SOURCES OF DUAL-TASK INTERFERENCE IN VISUOMOTOR TRACKING ASSESSED WITH BEHAVIORAL AND fMRI ANALYSES

by

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Abstract

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Compensatory tracking was studied alone and simultaneous with a speeded go-no-go task using behavioral and neuroimaging with BOLD fMRI. In the dual-task condition, subjects used their right hand to track while making button presses with their left hand to respond to the secondary task. The study was replicated in two experiments. Replication was tested both behaviorally and with neuroimaging analyses using multivariate linear modeling. Tracking error and joystick velocity were binned into 640 ms and 100 ms intervals centered at secondary task stimulus onset and response in separate analyses to locate the time points at which the tracking behavior showed an interference effect due to the secondary task. Neuroimaging analyses located brain regions associated with compensatory tracking and with dual-task coordination. The binned time-series analyses revealed interference effect in joystick velocity about 200 ms before secondary task response. This finding combined with decreased activation in the left motor cortex during left hand response to a secondary task demonstrated that dual-task interference occurred in the motor preparation stage.

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INTRODUCTION

Both tracking and dual-task designs have been well studied in a variety of experiments (Pashler, 1994a; Poulton, 1974). Cognitive neural research in error correction is still lacking a definitive circuit for the mechanism (Ogawa, Inui, & Sugio, 2007). In dual-task interference, the stages of processing interrupted by dual tasking require further investigation. Using tracking in a dual-task paradigm is advantageous to studying visuomotor error correction as well as understanding dual-task interference. Behavioral and cognitive research in tracking and dual-task paradigms are reviewed separately in this introduction in the first two sections. Advantages of integrating tracking in a dual-task design are then discussed in the last section.

Tracking

The tracking task has been a standard experimental tool that enables researchers to study a variety of cognitive processes and neural deficits. The goal of the task is for subjects to minimize the amount of error between a target object being tracked and a cursor controlled by the subject. The task requires continuous visual and motor processing as well as motor execution (Poulton, 1974). A large array of cognitive processes is recruited to track successfully (Ogawa, Inui, & Sugio, 2007). Visual processes perceive the target and the cursor movement. Integrating processes calculate the tracking error from the target and translate it into motor instructions. Motor functions then execute the behavior. This vast system of cognitive processes allows for a variety of experimental manipulations, making it an ideal experimental task for cognitive research.

Tracking can be a quick, one-step movement such as when reaching for an apple. It can also be a continuous motion that lasts for 30 minutes, which occurs, for example, when operating a vehicle. Researchers use step tracking instead of continuous tracking to study the neurophysiology of movement because step tracking is a simplified version of continuous tracking. A step track trial consists of the most basic elements of motion: preparation and execution. Its simplicity enables researchers to examine motor processes without confounding factors derived from activation of other cognitive systems, allowing any experimental effect to be readily observable. Step tracking has been studied in animal lesion studies to localize brain functions. Hoffman & Strick (1995) lesioned the primary motor cortex in a monkey and measured its performance in rapid step tracking. The researchers found that the primary motor cortex contributes to proper temporal and spatial control of muscle contraction during step tracking movement. Other studies have used step tracking to model cognitive processes. Fishbach, Roy, Bastianen, Miller, & Houk (2007) introduced random perturbations during step tracking to model error correction. Normal monkeys were trained to reach two targets in a series within 500 ms. The targets were randomly perturbed. The error resulting from the target movement was used to calculate error-processing parameters. Krakauer, Pine, Ghilardi, & Ghez (2000) also used perturbation in step tracking. They utilized two types of perturbations: directional and extent. Directional perturbation required subjects to adapt to a remapping in hand direction to the cursor's directional movement on screen. Extent perturbation induced subjects to learn a remapping of the magnitude of manual movement to the cursor movement. They observed the differences in the acquisition of the two remapping types to examine the cognitive planning and error correction model for a reaching action.

