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The Neural Correlates of Within-Session Practice Effect During Executive Function Task

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Abstract

The Neural Correlates of Within-Session Practice Effect During Executive Function Task

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There is a growing interest that practice effect may role as a behavioral marker of learning potential and flexible adaptability. However, the relationship between performance change during a brief task (i.e., within-session practice effect) and other cognitive abilities is still unclear. Assuming behavioral flexibility is associated with flexible components of executive function, it was hypothesized that there would be common neural correlates between within-session practice effect and flexible components of executive function. Based on previous reports that frontoparietal network engages in flexible control process, we investigated the association between the brain marker of within-session practice effect and frontoparietal network using task fMRI.

In this study, task performance and brain changes between early and late phase of multi-source interference task were tracked with task fMRI. We first tested the significance of brain changes by paired t-test. To test specificity of their association with frontoparietal network, spatial decoding was done for activation results and eight different large-scale networks were compared for connectivity results. To define brain markers of within-session practice effect, correlation analyses examined predictive power of such brain markers on the amount of within-session practice effect. Lastly, correlation between obtained brain markers and neuropsychological measures of flexible executive function was tested to decide whether the role of brain marker can be generalized to other task settings.

As a result, brain regions and functional connectivities which significantly predicted practice effect were primarily associated with frontoparietal network. Specifically, activation decline in bilateral superior parietal lobule, left superior and inferior frontal gyrus and decline in frontoparietal network intra-network connectivity and frontoparietal-cerebellum inter-network connectivity significantly predicted greater practice-related gain. Spatial decoding advocated the dominant engagement of frontoparietal network in the short-term learning process. Lastly, the brain markers of practice effect were consistently correlated with digit span backward score. These suggest that frontoparietal network serves as the common neural correlates between practice effect and flexible executive function.

Keywords : practice effect, executive function, working memory, frontoparietal network, task fMRI, functional connectivity

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Introduction

Over the past decades, numerous cognitive intervention programs have been designed to enhance cognitive ability. One of such endeavor is to train executive function among adolescents given their rapid development in frontal lobe and the centrality of executive function in adaptive functioning in life (Jolles & Crone, 2012; Karbach & Unger, 2014; Kim-Spoon et al., 2017; Luna, 2009). Process-based training paradigm widely used in those studies is based on the premise that repeated performance (i.e., practice) of demanding executive function tasks can lead to plastic change in executive function and its neural correlates.

However, there still remain some points to be explicated in training studies. First, it could be questioned which brain regions are specifically crucial in drawing changes in behavioral performance. Although previous studies have thoroughly investigated the reorganization process of brain circuitries after practice (Kelly, Foxe, & Garavan, 2006), there was less focus on the relationship of certain region and the magnitude of performance change. Moreover, another important issue in training studies is to reveal cognitive and brain characteristics of people who get more benefits from equivalent practice (Jolles & Crone, 2012; Karbach & Unger, 2014). Answering such question will not only reveal how one's capacity to change is differently shaped by brain characteristics, but also help design efficient training programs for each individual.

Unfortunately, despite the breadth of cognitive training studies, it is still insufficient to make better understanding on what happens in our mind and brain during those tasks and how difference in brain supports the individually different magnitude of shift in cognitive states. The aim of this study is to partly answer those questions by exploring short-term neural and behavioral changes during an executive function task. Some of the findings might contribute to our understanding of both the potential benefits of practicing executive function tasks and the secrets behind the individual difference in practice-related gain.

1. Practice effect

A hallmark of human cognition is flexible adaptation of behavior in a novel environment. In response to changing demands, we can rapidly and flexibly adjust our thoughts and behavior to achieve goal. One of the behavioral manifestations of adaptive process can be found from ‘practice effect’ (Koziol & Budding, 2009). It refers to improved task performance as a result of repetitive practices (Goldberg, Harvey, Wesnes, Snyder, & Schneider, 2015). For example, in repetitive speeded choice task, practice effect can be depicted by decreased reaction time and increased accuracy as a function of time.

Developing the knowledge on practice effect can be useful and crucial in clinical studies. Especially, studies designed to evaluate training effect on cognition inevitably confront practice effect on task performance. For example, neuropsychologists have to judge whether or not the performance change after practice is a significant indicator of cognitive enhancement. Traditionally, practice effect due to repetitive trials was regarded as a source of error that inflates cognitive test score in serial assessments (Calamia, Markon, & Tranel, 2012; Goldberg et al., 2015). However, this conventional perspective is recently being challenged. Some researchers suggested that practice effect carries clinical information beyond test score itself (Duff, Callister, Dennett, & Tometich, 2012). Duff and his colleagues (2012) found that smaller than expected practice effect was associated with a declining trajectory in cognition (Duff et al., 2011) and greater risk of Alzheimer’s disease (AD) pathology such as amyloid deposition and brain hypometabolism (Duff, Hammers, Dalley, Suhrie, Atkinson, Rasmussen, & Hoffman, 2017; Duff, Horn, Foster, & Hoffman, 2015) among people with mild cognitive impairment (MCI).

Another line of results provokes the idea that practice effect can be the behavioral index of learning potential and flexibility. Given the adverse effect of age-associated brain changes on memory function, people with more progressed aging were expected to show less practice effect than other with intact cognitive function. Indeed, Duff and colleagues (2010; 2015) demonstrated that practice effect informs spared learning abilities among the normal elderly. Magnitude of short-term practice effect predicted better response to long-term cognitive training after 5 weeks (Duff, Beglinger, Moser, Schultz, & Paulsen, 2010). Also, short-term responsiveness within 150 trials of motor task predicted long-term retention of skill after 1 month (Schaefer & Duff, 2015). Similar results were also found in schizophrenia patients (Watzke, Brieger, Kuss, Schoettke, & Wiedl, 2008), suggesting that practice effect reflects the individual difference of flexible adaptability over heterogeneous population.

Nevertheless, the explanatory power of practice effect in more generalized population have been less studied. Although some attempted to confirm whether short-term practice effect predicts future learning outcome among normal young adults (Bassett et al., 2011), they mainly focused on practice effect on brain, rather than task performance. However, capturing individual difference in responsiveness to certain experience can be crucial in researching not only cognitive aging but also cognitive development of younger population.

1.1 Cognitive accounts on practice effect

There are several accounts on how behavioral improvements during practice emerge through cognitive process. This, in turn, can reach to the question which cognitive process mostly accounts for the variance of practice effect. Some researchers suggested that practice effect primarily reflects adaptive process based on learning and memory system, especially procedural memory (Koziol & Budding, 2009). Some explained that practice creates memory traces to readily direct attention to appropriate stimulus (Kelley & Yantis, 2009; Logan, 1988; Shiffrin & Schneider, 1977). Others speculated that practice primarily affects response selection stage (Pashler & Baylis, 1991; Welford, 1976).

Still, practice effect can represent other types of cognitive process. Some may argue that sustained attention harnesses continuously improved performance during task. Considering the proposal that stable attention actually leads and supports the flexible switching ability (Benitez, Vales, Hanania, & Smith, 2017), the behavioral flexibility measured by practice effect can reflect the ability to sustain attentional focus.

Alternatively, a line of studies suggested that flexible control process primarily involves in the acquisition of asymptotic level of performance during practice (Kelly & Garavan, 2005; Petersen, van Mier, Fiez, & Raichle, 1998). Flexible control process is assumed to underlie cognitive abilities that endows dynamic modulation of behavior, such as updating and shifting (Miyake et al., 2000). Indeed, it was found that flexible control process is actively recruited to cope with a novel task especially at the early phase of practice (Chein & Schneider, 2005; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). This implies that adaptive modulation of information and response is led by flexible control process.

Several neuroimaging studies offered empirical evidence of cognitive mechanisms that may underlie practice effect (Chein & Schneider, 2005; Kelly & Garavan, 2005; Poldrack, 2000). First, the accounts that emphasizes procedural memory were previously noted by motor skill learning studies (Kantak & Winstein, 2012; Karni et al., 1998; Ungerleider, Doyon, & Karni, 2002). For example, an fMRI study showed that both strengthening of stimulus-response mapping and item repetition priming are correlated with striatofrontal neural networks in neural level and that modulation in these networks explains performance change during mirror-reading task (Poldrack & Gabrieli, 2001).

On the other hand, findings on the continuous engagement of cinguloopercular network during task epochs advocate the importance of sustained attention in guiding more practice-related performance gain. In a variant of Go/NoGo task and cued global/local attention task, the augmentation of medial frontal regions such as dorsal anterior cingulate cortex were simultaneously detected with overall performance gain (Kelly, Hester, Foxe, Shpaner, & Garavan, 2006; Weissman, Woldorff, Hazlett,

& Mangun, 2002). When conceding that these regions are associated with stable top-down control (Dosenbach et al., 2007) and tonic alertness (Sadaghiani & Esposito, 2015), stable control process can be the key to generate larger practice effect.

Furthermore, a number of neuroimaging studies showed the relevance between flexible control process and practice effect. Representatively, Petersen and colleagues (1998) compared brain activation patterns during a novel and those during highly practiced verbal and motor task with PET. As a result, brain activation changes were characterized by reorganization, especially among specific regions related to flexible control process. Similarly, other studies using higher cognition tasks also showed consistent results that practice modulates brain activities in frontal and parietal regions (Kelly et al., 2006; Landau, Schumacher, Garavan, Druzgal, & D'Esposito, 2004; Weissman, Woldorff, Hazlett, & Mangun, 2002).

Although each account on practice effect provides valuable insights in certain circumstances, they still harbor some limitations. First, procedural learning can be critical during a limited type of task which requires simple motor response. It is uncertain that practice-related gain during task which demands higher cognitive load but lower motor control is chiefly guided by procedural learning. For example, practice effect in N-back task, is less likely to benefit from procedural learning since response rule itself is simple. Also, both sustained attention-related brain areas and flexible control-related brain areas were found to involve during task in the same studies (Kelly, Hester, Foxe, Shpaner, & Garavan, 2006; Weissman, Woldorff, Hazlett, & Mangun, 2002). They only exhibited different temporal dynamics, making us hard to determine which brain change contributes more in inducing practice effect. Further, we cannot easily decide which brain change should be beneficial or deleterious for practice effect without testing the direction or magnitude of brain-behavior relationship. Therefore, future studies can include methodological considerations to complement limitations: the consideration of task domain, the comparison between multiple brain areas, the testing of brain-behavior relationship

Despite countless endeavor so far, practice effect still attracts many researchers due to the difficulty in making conclusive remarks on its mechanism. Kelly and colleagues (2006) asserted that we still need more careful explanation that bridges behavioral, cognitive, and neural levels of analysis, at the same time, to offer more comprehensive view. How practice induces behavioral flexibility, and whether we can measure such flexible cognitive characteristic by practice effect should be further examined.

As final note, an important factor in studying practice effect is the timescale used to measure it. While most studies followed between-session design, some studies used within-session practice effect (Duff, Chelune, & Dennett, 2012; Hauptmann, Reinhart, Brandt, & Karni, 2005; Schaefer & Duff, 2017). Between-session practice effect is typically measured between different time points in longitudinal cognitive assessments. On the contrary, within-session practice effect is measured within a session of brief tasks. Practice effect may have a different predictive power over cognitive function depending on timescale. Within long timescales (e.g., weeks and months), it can reflect the consolidation of long-term memory (Hauptmann et al., 2005). In contrast, within short timescales (e.g., minutes), the amount of practice effect might be better associated with short-term memory or control process.

