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Toward an understanding of the neural mechanisms underlying dual-task performance: Contribution of comparative approaches using animal models

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ABSTRACT

The study of dual-task performance in human subjects has received considerable interest in cognitive neuroscience because it can provide detailed insights into the neural mechanisms underlying higher-order cognitive control. Despite many decades of research, our understanding of the neurobiological basis of dual-task performance is still limited, and some critical questions are still under debate. Recently, behavioral and neurophysiological studies of dual-task performance in animals have begun to provide intriguing evidence regarding how dual-task information is processed in the brain. In this review, we first summarize key evidence in neuroimaging and neuropsychological studies in humans and discuss possible reasons for discrepancies across studies. We then provide a comprehensive review of the literature on dual-task studies in animals and provide a novel working hypothesis that may reconcile the divergent results in human studies toward a unified view of the mechanisms underlying dual-task processing. Finally, we propose possible directions for future dual-task experiments in the framework of comparative cognitive neuroscience.

1. Introduction

The dual-task paradigm is a behavioral procedure in which subjects are required to perform two different tasks simultaneously. The dual-task paradigm can involve a wide range of dual tasks, such as two speeded sensory-to-motor tasks, two perceptual tasks, two working memory tasks, or multiple simulated errands in daily living such as cooking and shopping. Accordingly, across different types of dual tasks, the time range of one trial could differ significantly, from less than a second to several minutes, as could the complexity of the task demands.

Despite such variety, dual-tasking often results in poorer performance in one or both of the component tasks compared to when each component task is performed separately. This effect, known as dual-task interference or dual-task cost, has been considered to be one of the most typical demonstrations of a strict bottleneck in information processing in the human brain. The ubiquity of this dual-task interference effect has frequently been associated with the concept of cognitive (mental) resource, which corresponds to the brain's task-general information-processing capacity that is shared across simultaneous tasks. Indeed, early interest in human dual-task performance in experimental psychology was derived from general questions about human cognitive

resources (Kahneman, 1973; Moray, 1967; Wickens, 1980). For example, based on event-related potentials obtained in human participants performing dual tasks, Wickens et al. (1983) searched for neural signatures of cognitive resources in the human brain. The concept of capacity-limited cognitive resource has been frequently used to explain dual-task interference, as well as the performance limitation observed in a variety of cognitive functions such as attention and working memory.

The dual-task paradigm has also received considerable interest among researchers with regard to higher-order cognitive functions because this paradigm is considered to be the gold standard for investigating the 'central executive system' (Baddeley, 1996; Just and Carpenter, 1992). For example, based on dual-task performance by healthy participants, Baddeley (1992) proposed the concept of a central executive system that actively allocates cognitive resources to coordinate information processing in the phonological loop and the visuospatial sketch pad. Theories of higher-order cognitive functions often highlight the link between dual-task performance and the component functions of the executive systems, such as planning, shifting, inhibition, coordination, and dividing of attention (Meyer and Kieras, 1997; Sigman and Dehaene, 2006). In human neuroimaging studies, use

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of the dual-task paradigm has contributed significantly to the formulation of the recently popular hypothesis of a hierarchical functional subdivision of the prefrontal cortex along the anterior-posterior axis (Badre and D'Esposito, 2009; Koechlin and Summerfield, 2007). Thus, it has been widely thought that elucidation of the neural mechanisms underlying dual-task performance should significantly contribute to our understanding of the neural mechanisms that support complex cognitive control.

Despite decades of investigation, our understanding of the neurobiological basis of dual-task performance is still limited. Neuroimaging studies that examined the neural mechanisms of dual-task performance and the dual-task interference effect have shown divergent results regarding two central questions: (1) whether or not there exist brain areas that are specifically related to the performance of dual-tasks? and (2) what are the neurobiological substrates of cognitive resource and the mechanisms for its allocation?

2. Neural basis of dual-task processing: human studies

A widely held view is that the simultaneous performance of two tasks requires more mental effort than performance of the individual tasks themselves. Accordingly, it is natural to consider that, to accommodate such an increase in processing demands in dual tasks, the activation of additional, spatially separate brain areas that were not activated in the performance of a single task would be necessary. According to this view, performance deficits in dual tasks arise from limitations in, or malfunctioning of, information processes in these brain areas that are devoted to the processing of dual-task-specific demands. In fact, neuropsychological studies of patients with focal frontal lesions (Baddeley et al., 1997), Alzheimer's disease (Baddeley et al., 1991), traumatic brain injury (McDowell et al., 1997; Park et al., 1999), and multiple sclerosis (D'Esposito et al., 1996) showed that the patients exhibited prominent performance deficits only in dual-task conditions, while their single-task performance remained relatively intact, which suggests the presence of distinct neural modules that are specifically involved in dual-task processing. Analyses of the behavioral performance of frontal patients in more realistic multitasking situations, such as cooking (Frisch et al., 2012; Godbout et al., 2005) and shopping (Shallice and Burgess, 1991), have further strengthened this view. In these studies, multiple tasks with different characteristics were interleaved with each other within a trial that lasted for several tens of minutes. For example, in the "Multiple Errands Test" (Shallice and Burgess, 1991), the participants were asked to perform several real-world tasks, such as buying specific items in different shops, collecting specific information, and arriving at a certain location at a certain time to meet the experimenters. The study found that frontal patients with lesions in the anterior lateral prefrontal cortex (MPFC) subtending Brodmann's areas 46 and 10 exhibited marked deficits in the simultaneous performance of multiple tasks, despite their relatively unaffected performance in conventional psychological tests such as a memory or IQ test, and even in some executive tasks that are normally associated with prefrontal function, such as the Wisconsin Card-Sorting test and the Verbal Fluency test (Burgess, 2000; Frisch et al., 2012; Godbout et al., 2005). Thus, these results suggest that there are distinct processing modules in the brain that are selectively recruited in dual-task situations, and that these modules reside, at least in part, in the prefrontal cortex.

2.1. Brain areas selectively activated during the performance of dual tasks

In a seminal fMRI study, D'Esposito et al. (1995) attempted to localize dual-task-specific brain areas by comparing brain activations under single-task and dual-task conditions. The dual-task condition was comprised of two non-working-memory tasks: a semantic-judgement task and a spatial-rotation match-to-sample task (Fig. 1A). In the dual-task condition, a significant increase in activation relative to the single-

task condition was observed in the dorsolateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC) (Fig. 1B). In the single-task condition, these areas did not show significant activation relative to the resting baseline. Based on these results, the authors suggested that the dual-task-specific activation in the DLPFC reflected the addition of dual-task-specific processing requirements (i.e., the allocation and coordination of attention between visual and auditory processing) that were absent in the single-task condition. The authors further suggested that these distinct regions in the DLPFC corresponded to the central executive component of working memory systems (Baddeley, 1992).

In another fMRI study, Koechlin et al. (1999) used a dual-task paradigm that required working memory. The task consisted of a main task and a sub-task that was embedded within the main task, and the participants were asked to keep the main goals in mind while allocating attention to process subgoal information (Fig. 1C). The fMRI BOLD responses were compared among this dual task and three other task conditions: the main task performed alone (control condition); the main task performed alone with the insertion of a delay period between responses (working memory condition); and the main task and the sub-task performed separately, but in frequently alternating blocks (task-switching condition) (Fig. 1D). The results showed that only the bilateral anterior LPFC (Brodmann's area 10) was selectively activated in the dual-task condition that required cognitive branching, while this region was not activated either when retaining a goal across the delay period (working memory condition) alone or when frequently allocating attentional resources between different goals (task-switching condition) alone. This dual-task-specific activation of the anterior LPFC was also observed in a separate control experiment that compared brain activation between the dual-task condition and a new task-switching condition which was made more difficult than the dual-task condition by using vague cue stimuli. The conclusion that the anterior LPFC plays a key role in dual-task processing was further supported by another fMRI study that used a similar cognitive-branching paradigm (Braver and Bongiolatti, 2002). In addition, using the same dual tasks as Koechlin et al. (1999), a recent human lesion study showed that the size of a lesion in area 10 but not the total volume of a brain lesion was correlated with error rates in the dual-task condition (Dreher et al., 2008).

