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## **Primate models of interference control** Kei Watanabe<sup>1,2,3</sup> and Shintaro Funahashi<sup>2</sup>



### Abstract

Interference control is the ability to protect ongoing cognitive processing from internal or environmental distraction. For an individual to achieve interference control appropriately, either a control mechanism to coordinate multiple processing streams, such as the central executive in working memory, a mechanism to flexibly allocate the cognitive resource with a limited capacity for performing each task, or both, are needed. Through the use of dual-task paradigms, animal studies have provided important information to elucidate the neural mechanisms of the central executive and the flexible allocation of cognitive resource. These animal studies should help to promote our understanding of the neural mechanisms of interference control.

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### Introduction

Interference control, which is the ability to protect ongoing cognitive processing from internal or environmental distraction, has long been a subject of interest in cognitive psychology. The ability to achieve interference control is strongly correlated with the performance of higher-order cognitive functions such as language comprehension, problem-solving, and fluid intelligence. Human cognition studies have focused on inhibitionrelated functions [1–3], and dual-task paradigms have been used to investigate the mechanisms that underlie interference control. The general principle of the dualtask paradigm is for subjects to perform two relatively complex tasks simultaneously, each of which includes a distinct goal and stimulus-response association. Despite the remarkable flexibility of cognitive abilities, human subjects often exhibit decreased performance in either or both component tasks of the dual-task paradigm, since information processing for one task interferes with the other [4<sup>•</sup>]. The addition of a more cognitively demanding secondary task can strongly disrupt performance of the primary task. Since heavy cognitive demands on the information processing system are thought to produce dual-task interference, either a control mechanism to coordinate multiple processing streams, such as the central executive in working memory model [5,6], or a control mechanism to flexibly allocate cognitive resource for each task [7,8], is required in addition to the control process for each component task. Recent behavioral studies have indicated that humans and animals exhibit a similar dual-task interference effect. Therefore, animal studies may be able to provide valuable insight to understand the neural mechanisms of interference control. This review focuses on the results obtained using dual-task paradigms and explains how animal studies help to elucidate the neural mechanisms of interference control.

# Behavioral analyses of the dual-task interference effect in animals

Behavioral analyses of the interference effect in dual-task conditions have been conducted in studies using animals (Table 1). Although these experiments were conducted under dual-task conditions, some examined the functional similarity of short-term memory (STM) processes between humans and animals, rather than the psychological mechanisms related to dual-task interference. In humans, rehearsal is negatively affected when a secondary task is introduced during the retention period of the primary STM task. Therefore, if the STM is a functionally equivalent process in humans and animals, a similar negative effect on the rehearsal process would be expected in behavioral performance of dual tasks in animals.

Moise [9] examined this issue using monkeys. In the dual-task, a reaction time (RT) task was repeatedly inserted during the retention interval (<30 s) of a delayed matching-to-sample (DMS) task. In the RT task, monkeys were required to quickly touch an illuminated cue. The rationale was that, if the monkey's maintenance of memoranda relied on effortful rehearsal processes, the introduction of RT trials during the retention period should disrupt the performance of the DMS task, since effort was required to perform RT trials. In fact, DMS performance was markedly disrupted by the insertion of RT trials to a degree proportional to the number of inserted RT trials. The author concluded that the performance in both the DMS and RT required some degree