2. Executive function and practice effect

Practice effect is a prevalent phenomenon observed in a wide variety of tasks, from complex tasks requiring effortful control to simple motor learning tasks. In this sense, its relationship with higher cognition such as executive function has been rarely explored. However, considering the central role of executive function in learning, one of the most primitive form of learning, practice effect, can be highly associated with executive function. Previous studies supported this notion.

2.1 Executive function

Executive function (EF) is a multi-faceted construct that supports goal-directed behavior, encompassing a number of basic cognitive processes: maintenance of internal representation of goal, updating of it with changing contexts, selective attendance to goal-relevant information, and inhibition of prepotent responses (Diamond, 2013; Miller & Cohen, 2001). Although their characteristics are heterogeneous, their contribution in behavioral adaptation was consistently implicated in the literature (Koechlin, 2016; Miller & Cohen, 2001).

Inhibition, updating, and shifting are viewed as three core components of EF (Miyake et al., 2000; Miyake & Friedman, 2012). Inhibition is the ability to override prepotent response in the face of interference. For example, in Stroop task (Stroop, 1935) subjects have to put attention toward the ink color away from the prepotent inclination to read the word. Because naming an ink color of incongruent color words (e.g., word 'blue' colored in green) delays response than naming a word, the difference in reaction time reflects the attentional resources additionally recruited to resolve interference.

Compared to inhibition that stably maintains attentional focus on the goal, other two components, updating and shifting, are presumed to be associated with behavioral flexibility. Updating is the ability to update and monitor goal-related information, which fundamentally stems from working memory (Gratton, Cooper, Fabiani, Carter, & Karayanidis, 2018; Miyake & Friedman, 2012). It serves to mentally relate, integrate and recombine information across different time scales. That is, updating mentally connects the outcome of the past with the future outcome to lead to goal-directed decision making. Hence, updating is critical and necessary for all types of thinking that prospectively transforms mental representation based on earlier experience.

Also, shifting is another major source for behavioral flexibility. It refers to the ability to shift between tasks, goals, or mental sets. Set, here is defined as the property of stimulus that is relevant in a given trial (Ravizza & Carter, 2008). For instance, in Wisconsin Card Sorting Task (WCST) (Grant & Berg, 1948) the correct sorting rule among color, shape, and number is defined as set. Shifting helps intentional disengaging from previous task set or overlearned stimulus-response association to meet the needs of new goal. In WCST, people with good shifting ability quickly learn when to apply different sorting rule based on the feedback.

A leading notion on the latent structure of EF highlights heterogeneity between different components of EF. Recent factor analyses demonstrated that inhibition, updating, and shifting are indeed separable (Friedman, Miyake, Robinson, & Hewitt, 2011). Whereas the variance in inhibition tasks was entirely accounted for by commonality among EF tasks, updating and shifting additionally captured unique variance. That is, performance in updating task such as n-back task uniquely requires updating ability, but simultaneously recruits inhibition as well. From these results, researchers suggested that common EF factor which perfectly overlaps with inhibition underlies sustaining task-set in a stable manner, while updating and shifting underlies efficient gating and clearing of representations in a flexible manner (Miyake & Friedman, 2012). In this aspect, EF factors can be separated into stable EF (i.e., inhibition) and flexible EF (i.e., updating, shifting).

Neuroimaging studies found the physiological origin of executive function from distinct top-down control signals processed by brain (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, 2013; Dosenbach et al., 2008). The neural models of executive function also agree with the distinction between stable and flexible control process. According to a dual networks model, frontoparietal network and cinguloopercular network process distinct top-down signals (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Dosenbach et al., 2006). Frontoparietal network processes transient signal that significantly appears in the beginning of task block and operates in trial-by-trial manner. This indicates that frontoparietal network is a basis of flexible control process and guides the mechanism of updating and shifting. In comparison, cinguloopercular network processes sustained signal during overall task epochs. In this regard, cinguloopercular network can be thought as a basis of stable control process maintaining goal-representation in background (Dosenbach et al., 2008).

2.2 Executive function and learning

Components of executive function (EF), especially updating and shifting can be speculated to help flexible changes in mental representation and response. Accordingly, their putative role in learning were discussed by previous studies.

Previous findings demonstrated that individual differences in flexible components of EF predicts learning outcomes in real life. For example, working memory capacity was a central predictor of life outcomes including academic attainments after 5 years of follow-up among children (Alloway & Alloway, 2010) and math achievements among preschoolers and children (Bull, Espy, & Wiebe, 2008). Since working memory capacity guides successful operation of updating, it can be concluded that flexible EF provides a basis of learning. Compared to updating, the role of shifting has rarely been discussed in terms of learning. Nevertheless, perseveration or repeating the same response over and over even when it becomes inappropriate is one of the key symptoms of frontal lesions (Luria, 1980; McDonald, Delis, Norman, Tecoma, & Iragui-Madoz, 2005; Stuss & Benson, 1984) and other psychological disorders (Pantelis et al., 1999). Since these neurological conditions feature deficits in learning and adaptability as well, the role of shifting in learning can be inferred.

A number of brain studies also support the role of flexible control process in brief task learning. Several studies found that most prominent brain change during task practice is upregulated activation in working memory-associated areas (Chein & Schneider, 2005; Kelly et al., 2006; Landau et al., 2004; van Raalten, Ramsey, Duyn, & Jansma, 2008; Weissman et al., 2002). According to Petersen's 'scaffolding-storage' framework (1998), a set of brain regions provides 'scaffold' to guide early phase of learning, sending signal to task-specific regions where task-specific sensorimotor mapping are stored (Petersen, van Mier, Fiez, & Raichle, 1998). Scaffolding regions included prefrontal cortex, anterior cingulate cortex, and posterior parietal cortex, which are significantly associated with working memory (van Raalten et al., 2008). And their activation decreased after the process becomes automatized when additional control becomes needless.

Consistently, recent functional network studies provided more detailed view on the role of executive function-related networks during task practice. For example, Cole and colleagues (2013) found that dynamic reconfiguration of frontoparietal network is a neural basis of flexible adaptation. However, Mohr and colleagues (2016) provided different results. They found that functional brain correlates of practice-related gain during motor learning is increased connectivity between cinguloopercular network and dorsal attention network (Mohr et al., 2016).

Overall, previous results suggest the engagement of executive control process during learning process, being the basis of practice effect observed during short time scales. Majority of studies viewed that flexible control, which presumably supports updating and shifting ability, draws behavioral adaptation during practice and learning. Still, there are inconsistent proposals on the neural basis of practice effect from different regions of brain, or networks.

3. Objective and Hypotheses

Practice effect can be studied in its relationship with flexible components of executive function (EF) especially in short timescales. Specifically, the practice effect within a brief task is defined as ‘within-session practice effect.’ Assuming the role of flexible EF in learning, it can be hypothesized that the amount of within-session practice effect will reflect the individual difference in flexible EF. Previous studies offered that frontoparietal network regions decline in activity during task practice. It leads to the proposal that the activity change in this network underlies practice effect on task performance.

However, previous studies had several limitations. Many studies did not explicate how these activation changes support more efficient reorganization, raising the need for further sophistication of mechanism (Kelly & Garavan, 2005; Landau et al., 2004; Weissman et al., 2002). In this sense, functional connectivity can supplement the previous results. Also, previous studies did not check the association between brain changes and performance changes by correlation or regression analysis. However, the directionality or strength of brain-behavior relationship, if they are conjointly used to predict practice effect, can increase predictive power. Lastly, few studies examined practice effect during executive function task, compared to motor skill task. But, as Kelly and Garavan (2005) stated, the underlying mechanism of practice effect can be different depending on task domain. Therefore, more evidence from executive function task will broaden our knowledge.

In this regard, the aim of this study was to investigate the neural correlates of within-session practice effect by observing brain activation and functional connectivity changes during executive function task. Ultimately, it was expected to answer the question whether practice-related gain predicts cognitive abilities regarding flexible executive function.

In doing so, we first measured performance change and brain changes during practice by comparing activation and functional connectivity between early and late phase of executive function task. Paired t-test examined the significance of change. We further tested whether the significant activation changes were found in flexible executive function-related brain regions, frontoparietal network. In case of activation result, spatial decoding was conducted to complement interpretation.

Next, the relationship between brain change and performance change was tested to define the brain marker of practice effect. Correlation analysis found the activation change and connectivity change which significantly predicted practice-related gain in performance. Again, the association with frontoparietal network of the brain marker was evaluated.

Finally, we tested whether the index from brain marker of practice effect and neuropsychological measures of EF are correlated. It was expected that the neural correlates of practice effect could predict the neuropsychological measures, if they reliably reflect flexible control process.

Hypotheses of this study were as follows: 1) change in activation and functional connectivity can be found within frontoparietal network, 2) the amount of practice-related change is correlated with brain changes within frontoparietal network, 3) the associated brain changes are also correlated with neuropsychological measures of updating and shifting.

Methods

1. Participants

Seventy-one healthy adolescents aged 12-14 (average =13.16 years old, male n=39, female n=32) were recruited by online advertisements from urban communities of South Korea for cognitive training research. Semi-structured interview of legal parents revealed that some participants had a history of psychiatric or developmental disorders and were excluded (n=4). Also, subjects who did not fully engaged or dropped out were excluded (n=8). Finally, due to technical problems during MRI scan (n=2), a total of fifty-seven participants (mean age = 13.21 years old) were finalized as the dataset (male: n=30, female: n=27). All participants were right-handed according to Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. Informed consent was obtained from both subjects and their parents in accordance with procedures approved by the Institutional Review Board of Seoul National University.

2. Materials

2.1 Experimental task

A modified version of Multi-Source Interference Task (Bush, Shin, Holmes, Rosen, & Vogt, 2003) was used as executive function task during functional magnetic resonance imaging (fMRI). It involved inhibitory control like stroop, simon, and flanker task with less demand in working memory. Therefore, it was expected that practice-related gain during this task could maximally extract individual difference in behavioral flexibility. According to previous studies, this task reliably activates the pattern of fronto-cingulo-parietal network (Bush & Shin, 2006), and captures with high sensitivity individual differences of brain and cognitive function (Bush et al., 2008; Cocchi et al., 2012; Liu, Angstadt, Taylor, & Fitzgerald, 2016; Zamorano et al., 2017).

The task had two conditions, ‘congruent’ and ‘incongruent.’ While congruent condition simply recruited motor control in the absence of interfering component, incongruent condition required inhibition due to presence of conflicting stimuli. The stimulus presentation and correct response is illustrated in Figure 1. Inside MRI scanner, subjects were presented with three numbers among 1, 2, 3 through monitor and asked to respond via button box. Two of stimuli were always same, while one different number was defined as target. Each button was designated to each answer (i.e., 1, 2 and 3) and to each finger (i.e., index, middle and ring finger of right hand). Subjects were asked to respond to this target as fast and accurate as possible.