Thus, this initial evidence highlighted the selective and essential involvement of the prefrontal cortex in dual-task processing. These findings were further supported by subsequent neuroimaging studies (Collette et al., 2006; Dux et al., 2006, 2009; Hesselmann et al., 2011; Johnson and Zatorre, 2006; Ramsey et al., 2004; Szameitat et al., 2002; Thomsen et al., 2004). Among these, of particular interest are studies that used a psychological refractory period (PRP) paradigm, in which participants must perform two simple sensory discrimination tasks simultaneously or in rapid succession (Dux et al., 2006, 2009; Hesselmann et al., 2011; Sigman and Dehaene, 2008). It has been repeatedly observed that the onset timing of activation in the left posterior LPFC alone (Dux et al., 2006, 2009) or the bilateral frontoparietal network including the left posterior LPFC (Hesselmann et al., 2011; Sigman and Dehaene, 2008) was strongly correlated with the magnitude of behavioral dual-task interference that was measured as an increase in response times (RTs) under dual-task conditions (i.e., the PRP task) relative to single-task conditions. Furthermore, one of these studies (Dux et al., 2009) showed that extensive practice in PRP tasks led to a selective reduction of activation in the left posterior LPFC, the magnitude of which was directly proportional to the degree of improvement in PRP performance. Correspondingly, a decrease in the excitability of the left posterior LPFC by transcranial direct cathodal current stimulation (tDCS) has been shown to significantly improve RT performance in dual-task trials (Filmer et al., 2013; but see, Zhou et al., 2014 and Hsu et al., 2015, which reported improvement of dual-task performance under anodal tDCS over the left DLPFC). The precise mechanism by which tDCS over the left LPFC improves RT is unclear.
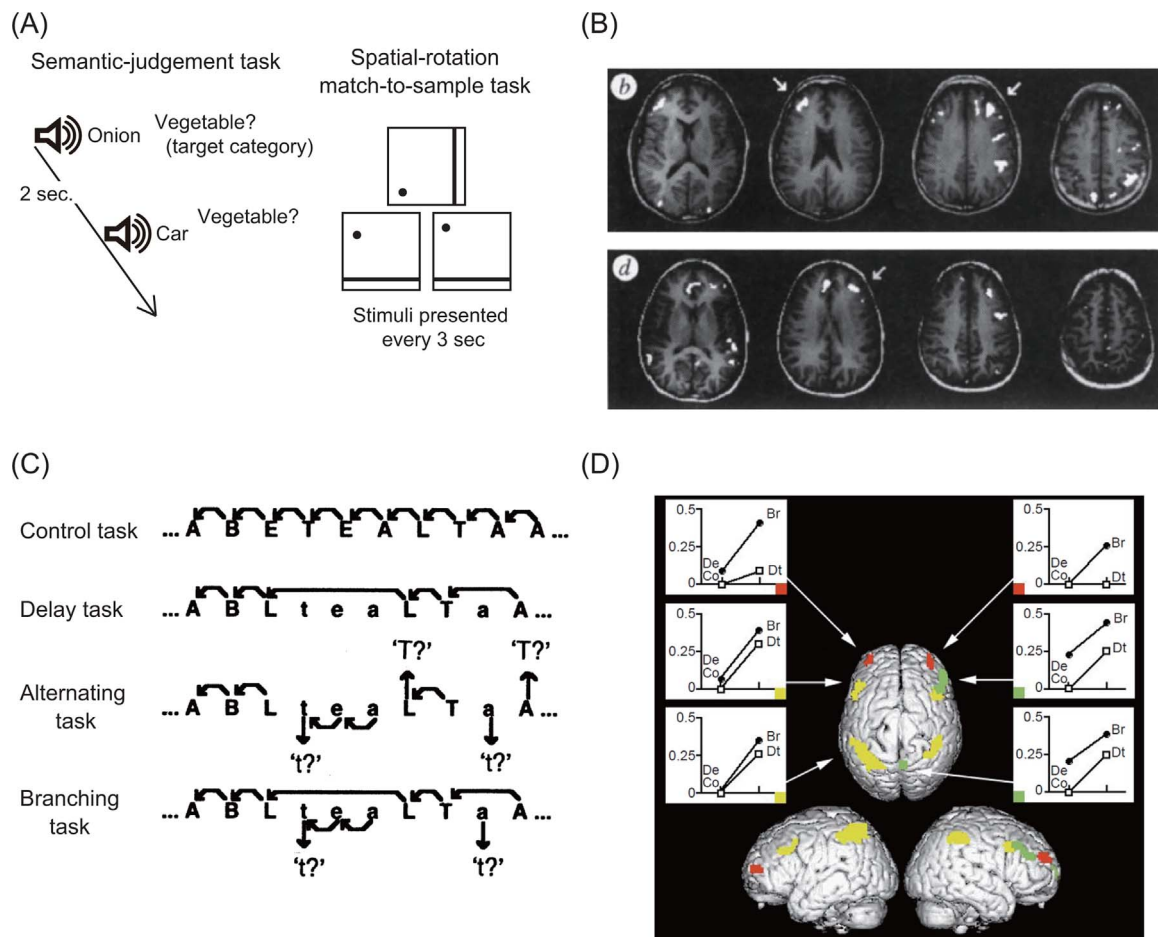
Fig. 1. Functional neuroimaging evidence for the presence of brain areas that are specifically recruited in dual-task performance. (A) Two component tasks used by D'Esposito et al. (1995). In the semantic-judgement task, participants were asked to respond to exemplars of a pre-defined target category ('vegetable') in a series of aurally presented words at a rate of one word every 2 s. In the spatial-rotation match-to-sample task, participants were asked to indicate which of the lower squares had the dot in the same location, relative to a double line, as the upper square. Visual stimuli were presented every 3 s. The dual-task condition required concurrent performance of these two single tasks. (B) Comparison of the BOLD response between the single-task, dual-task, and control conditions revealed dual-task-specific activation in the anterior DLPFC (arrows). Top: Dual-task condition minus semantic-judgement task (single-task condition). Bottom: Dual-task condition minus spatial-rotation match-to-sample task (single-task condition). In the single-task condition, these areas did not show significant activation relative to the resting baseline (control). Adapted from D'Esposito et al. (1995). (C) Behavioral tasks used by Koechlin et al. (1999). In all four tasks, visual stimuli consisted of a pseudo-random sequence of upper-case and/or lower-case letters from the word "tablet". Control task: Participants were asked to judge whether two successively presented upper-case letters were in immediate succession in the word "tablet". Delay task: Lower-case letters were occasionally inserted between upper-case letters. Participants had to ignore lower-case letters and judge whether two successively presented upper-case letters were in immediate succession in the word "tablet". Alternating task: Participants were asked to respond as in the control task for both upper-case and lower-case letter sequences. Participants were also asked to judge whether every first letter that marked a case change was the letter T (or t). Branching task (dual-task condition): Participants were asked to respond to upper-case letters exactly as in the delay task and to lower-case letters exactly as in the alternating task. (D) Brain regions (red) that were activated only in the branching task (dual-task condition). Across the entire brain, only two regions in the left and right dorsal fronto-polar prefrontal cortex (BA 10) exhibited an increase in activation specifically associated with performance of the branching task (dual-task condition) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).
Adapted from Koechlin et al. (1999).

However, these findings in PRP studies appear to support the notion that the central bottleneck of information processing that defines the limitation in human dual-task performance is localized in distinct brain regions.

In a broader perspective, these findings that highlight the presence of dual-task-specific prefrontal activation have contributed significantly to the formulation of recently prevalent hypotheses which postulate that there is a functional gradient along the anterior-posterior axis in the LPFC, based on the level of action control (Information Cascade hypothesis, Koechlin et al., 2003; Koechlin and Summerfield, 2007) or the abstractness of task-relevant rules (Badre, 2008; Badre and D'Esposito, 2009). These hypotheses postulate that more anterior regions of the LPFC participate in the processing of more complex, abstract action information, while more posterior regions of the LPFC process more concrete action information that is closer to specific motor command. At the apex of this hierarchy, the most anterior end of the LPFC (Brodmann's area 10) participates in the parallel processing of

main-goal and sub-goal information (i.e., dual-task processing).

2.2. Presence or absence of dual-task-specific brain areas

The neuroimaging and neuropsychological studies reviewed so far have shown that distinct regions in the prefrontal cortex are selectively recruited in dual-task performance. However, opposite results were reported in several other studies, which indicated that dual-task performance did not activate additional brain areas relative to those activated in single-task performance. In a Positron Emission Tomography (PET) study, Klingberg (1998) measured regional cerebral blood flow while participants were engaged in four different task conditions: an auditory working memory task, a visual working memory task, a dual task comprised of these two tasks, and a control task (passive viewing of stimuli). In the auditory working memory task, a brief tone was presented every 2–5 s (Fig. 2A). The participants were asked to continuously compare each tone with a preceding tone and to press a
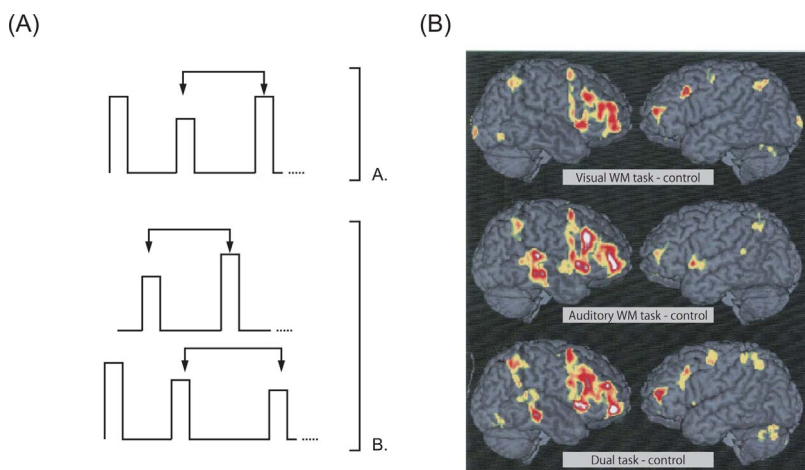
(A)

(B)

Fig. 2. Functional neuroimaging evidence against the presence of brain areas that are specifically activated in the dual-task condition. (A) Schematic diagram of the two component tasks (top) and the dual task (bottom) used by Klingberg (1998). Top: In both the auditory and visual working memory tasks, a stimulus (brief tone or circular visual stimulus, respectively) was presented every 2–5 s. Participants were asked to continuously compare the pitch (or brightness in the visual task) of the current stimulus to that of a preceding one. Bottom: In the dual-task condition, the two working memory tasks were performed simultaneously. (B) Comparison of the increase in rCBF relative to the control condition in the single-task and dual-task conditions showed no dual-task-specific activation throughout the brain including the PFC. In the control condition, the participants passively viewed the stimuli. Top: Visual working memory task minus control. Middle: Auditory working memory task minus control. Bottom: Dual task minus control.
Adapted from Klingberg (1998).

response button if the current tone was lower in pitch than the preceding tone. Similarly, in the visual working memory task, the participants compared the brightness of sequentially presented circular visual stimuli. In the dual-task condition, the participants performed both tasks simultaneously (Fig. 2A bottom). The results demonstrated that, compared to the control condition, both working memory tasks activated common cortical areas in the DLPFC and the ACC. However, no brain area was activated only in the dual-task condition, which suggested that brain areas that are specifically involved in dual-task processing are not present in the frontal lobe (Fig. 2B). Adcock et al. (2000) also reported the absence of dual-task-specific frontal activation during the performance of two kinds of dual tasks, one of which was the same dual task as that used by D'Esposito et al. (1995). Other studies using a variety of dual tasks have shown a similar absence of dual-task-specific frontal activation (Bunge et al., 2000; Erickson et al., 2005; Jaeggi et al., 2003; Just et al., 2001; Newman et al., 2007; Salo et al., 2015).

Some reports have stated that the simple manipulation of task difficulty in a singly-performed perceptual task, the performance of which hardly required complex cognitive control, elicited significant activation throughout the DLPFC (Crittenden and Duncan, 2014; Jiang and Kanwisher, 2003a,b). This activation in the DLPFC included areas that were anterior to, or overlapped with, areas that have been reported to be specifically activated in dual-task performance (Braver and Bongiolatti, 2002; D'Esposito et al., 1995; Koechlin et al., 1999; Sigman and Dehaene, 2008). For example, Crittenden and Duncan (2014) used a simple visual search task, in which participants were asked to indicate the position of the shortest (oddball) of four vertical lines presented on a screen, by pressing the spatially corresponding key in a response box (baseline condition). The difficulty of the task was manipulated in three simple ways: (1) by increasing the number of lines from four to eight (8L condition), (2) by decreasing the difference in length of the shorter line (FD condition), and (3) by changing the stimulus-response mapping using spatially non-corresponding arrangements of response keys (MS condition). They showed that changing from natural to unnatural stimulus response mapping (MS condition) produced the greatest increase in activation throughout the bilateral PFC including the bilateral anterior DLPFC. A similar increase in activation across the rostro-caudal PFC, though more restricted to the left hemisphere, was observed by reducing the difference in the length of the shorter line (FD condition). The authors concluded that complex task demands, such as cognitive branching or comprehension of an abstract task-rule are not the only factors that can recruit the anterior regions of the DLPFC, which has been implicated as the locus of dual-task processing (Burgess et al., 2007; D'Esposito et al., 1995; Koechlin et al., 1999; Koechlin and Summerfield, 2007), and instead such recruitment can occur even with the simple manipulation of task difficulty in perceptual tasks.

Recent fMRI studies have suggested that an increase in the inter-regional synchronization of neural activity mediates dual-task-specific processing requirements (Buchweitz et al., 2012; Mizuno et al., 2012). Buchweitz et al. (2012) compared the strength of the inter-regional synchronization of brain activity between the simultaneous comprehension of two streams of dichotically-presented spoken input (dual-task condition) and the comprehension of a single speech stream (single-task condition). The inter-regional synchronization of brain activity was measured as the correlation between the average time courses of BOLD signal intensity in the three cortical nodes for language processing: the left frontal lobe (Broca's area), the left temporal lobe (Wernicke's area), and the right temporal lobe. As a result, inter-regional synchronization was significantly stronger in the dual-task condition than in the single-task condition: left frontal activation changed between the single-task and dual-task conditions such that synchronization with bilateral temporal areas was increased. These results suggest that the increase in inter-regional synchronization in the dual-task condition is related to the processing of greater and more complex demands placed on the cognitive system that were not present in the single-task condition. In this view, the search for brain regions that are specifically related to dual-task performance should focus on the coherent modulation of activity at the network level, rather than on activity within individual brain areas.

Thus, these human neuroimaging studies support the view that there are no distinct brain areas that are specifically involved in dual-task performance, and instead suggest that the performance of dual tasks depends largely on the interaction between brain areas that are already activated by the individual component tasks themselves.