#### Table 1

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	Species	Combination of tasks
Behavioral studies		
Moise [9]	Monkey	DMS <sup>a</sup> + simple reaction time task
Washburn and Astur [10]	Monkey	DMS + overt OT <sup>b</sup> or numerical judgment task
Basile and Hampton [11*]	Monkey	DMS + motor, image perception, or image classification tas
Smith et al. [12]	Monkey	DMS or DMP <sup>c</sup> + perceptual confidence judgment
Kendrick and Rilling [13]	Pigeon	DMS + VI <sup>d</sup> , EXT <sup>e</sup> , or DRO <sup>f</sup> schedule
Calder and White [14]	Pigeon	DMS + VI schedule
Maki et al. [15]	Rat	8-arm WS <sup>g</sup> radial maze + 4-arm WS <sup>h</sup> radial maze
Beatty and Shavalia [16]	Rat	8-arm WS radial maze + 8-arm WS or WS radial maze
Roberts [17]	Rat	8-arm WS radial maze + 8-arm WS radial maze
Cook and Brown [18]	Rat	12-arm WS radial maze + 12-arm WS radial maze
Jarrard and Elmes [19]	Rat	12-arm WS radial maze + 4-arm WS radial maze
Harper et al. [45]	Rat	SPR <sup>i</sup> in 12-arm maze + food consumption
Neurophysiological studies		
Lebedev et al. [30]	Monkey	memory-guided saccade + luminance discrimination
Messinger et al. [31*]	Monkey	memory-guided saccade + luminance discrimination
Miyazaki et al. [32]	Monkey	memory-guided + visually-guided bimanual motor task.
Watanabe and Funahashi [33**]	Monkey	DMP + spatial attention task

<sup>a</sup> DMS: delayed matching-to-sample task.

<sup>b</sup> OT: object tracking task.

<sup>c</sup> DMP: delayed matching-to-place task.

<sup>d</sup> VI: variable interval.

<sup>e</sup> EXT: extinction.

<sup>f</sup> DRO: differential reinforcement of other behavior.

<sup>g</sup> In the WS (delayed spatial win-shift) radial maze task, animals are required to retain spatial information for visited arms both during task performance and across a delay. Optimal behavior consisits of visiting each arm without repetition. <sup>h</sup> WS: spatial win-shift task.

<sup>i</sup> SPR: serial probe recognition task.

of active processing which taxed a common capacitylimited cognitive resource, and that the nature of memory maintenance in DMS performance in monkeys was reminiscent of active rehearsal in human STM.

On the other hand, Washburn and Astur [10] also investigated whether or not monkeys could rehearse visual short-term memoranda. They inserted two secondary tasks during a variable retention interval (<48 s) in the DMS task. The secondary task was either manual tracking of a moving circle or judgment of the number '2'. Insertion of these secondary tasks disrupted the performance of the DMS task. However, manual tracking produced no more disruptive effects than passive viewing of a moving circle, and the response times in the numerical judgment task were comparable during a retention interval and an intertrial interval of the DMS task. Therefore, the authors concluded that monkeys did not rely on active rehearsal processes to maintain memoranda.

Although contradictory results have been obtained from experiments that examined the cross-species similarity of STM, these studies showed that, with the addition of relatively simple secondary tasks, a dual-task interference effect can be observed in monkeys. Subsequent studies demonstrated that not only monkeys [11,12] but also pigeons [13,14] and rats [15-19] can also perform dualtasks in various conditions and also exhibit dual-task

interference effects analogous to those in humans (Table 1). Recently, Smith et al. [12] applied the dual-task method to examine whether or not metacognitive process can be dissociated from perceptual-level process using monkeys. In the dual-task condition, a metacognitive task was inserted during the retention period of a DMS task or a STM task. The metacognitive task included a sparsemiddle-dense discrimination of random dots and the 'uncertain' response when the monkey was difficult to discriminate. As a result, a dual-task interference effect was observed. In addition, they found that the number of 'uncertain' responses dramatically decreased in the dualtask condition, while the performance of the sparsemiddle-dense discrimination was not affected. These results indicate that the dual-task method can dissociate a lower level perceptual process from a higher level decisional process, such as metacognition. Thus, the dual-task paradigm is useful not only for examining the mechanism of interference control but also for examining other higher cognitive functions such as metacognition.

The load-dependent effect of dual-task interference is an important characteristic of human dual-task performance [20,21] and an important phenomenon to examine the mechanism of interference control. Basile and Hampton [11<sup>•</sup>] showed that this effect was also evident in monkey dual-task performance. In their study, a DMS task was coupled with one of four secondary tasks that required

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