Incongruent trial included two types of incompatibility which led to delayed response. The item incompatibility between the answer and other neighboring stimuli caused interference in selective attention (*flanker effect*), while the spatial incompatibility between answer and response button caused interference in response (*simon effect*). Instead, congruent trial displayed two Xs and the other number which was the answer of each trial and simultaneously spatially matched to response button.

Each subject performed two runs of block-designed MSIT. Each run lasted for 398.4 sec (around 6 minutes) including 7.2 seconds of fixation in the beginning and the end. 12 trials of condition block alternately repeated eight times (i.e., C-I-C-I-C-I-….) without counterbalance. Each trial lasted for 1750 msec and was self-paced so that the screen jumps to fixation cross along with response. Fixation continued until 250 msec of intertrial interval ended. In total, running two runs resulted in 384 trials. Stimulus presentation and the recording of response data were executed using Matlab R2015b. (The Mathworks, Natick, MA). Before the main experiment, participants were provided with full instructions on task rules and a brief practice session which included 12 incongruent and congruent trials.

For data analysis, only 192 trials were included in the final dataset in order to examine different neural responses between early and late phase (Figure 2). Therefore, 96 trials (48 trials for each condition) in the beginning of the first run and the counterpart at the end of second run were concatenated as 'Early' and 'Late' trials. Similar concatenation of task trials were attempted by previous studies investigating practice effect or short-term adaptation (Landau et al., 2004; Mohr et al., 2016).

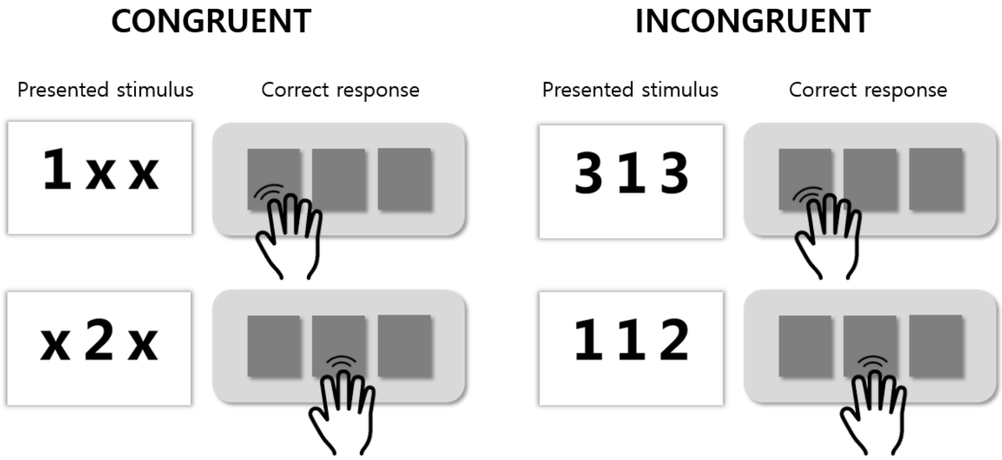

Figure 1. Schematic representation of the Multi-Source Interference Task

Example stimulus (left) and correct response of its trial types (right).

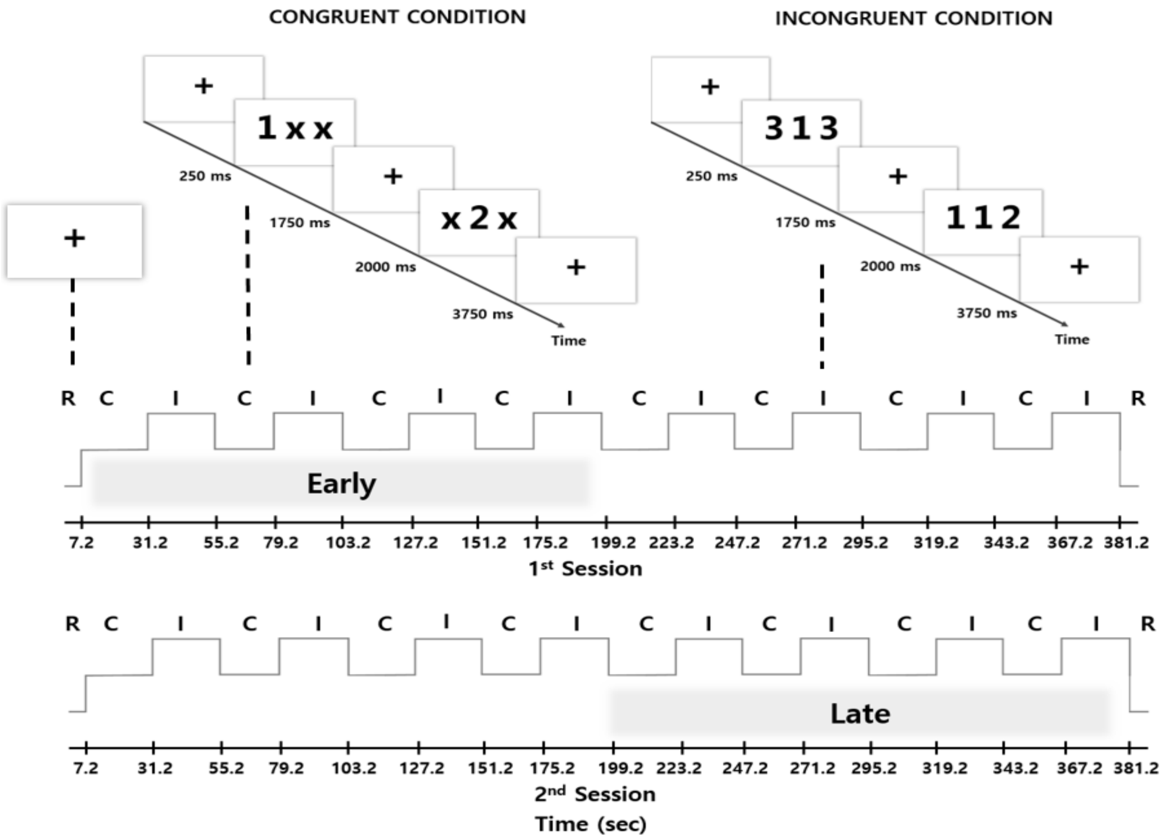

Figure 2. Experimental design and time course of trial presentation.

Rest (R), Congruent (C), Incongruent (I) conditions in block-designed. ‘Early’ and ‘Late’ phases (grey bar) were analyzed.

2.2 Neuropsychological tests

Neuropsychological tests were conducted to assess different components of executive function: updating, shifting, and inhibition.

Updating. Subsets of Digit span task in K-WAIS-IV (Hwang, Kim, Park, Chey, & Hong, 2012) assessed working memory (updating). In digit span backward (DSB), subjects had to recall the numerical items in backward. In digit span sequence (DSS), the rule was to reorder and recall items in numerical order. Both tasks required short-term storage and manipulation of mental representation. Digit span forward (DSF) in the same battery was also used to measure working memory retention.

Shifting. Task-set shifting was assessed by Trail making test (TMT) interference score in CERAD-K (Lee et al., 2002). In TMT A, subjects had to connect 25 number circles in numerical order (i.e., ①-②-③-④-⑤-…) as fast as they could. Instead, in TMT B they had to connect 13 number circles and 12 letter circles alternately in sequential order (i.e., ①-㉠-②-㉡-③-㉢-...). The interference index, calculated by the difference of reaction time between A and B condition, measured shifting. As the index reflected the additional cognitive load required for set-shifting, smaller index indicated better shifting ability.

Inhibition. Inhibition was assessed by Children's version of color-word stroop test (Shin & Park, 2006). In color reading condition XXX colored by red, yellow, blue and green color were presented. In word reading condition, words ('RED', 'YELLOW', 'BLUE', 'GREEN' colored in black) were presented. Color-word reading condition showed incongruent words (e.g., BLUE in green color). Subjects had to read the words as many as he could according to naming rule. In color-word reading condition, subject had to name the color of incongruent word. The interference index was calculated by the difference of the number of words read in color-word and word condition. Bigger index indicated the worse inhibition of prepotent tendency to read the word.

2.3 Functional magnetic resonance imaging

Functional magnetic resonance imaging is in vivo imaging technique that detects functional activation over brain regions, indicated by blood-oxygen-level dependent (BOLD) signal. Task fMRI not only provides maps of how a particular cognitive function is represented within the brain but also evaluates relative strengths of functional relationship among different brain regions and large-scale networks through coactivation patterns (Huettel, Song, & McCarthy, 2004).

Data acquisition. All imaging data were collected on 3-T Siemens MAGNETOM Trio MRI scanner in Seoul National University Neuroimaging Center. A foam pad within the head coil and noise-protection earplugs were provided to minimize head motion and noise of MRI scanner. Participants who required correction for vision were provided with fMRI compatible glasses for optimal task performance. Task functional images, structural images and resting-state functional images were acquired in order. Resting-state images were not included in the present study. The total scanning time was 26 minutes for each participant. Whole-brain functional images were acquired using following parameters: T_2^*-weighted echo planar imaging sequence with TR=2400 ms, TE=30 ms, FOV=240 x 240 mm, FA=79°, 3 x 3 in-plane resolution, 36 3-mm-thick oblique transversal slices with 1mm interslice gap in bottom-up interleaved order. Structural T1-MPRAGE images were acquired for coregistration and spatial normalization (TR=2300 ms, TE=2.36 ms, FOV=256 x 256 mm, FA=9°, voxel size 1 x 1 x 1mm^3). A total of 332 volumes (14 mins) were collected during the task (166 volumes per session) and 224 volumes (5 mins) for structural images.

3. Data analysis

3.1 Behavioral data analysis

MSIT Reaction time and accuracy. Reaction time (RT) and accuracy were calculated for both congruent and incongruent trial. Due to predicted ceiling-effect in accuracy and general interaction between RT-ACC (i.e., RT-accuracy tradeoff), we mainly analyzed response time of correct trials.

Interference index. Conventional subtraction method that contrasts experimental and control conditions is commonly used to measure additional load demanded for cognitive processing of interest. However, the interference effect measured by raw difference can be affected by baseline differences in RT (i.e., the speed required for simple motor control in congruent condition). Thus, adjusting baseline reaction time in interference scoring has been attempted in case of Stroop task (Scarpina & Tagini, 2017; Van Der Elst, Van Boxtel, Van Breukelen, & Jolles, 2006). Following these methods, we have calculated interference index as follows (1). Lower score implies better performance.

$$\text{Interference Index} = \frac{mean\ RT\ (incong) - mean\ RT\ (cong)}{mean\ RT\ (cong)} \quad (1)$$

Within-session practice effect ('Residual gain score'). Practice-related gain of each subject was obtained by regression method. A linear regression model which predicts later performance ("late phase") by earlier performance ("early phase") of all subjects was established. In that model, each residual term (ε), the difference between dependent variable (y) and predicted value (ŷ), was defined as residual gain score. Statistically, it referred to the variance of later phase performance which cannot be explained by baseline performance.

$$\text{Interference Index}_{\text{LATE}} = b \text{ x Interference Index}_{\text{EARLY}} + \varepsilon \qquad (2)$$

As lower interference index reflects faster, thus better, resolution of disturbing stimuli, the index should diminish if subjects acquire task proficiency over time. Therefore, negative value of residual gain score indicates practice-related gain, while positive value does practice-related loss. For ease of interpretation, the inverse of residual term was dubbed 'residual gain score' to quantify the amount of within-session practice effect.

$$\text{Residual gain score} = -\varepsilon \qquad (3)$$

Statistical analyses. Mean and standard deviation of behavioral indices were calculated for each phase. Significance of change between each phase was tested by paired t-test (significance level at p=0.5) in SPSS version 23.0 (SPSS, Chicago, IL).