2.3. Possible reasons for discrepancies

As described above, there is considerable uncertainty regarding the nature of the neural mechanisms that underlie information processing in dual tasks. There has been a longstanding debate on whether distinct brain areas are involved in dual-task-specific processing or such processing occurs in brain areas that have already been recruited in single tasks, and even on whether the assumption of dual-task-specific processes is an appropriate metaphor at all.

There are at least three possible reasons why these issues have not been resolved in human neuroimaging studies. First, despite their significant contributions in the mapping of a dual-task network at the whole-brain level, the relatively coarse spatial and temporal resolutions of neuroimaging techniques (PET and fMRI) are likely to have limited our understanding of the fine details of the neural processes that underlie dual-task performance. This possibility has already been addressed in previous neuroimaging studies. For example, in one PRP study, Jiang and Kanwisher (2003a) raised the possibility that the neural populations that underlie the central bottleneck of response

selection *per se* may be so closely intermingled with those that underlie perceptual processing that these two neural populations cannot be distinguished by fMRI due to limitations in spatial resolution. They also pointed out that if the same neural population performs two or more functions simultaneously, or in close temporal order, it may be difficult to dissociate these functions into temporally distinct processing stages by fMRI due to limitations in temporal resolution.

Second, the differences between the behavioral paradigms used in previous studies may have led to the inconsistent results. By definition, dual tasks can consist of any combination of two component tasks. Therefore, performance in dual tasks that are comprised of highly different component tasks across studies may require different kinds of cognitive processes. In previous studies, there were substantial differences in working memory demands in the component tasks. For example, D'Esposito et al. (1995) used two non-working memory tasks as component tasks, while Klingberg (1998) used two working memory tasks as component tasks. In fact, a comparison of these two studies indicates that this difference in working memory demands in the component tasks caused different degrees of neural recruitment even in the single-task conditions; experiments that used two working memory component tasks showed significant activation across wide brain areas including the LPFC even in the single-task conditions, while those that used two non-working memory tasks tended not to show such an increase in activation.

Third, individual differences in task-proficiency could have resulted in the differential recruitment of brain areas in dual-task conditions. It has been repeatedly shown that extensive training in working memory tasks leads to a decrease in neural activity related to working memory processes (Jansma et al., 2001; Milham et al., 2003; Ramsey et al., 2004). In fact, extensive practice can enhance the automatization of one or both component tasks in a dual task and reduce the dual-task interference effect (Pashler et al., 1993; Passingham, 1996; Ruthruff et al., 2001). Correspondingly, task-related activation patterns across brain regions as measured by fMRI could show significant differences between before and after training of the dual task (Dux et al., 2009; Erickson et al., 2007). Notably, when the same dual task was performed by good and poor performers (i.e., those who showed a weak and strong dual-task interference effect, respectively), dual-task-specific activation in the DLPFC was observed only in the poor performers (Smith et al., 2001). In addition, studies that showed no dual-task-specific activation in the frontal lobe tended to involve no (Bunge et al., 2000) or negligible (Adcock et al., 2000) behavioral interference effect. When the task difficulty was matched across single- and dual-task conditions, a difference in neural activation between these conditions was found only in the sensory areas, and not in the prefrontal areas (Nebel et al., 2005).

Even in studies which reported that no brain areas were specifically activated in dual-task performance, it was often observed that the total volume of significantly activated brain area was larger in the dual-task condition than in the single-task condition (e.g., Klingberg, 1988, Fig. 2B). Furthermore, it was often observed that the brain areas that were commonly activated in both single tasks were more strongly, if not significantly, activated in the dual-task condition. However, these studies still concluded that no brain areas were selectively recruited in the dual-task condition, because voxels that exhibited a dual-task-related increase in activation did not constitute any spatially separate clusters, but were mere extensions of, or parts of, the neural clusters that were activated during single-task performance (Buchweitz et al., 2012). Therefore, based on this observation, together with (1) the limitations in imaging resolution, (2) the differences in behavioral paradigms, and (3) the differences in the participants' performance level across previous studies, we propose a hypothesis that may explain the cause of the inconsistent observations among previous neuroimaging studies: although the processing of dual-task-specific demands depends on distinct neural clusters that are different from those involved in single-task processing, these two neural clusters exist in an interdigitated fashion within overlapping brain regions. Consequently, the limitations in

spatial and temporal resolutions in neuroimaging techniques have made it difficult to distinguish these two neural clusters in different studies that used participants with different performance levels and a wide variety of dual tasks. As we will discuss later, this hypothesis is supported by accumulating neurophysiological evidence in animal studies.

3. Exploring the neural basis of cognitive resource: human studies

Apart from the debate on the presence of dual-task-specific brain areas, another line of research has sought to identify the neural basis of cognitive resource. Cognitive resource has been thought to be limited in capacity, sharable across different kinds of cognitive processes, and reside somewhere in the brain. Prominent theories in cognitive psychology have repeatedly suggested that there is an inseparable relationship between dual-task performance and cognitive resource (Kahneman, 1973; Moray, 1967; Wickens, 1980, 2002). In these theories, cognitive resource is thought to correspond to the brain's information-processing capacity that is shared reciprocally and competitively between simultaneous tasks in a graded manner. Presumably, the amount of available resource defines the upper limit for the amount of information that can be processed at a time, and dual-task interference is thought to occur if two tasks that are accessing this finite resource simultaneously exceed the total amount of available resource. However, it is not clear whether the cognitive resource is comprised of a modality-general (i.e., process-general) resource maintained in a single reservoir (Kahneman, 1973), modality-specific (i.e., process-specific) resources composed of multiple reservoirs (Wickens, 2002), or two independent resources controlled by each cerebral hemisphere (Friedman and Polson, 1981).

The notion that the capacity-limitation in cognitive resource is a determining factor of dual-task interference was first supported by studies using P300 component of event-related potentials (ERPs) (Isreal et al., 1980; Wickens et al., 1983). P300 is usually elicited when participants attend to the low-probability target items (oddball) that are embedded within the presentation sequence of high-probability primary items. P300 is considered to reflect endogenous processes that correspond to participants' internal processes related to stimulus evaluation or categorization. Thus, the amplitude of P300 at a given stimulus indicates the strength of attention directed to that stimulus. Wickens and colleagues measured the amplitude of P300 in the parietal electrode while participants performed a dual task comprised of a primary visual object-tracking task and a secondary visual or auditory stimulus-counting task (Fig. 3). In the visual object-tracking task, a visual target executed a series of horizontal jumps of random distance every 3 s, and the participants were required to manipulate a joystick so that a cursor was superimposed on the moving target. There were three levels of task difficulty: in the easy condition, the movement of the target followed a predictable right-left sequence, and constant displacement of the joystick moved the cursor at a constant velocity; in the intermediate condition, the direction of the target's jumps was unpredictable; in the difficult condition, the direction of the target's jumps was unpredictable, and constant displacement of the joystick accelerated the movement of the cursor. In the secondary stimulus-counting task, participants had to count the number of pre-specified auditory or visual signals among a stream of stimuli. When these tasks were performed simultaneously, as the object-tracking task became more difficult, the magnitude of P300 associated with the presentation of the stimulus for the secondary counting task decreased (Fig. 3). Importantly, when the object tracking task was performed alone, increasing the difficulty of the object tracking task resulted in an enhancement in the amplitude of P300 elicited by the series of horizontal jumps of a visual target. Thus, the decrease of P300 associated with the stimulus for the secondary tasks in the dual-task condition was likely to reflect a process in which some portion of the resource was withdrawn from the counting task and allocated to the primary object-tracking task
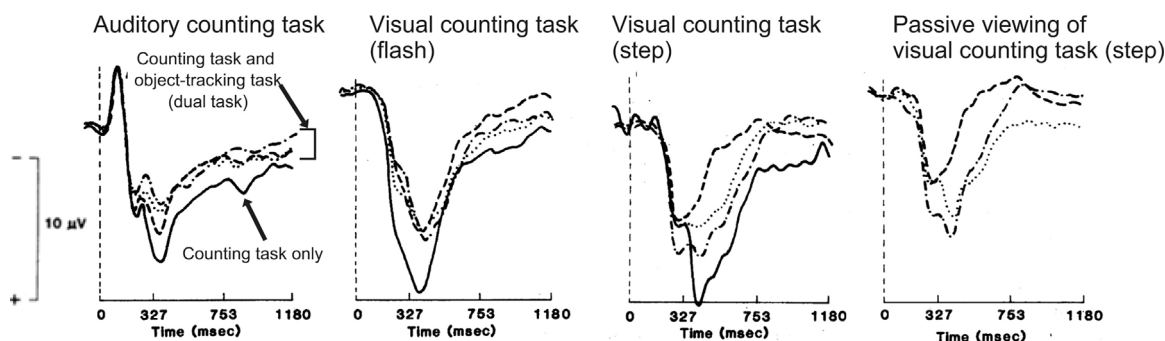
Task conditions

Fig. 3. ERP signals elicited by the presentation of auditory and visual stimulus used in the counting tasks. Data are shown for both the single-task (counting task only) condition (solid line) and the dual-task condition in which the counting task or passive viewing of the visual counting task was performed together with the object-tracking task (dashed lines). Adapted from Wickens et al. (1983).

to cope with the increase in difficulty of the latter.

Similar tradeoffs of ERP signals between two simultaneous tasks have been reported in subsequent studies (for a review, see Kok, 2001). Thus, although these ERP studies did not reveal the neural mechanisms underlying the limitations in cognitive resource, they did provide the initial evidence that the cognitive resource, a widely-held hypothetical construct in psychology, has a neurobiological basis, and that use of the dual-task paradigm is highly effective in examining the neural mechanisms of the cognitive resource.

3.1. Evidence for modality-specific multiple resources: overlap hypothesis

A more specific relationship between dual-task performance and the cognitive resource was proposed in the 'overlap hypothesis' (Kinsbourne and Hicks, 1978; Roland, 1985). The overlap hypothesis postulates that the magnitude of the dual-task interference in a dual task is determined by the 'functional cerebral distance' (i.e., functional similarity) between brain areas activated by each component task alone. If the individual performance of two tasks relies on the activation of common brain regions, there should be a strong competition for resources between the two tasks when they are performed simultaneously, which would give a prominent dual-task interference effect. Using positron emission tomography (PET), Klingberg and Roland (1997) and Klingberg (1998) searched for neural evidence to support the overlap hypothesis. They compared the volume of overlap in cortical activation between two kinds of dual tasks: one dual task consisted of auditory and visual go/no-go tasks, and another consisted of auditory and visual working memory tasks. The rationale underlying the experiment was that, according to the overlap hypothesis, if activations during the individual performance of tasks A and B showed greater overlap of brain activation than those for tasks C and D, then the simultaneous performance of tasks A and B would produce greater behavioral interference than that of tasks C and D. The results confirmed this prediction. At the behavioral level, the dual task that consisted of auditory and visual working memory tasks showed greater performance deficits, as measured by response times and percent correct rates, than the dual task that consisted of auditory and visual go/no-go tasks. At the neural level, although an overlap in activation between the two component tasks in each dual task was observed in many parts of the cortex including the superior and inferior frontal gyri, the degree of overlap was significantly stronger in the dual task that consisted of two working memory tasks than in the dual task that consisted of two go/no-go tasks. Another important finding was that the area that exhibited

a decrease in activation in one component task (e.g., auditory working memory task) never overlapped the area that showed an increase in activation in the other component task (e.g., visual working memory task), suggesting that there was no competition for resource between different processing modalities (e.g., auditory processing vs. visual processing). Similar results have been reported in subsequent studies (Alavash et al., 2015; Herath et al., 2001; Mochizuki et al., 2007; Nijboer et al., 2014). In particular, Nijboer et al. (2014) compared brain activation using three kinds of dual tasks and showed that the degree of overlap in single-task activation patterns correlated with the magnitude of performance decrements in dual-task performance.

