation not present in the multiple demand network in Duncan (2010). Thus, despite the partial overlap with previously identified networks, the task-learning regions we uncovered do not map onto a single known network. Future work should determine if the task-learning network reflects a reconfiguration of known intrinsic networks or constitutes a unique task network.

The current study has several limitations. While our results constitute a critical step in establishing the domain generality of task learning, they reveal little about the functions of the specific

brain areas identified here (bilateral IFG, bilateral IPS, and left cerebellum). For example, we found that the left cerebellum has weak connectivity to the remaining 4 frontoparietal areas, and is thus likely to have a different function than the remaining regions. It is possible that the cerebellum is involved in learning how to transform internal variables into motor commands, but it is also possible that it engages in other high-level cognitive functions that are not specifically motor-related (Strick et al. 2009; Buckner 2013). Similarly, both the bilateral parietal and frontal areas identified here have been associated with a large array of high-level functions from attention, to working memory, to cognitive control (Corbetta and Shulman 2002; Power and Petersen 2013; Vossel et al. 2014; Ptak et al. 2017), and therefore it is difficult at this point to isolate the cognitive processes that these areas are likely to subservise in the context of task learning. Follow-up studies should therefore specifically focus on determining the precise function that each area is performing. In addition, as already mentioned, although our 6 tasks rely on different domain-specific brain regions, they do not capture the wide variety of tasks that exist in the literature. We chose our design to gain maximum power for each task while keeping the testing session under 2 h. However, future work is needed to test whether our results generalize to the wide array of tasks used in cognitive neuroscience.

## Authors' contributions

Jiwon Yeon (Data curation, Formal analysis, Investigation, Software, Visualization, Writing – original draft, Writing – review & editing), Alina Sue Larson (Data curation, Writing – review & editing), Dobromir Rahnev (Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing), and Mark D'Esposito (Conceptualization, Writing – review & editing)

## Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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