3.2 Functional activation analysis

Preprocessing. Imaging preprocessing was performed using SPM12 software (Welcome Department of Imaging Neuroscience, Institute of Neurology, London, UK) for functional activation and functional connectivity analysis. All functional images were corrected for field inhomogeneity, realigned with six rigid body movement correction (three translation and three rotation parameters) and corrected for slice timing. After coregistrating EPI images to T1 images, the nonlinear deformation of T1 to Montreal Neurological Institute (MNI) space was used for spatial normalization of EPI images to the same standard space. The images were then smoothed with an 8mm full-width half maximum Gaussian kernel.

Estimation of activation change. Concatenated volumes (early and late phase) were included for model estimation of early phase and late phase, respectively. For each phase, functional activation was measured by beta estimates of general linear model(GLM) which predicts raw BOLD signal by a set of variables. This were done by following steps: (1) The fixed effect model tested the effect of task conditions and other realign parameters in subject level, resulting in contrast map of individual subject (Friston, Jezzard, & Turner, 1994). (2) The random effect model tested the effect of between subject variables in group level (Holmes & Friston, 1998).

In subject level, the task conditions of MSIT were contrasted (i.e., [Incongruent, Congruent]=[1,-1]) in order to discount brain activation irrelevant to executive function. Trial RT was parameterized to modulate hemodynamic response modeling, based on reports that the effect of RT on brain activity obscures conditional differences in brain activity (Carp, Kim, Taylor, Fitzgerald, & H.Weissman, 2010; Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2009).

In group level, we compared activation map at early phase and late phase by using paired t-test (FWE-corrected $p<0.05$ in cluster-level, $k>20$) to estimate temporal change of activation during the task. As covariates, interference index of each phase and demographic variables (sex, age) were included.

Peak MNI (Montreal Neurological Institute) coordinates of significant clusters were set as region of interests (ROIs) and mean beta estimates were extracted from 8mm spheres centering the peak voxel, from early and late phase main effect map, respectively. Activation change was defined as follows.

$$\text{Activation change} = B1 - B2$$

B1 : Beta estimate at early phase; B2 : Beta estimate at late phase

For supplementary, the main effect map from whole task session was acquired by general linear model. It was used for discussion of results. MarsBar ver 0.44 (Brett, Anton, Valabregue, & Poline, 2002) was used for extraction. Visualization of t score (SPM {t} map) and anatomical identification were performed with bspmview toolbox (http://www.bobspunt.com/software/ bspmview/) and MRIcron (https://www.nitrc.org/projects/mricron).

Spatial decoding. To address the functional interpretation of activation results, spatial decoding method provided by Neurosynth was applied (Gorgolewski et al., 2015; Rubin et al., 2017; Yarkoni, Poldrack, & Nichols, 2011). It calculated the spatial similarity between current activation map and meta-analysis based maps that are specifically related to brain or cognitive terms, such as ‘frontoparietal network’, ‘executive function’. The maps (reverse inference map) were created based on meta-analytic studies and depicted the likelihood that such term is mentioned in a study given the presence of the activation in a brain region (i.e., P(Term | Activation)). That likelihood is distinguishable from the likelihood that the same brain region is activated given the term is used in that study (i.e., P(Activation | Term)). They provide ‘which brain region is necessary for cognitive process.’ Thus, the comparison with this map was to test whether and the degree to which neural changes observed in this study was linked to certain brain or cognitive term.

Decoding process was entirely implemented in Neurosynth (Yarkoni et al., 2011) (http://neurosynth.org/) and NeuroVault (Gorgolewski et al., 2015) (https://neurovault.org/) platform. We uploaded the unthresholded SPM t map from paired t-test at NeuroVault repository and received the correlation coefficient, a quantitative measure of spatial resemblance of the input map and meta-analysis based maps. Such spatial correlation was represented by Pearson’s correlation r without p values.

3.3 Functional connectivity analysis

Preprocessing. In addition to identical preprocessing step used in functional activation, denoising was performed using Conn toolbox v.17f (http://www.nitrc.org/projects/conn). Band-pass temporal filtering (0.008-0.09) was applied to exclude irrelevant physiological noise signal. The Artifact Detection Tools (ART) was used to identify motion and signal intensity outlier images. Images with global mean intensity Z-value >5 and movement > 0.9mm were identified as outlier. Estimated motion parameters and outlier images were used as nuisance covariates in the time-series linear regression.

Network node identification. A set of nodes that represent whole brain networks were determined as ROIs. MNI coordinates were defined from CONN's Independent Component Analysis (ICA) of HCP(Human Connectome Project) dataset (n= 497) provided by CONN toolbox v.17f (Appendix I). These included the nodes of frontoparietal (4 ROIs), cignuloopercular (7 ROIs), dorsal attention (4 ROIs), default mode (4 ROIs), sensorimotor (2 ROIs), visual (4 ROIs), language (4 ROIs), and cerebellar (2 ROIs) network. The organization of functional networks were based on previous studies (Power et al., 2011; Yeo et al., 2011).

Generalized Psychophysiological Interaction (gPPI). gPPI analysis was applied to measure context-dependent functional connectivity. (McLaren, Ries, Xu, & Johnson, 2012). gPPI analysis reduces the chance that functional connectivity estimates were driven by simple coactivation without inter-regional communication between seed and target ROI (Cole et al., 2013). This method affords the opportunity to examine the interaction effect between seed ROI BOLD time-series and task condition when predicting target ROI time-series. The interaction factor was convolved with hemodynamic response function and linear interactions were modeled on the resulting BOLD-level signal. Both the generation of interaction term and statistical testing were conducted by Conn toolbox v.17f.

Estimates of connectivity change. Connectivity estimates (z-transformed correlation coefficient) of each phase were imported from whole-network ROI-to-ROI analysis. Change of connectivity strengths during task was calculated by the difference (i.e., [(Incong - Cong) late – (Incong – Cong) early], and obtained over 32 ROIs for each subject.

The estimates of all edges were summed to calculate network connectivity across networks. Since gPPI adjacency matrix (32 x 32 ROIs) is non-symmetrical, upper and lower diagonal values were both included in average calculation. For example, to calculate inter-network connectivity between sensorimotor (2 ROIs) and cerebellar network (2 ROIs), 4 edges (2 x 2 ROIs) were included in the calculation. In case of intra-network connectivity which refers to connectivity strengths between different nodes within a network, default mode network (4 ROIs) intra-network connectivity was computed by averaging 12 edges. The whole process resulted in 8 intra- and 28 inter- network connectivity values for each participant. Finally, one sample t-test ($p<0.05$) was done to test the significance of change in network connectivity.

For complement analysis in network level, post hoc ROI-to-ROI analysis tested the significance of connectivity change between nodes (FDR-corrected $p<0.05$ intensity-level). The statistical analyses were done with Matlab R2015b and SPSS ver 23.0.

3.4 Brain-behavior relationship analysis

Correlation between brain change and MSIT practice effect. For activation change estimates and connectivity change estimates, the relationship with MSIT residual gain score was analyzed by partial correlation ($p<0.05$). Due to multiple comparison problem, only activation change estimates which were found significant in above paired t-test were used in analysis. Those found significant were defined as the neural correlates of within-session practice effect.

Correlation between brain change and neuropsychological test. To test the predictive value of the neural correlates of practice effect, we compared the correlation with this neural correlates and neuropsychological measures. Total scores from Digit span forward, backward, sequence and interference indices from Trail making test and Stroop test were used. Since the effects of age, sex were already removed in previous steps, bivariate correlations ($p<.05$) were tested. All correlational analyses were done with SPSS ver 23.0.

Results

1. Practice effect on task performance

Replicating several studies using multi-source interference task (MSIT) (Bush & Shin, 2006; Dwyer et al., 2014; Weissman & Carp, 2013), mean reaction time (RT) was slower in incongruent (IC) than in congruent (C) trials (*t*(56)=34.04, *p*<.0001). Similarly, mean IC accuracy was lower than C accuracy trials (*t*(56)=9.472, *p*<.0001). Conditional difference on RT and accuracy (incongruent > congruent) was respectively 0.296 sec (SD=0.06) and –0.05% (SD=0.04) in raw scale. There was no correlation between age and interference index (*r*= –.235, *p*= .354). Also, after controlling for RT, there was no correlation of age with IC accuracy (*r*=.262, *p*=0.52).

Task performance significantly improved between early and late phase of task execution (Table 1). Although there were fluctuations during four successive phases, the comparison between early (1st phase) and late (4th phase) clearly demonstrated that there was significant decrease in MSIT interference index (*t*(56)=3.1, *p*<.001). Accuracy also improved, although the change was only significant in congruent condition when early and late phase were compared (*t*(56)=2.54, *p*<.001).

There was substantial individual difference in practice-related gain. Two thirds (n=38) of 57 subjects gained from practice (i.e., reduction in interference index) during the task. On the other hand, the remaining third (n=19) showed increase in interference index, implying practice-related gain was not consistent between individuals. The baseline performance at early explained only 25% of the performance at late in linear regression (Figure 3). Furthermore, there was no effect of sex and age on the amount of practice-related gain. In part, this supports that this behavioral index could explain individual differences in cognition that is not predicted by developmental factor or gender.

Table 1.

Average task performance and its change.

	Behavioral index				Change of behavioral index		
	Interference Index Mean (SD)	Accuracy (%)			Interference Index *t*(56)	Accuracy *t*(56)	
		Cong	Incong			Cong	Incong
1st phase (“EARLY”)	0.568 (0.157)	99.6	93.9	-	-	-	-
2nd phase	0.557 (0.153)	99.5	94.4	1vs.2	0.64	0.32	–0.70
3rd phase	0.568 (0.158)	99.3	95.8	1vs.3	0.02	0.88	**–3.62 ***
				2vs.3	–0.72	0.6	**–3.21 ***
4th phase (“LATE”)	0.505 (0.150)	98.4	94.4	1vs.4	**3.1 ***	**2.54 ***	–0.74
				2vs.4	**3.4 ***	**2.49 ***	–.01
				3vs.4	**4.4 ***	**2.75 ***	**2.4 ***

note. Paired t-test on whether each performance index changed compared to that of former phase. For example, 1vs.2 tests whether the index of 1st phase was higher than that of 2nd phase. *: $p<.001$

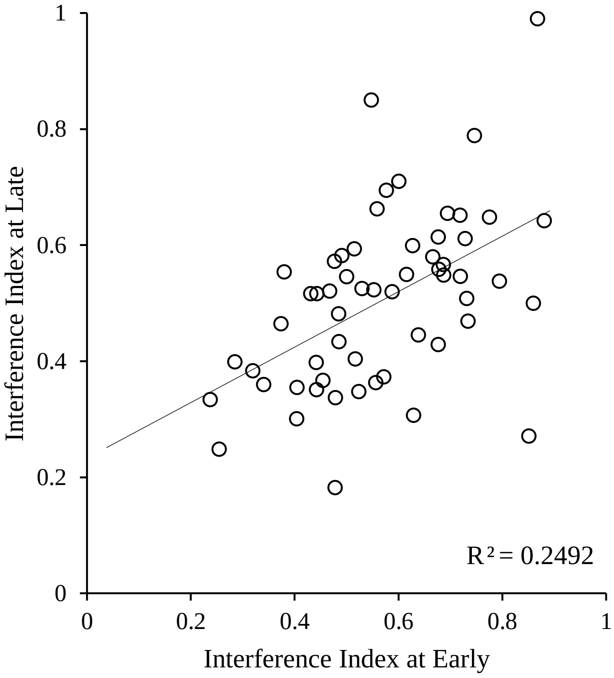

Figure 3. Scatterplot of early and late phase task performance

2. Practice effect on brain function

2.1 Activation change

The activation change between early and late phase were significant among various regions throughout frontal and parietal cortices (p_{FWE}<.01 at cluster-level and p<.001 uncorrected at peak-level, Table 2). As expected, activation primarily declined. For all regions reported significant, activation level diminished and no region showed significant increase of activation.