Theoretically, the overlap hypothesis and the multiple resource model (Wickens, 2002) make similar predictions. They both suggest the presence of modality-specific, or process-channel-specific, multiple resource reservoirs in the brain. Competition to obtain a necessary amount of resources occurs predominantly within the same neuronal processing channel. Therefore, the recruitment of one particular channel should have little effect on the state of other channels. This notion has been supported by observations in some human psychophysical studies, which demonstrated that the interference between concurrently attended or memorized objects is predominantly restricted within visual quadrants (Carlson et al., 2007) or visual hemifields (Alvarez and Cavanagh, 2005) that are represented by non-adjacent early visual cortices. Similarly, there is behavioral evidence that independent resources are controlled by separate cortical modules, each of which is responsible for processing different categories of high-level visual stimuli (faces, bodies, scenes, or objects) (Cohen et al., 2014). Thus, these results support the notion that cognitive resources are comprised of multiple reservoirs, which reside in functionally and spatially distinct brain regions.

3.2. Evidence for a modality-general single resource: under-additivity of dual-task activation

Although the overlap hypothesis has been supported by several lines of evidence, it has been challenged by opposing evidence of the interdependent modulation of activity between two functionally and anatomically distant cortical areas in some dual tasks. Using fMRI, Just et al. (2001) showed that two highly dissimilar tasks, each of which recruited spatially and functionally discrete cortical areas, interfere with each other at both the behavioral and neural levels in the dual-task condition (Fig. 4). The dual-task used in this study was comprised of two tasks that taxed different processing modalities: an auditory
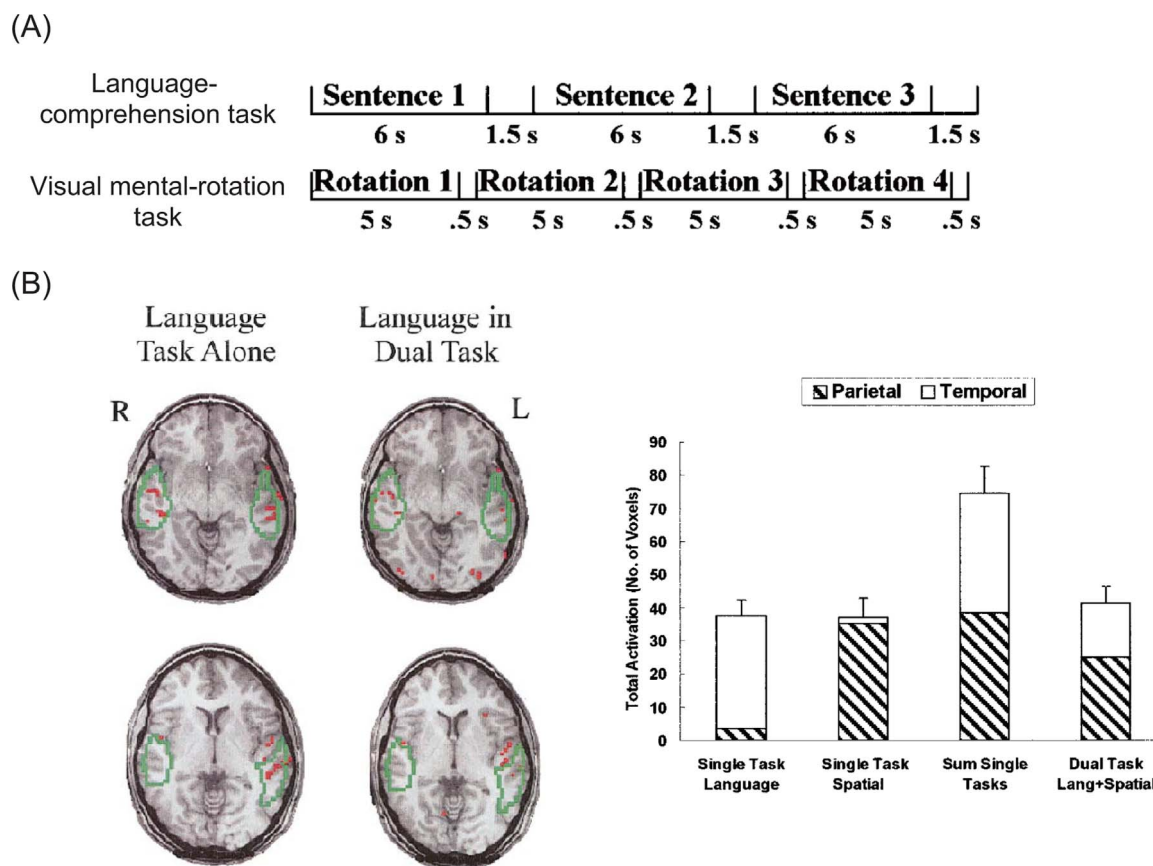
Fig. 4. Evidence for cross-modal dual-task interference in the brain (under-additivity of dual-task activation). (A) Schematic diagram of the timing of the dual-task condition. In the auditory language-comprehension task, participants listened to sentences regarding general knowledge and were asked to make true/false judgements. Each sentence took about 6 s to articulate. In the visual mental-rotation task, participants viewed a pair of complex, 3D figures and were asked to make same/different judgements. Each pair of figures was presented for 5 s. (B) Left: Comparison of brain activation in the temporal cortex ROIs (green border) in the language task between the single-task (left column) and dual-task conditions (right column). In the dual task, the number of activated voxels in the temporal cortex was significantly smaller than that in the single-task condition. Right: In the dual-task condition, the total number of activated voxels (rightmost bar) was significantly less than the sum of the two single-task conditions (second bar from the right). When the two component tasks were performed separately, these two tasks elicited activations in largely non-overlapping brain areas: the language task activated the temporal lobe, and the mental-rotation task activated the parietal lobe (two leftmost bars). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Adapted from Just et al. (2001).

language-comprehension task and a visual mental-rotation task (Fig. 4A). When these tasks were performed separately, activations were observed in discrete areas of the association cortices in a non-overlapping manner, such that the language task activated the temporal cortex, while the mental-rotation task activated the parietal cortex (Fig. 4B). The rationale for the experiment was that if the competition for resource occurs only within the same neuronal processing module, as was suggested by the overlap hypothesis, then the total volume of activation in the dual-task condition should be equal to the sum of the volume of activation that was produced during independent performance of the two component tasks. In contrast, if the simultaneous performance of these two tasks depends on a modality-general cognitive resource, the total volume of activation in the dual-task condition should be less than the sum of the volume of the activation observed during independent performance of the two component tasks. The results showed that, in the dual-task condition, the total volume of activation in the critical brain areas was substantially less than the sum of those observed during independent performance of the two component tasks (Fig. 4B right). This effect has been referred to as 'under-additivity' of the activation in the dual-task condition (Just et al., 2001). The presence of this under-additive effect suggests that, despite the absence of anatomical overlap, language and spatial processing systems operate in an interdependent manner when these systems are recruited simultaneously. In a subsequent study, Just et al. (2008) further demonstrated that the simultaneous performance of a visuospatial driving

task and an auditory language-comprehension task resulted in a decrease in brain activation associated with the performance of the visuospatial driving task, despite the fact that these two tasks recruited largely non-overlapping brain areas when they were performed separately. Similar results have been reported in other studies (Newman et al., 2007; Tombu et al., 2011).

The results of these neuroimaging studies are in line with the observations in some classic behavioral studies in experimental psychology (Posner et al., 1989; Strayer and Johnston, 2001; Sullivan, 1976). These psychological studies demonstrated that, although studies supporting the overlap hypothesis have highlighted strong interference between tasks that use the same processing modality (e.g., Alvarez and Cavanagh, 2005), the behavioral evidence for cross-modal interference is equally strong in dual tasks that use two dissimilar component tasks, such as verbal shadowing and visual detection tasks (Sullivan, 1976), verbal shadowing and visuo-spatial orienting tasks (Posner et al., 1989), and cell-phone conversation and driving, (Strayer and Johnston, 2001).

These behavioral and neuroimaging studies suggest that the assumption that dual-task interference can be explained by the limited capacity of the modality-specific resource is an oversimplification, and instead suggests that some mutual inhibitory mechanisms come into play across anatomically and functionally distant brain areas when these areas are simultaneously recruited in dual-task performance. At a given point in time, there may be an activation quota at the whole-brain

level. When the quota is about to be exceeded in dual tasks, the volume of activation in two discrete brain areas recruited by each component task is regulated via some mutual inhibition mechanisms.

Taken together, previous behavioral and functional neuroimaging studies have not been successful in resolving the debate between the general resource model (Kahneman, 1973) and the multiple resource model (Wickens, 2002). The existing behavioral evidence in experimental psychology indicates that not only two similar tasks but also two dissimilar tasks interfere with each other, and that similar tasks tend to interfere with each other more strongly than dissimilar tasks (Bourke, 1997). Consequently, the results of neuroimaging studies also support both models; while some evidence supports predictions of the overlap hypothesis and the presence of modality- and process-specific multiple resource pools (e.g., Klingberg, 1998), other evidence supports the presence of a task-general whole-brain activation quota, which suggests the existence of as modality- and process-general single resource pool (e.g., Just et al., 2001).

4. Advantages of animal studies in examining neural information processes for dual-task performance

The use of animal subjects in dual-task research should help to clarify the nature of the cognitive resource and the causes of the dual-task interference effect, because various physiological techniques can be used to examine neural activity related to dual-task performance in higher temporal and spatial resolutions. With regard to the question concerning the existence of dual-task-specific brain areas, recordings obtained from single neurons in putative dual-task-specific areas should provide new insights, by clarifying the possibility that dual-task-specific circuits are intermixed with neural circuits for single-task processes. Interventional approaches, including inactivation and electrical stimulation, should enable us to study the causal relationships between the activation of dual-task-specific neural circuits and behavioral performance in dual tasks. With regard to the question concerning the neural basis of cognitive resource, a neurophysiological approach should help us clarify whether dual-task performance affects the activity of task-related brain regions in a manner than could account for the behavioral dual-task interference effect. If the overlap of brain activations in two simultaneous tasks could be observed at the level of single neuron activity, it would constitute unequivocal neurobiological evidence for the notion of resource competition in dual-task performance. The presence of a neuronal activation quota can be directly tested for both within and across functionally distinct brain areas by comparing the firing rate or the strength of selectivity for task-related information between single-task and dual-task conditions. Therefore, although much has been learned from human neuroimaging studies, to more finely characterize the mechanisms that underlie information-processing in dual tasks, knowledge gained from animal models of dual-task performance would be highly useful for addressing the issues that have long been debated in human dual-task studies.

Because the performance of dual-tasks requires complex cognitive processing, it is often presumed that nonhuman animals are not able to perform dual-tasks. To date, dual-task performance in animals has been reported only sporadically (Watanabe and Funahashi, 2015a). However, these pioneering behavioral studies using pigeons, rats, and monkeys have demonstrated that nonhuman animals possess sufficient information-processing ability to perform dual tasks, and paved the way for the use of nonhuman animals in neurobiological investigations (Table 1). In addition, the detailed methods of dual-task training in animals reported in several studies have indicated that nonhuman animals can learn how to perform dual tasks without a prohibitive training time (Kleinman et al., 2016; Moise, 1970; Watanabe and Funahashi, 2015b).

5. Dual-task performance in monkeys

Moise (1970) trained stumptail monkeys in a dual task in which a simple reaction time (SRT) task and a delayed match-to-sample (DMTS) task were performed simultaneously. In the SRT task, monkeys were required to make a speeded manual response when a visual cue was illuminated. In the dual-task condition, the SRT task was repeatedly inserted during a variable delay period (< 30 s) in the DMTS task. In the dual-task condition, the percent correct rate in the DMTS task decreased significantly as the number of inserted SRT trials increased. This detrimental effect of the insertion of SRT trials on the performance of the DMTS task was consistent throughout the weeks of testing, suggesting that the interference effect caused by insertion of the SRT trials reflects basic properties of dual-task processing in monkeys. This study was the first demonstration of a dual-task interference effect in monkeys. Consistent with the evidence in human studies that used similar paradigms (e.g., Peterson and Peterson, 1959), this finding suggests that both performance of the SRT task and the maintenance of short-term memory in the DMTS task taxed a common capacity-limited processing resource, and that the degree of a dual-task interference effect in one component task is determined by the demand of the other concurrent task. Thus, a simple arithmetic regarding the hypothetical cognitive resource appears to hold true in nonhuman animals: at any given moment, there is a limited amount of resource that can be allocated to simultaneous tasks, and as more resource is allocated to one task, less resource is available for the other task.

Washburn and Putney (1998) directly followed this logic, and examined the presence of such a tradeoff relationship between the two component tasks of a dual task using both humans and rhesus monkeys as participants. They used a dual task in which a secondary perceptual judgement task was inserted during the performance of primary tasks (a two-choice discrimination learning task or a same-different task). For both species, response times in the secondary task increased when the primary task became more demanding. This result indicates that the tradeoff in resource allocation in dual-task situations commonly occurs in both humans and monkeys, suggesting that common neural mechanisms underlie cognitive resource allocation in these two species.

Similar results were also reported by Basile and Hampton (2013), who manipulated the difficulty of the two component tasks in a dual task. In this study, a DMTS task was used as a primary task. In the dual-task condition, one of the following four secondary tasks was inserted during the delay period of the DMTS task. These secondary tasks were associated with four levels of mental effort: (1) no secondary task (control); (2) motor-only task, in which monkeys were required to touch a blue square presented at one of the four corners of the screen; (3) image perception task, in which monkeys were required to touch a photograph of a complex image presented in a corner of the screen; and (4) image classification task, in which monkeys were required to classify an image as a flower, fish, bird, or person by touching the corresponding symbol stimulus in one of the four corners of the screen. The difficulty of the primary DMTS task was also manipulated. In the DMTS task, either a set of four images (small-set DMTS task) or a set of 1400 images (large-set DMTS task) was used. In the small-set DMTS task, due to frequent, repetitive presentation of the same images across different trials, a target image could not be distinguished from distractors during the test period based solely on familiarity. In contrast, the large-set DMTS task was less demanding than the small-set DMTS task, because infrequent repetition of a target image made it possible to distinguish it from distractors during the test period based on relative familiarity. The critical finding was that performance of the primary DMTS was disrupted only when a more difficult secondary task was coupled with the small-set DMTS task. The observed effect of the interaction of the difficulties of the primary and secondary tasks on the magnitude of the performance deficit in the primary DMTS task corroborates the tradeoff of resource allocation in dual-task performance, and provides a strong parallel with human dual-task performance.

Table 1
Dual-task studies using animal subjects.

	Species	Tasks
Behavioral studies		
Moise (1970)	Monkey	Visual Delayed Match-to-Sample (DMTS) task + Simple Reaction Time (SRT) task
Maki et al. (1979); Beatty and Shavalia (1980); Roberts (1981); Jarrard and Elmes (1982) and Cook and Brown (1985)	Rat	Spatial Win-Shift (SWSh) radial maze task + SWSh radial maze task
Kendrick and Rilling (1984)	Pigeon	Visual DMTS task + Variable Interval (VI), Extinction (EXT) or Differential Reinforcment of Other behavior (DRO) schedule
Meck and Church (1984) and Matsuo et al. (2016)	Rat	Simultanoues Temporal Processing (STP) task
Harper et al. (1993)	Rat	Serial Probe Recognition (SPR) task + food consumption task
Washburn and Putney (1998)	Monkey	Two-choice discrimination learning task or same-different task + perceptual judgement task
Washburn and Astur (1998)	Monkey	Visual DMTS task + visual object tracking or numerical judgement task
Roberts and Mitchell (1994); Fetterman and Killeen (1995); Leak and Gibbon (1995); Sutton and Roberts (1998); Lejeune et al. (1999); Sutton and Roberts (2002) and Aum et al. (2004);	Pigeon	Variant of STP task
Basile and Hampton (2013)	Monkey	Visual DMTS task + motor, image perception, or image classification task
Smith et al. (2013)	Monkey	Visual DMTS or Delayed Match-to-Place task + perceptual confidence judgement task
Calder and White (2014)	Pigeon	Visual DMTS task + VI schedule
Watanabe and Funahashi (2015b)	Monkey	Memory-guided saccade task + visuospatial attention task
Gray et al. (2016)	Monkey	Visual DNMTS + two-choice object discrimination task, food consumption task or passive viewing of objects
Kleinman et al. (2016)	Monkey	STP task
Neurophysiological studies		
Meck (1987); Olton et al. (1988); Meck and Williams (1997) and Pang et al. (2001)	Rat	STP task
Lebedev et al. (2004) and Messinger et al. (2009)	Monkey	Memory-guided saccade task + luminance discrimination task
Watanabe and Funahashi (2011, 2014)	Monkey	Memory-guided saccade task + visuospatial attention task
Miyazaki et al. (2013)	Monkey	Memory-guided bimanual motor task + visually-guided bimanual motor task
Mansouri et al. (2015)	Monkey	Wisconsin card sorting task + image discrimination task or food consumption task

Recently, two studies have demonstrated that the use of dual-task paradigms in monkeys is effective beyond evaluating tradeoff relationships concerning the allocation of cognitive resources between two simultaneous mental processes. In the first study, Smith et al. (2013) applied the methodology of dual-task dissociation to examine whether or not a cognitive function of interest ('metacognitive' processing in monkeys) could be dissociated from another function (lower-level perceptual processing). The monkeys were required to perform a metacognitive task involving a perceptual sparse-dense discrimination of a static random-dot patch, within which a third, 'uncertain', response let them opt out of difficult trials, or a 'middle' response let them identify stimuli with intermediate dot density at their own initiative. In the dual-task condition, this metacognitive task was inserted during the retention period of a visual DMTS task or a visuo-spatial short-term memory (STM) task. The rationale of the experiment was that if the uncertain response and sparse-middle-dense response were dependent on different levels of information processing, these two responses would be affected differently by the addition of concurrent DMTS and STM tasks. The result showed that the addition of these tasks dramatically reduced the number of uncertain responses, while leaving intact the use of perceptual sparse-middle-dense responses. Based on this result, the authors suggested that the uncertain response reflected higher-level cognitive assessments about the indeterminacy of perceptual discrimination (i.e., confidence), while differentiating this process from merely perceptual sparse-middle-dense responses. Although, in a more parsimonious interpretation, the observed dissociation between the uncertain response and sparse-middle-dense response does not directly confirm that the use of uncertain response in monkeys is stemmed from the operation of some 'higher-order' metacognitive processes, this study clearly demonstrated that the methodology of dual-task dissociation is applicable to nonhuman primates. The methodology of dual-task dissociation has played an essential role in identifying the modular organization of human cognitive systems, the most prominent case of which

is the characterization of subcomponents of human working memory systems (Baddeley and Hitch, 1974). The study by Smith et al. (2013) strongly suggests the effectiveness of examining functional modularity of working memory systems in nonhuman animals by using dual-task paradigms that are analogous to those originally used in human working memory experiments.

In the second study, Gray et al. (2016) adopted the dual task used by Basile and Hampton (2013) within their battery of multiple executive tasks to examine whether the three major separable components of central executive functions proposed in human studies (Miyake et al., 2000), i.e., mental set shifting ('Shifting'), information updating and monitoring ('Updating'), and inhibition of prepotent responses ('Inhibition'), are also dissociable and independently impacted by normal aging in monkeys. While earlier studies in marmosets have shown that mental set-shifting was independent of inhibition (Dias et al., 1996), and that these two independent components of central executive functions correlated independently with phenotypic variations of trait anxiety (Shiba et al., 2014), Gray et al. (2016) approached this problem by using the dual-task paradigm.

The authors used two cohorts of bonnet monkeys: young (mean age: 10.5 years) and aged (mean age: 23.4 years) groups. In the dual-task condition, the monkeys had to perform a delayed nonmatch-to-sample (DNMTS) task as a primary task, while three different levels of secondary-task interference were inserted in a 30-s delay period of the DNMTS: (1) an 'Interruption Condition', in which the monkeys had to perform a two-choice object discrimination task involving four pre-learned object pairs, (2) a 'Relevant Distraction Condition', in which the monkeys had to displace a single object for a food reward, and (3) an 'Irrelevant Distraction Condition' in which a single object was presented to the monkeys behind a transparent barrier. This DNMTS dual-task paradigm has been used in human studies, and is known to tax the attentional updating and monitoring component of the central executive functions (Clapp et al., 2011; Clapp and Gazzaley, 2012). In a

critical comparison of this study, the authors compared animals' performance in this dual task to that in another executive task, an object reversal learning task, which is known to tax the shifting component of the central executive functions (Fellows and Farah, 2003; Izquierdo et al., 2016). In this object reversal learning task, the monkeys were first required to learn 40 object discrimination problems that were presented once per session in the same order across days (sessions). After the monkeys learned which object in the pair was rewarded, the object-reward association was reversed (reversal learning phase), and the monkeys had to learn this novel association. Behavioral performance in this task was measured as the number of days required to learn the reversed object-reward association. The result showed that, although the young group showed better performance than the aged group in both the DNMTS task under the 'Interruption Condition' and the object reversal learning task, there was no significant correlation between the performance levels in these two tasks in either group. The authors concluded that, as in humans, information updating, and monitoring and mental set shifting are separable functions in monkeys, and these two functions are impacted differently by normative aging.

6. Dual-task performance in rats and pigeons

It has been shown that rats are capable of performing dual tasks, and that their dual-task performance typically exhibits dual-task interference. For example, in a dual radial-maze task, in which a secondary win-shift radial-maze task was inserted during the performance of a primary win-shift radial-maze task, spatial memory for a primary maze was disrupted only when the primary maze involved a large number of to-be-remembered arms and the secondary maze required a substantial number of arm-visits (Cook and Brown, 1985; Roberts, 1981). Interference between the two mazes was not observed if either the primary or secondary maze had a small number of arms (Beatty and Shavalia, 1980; Maki et al., 1979).