Notably, main loci of change were bilateral superior parietal lobule (SPL) and bilateral middle/superior frontal gyri (MFG, SFG) (Figure 4). Parietal cluster also included dorsal intraparietal sulcus (IPS) and lateral occipital cortex. Frontal clusters covered wide areas reaching posteriorly to premotor, frontal eye field and ventrally to subparts of inferior frontal gyri. These regions of frontal and parietal lobe corresponded to previous parcellations of task-positive network (Fox et al., 2005) and of frontoparietal network (Dosenbach et al., 2006; Power et al., 2011; Yeo et al., 2011). This was also evident when the task main-effect map was compared with activation change map (Figure 5).

Although it did not reach the threshold, there was a trend in activation increase among left anterior cingulate gyrus ($t(55)$=2.8762, k=100, p<.05 uncorrected), right inferior frontal gyrus ($t(55)$=2.387, k=105, p<.05 uncorrected), left frontal pole (t=2.385, k=68, p<.05 uncorrected).

Table 2.

Paired t-test on activation change (Early > Late)

Brain region	Cluster size (k)	MNI Coordinates (x, y, z)	*t*(55)
Frontal			
R superior frontal gyrus	624	24, 2, 48	4.72
R frontal eye field	624	24, -2, 60	4.67
L middle frontal gyrus	759	-24, -4, 46	4.68
L superior frontal gyrus	759	-22, -6, 54	4.43
L precentral gyrus	364	-52, 6, 48	4.47
L inferior frontal gyrus pars opercularis	364	-52, 16, 38	4.20
L inferior frontal gyrus pars triangularis	364	-36, 16, 28	4.06
Parietal			
L post-central gyrus	1372	-32, -38, 42	5.21
L lateral occipital cortex, superior	1372	-12, -60, 60	4.51
L superior parietal lobule	1372	-26, -44, 54	4.29
R post-central gyrus	1448	36, -32, 44	4.91
R superior parietal lobule	1448	34, -46, 66	4.86

note. Brain regions which survived at cluster threshold ($p_{\text{FWE}} < .01$) and height threshold ($p < .0001$, uncorrected) in whole-brain search. R: right; L: left.

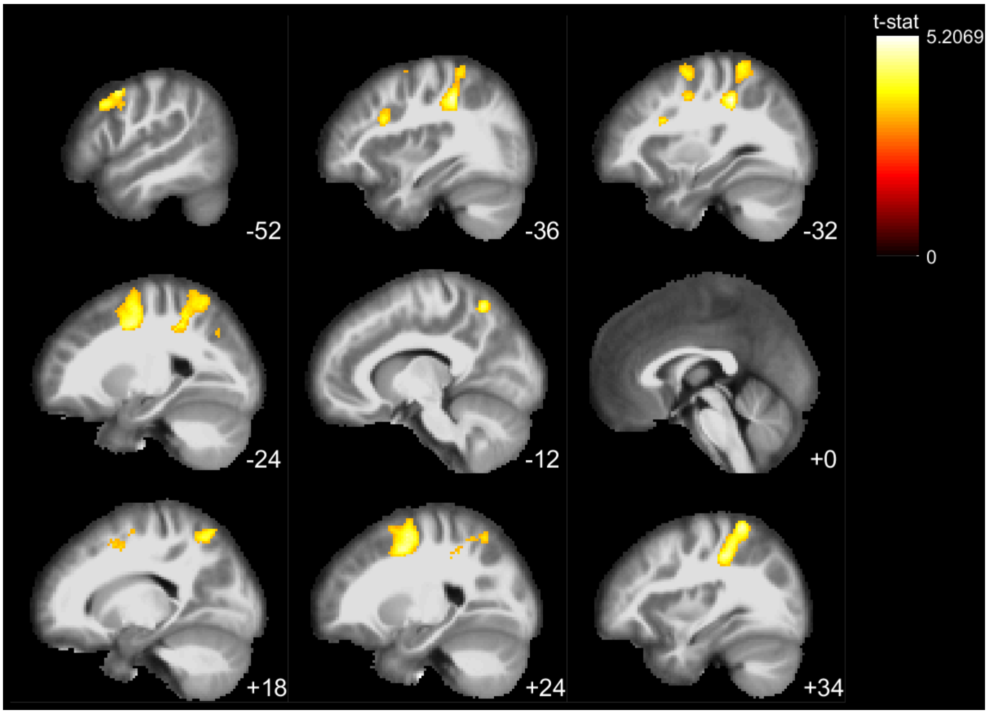

Figure 4. Clusters of which activation significantly reduced.

Colored regions superimposed on sagittal map depict significant regions (p_{FWE}<.01 with k>340).

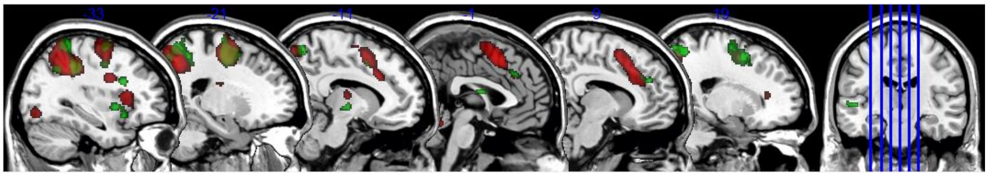

Figure 5. Overlap between MSIT main-effect map and change map.

(Red) average main-effect map. (Green) activation change map.

2.2 Spatial decoding of activation change

Despite the inclusion of typical regions of frontoparietal network, weak *p* values from whole brain analysis made it difficult to confirm whether these distinct regions collectively represented frontoparietal network. In this regard, Neurosynth image decoder was applied to interpret topographical pattern of neural changes (Gorgolewski et al., 2015; Yarkoni et al., 2011) (Table 3).

The result revealed that affected regions more corresponded to frontoparietal network (r=.198) than other types of networks, such as cinguloopercular or dorsal attention network (r= –0.002), which are executive function or attentional control associated networks. Since correlation coefficient of cinguloopercular network was not available in Neurosynth database, frontal operculum (r=0.041) and anterior cingulate cortex (r=0.077) were alternatively used for decoding. Also, correlation was higher for parietal area (intraparietal sulcus r=0.355) than for frontal areas (premotor r=0.232 and frontal eye field r=0.226). These demonstrated that parietal areas were primarily affected than frontal areas during practice.

Decoding result of cognitive terms, however, demonstrated lower correlation with executive function (r=0.071). Instead, working memory revealed higher correlation (r=0.23). Nevertheless, the highest correlation was found in ‘action’ which implies motor response (r=0.237). Also, meta-based map of attention showed considerable correlation (r=0.186).

Table 3.

Spatial decoding result for activation change.

Decoding term (Cognitive term)	Correlation coefficient	Decoding term (Brain term)	Correlation coefficient
Action	0.237	Parietal	0.426
Working memory	0.23	Intraparietal sulcus	0.355
Attention	0.186	Premotor	0.232
Interference	0.096	Frontal eye field	0.226
Executive	0.071	Frontoparietal network	0.198
		Dorsal attention network	-0.002
		Anterior cingulate cortex	0.077
		Frontal operculum	0.041

note. Only cognitive terms used by Yarkoni et al. (2011) were listed due to its frequent use and validated meta-analysis.

2.3 Functional connectivity change

Change in functional connectivity were reported in both intra- and inter-network connectivity during practice (Table 4). However, t-test results became different depending on control of demographical variables.

When age, sex were not adjusted, frontoparietal network ($t(56) = 2.84$, $p < .005$) and cerebellum network ($t(56) = 2.34$, $p<.05$) showed profound positive changes in their intra-network connectivity. Their inter-network connectivity also increased as a result of practice ($t(56) = 2.64$, $p<.05$). These seemed to resonate with activation results that showed frontoparietal network-centered neural change. But connectivity results additionally reported the modulation of cerebral-cerebellar communication. The role of cerebellum in cognitive tasks have been implicated by previous studies (Chein & Schneider, 2005; Ungerleider et al., 2002).

However, after age and sex control, significant change were only observed in inter-network connectivity between frontoparietal-default mode network ($t(54)= -2.45$, $p<.05$) and that between cinguloopercular-sensorimotor network ($t(54)= 2.41$, $p<.05$). It implies that practice effect on connectivity was largely affected by developmental factor. Accordingly, those connectivities of which change were unaffected by such covariates can rather be regarded as generic effect of practice.

Nevertheless, supplementary ROI functional connectivity result suggested that these changes were purely time-related for they could not predict practice effect on task performance. Changes of cinguloopercular network connectivity were purely time-related (Table 5). Specifically, left and right medial prefrontal cortex (mPFC) connectivity, one of the edges of cignuloopercular network, significantly decreased ($t(53)= -3.34$, $p_{FDR} <.05$) irrespective of MSIT performance gain. Also, Left posterior parietal cortex (PPC)-dorsal anterior cingulate cortex (dACC) connectivity significantly increased ($t(53)=3.13$, $p_{FDR} <.05$) when residual gain score was controlled for.

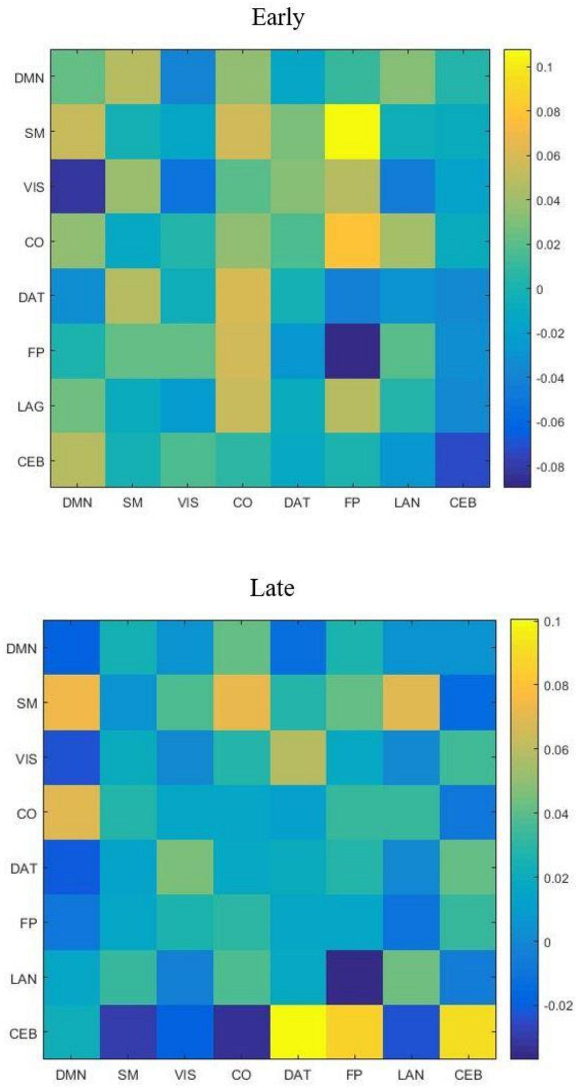

Figure 6. Mean functional connectivity matrices at early (above) and late (below).

note. connectivity strengths between 32 ROIs were summed to represent intra- and inter-network connectivity.