The robust capability of rats in timing behavior has also been used to study dual-task performance (Meck and Church, 1984; Olton et al., 1988). These studies used a simultaneous temporal processing (STP) task in which rats had to time two different intervals. The STP task is a variant of the trial-discrete fixed-interval (FI) reinforcement schedule that involved the successive presentation of two sensory stimuli (e.g., white noise and house light), each of which was associated with a different FI reinforcement schedule (e.g., 10 and 20 s). The interval timing of the shorter FI was embedded within that of the longer FI, and rats were required to simultaneously time two different intervals. An analysis of behavioral performance in the STP task showed that rats could simultaneously time both intervals without significant interference. Further investigations that used longer intervals (i.e., 10 s vs. 40 s, and 10 s vs. 50 s) also showed that rats can simultaneously time two different intervals virtually without interference (Matsuo et al., 2016; Pang et al., 2001).

In pigeons, dual-task performance has been investigated using variants of the STP procedure. In some cases, the dual-task situation has led to the deterioration of timing performance, which is suggestive of resource tradeoff between the interval-timing task and other simultaneous tasks (Aum et al., 2004; Lejeune et al., 1999; Sutton and Roberts, 2002). In other cases, pigeons were capable of performing an interval timing task together with other temporal (Fetterman and Killeen, 1995; Leak and Gibbon, 1995) and non-temporal tasks (Roberts and Mitchell, 1994; Sutton and Roberts, 1998) without interference. Recently, Kleinman et al. (2016) adapted the STP procedure for use in rhesus monkeys. The monkeys were trained to time two different intervals (8 and 16 s) simultaneously by using saccadic eye movement for a behavioral report. The results showed that the monkeys could simultaneously time two different intervals highly accurately with only weak dilation of time perception for the second interval.

7. Neurophysiological investigation of dual-task processing

7.1. Neurophysiological investigation using rats

An early neurophysiological experiment in animals performing dual tasks was performed by Olton et al. (1988), who investigated the effect of circumscribed brain lesion on the performance of rats in the simultaneous temporal processing (STP) task. Normal rats could effectively divide their attention between the two stimuli and demonstrated a robust ability to time each stimulus in parallel. However, lesion of the lateral agranular frontal cortex (FC), which the primary motor cortex with a somatotopic representation in rat, induced a severe deficit in the STP task. When a second stimulus (short stimuli) was presented during timing of the first stimulus (long stimuli), the FC lesioined rats only attended to and timed the second stimulus correctly. In contrast, the lesion did not affect their ability to time each stimulus separately. These findings suggest that the rat lateral agranular FC plays a critical role in the rat's ability to attend to two stimuli simultaneously.

A subsequent single-unit recording experiment using the STP task (Pang et al., 2001) demonstrated that a large proportion of FC neurons (30% of all recorded neurons, corresponding to 60% of task-related neurons) showed activity modulation during the simultaneous interval timing of two stimuli ('compound short' and 'compound long' conditions; Fig. 5A, left), but not during the timing of either stimulus alone ('simple short' and 'simple long' conditions). Importantly, this dual-task-specific activation of FC neurons was triggered by the onset of the second stimulus associated with the shorter of the two FI schedules, corresponding to the onset of the period when simultaneous timing of the two stimuli was required. This suggests that the activity of these neurons reflects the behavioral requirement of dividing attention in the dual-task situation. Nevertheless, as Pang et al. (2001) pointed out, the dual-task-specific activation in type 1 neurons continued even after termination of the period when simultaneous timing of the two stimuli was required. This leaves open the possibility that type 1 neurons are not directly involved in the division and allocation of attention in the dual-task situation, but rather their activation reflects an increase in behavioral motor activity associated with a lever-press response (see Fig. 1 in Pang et al., 2001), or the integration of inputs from dual-task-specific neurons in other brain areas.

Another important finding was that these dual-task-specific neurons ('Type 1' neurons, Fig. 5A, right) did not form an independent cluster in a circumscribed sub-region of the FC, but rather, across the entire FC, type 1 neurons existed in an interdigitized fashion among neurons that showed response patterns that were not specifically related to dual-task performance (type 2, 3, and 4 neurons). These non-dual-task-specific neurons showed activity modulation in both the single- and dual-task conditions (type 2), in one of the two single-task conditions and in the dual-task condition (type 3), or only in one of the two single-task conditions (type 4). Thus, the coexistence of dual-task-specific type 1 neurons and other neuron types in the rat FC suggests the possibility that dual-task processing depends on distinct neural circuits comprised of neurons such as type 1 neurons, but critically, the dual-task-specific neural circuits are not localized to spatially separate brain areas relative to neural circuits involved in single-task processing.

Psychopharmacological experiments conducted using the STP paradigm have suggested that specific neurotransmitter systems such as the cholinergic system may be important for the effective parallel processing of temporal information. Prenatal choline supplementation improved the performance in the simultaneous interval timing of two stimuli, presumably by increasing the speed of signal processing in brain regions related to attention and memory. In contrast, prenatal choline deprivation induced deficits in STP performance (Meck and Williams, 1997). The administration of vasopressin, which is known to increase and maintain the level of acetylcholine in the central nervous system, also facilitated STP performance (Meck, 1987). In addition, lesions of the nucleus basalis magnocellularis (NBM), which contains a
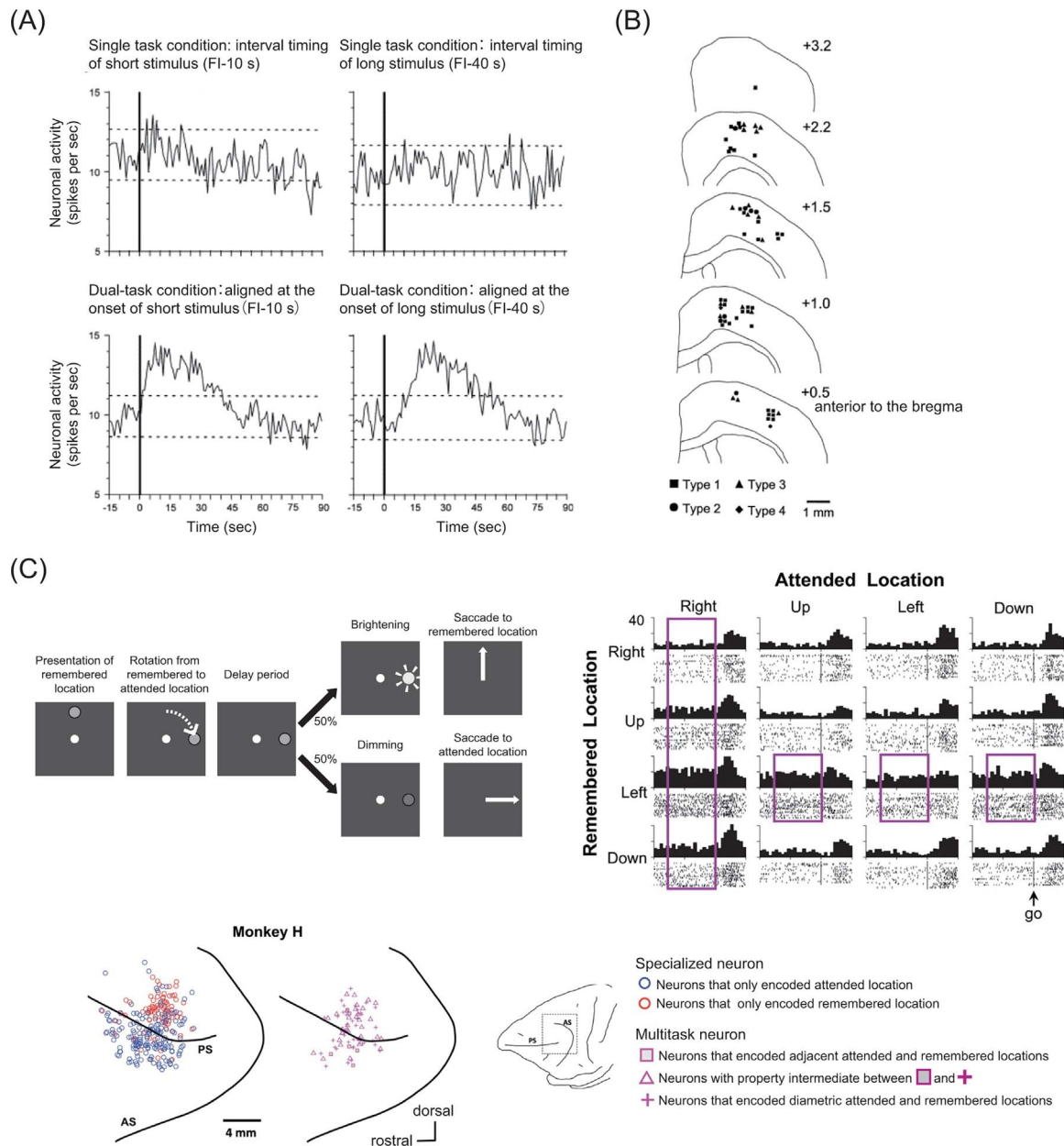
Fig. 5. Neurophysiological evidence for the presence of neural circuits specifically related to dual-task performance. (A) An example of a rat FC neuron that was specifically activated in the dual-task condition (compound short and long), but did not respond to either single-task condition (simple short and long). The short stimulus was associated with a fixed interval of 10 s (FI-10) and the long stimulus was associated with FI-40. Histograms are aligned at the onset of the stimulus. The two dotted horizontal lines indicate the 95% confidence interval of the mean spike rate in the baseline period (−15 to 0 s relative to stimulus onset). (B) Location of 60 task-related neurons recorded from nine rats. The distribution of Type 1 (i.e., dual-task-specific) neurons (square) overlapped those of other non-dual-task-specific neurons (Types 2, 3, and 4). Adapted from Pang et al. (2001). (C) Activity of the monkey LPFC in a dual-task-like situation. Top left: Schematic diagram of the task. Top right: An example of a 'hybrid' neuron that encoded both the attended and remembered locations with a diametric spatial preference. Bottom: Location of hybrid (purple) and specialized neurons (blue and red) in the LPFC. Hybrid neurons did not form a cluster that was spatially separate from specialized neurons.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Adapted from Lebedev et al. (2004) and Messinger et al. (2009).

population of cholinergic neurons that innervate the entire neocortex including the lateral agranular FC (Rye et al., 1984; Wenk, 1997), produced deficits in STP performance while leaving the ability to time each stimulus separately (i.e., single-task performance) unaffected. This effect was comparable to that of lesion in the agranular FC (Olton et al., 1988).

Although it is still not clear whether the agranular FC and the nucleus basalis magnocellularis are the only brain regions in rats that play a crucial role in divided attention in support of parallel temporal processing, these findings represent an important demonstration that investigation of the neural mechanisms underlying dual-task performance

is well within the scope of a systems neuroscientific approach using nonhuman animals. Further investigations with the rodent STP paradigm may help us clarify how this animal model relates to the mechanisms underlying human dual-task performance. It remains to be seen whether the rat medial prefrontal cortex, a putative homologue of the primate lateral prefrontal cortex (Seamans et al., 2008; Uylings et al., 2003; but see, Passingham and Wise, 2012), and the hippocampus, an area which is known to participate in temporal information processing (Meck et al., 1984; Nakazono et al., 2015), contain neurons that exhibit dual-task-specific modulation, the duration of which corresponds to the time epoch in which there is a behavioral demand for

dual-task processing. A comparison of the anatomical distribution of dual-task-specific neurons to that of neurons involved in a single-task process alone across these brain regions would be of particular interest.

7.2. Neurophysiological investigation using monkeys

In monkeys, Wise and colleagues investigated neural mechanisms in the lateral prefrontal cortex (LPFC) underlying effective parallel processing in dual-task-like situations (Fig. 5B) (Lebedev et al., 2004; Messinger et al., 2009). In their task, while monkeys looked at a fixation point at the center of a screen, a visual cue was first presented at one position (remembered location) and then revolved around the fixation point to the second position (attended location) (Fig. 5B, top left). Because brightening or dimming of this cue that occurred after a few-second delay period indicated whether the monkeys should make a saccade to the remembered or the attended location, respectively, monkeys were required to attend to a visual cue at the second position while remembering the first position during the delay period. While this task design differs from the dual tasks described earlier in rhesus monkeys that employed two independent tasks, each of which involved a distinct goal with unique stimulus-response association (e.g., Basile and Hampton, 2013), this task design did required the monkeys to engage in separate attentional and mnemonic processing. Thus this task taxed the ability to engage in parallel processing of two independent streams of information, which is the hallmark of dual-task processing. Thus, this task enabled the researchers to investigate the prefrontal activity related to dual-task processing. The authors found that besides 'specialized' neurons that encoded either the remembered or the attended location, the monkey LPFC contained a population of 'hybrid' neurons that encoded both remembered and the attended locations simultaneously (Fig. 5B, top right). Hybrid neurons exhibited several computational advantages over specialized neurons in parallel spatial-processing required in this task: (1) hybrid neurons encoded different (often diametrically opposite) locations for attention and memory, and exhibited stronger spatial tuning than specialized neurons, (2) ensembles of hybrid neurons gave significantly higher accuracy in decoding both the remembered and the attended locations in a given trial than ensembles of specialized neurons of the same size, suggesting that hybrid neurons represented task relevant information more efficiently than either type of specialized neurons. While it has been established that the monkey LPFC contains many neurons that can encode, in single-tasks situations, a conjunction of more than one location (Inoue and Funahashi, 2002), object (Warden and Miller, 2007), or both (Rao et al., 1997), the properties of hybrid neurons were different, in that hybrid neurons could represent remembered and attended locations independently of each other. Thus, dual-task resilient information processing may be mediated by the activities of hybrid neurons in the LPFC that encode information for two concurrent tasks independently and more efficiently than populations of specialized neurons of the same size, and this view corroborates findings in human studies which suggested that the LPFC plays a crucial role in resolving interference between two simultaneous tasks through adaptive task coordination (Baddeley et al., 1997; D'Esposito et al., 1995).

Messinger et al. (2009) reported that hybrid neurons comprised 17% of all recorded neurons, corresponding to 30% of task-related (i.e., spatially-tuned) neurons in the monkey LPFC. Although, due to the differences in behavioral paradigms and recording areas, this result cannot be directly compared with those obtained in the rat primary motor cortex (FC) in the STP paradigm (Pang et al., 2001), the proportion of hybrid neurons in the monkey LPFC was much lower than that of type 1 neurons in the rat FC (30% of all recorded neurons) (Pang et al., 2001). In addition, it is not clear whether hybrid neurons in the monkey LPFC have the same function as type 1 neurons in rat, because the activity of hybrid neurons in the monkey LPFC has not been examined under single-task conditions. Dual-task-specific neurons, by definition, should exhibit task-relevant selectivity only during the time

period in which cognitive multitasking is required. Thus, it remains to be seen whether specialized and hybrid neurons in the monkey LPFC show task-related activation in the single-task condition. If, for example, hybrid neurons do not show activity modulation in the single-task condition, it can be concluded that the activity of hybrid neurons underlies information processes specifically related to dual-task performance.

Nevertheless, the critical finding reported by Messinger et al. (2009) is that in the monkey LPFC, locations of hybrid neurons did not differ significantly from those of specialized neurons, which indicated that both hybrid neurons and specialized neurons did not form a cluster that was spatially separate from each other (Fig. 5B, bottom), indicating that neural populations for hybrid neurons. Thus, If these hybrid neurons indeed correspond to the hypothesized dual-task-specific neurons, this result would help to reconcile a long-standing debate regarding the presence of anatomically distinct dual-task-specific brain areas (D'Esposito et al., 1995; Klingberg, 1998). On one hand, the overlap of the anatomical distributions of hybrid and specialized neurons suggests the presence of dual-task-specific neural processes (e.g., D'Esposito et al., 1995). On the other hand, it can also explain the absence of spatially separate dual-task-specific regions in the LPFC in some neuroimaging studies (e.g., Klingberg, 1998). Given the relatively small proportion (17%) of hybrid neurons among all recorded samples (Messinger et al., 2009), it is conceivable that, during dual-task performance, such anatomical configurations in the LPFC would show a moderate increase in activity at the macroscopic level, as observed in neuroimaging studies which had reported the absence of a dual-task-specific area in the PFC. Further neurophysiological investigations in monkey behavioral dual-task models could shed new light on this issue. The important next step would be to determine whether hybrid neurons are specifically activated during dual-task performance by examining the activity of hybrid neurons in the single-task condition.

In addition to the question regarding the presence of dual-task-specific neuronal activity, another line of single-neuron recording studies attempted to elucidate the neural basis of the hypothetical cognitive resources. Watanabe and Funahashi (2011, 2014) tested the validity of the overlap hypothesis by comparing neuronal activities in the monkey LPFC in single-task and dual-task conditions (Fig. 6). The recording was done in the posterior third of the principal sulcus including the prearcuate region, the area similar to that investigated in Lebedev et al. (2004) and Messinger et al. (2009). In this experiment, monkeys were required to remember the location of a visual cue that was briefly presented in the far-peripheral visual field for a memory-guided saccade that could only be executed after the end of the memory delay period (memory task). At the same time, they were required to attend to a small circle presented at various locations on the monitor until partway through the memory delay period, and make a lever-release response upon detecting a slight change in its color (attention task) (Fig. 6A). Furthermore, to examine the load-dependency of the dual-task interference effect, the difficulty of the attention task was parametrically manipulated by varying the location of a to-be-attended circle. Performance of the memory and attention tasks is known to require an intact LPFC (Funahashi et al., 1993; Rossi et al., 2007) and recruits the activation of many LPFC neurons (Funahashi et al., 1989; Kadohisa et al., 2013; Spaak et al., 2017). Therefore, it was expected that the simultaneous performance of these two LPFC-demanding tasks would cause an interference effect, because the monkeys would be required to engage in the processing of two simultaneous tasks that overlapped with respect to both time and processing modality. The rationale of the experiment was that if the LPFC is related to the dual-task interference effect, sustained delay-period activity in the LPFC that represents a memory trace of cue stimuli for the memory task (Funahashi et al., 1989; Kubota and Niki, 1971; Watanabe et al., 2006; Watanabe and Funahashi, 2007) would show different activities depending on the difficulty of the simultaneously performed attention task.
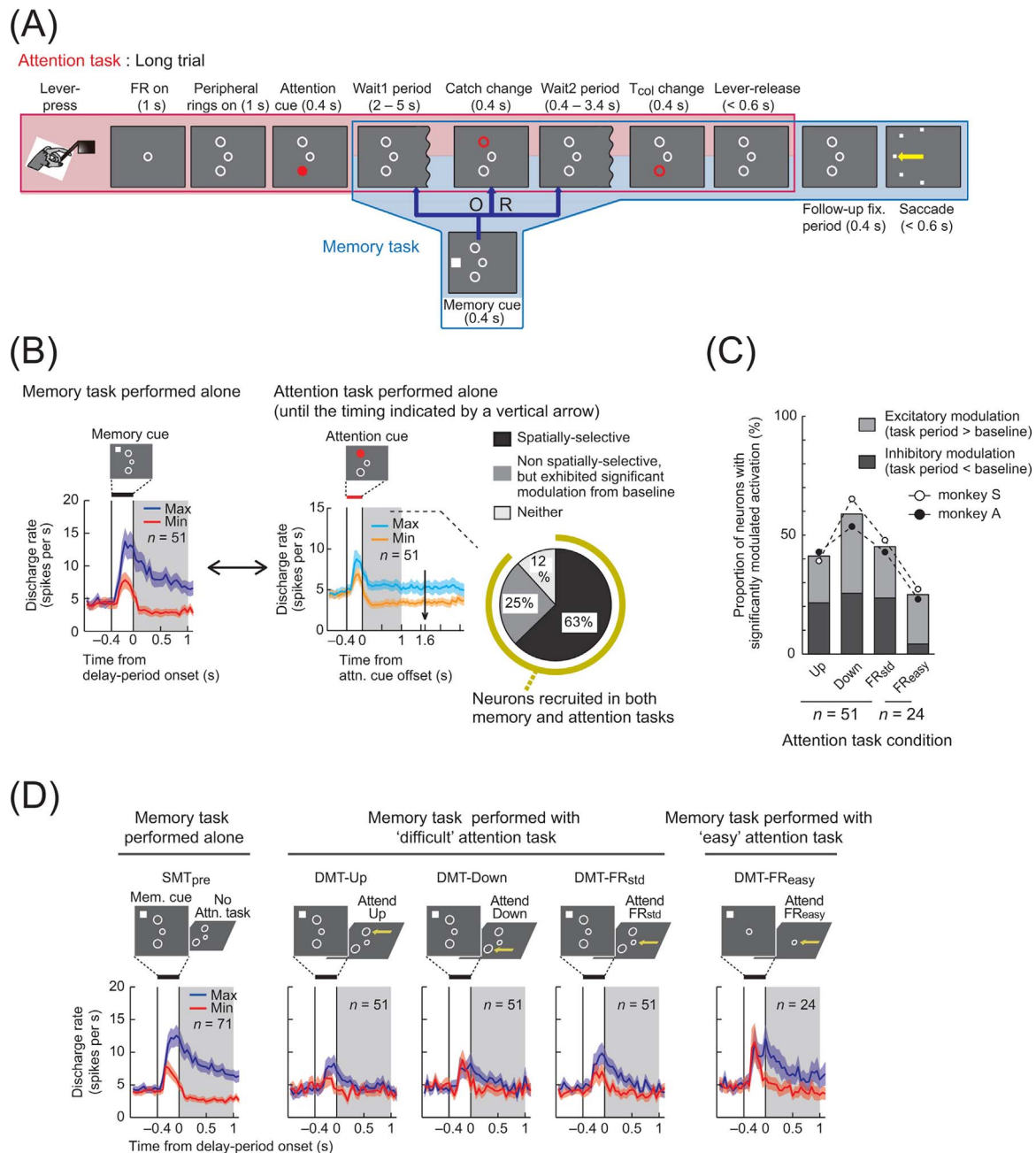
Fig. 6. Neuronal substrates of capacity-limited cognitive resources in the primate PFC. (A) Schematic diagram of the tasks. Top: Attention task (single-task condition). Middle: Memory task (single-task condition). Bottom: Dual-task condition. After completion of the attention task component, monkeys were required to make a memory-guided saccade to the location that had been indicated by a memory cue. Fixation on the fixation ring (FR) was required throughout the trial. (B) Neuronal evidence supporting the overlap hypothesis. In the single-task conditions, most (88%) LPFC neurons that encoded the location of the memory cue in the delay-period of the memory task (grey-shaded area in the left histogram) also encoded the location of the attention cue in the attention task (grey-shaded area in the right histogram). The simultaneous performance of these two tasks resulted in a significant behavioral dual-task interference effect. (C) Proportion of memory-task-related neurons that were also recruited in each of the four attention task conditions. The degree of recruitment overlap between the memory and attention tasks changed as a function of the difficulty of the attention task. When the memory task was coupled with the easiest attention task condition (FR$_{easy}$), the overlap of neuronal recruitment was smallest, which coincided with the weakest manifestation of the dual-task interference effect at both the behavioral (as in Fig. 2c in Watanabe and Funahashi, 2014) and neuronal levels (as in panel (D)). (D) Population averaged delay-period activity (grey-shaded area) in the five memory task conditions. Greater attenuation of mnemonic delay-period activity was observed when the memory task was concurrently performed with more difficult attention task conditions.
Adapted from Watanabe and Funahashi (2014).