DMN: default mode network; SM: sensorimotor network; VIS: visual network; CO: cinguloopercular network; DAT: dorsal attention network; FP: frontoparietal network; LAG: language network; CEB: cerebellum network.

Table 4.

Functional connectivity change and its correlation with practice effect

Network connectivity		Change (Late – Early)				MSIT residual gain
		age, sex unadjusted		age, sex adjusted		
Network	Network	$t(56)$	*P*	$t(54)$	*P*	^{a}Correlation (r)
Intra-network connectivity						
Frontoparietal	Frontoparietal	2.84	$p < .005$			**-.265***
Visual	Visual	2.005	$p = .05$			
Cerebellum	Cerebellum	2.34	$p < .05$			
Inter-network connectivity						
Frontoparietal	Cerebellum	2.64	$p < .05$			**-.267***
Frontoparietal	Default mode			-2.45	$p <.05$	
Cinguloopercular	Sensorimotor			2.41	$p <.05$	
Dorsal attention	Cerebellum	2.148	$p < .05$			

note. a. Correlation: partial correlation coefficient controlling for age, sex. *p<.05.

Table 5.

Functional connectivity change among ROIs

ROI-to-ROI connectivity		Change (Late – Early)			
		Performance gain unadjusted		Performance gain adjusted	
Region ([a]Network)	Region (Network)	*t*(54)	[b] P_{FDR}	*t*(53)	[b] P_{FDR}
Intra-network connectivity					
left mPFC (CO)	right mPFC (CO)	-3.18	0.0342	-3.34	0.0219
left PPC (FP)	right DLPFC (FP)	-2.86	0.0278	-	-
Inter-network connectivity					
left PPC (FP)	dACC (CO)	3.02	0.0342	3.13	0.0392
right PPC (FP)	right FEF (DAT)	2.92	0.0278	-	-

note. Some of connections significant in the model without performance covariate became insignificant in the model with performance covariate. [a]Network : network membership. [b] P_{FDR} : Significance tested at $p_{\text{FDR}} <.05$ at seed-level.

CON: Cinguloopercular network FPN: Frontoparietal network; DAT: Dorsal attention network; mPFC; middle prefrontal cortex; PPC: posterior parietal cortex; DLPFC; dorsolateral prefrontal cortex; dACC; dorsal anterior cingulate cortex; FEF: frontal eye field.

3. The neural correlates of within-session practice effect

3.1 Practice effect-related activation change

Partial correlation analysis examined which activation changes explained practice-related gain. To reduce the problem of multiple comparison, correlation was tested only among the regions where activation change was significant. As a result, left superior frontal gyrus (r= .267, p <.05), left post-central gyrus (r= .259, p <.05) left superior parietal lobule (r= .330, p <.01) and right superior parietal lobule (r=.307, p <.05) were positively correlated with MSIT residual gain score (Figure 7). Consistent with previous studies (Mohr et al., 2016), more decrease in frontoparietal activation accompanied more practice-related gain. This implies that individuals who showed more flexible adaptation during practice had a tendency to reduce frontoparietal activities to a greater degree.

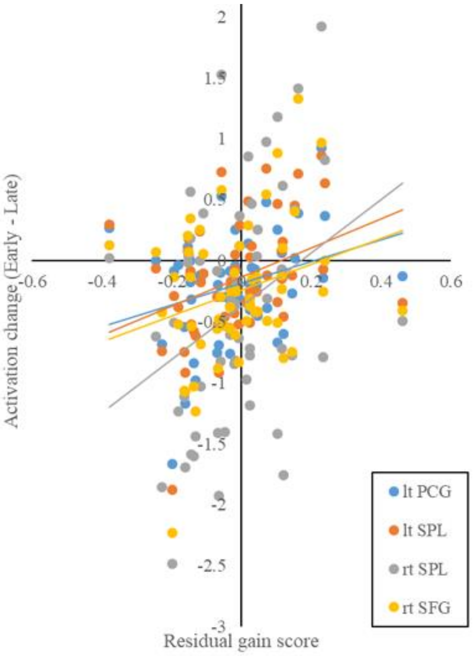

Figure 7. Practice effect-related activation change.

Scatterplot of beta changes (Early – Late) as a function of residual gain score.

(Blue) left postcentral gyrus; (Orange) left superior parietal lobule; (Grey) right superior parietal lobule; (Yellow) right superior frontal gyrus.

3.2 Practice effect-related functional connectivity change

Correlation analysis revealed that only frontoparietal network connectivity changes significantly predicted MSIT residual gain (Table 4). Frontoparietal intra-network connectivity (r=-.265, p<.05) and frontoparietal-cerebellum network connectivity (r=-.267, p<.05) significantly predicted MSIT residual gain score. It was a stark contrast with the finding that cinguloopercular network associated changes did not predict any behavioral outcome (Table 4, Table 5).

Likewise, correlation of practice-related gain with ROI-to-ROI connectivity change also showed consistent findings (Figure 8). The reduction in bilateral dorsolateral prefrontal cortex (DLPFC) connectivity (r=-.413, p<.005), and the increase (r=.393, p<.005) in left post parietal cortex (PPC)-right supramarginal gyrus (SMG) connectivity were significantly correlated with MSIT residual gain. This was consistent with network connectivity result above because these connections were primarily associated with frontoparietal network. Collectively, this provided a rough outline of brain pattern that induces practice effect; the individuals who gained more from practice showed tendency to reduce lateral prefrontal communication and boost parietal connection.

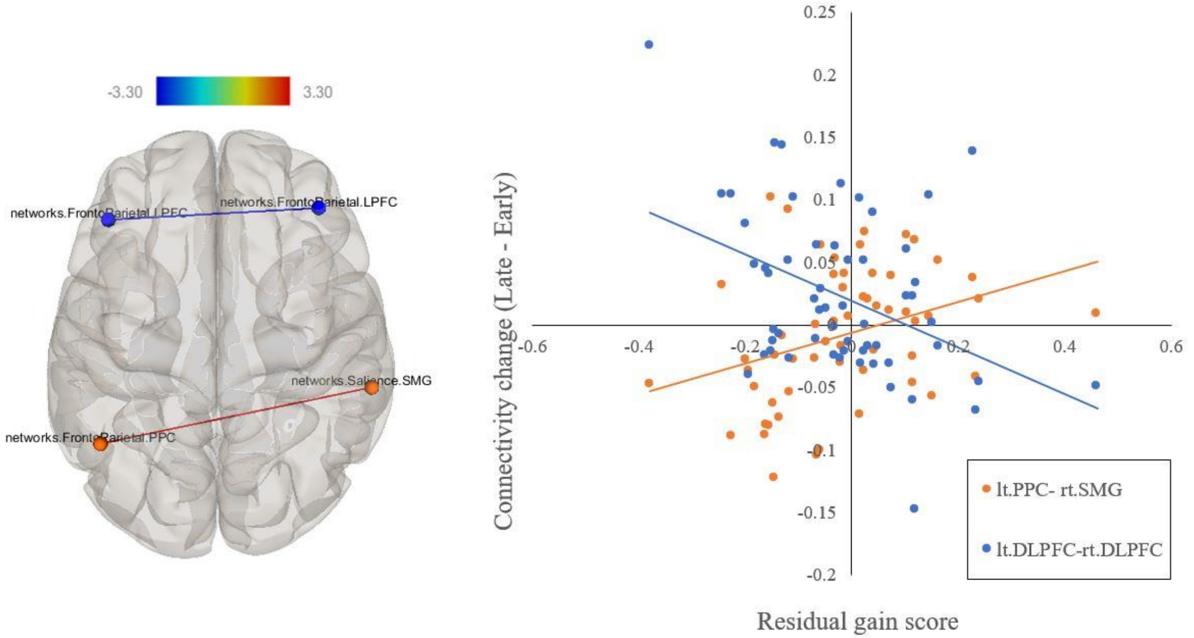

Figure 8. Practice effect-related ROI connectivity changes

(Left) 3D Axial map of significant ROIs and their connection. Connectivity strengths and directions are marked by color map.

(Right) Scatterplot of functional connectivity change (Late – Early) as a function of MSIT residual gain score.

Decrease in bilateral DLPFC (blue) and increase in left PPC-right SMG (orange) connectivity explained more performance gain.

3.3 Correlation with neuropsychological measures

Activation change significantly predicted MSIT residual gain score can be inferred as neural correlates of practice-related gain. Therefore, their relationship with neuropsychological measures of working memory (updating, shifting) and inhibition was tested by correlation analysis. There was no correlation between MSIT residual gain and neuropsychological measures. However, correlations between neuropsychological measures and the brain marker of practice effect were significant (Table 6). Activity changes in left SFG (r=-.229, p<.05), left SPL (r=-.268, p<.05), and right SPL (r=-.280, p<.05) were significantly correlated with digit span backward score, but not with other measures.

Likewise, connectivity changes associated with MSIT residual gain score were thought as the neural correlates of practice effect in the form of connectivity (Table 7). Similar to activation, negative correlation with digit span backward score was found in frontoparietal intra-network connectivity (r=–0.219, p<.05). It indicates that people who were better at updating more strongly decreased integration of FP network during MSIT. The negative correlation with updating score corresponded with negative correlation with practice-related gain.

Table 6.

Correlation between activation change and neuropsychological tests

	Activation change	1	2	3	4	DSF	DSB	DSS	TMT	Stroop
1	L superior frontal gyrus	1	**.844****	**.879****	**.843****	-.038	**-.229***	.07	-.08	-.110
2	L post-central gyrus		1	**.897****	**.787****	-.066	-.191	-.024	-.14	-.066
3	L superior parietal lobule			1	**.876****	-.075	**-.268***	-.017	-.096	-.157
4	R superior parietal lobule				1	-.013	**-.280***	-.017	-.008	-.040

Note. *:p<.05 **:p<.005. DSF: Digit span forward, DSB: Digit span backward, DSS: Digit span sequence, TMT: Trail making test interference, Stroop : Stroop test interference.

Table 7.