As predicted, this dual task produced a typical pattern of dual-task interference in memory task performance that scaled with the difficulty of the attention task component. Memory task performance was impaired by the addition of an attention task component, and a more difficult attention task produced greater impairment. Analyses of LPFC neuron activities showed that both memory and attention tasks recruited the activation of a largely overlapping LPFC neuronal population (Fig. 6B). In agreement with the overlap hypothesis, the degree of

overlap in the neuronal recruitment by the two tasks was correlated with the magnitude of the behavioral dual-task interference effect; the condition that showed greater behavioral interference showed a higher degree of recruitment overlap (Fig. 6C). Critically, sustained delay-period activities that encoded the location memorandum for the memory task were significantly attenuated by the concurrent attention task, and greater attenuation was observed under a more difficult attention task condition associated with a higher degree of recruitment

overlap (Fig. 6D). These results suggest that cognitive resources, at least those associated with spatial processing, are represented in the brain as limitations in the computational capacity of single neurons in the LPFC. These results support the overlap hypothesis (Klingberg, 1998; Passingham, 1996) by demonstrating that the dual-task interference effect is likely to originate in competitive, overloaded recruitment of an overlapping LPFC neuronal population by two concurrent tasks.

The mechanisms of interference proposed by the overlap hypothesis have also been corroborated by evidence from recent single-unit recording experiments that investigated the neural basis for visual short-term memory for locations (Matsushima and Tanaka, 2014) and objects (Buschman et al., 2011). These studies showed that when two locations or object memoranda were presented in the same visual hemifield, stimulus selectivity among the monkey LPFC neurons was significantly attenuated relative to when the two cues were presented in different hemifields. Considering the anatomical evidence that information from different visual fields reaches interdigitized, but spatially distinct, columns in the monkey LPFC (Goldman-Rakic and Schwartz, 1982), these results strongly suggest that the competitive interaction of multiple representations occurs only when these representations are held by the same neuronal population.

Thus, accumulating neurophysiological evidence suggests the possibility that the mechanisms of interference proposed by the overlap hypothesis can be generalized to the mechanisms underlying the limitation of neuronal representational capacity and consequent loss of behavioral performance in various types of complex cognitive tasks.

Recently, based on the framework of the overlap hypothesis, Marcos et al. (2017) examined whether cross-modal behavioral interference between the estimation of space and time could be explained by the magnitude of overlap of activation in the LPFC. In this study, the monkeys were trained to report which of two visual stimuli (blue circle and red square) was presented longer than the other (the duration discrimination task) and which had greater distance from the fixation spot (the distance discrimination task). The monkeys performed these tasks separately. The recording was done in the posterior half of the principal sulcus and the periarcuate region. While the monkeys performed these single tasks, the authors identified two independent neural populations participating in the estimation of distance and duration and concluded that the cross-modal interference between time and space perception cannot be explained by the activity of LPFC neurons. This result, however, is based solely on the analysis of neuronal activity in the single-task performance. The investigation of how these two independent neural population would react in the dual-task condition, in which the monkeys are required to encode both duration and distance of the stimuli and indicate duration or distance judgement based on the second instruction cue, would be another good test for the overlap hypothesis.

8. Future directions

Emerging neurophysiological evidence in animal models of dual-task performance are beginning to provide a unique window into the neural mechanisms of cognitive multitasking and the nature of hypothetical cognitive resources. Some studies have provided evidence for the presence of neural circuitries devoted to the dual-task-specific information-processing demand (Lebedev et al., 2004; Messinger et al., 2009; Olton et al., 1988; Pang et al., 2001). These dual-task circuits have been shown to be interwoven within the neuronal circuits for single-task processing in the PFC. Further investigations in animal models may reconcile the long-standing debate in human studies concerning the presence of brain areas specifically involved in dual-task processing. Another line of studies that focused on the neuronal underpinnings of performance limitation in dual tasks (Watanabe and Funahashi, 2011, 2014) and multiple-item working memory tasks (Buschman et al., 2011; Matsushima and Tanaka, 2014) has identified neurobiological substrates of the hypothetical cognitive resource as the

total amount of neuronal selectivity representing task-relevant information in the PFC. Such neuronal selectivity was shown to be capacity-limited and sharable across multiple concurrent tasks or task contents. This finding appears to support the overlap hypothesis of the dual-task interference effect (Kinsbourne and Hicks, 1978; Roland, 1985). In relation to the recent debate on whether working memory is held by sustained firing of neurons in the fronto-parietal network or other mechanisms (Constantinidis and Klingberg, 2016), further investigations into neuronal activity in these behavioral paradigms may provide new insights, because the majority of neurophysiological studies conducted so far on this issue have used single-item working memory tasks in single-tasking situations.

Despite these intriguing new findings in animal studies, clearly there is still much work to be done. For example, the available neurophysiological evidence so far appears to support the presence of both a dual-task-specific neuronal process (Lebedev et al., 2004; Messinger et al., 2009) and a moment-to-moment quota of neuronal selectivity allocated to tasks at hand (Buschman et al., 2011; Watanabe and Funahashi, 2014). However, it would be natural to deduce that these two neuronal processes would have opposite effects on dual-task performance, such that the former would facilitate, and the latter would impose a limitation on, dual-task processing. It will be important to investigate how these two seemingly opposing mechanisms interact with each other in brain areas that are related to dual-task performance.

Another important issue is to clarify the presence or absence of the whole-brain activation quota at the level of single-neuron activity. To this end, it will be necessary to expand the repertoire of behavioral dual-task paradigms in animal neurophysiology. All of the existing dual-task neurophysiology studies in animals have used a combination of two similar tasks that tax the same processing modality. Future studies in animals should involve dual tasks comprised of two highly dissimilar tasks (e.g., an auditory DMTS task and a spatial delayed response task), because the hypotheses regarding the presence of a whole-brain activation quota and the presence of general resources can only be tested by using a combination of highly dissimilar component tasks that activate non-overlapping brain regions.

The proposal that interregional activity synchronization plays an important role in coping with intensified processing demands in dual-task situations (Buchweitz et al., 2012) is directly amenable to neurophysiological investigation using the simultaneous recordings of neuronal activities from multiple brain areas. A task-related increase in synchronization has been observed between prefrontal and posterior brain areas in monkeys in a variety of cognitive tasks such as attention (Buschman and Miller, 2007), decision-making (Pesaran et al., 2008) and working memory tasks (Salazar et al., 2012). Therefore, an examination of neural synchrony across multiple brain areas may provide important clues regarding the role of synchronization in dual-task processing.

At the level of experimental design, we propose that future studies should include comparisons of neuronal activity among (1) a single-task condition, (2) an easy dual-task condition without behavioral interference, and (3) a difficult dual-task condition with behavioral interference. The comparison of neuronal activity between the first and latter two conditions should enable us to directly examine whether dual-task-specific neural circuitry coexists with the neural circuit for single-task processes in an interdigitated manner. The comparison of dual-task conditions with and without behavioral interference should allow us to clarify the long-standing debate as to whether the loss of behavioral performance due to the increased task-difficulty can be attributed to (1) competition for neuronal recruitment and consequent overloading of the overlapping neuronal population (e.g., Klingberg and Roland 1997), or (2) the malfunctioning of dual-task-specific neuronal processes (e.g., Baddeley et al., 1997).

The framework for future studies presented so far has highlighted possible directions to resolve the existing debate. It will also be important to study the wider context within which the functional

significance (i.e., benefit) of cognitive capacity limitation is characterized. Previous studies, implicitly or explicitly, tended to regard capacity limitation as an intrinsic defect in cognition. However, if greater capacity is advantageous in the competition for survival, why does our cognition have a severe capacity limitation as a product of evolution? This question has been largely neglected in the previous literature. However, there have been a few intriguing proposals (Miyake and Saito, 2001; O'Reilly et al., 1999). For example, O'Reilly et al. (1999) suggested that the presence of capacity limitation avoids the unrestrained representation of information that is irrelevant to the current goal, and thus promotes focused and coherent information processing. Without such constraints, even one simple goal would not be efficiently accomplished, due to unrestrained 'runaway activity'.

Related to this proposal, Duncan et al. (1996) showed that patients with major damage in the frontal lobe often exhibit a form of performance failure that they termed *goal neglect*. A person with goal neglect often ignores some task requirement during the performance of complex tasks, although he or she is able to describe the requirement *per se* that had slipped out of their mind. This is consistent with the recent finding in a nonhuman primate study that sustained neuronal activity in the LPFC representing a particular sub-goal is elevated only when the immediate next requirement corresponds to the execution of that sub-goal, while this activity undergoes significant suppression when the current task context required that sub-goal to be maintained in the background (Watanabe and Funahashi, 2014). Similar observations have been reported in human neuroimaging studies (Lewis-Peacock et al., 2012; Wolff et al., 2015). Thus, the LPFC appears to play a key role in the timely and focused activation of a current goal, which is critical for the smooth execution of complex behaviors that are comprised of multiple sub-goals. In this context, the presence of capacity limitation appears to be beneficial because it will naturally act in the direction of avoiding the limitless activation of irrelevant goals if the subject can construct an appropriate capacity-allocation policy.

A recent lesion study in a nonhuman primate suggested that the making of an appropriate capacity-allocation policy is mediated by the frontopolar prefrontal cortex (Mansouri et al., 2015). This study showed that when a novel, secondary goal is inserted during pursuit of the primary goal, the frontopolar PFC plays an essential role in the reorientation of attention from the current goal to a novel goal to effectively explore the new goal. This finding is consistent with the observation in some human studies that the activity of the frontopolar PFC plays an important role in cognitive branching that requires the halting of current-goal processing to respond to new environmental demands (Domenech and Koechlin, 2015; Koechlin et al., 1999). Thus, it appears that, in contrast to the LPFC, which is important in focusing the limited resource onto the most relevant goal at hand, an important function of the frontopolar PFC is to juggle between several, temporally distant goals by guiding the allocation and reallocation of resources to each goal. The fact that primate brains are equipped with these two complementary functions suggests that capacity limitation is not merely a defect in cognitive processes that is desirably pruned away during evolution. Rather, capacity limitation has been selected as an advantageous characteristic that permits flexible and coherent goal-directed behavior under complex goal-tree structures.

9. Concluding remarks

The problem of dual-tasking is one of the central issues in human cognitive psychology and cognitive neuroscience. It has provided a critical backbone to theories of capacity-limited cognitive resources and models of higher-order cognition, including attention and working memory. However, the results obtained in previous human behavioral and neuroimaging studies have been divergent. Investigation of the behavioral and neuronal correlates of dual-task performance in animals is beginning to provide intriguing evidence regarding how dual tasks are processed in the brain. Cross-species similarity in the pattern of the behavioral performance in a variety of dual tasks supports the view that the fine details of the mechanisms underlying dual-task performance obtained in animal models are useful for understanding the mechanisms of human dual-task performance. The problem of cognitive multitasking has been largely neglected in animal studies, and clearly there is still much work to be done. The findings obtained in future animal behavioral neurophysiology studies should help to resolve the long-standing debate in human studies, and provide a unified account of the mechanisms that underlie cognitive multitasking in the brain.

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Acknowledgements

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