Correlation between connectivity change and neuropsychological tests

	Connectivity change	1	2	DSF	DSB	DSS	TMT	Stroop
1	Frontoparietal inter-network	1	-.203	-.020	**-.219***	-.165	.171	.115
2	Frontoparietal-cerebellum inter-network		1	.213	.141	.016	.055	-.03

note. *p<.05, **p<.005. DSF: Digit span forward, DSB: Digit span backward, DSS: Digit span sequence, TMT: Trail making test interference index, Stroop: Stroop interference index

Discussion

In the present study, we identified that brain changes within frontoparietal network are the neural correlates of within-session practice effect during executive function task. Moreover, these neural correlates significantly predicted cognitive measure of flexible executive function. From these results, the link between practice effect and flexible control process was supported.

Our main findings can be summarized as follows. First, we found that dynamic alteration of frontoparietal network activation and connectivity predicted the individual difference in practice-related gain. In functional activation analysis, practice effect in task reaction time was predicted by activation decline in left superior frontal gyrus and bilateral superior parietal lobule. Spatial decoding result also favored the primary engagement of frontoparietal network and working memory process. Consistently, functional connectivity analysis revealed that practice effect-related change occurred in frontoparietal network and cinguloopercular network. However, connectivity changes which were associated with practice-related gain were detected only in frontoparietal intra-network connectivity and frontoparietal-cerebellum inter-network connectivity. Based on these results, we argue that successful short-term learning in executive function task requires flexible modulation in frontoparietal network. Our result further clarifies the mechanism of 'scaffolding-storage process' proposed by Petersen and colleagues (1998).

Furthermore, the link between practice effect and flexible executive function was supported by their concurrent correlation with frontoparietal intra-network connectivity. Among several neural correlates of within-session practice effect, the connectivity changes in frontoparietal intra-network showed correlation with digit span backward score in the same direction. Evidently, this pattern was not found from other neural correlates, such as activation changes of frontal and parietal ROIs. It implies that a portion of practice-related gain that is attributable to working memory is represented by frontoparietal intra-network connectivity change in neural level. Taken together, we suggest that flexible executive function, especially working memory, serves as a major cognitive process behind practice-related gain.

1. Frontoparietal network change accounts for practice effect

1.1 Pure time effect and practice effect

A uniqueness of the present study lies upon the dissociation between brain changes those were time-related and those were practice effect-related. While the former refers to temporal brain changes irrelevant to learning in behavior, the latter refers to those predict the amount of practice-related gain. In behavioral aspect, the latter attains psychological implication than the former.

Whether the plastic brain changes during brief task supports flexible modulation of cognitive states and performance is disputable according to previous studies. Previous study by Landau and colleagues (2004) tested the main effect of practice-related gain, but found no significant correlation between behavioral changes and brain changes. However, other researchers claimed that dynamic changes are linked to faster and more accurate performance (Bassett et al., 2011; Mohr et al., 2016; Poldrack & Gabrieli, 2001). Therefore, we tried to test the possibility that some brain changes would predict practice-related gain while others not. In the meantime, we could test the fitness of our prior hypothesis that within-session practice effect is guided by cognitive process of updating (working memory) and shifting. As provided, this hypothesis can be challenged by other tenable accounts, such as task automatization or sustained attention.

One of our main findings was that frontoparietal intra-network connectivity and frontoparietal-cerebellum inter-network connectivity significantly predicted the individual differences of practice-related gain. In contrast, even though frontoparietal-default mode inter-network connectivity and cinguloopercular-sensorimotor inter-network connectivity changes were statistically significant, they did not predict behavioral change. In the same manner, activation change among frontoparietal network regions significantly predicted practice-related gain. Left superior frontal gyrus and bilateral superior parietal lobule were associated with practice effect in reaction time.

Based on these findings, we concluded that the only behaviorally meaningful neural change occurs in association with frontoparietal network. Supplementary ROI-to-ROI connectivity analysis also supported this idea because the changes in cinguloopercular network connectivity were indeed significant after MSIT residual gain score was regressed out. As Sadaghiani and D'Esposito (2015) characterized the functional role of cinguloopercular network as tonic alertness, tonic alertness may not be sufficient for inducing behavioral change. It might be that pure time-related change in cinguloopercular network may underlie temporal changes in brain level but it may not manifest as modification of performance in behavioral level.

Distinct role of frontoparietal network and cinguloopercular network in within-session practice effect can be understood from Dosenbach's dual-network framework (2007, 2008). According to this framework, main signal processed by cinguloopercular network is stable top-down signal while frontoparietal network processes phasic signal in trial-by-trial manner. It implies that executive function component that underlies stable monitoring, inhibition, is guided mainly from cinguloopercular network while updating and shifting are based on frontoparietal network. Therefore, our result suggests that practice-related gain is guided by neural process of working memory, even though the neural process of inhibition is simultaneously on the move. Individuals who had more ability to modulate frontoparietal network gained benefit from practice more than others. This is in favor of our hypothesis that practice-related gain is supported by flexible executive function, especially working memory.

Meanwhile, it is also noteworthy that cinguloopercular and sensorimotor network connectivity increased during task. This may indicate facilitated sensorimotor control during repetitive practice (Pashler & Baylis, 1991). Or, it can reflect the modulation in response inhibition (Aron, Robbins, & Poldrack, 2014), as suggested by increased activation in cingulate gyrus and right inferior frontal gyrus.

However, since these changes could not explain behavioral change, the possibility that task automatization based on procedural memory process takes most parts in practice-related gain can be negated.

Furthermore, another pure time-related change was observed in decrease in frontoparietal and default mode network (DMN) connectivity. The anticorrelation between these networks is the most prominent features of functional connectivity during task (Greicius, 2008; Raichle et al., 2001). A common conceptualization on frontoparietal and DMN connectivity is that stronger antagonism invariably supports more active cognitive control in task context and resting state (Kelly, Uddin, Biswal, Castellanos, & Milham, 2008; Menon, & Uddin, 2011). Accordingly, it is expected that the antagonism might be lessened when cognitive load is released by various factor (Cocchi, Zalesky, Fornito, & Mattingley, 2013) and when more faster response becomes possible (Fornito, Harrison, Zalesky, & Simons, 2012). Considering such relationship, increased connectivity should have been observed from task practice, which is contrary to our result. The increase in anticorrelation can reflect that control demand was not easily released but rather increased for our subjects. It might be due to immature inhibitory control in early adolescence (Luna et al., 2015). However, since performance on average improves during task, there can be other reasons. Leech and colleagues (2012) demonstrated that some core parts (dorsal posterior cingulate cortex) of DMN is actually strongly integrated with frontoparietal systems when cognitive load is higher. They show opposite pattern from ventral posterior cingulate cortex, which is other part of DMN (Leech, Braga, & Sharp, 2012).

Of final note, we judged the pure time-related brain change as the evidence that certain cognitive process is less affected during task. But some researchers asserted that this change is also subject to functional interpretation. Kelly and colleagues (2006) argued earlier that a practice-based interpretation of activation changes is still of value even without the behavioral effects because the changed reaction time can confound the interpretation of activation changes (Poldrack, 2000). However, we attempted to control for the effect of timing on the task by parametric modulation of trial RT and covaring out average reaction time in activation analysis. Since the result of present study is relatively free from confounding effects, the dissociation of pure time-related change and practice effect-related change seems free from controversy.

1.2 The direction of brain change

According to scaffolding-storage framework, some prefrontal and parietal areas engage in task acquisition and diminishes its activity over time. As a function of time, practice produced a shift in activity to sylvian-insular, and other regions where task-specific representation were stored (Petersen et al., 1998).

Our results are in line with the previous notion and our hypothesis. Not only decline was observed among frontoparietal network, but also the its magnitude predicted the more gain from practice. The decline in most regions reflects that flexible control process, which underpins working memory, was massively recruited in early phase and became unnecessary after subjects gained efficiency.

The functional interpretation on activity decline needs careful scrutiny. Although low activation level was related to better task performance in previous studies (Landau et al., 2004; Rypma, Berger, & D'Esposito, 2002), decline can be possibly due to fatigue, which generally curtails brain activation. However, Landau and colleagues confirmed that fatigue is not a cause for decline because there were no difference in decline between high accuracy group and low accuracy group (Landau et al., 2004). Similarly, we found the positive relationship between decline in activity and practice-related gain. We concluded that deactivation in late phase of task mirrors increased in neural efficiency acquired by preceding recruitment of working memory process.

Most studies proposed that decline in activations suggests the efficient reorganization process (Kelly et al., 2006), and will demonstrate increased connectivity between those regions. However, coactivation pattern per se should be separated from functional connectivity between regions especially during task (Friston et al., 1997). Also, the pattern of activation and functional connectivity change may be congruent and incongruent according to regions (Gerchen & Kirsch, 2017). In this regard, we computed the change in connectivity strength to determine whether the activation decrease reflects integrated communication between frontoparietal regions. Different from common beliefs, our study found that frontoparietal intra-network connectivity strength actually decreased. Besides, the degree of decrease was associated with more behavioral gain.

The reason why decreased connectivity has more advantage in behavior can be discussed in several ways. First, the result can be attributed to a flexible nature of frontoparietal network. Cole and colleagues (2013) recently observed that frontoparietal network is dynamically reorganized according to task requirements. Under specific task conditions, frontoparietal network starts to connect with other neural networks in task-specific way, as suggested by highest variability of frontoparietal network connections (Cole et al., 2013). Furthermore, the pattern of frontoparietal functional connectivity with other neural networks was coded during practice and later emerged in novel task setting reflecting its role as hub in task learning (Cole et al., 2013). In this regard, practice during task might have encouraged task-specific connectivity with other neural networks. And this emergence of task-specific connection can be manifested by decrease in frontoparietal intra-network connectivity.

Second possibility is that some connections between within frontoparietal networks were strengthened while others not. ROI-to-ROI connectivity analysis is supportive to this notion, demonstrating connectivity has changed in a fashion that parietal connections wax and frontal connections wane. Increased parietal connection was reflected by right supramarginal gyrus and left posterior parietal cortex connectivity and reduced frontal connection was reflected by bilateral dorsolateral prefrontal cortex connectivity. Both of them were associated with more gain in behavioral performance.

Lastly, the decline in frontoparietal network connectivity can reflect subject-specific developmental trajectory. According to Marek and colleagues (Marek, Hwang, Foran, Hallquist, & Luna, 2015), brain network organization in the early adolescence go through changes in a way that reduces both intra-network connectivity and inter-network connectivity. In light of developmental trajectory, task practice might have stimulated the neural and cognitive process to accelerate maturation.

We mainly focused on the functional interpretation of frontoparietal intra-network connectivity. Nevertheless, frontoparietal-cerebellum network connection also significantly predicted practice-related gain. More decline in their connectivity was associated with more gain in performance. However, this was opposite to optimal developmental trajectory. Fair and colleagues (2007) provided that long-range connection between frontal regions and cerebellum develops and hard-wired across development. Based on this discrepancy, the role of this connection should be further examined by future investigation.

2. The link between within-session practice effect and working memory

2.1 Shared neural correlates

Within-session practice effect can be a mixed result from various cognitive processes. Indeed, there was no correlation between within-session practice effect and neuropsychological measures of updating, shifting, or inhibition. The lack of relationship among behavioral measures may imply either the absence of such process during task, or inversely, the difficulty to separate each contribution of various processes. In this regard, the results from neuroimaging can help elucidate the hidden link between cognition and behavior. The present study has taken frontoparietal network change as evidence that working memory process determines the individual difference in within-session practice effect.

It is noteworthy that the link between working memory and practice effect is only observed in neural level but not in behavioral level. However, a number of neuroimaging studies provided that some neural correlates of cognition may associate with other behavior, even in the absence of behavioral link (Kim-Spoon et al., 2017). For example, Galvan and colleagues (2011) found that neural correlates of response inhibition in Stop-signal task reliably predicted cigarette smoking in late adolescent, whereas the performance in task did not (Galván, Poldrack, Baker, McGlennen, & London, 2011). In that study, the disruption of inhibitory process by smoking was still raised despite the absence of behavioral manifestations. In the same perspective, we suggest that individual difference in updating is shaped into discrepant task-dependent change in frontoparietal network and manifested as different amount of practice-related gain. In this regard, frontoparietal network roles as a mediator in the relationship between working memory and practice-related gain.

2.2 Specificity of the relationship

Unlike previous studies, we took a step forward by probing the association between the neural correlates and neuropsychological measures. It was to see if the neural base of practice-related gain has specific relationship with working memory in other task settings. The correlation analyses demonstrated the specificity of relationship between the neural correlates and updating measure. When compared to other measures of retention (digit span forward), shifting (trail making test), and inhibition (stroop test), only digit span backward score revealed the significant correlation. Based on these results, we evince the specificity of working memory in producing practice-related gain.

As to specificity of updating in practice effect, we offer possible explanations. First, sustained goal-representation, largely measured in inhibition task, may not be sufficient to manifest as change in behavior. On the other hand, task property used in this study also can be a reason. Because inhibitory control is heavily adopted during multi-source interference task (MSIT), there can be less room for additional engagement. Based on previous notion on competitive relationship between working memory and inhibition (Diamond, 2013), it can be asked: if working memory task is used, brain correlates will be associated with inhibition, instead? However, previous study which used working memory task also reported similar brain modulation during practice (McEvoy, Smith, & Gevins, 1998). Still, that study did not observed whether similar patterns of brain change also explained practice-related gain. Thus, we might need more evidence to conclude that the present result is task-general.

The reason why shifting was unexpectedly unassociated with practice effect also can be attributed to task property. Because the rule of MSIT is invariably to find one different number in both congruent and incongruent trials, subjects do not have to intentionally switch attentional set. However, updating influences MSIT performance because target and competing stimuli are continuously changed on trial-by-trial basis. For example, when stimulus '212' is followed by '332' subject has to manipulate representation of '2' from distractor to target. The report that frontoparietal network acts in a more content-dependent manner is also in this stream (Sadaghiani & Esposito, 2015).

2.3 Connectivity change reliably measures working memory capacity

Whereas frontoparietal intra-network connectivity change predicted both working memory and practice-related gain in the same direction, brain activation changes did in opposite direction. More decline in frontoparietal activation was beneficial for practice-related gain, but individuals with higher working memory score tend to show lesser decline. Probable reason is that we used the change score. Individuals with higher working memory score are likely to show better performance at baseline. Assuming they used their cognitive resources enough at firsthand, they inevitably will have lesser practice effect.

In this sense, it is intriguing to find out that connectivity change did not show inverse direction between correlations. More decline in frontoparietal intra-network connectivity positively contributed for both practice-related gain and working memory. Since the physiological basis of connectivity change relatively less unclear than activation, we cannot assertively explain the reason. Our limited conclusion is that frontoparietal intra-network connectivity underlies the basic cognitive process regarding both practice effect and working memory.

3. Limitations and future considerations

For future search, following points can be considered. First, longitudinal outcome is required to evaluate generalized contribution of the neural correlates in learning in broad sense. We must limit our result to short-term practice effect because longitudinal training effect may arise from different neural mechanism (Hauptmann et al., 2005). To test the generalizability of our result, future study need to compare within-session practice effect with training gain. Following growing interest for neural marker of behavior, it is possible to summarize the neural correlates into factor score and test its explanatory power by applying to training gain.

Second, other factors such as age or sex need to be considered. We did not further analyze the effect of age when testing the hypotheses because it was not our main interest. However, developmental factor was considered as crucial factor to decide how brain networks are dynamically modulated. Although our subject age range was tightly controlled to 13-14 years old, even this gap affected the result. Indeed, our study showed that change in frontoparietal network connectivity was not significant in group level after age, sex adjustment. Also, the functional interpretation of connectivity change can be influenced by developmental stage (Fair et al., 2007; Marek et al., 2015).

Third, resting state connectivity can be considered as neural correlates. The primary reason why we looked at the changes in brain function was based on the view that context-dependent change of brain function is more powerful tool for explaining reflexive behavior than spontaneous activity at rest. There were consistent reports that task-dependent brain function reveals different features from intrinsic brain characteristics (Fornito et al., 2012). However, resting state may involve task-dependent coactivation as well (Buckner, Krienen, & Yeo, 2013; Yeo et al., 2011). Previous study found that intrinsic connectivity structure highly resembles functional connectivity structure obtained from multiple tasks (Cole et al., 2013). We mainly analyzed task-evoked connectivity and activation patterns, but it can be meaningful to validate the neural correlates of practice-related gain in resting-state networks.

Lastly, methodological limitation lies in assessment of cognitive constructs. We asserted the relationship with cognitive construct by measuring only one or two scores by each construct. However, updating, shifting, and inhibition are basically latent factors from structural modeling analysis (Miyake et al., 2000). More appropriate approach is to use several tasks and extract factor scores. Or, it is possible to design specific task that simultaneously measures each component score with various conditions.

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국문 초록

집행기능과제에서 수행의 향상과 뇌기능 변화

최근 연구결과들은 과제수행 동안의 연습효과, 즉 회기 내 연습효과(within-session practice effect)가 학습 잠재력 또는 유연한 적응 능력에 대한 행동적 지표가 될 수 있다는 점을 시사한다 (Duff et al., 2012). 그러나 주어진 과제를 연습하는 동안의 급격한 수행 변화가 어떠한 인지기능을 반영하고 안정적으로 예측하는지, 신경학적 방법을 통해 연구된 바는 드물다. 행동적으로 유연하게 변화하는 능력은 집행기능의 구성요소 중 최신화 및 전환 등의 요소에 의해 뒷받침되는 것으로 보인다 (Miyake & Friedman, 2012). 이러한 점에서 회기 내 연습효과가 최신화 및 전환과 같은 집행기능의 요소와 신경 기전을 공유할 가능성이 제기된다. 전두두정네트워크가 유연한 통제처리과정(flexible control process)을 담당한다는 기존 결과들을 토대로, 본 연구에서는 회기 내 연습효과의 신경학적 상관과 전두두정네트워크의 연관성을 기능적 자기공명영상을 통해 탐구하였다.

본 연구에서는 집행기능과제 중 하나인 다중간섭과제(multi-source interference task)를 수행하는 동안, 과제 초기와 후기 사이의 시행 반응시간 차이와 뇌영역 활성화 및 대뇌네트워크의 기능적 연결성 강도의 차이를 측정하였다. 우선, 과제수행동안 뇌기능 변화가 유의한지 공간패턴 해석(spatial decoding)과 대응표본 t 검정을 실시하였다. 이 중에서 연습효과 크기와 유의한 상관을 보이는 뇌기능 변화를

연습효과의 신경상관자로 정의하였다. 마지막으로, 결과가 특정 과제상황에 국한되지 않는지 확인하기 위해, 연습효과의 신경상관자와 집행기능을 측정하는 신경심리검사 점수들 간 상관이 분석되었다.

그 결과, 회기 내 연습효과의 상관자는 전두두정네트워크와 관련된 영역 및 기능적 연결성이었다. 해당 네트워크에 속한 양측 상두정엽, 좌측 상전두회 및 하전두회의 활성화가 과제 후기에 더 많이 감소할수록 더 큰 연습효과가 있었다. 또한, 전두두정네트워크 내부의 연결성, 전두두정 네트워크와 소뇌네트워크 간 연결성이 감소할수록 연습효과가 컸다. 공간패턴해석 결과 역시 일관되게 전두두정네트워크 중심의 변화를 지지했다. 마지막으로, 이러한 신경상관자는 작업기억을 측정하는 거꾸로 숫자 외우기 점수와 일관된 상관을 보였다. 종합적으로, 본 연구결과는 회기 내 연습효과와 유연한 통제처리과정의 공통된 신경상관자가 전두두정네트워크이며, 과제를 습득하는 초기 과정에서 해당 네트워크의 효율적 사용이 적응적으로 행동 변화를 도모하는 능력의 기반임을 시사한다.

주요어: 연습효과, 집행기능, 작업기억, 전두두정네트워크, 대뇌 활성화, 기능적 연결성

학번: 2016 – 20186

Appendix I. Network regions used in functional connectivity analysis

	Network	Anatomical label		MNI coordinates		
				x	y	z
1	DefaultMode	medial prefrontal cortex		1	55	-3
2	DefaultMode	lateral parietal	(L)	-39	-77	33
3	DefaultMode	lateral parietal	(R)	47	-67	29
4	DefaultMode	posterior cingulate cortex		1	-61	38
5	SensoriMotor	postcentral gyrus	(L)	-55	-12	29
6	SensoriMotor	postcentral gyrus	(R)	56	-10	29
7	SensoriMotor	precentral gyrus		0	-31	67
8	Visual	supracalcarine cortex		2	-79	12
9	Visual	occipital pole		0	-93	-4
10	Visual	lateral occipital cortex	(L)	-37	-79	10
11	Visual	lateral occipital cortex	(R)	38	-72	13
12	Cinguloopercular	anterior cingulate cortex		0	22	35
13	Cinguloopercular	anterior insula	(L)	-44	13	1
14	Cinguloopercular	anterior insula	(R)	47	14	0
15	Cinguloopercular	rostral prefrontal cortex	(L)	-32	45	27
16	Cinguloopercular	rostral prefrontal cortex	(R)	32	46	27
17	Cinguloopercular	supramarginal gyrus	(L)	-60	-39	31
18	Cinguloopercular	supramarginal gyrus	(R)	62	-35	32
19	DorsalAttention	frontal eye field	(L)	-27	-9	64
20	DorsalAttention	frontal eye field	(R)	30	-6	64
21	DorsalAttention	intraparietal sulcus	(L)	-39	-43	52
22	DorsalAttention	intraparietal sulcus	(R)	39	-42	54
23	FrontoParietal	lateral prefrontal cortex	(L)	-43	33	28
24	FrontoParietal	posterior parietal cortex	(L)	-46	-58	49
25	FrontoParietal	lateral prefrontal cortex	(R)	41	38	30
26	FrontoParietal	posterior parietal cortex	(R)	52	-52	45
27	Language	inferior frontal gyrus	(L)	-51	26	2
28	Language	inferior frontal gyrus	(R)	54	28	1
29	Language	posterior superior temporal gyrus	(L)	-57	-47	15
30	Language	posterior superior temporal gyrus	(R)	59	-42	13
31	Cerebellum	anterior cerebellum		0	-63	-30
32	Cerebellum	anterior cerebellum		0	-79	-32

note. Network information was provided by CONN 17f. (L): left, (R): right.