Continuous tracking involves a series of movements to minimize error. There are two types of continuous tracking: pursuit and compensatory, which differ in the type of information displayed. In pursuit tracking, the locations of both the tracked object and the subject's cursor are displayed as the target moves around the screen. Subjects are presented with the cursor's exact location relative to the target. For compensatory tracking, on the other hand, the target stays fixed in the center of the screen while the cursor drifts around the target. Subjects can only view the amount of deviation from the target but cannot see the tracking path. Tracking errors are indistinguishable from target movement since both variables cause the cursor to be displaced from the center. Without seeing the error, subjects cannot correct their errors properly. Based on this argument, Poulton (1974) believed that compensatory display results in worse subject performance than pursuit display.

Poulton (1974) presented a large collection of articles that supported the advantage of pursuit over compensatory display. Chernikoff, Birmingham, & Taylor (1956) simulated flight control in a task that followed four different courses. All courses consisted of three sine waves combined into one function but each course differed in frequency. Each course was presented in both display modes, pursuit and compensatory. At low frequency (less than four cycles per minute), subject performance was equal between the two display conditions. As frequency increased, tracking error during pursuit display was significantly lower than during compensatory display. The difference in performance between the two display modes was not exposed under low frequency due to the ease of the task, but for higher frequencies, the task difficulty sufficiently teased apart the advantage of pursuit over compensatory display.

Besides frequency and display modes, a third commonly manipulated tracking variable is the order of control subjects have on the cursor (Chernikoff & Taylor, 1957; Obermayer, Swartz, & Muckler, 1962; Poulton, 1974). A system with a zero order control allows subjects to direct the position of the cursor. The first order of control is the velocity of the cursor, and the second order is acceleration. The greater the order of control, the more a response is delayed from influencing the cursor movement. In order to perfectly track a target with velocity control, the subject has to change the velocity before the target changes position in order to compensate for the delay. For a simple sine wave, subjects can successfully predict the tracking path, but as the irregularity of the path increases, anticipating the target path becomes more difficult. Therefore, performance worsens as the order of control increases.

The advantages of pursuit over compensatory displays and of lower order controls over higher order controls are not always unambiguous. Chernikoff and colleagues (1957) explored the interaction between frequency of the tracking course, display modes, and orders of control. They varied compensatory and pursuit displays within three control order conditions for three different courses. The lower the frequency, the easier was the course. Their results showed a complicated interactive pattern between the three variables. While performance was generally better for lower frequencies than for higher frequencies, there was no obvious trend in performance under the various combinations of display modes and control orders. For example, rate control in pursuit display resulted in higher tracking error than in compensatory display for the lowest frequency course, but in the highest frequency course, performance was better in pursuit display than in compensatory display under rate control.

Most of the tracking research conducted before the 1980’s focused on the effect of various experimental manipulations on performance. As knowledge about the task accumulated, researchers began to explore tracking as a research tool. Tracking is a basic motor skill that can be an excellent indicator of cognitive effects. Clinicians use tracking to measure cognitive deficits in psychopathologies and to monitor drug effects (Hocherman, Moont, & Schwartz, 2004; Lemieux, Ghassemi, Jog, Edwards, & Duval, 2007; Purdon, Labelle, & Boulay, 2001; Silver & Feldman, 2005; Slaats-Willemse, Swaab-Barneveld, De Sonneville, & Buitelaar, 2005; Tirosh, Perets-Dubrovsky, Davidovitch, & Hocherman, 2006). Silver and Feldman (2005) used visuomotor tracking to measure sustained attention in schizophrenic patients and healthy controls. Participants tracked while subjected to different levels of distraction. Patients' performance suffered to a greater extent than controls under distraction. Purdon et al. (2001) evaluated the efficacy of a new antipsychotic drug. Tracking was used to measure the new medication's effect on motor skills. Hocherman, Moont, & Schwartz (2004) also used tracking to study sustained attention in Parkinson's disease patients. Tirosh et al. (2006) and Slaats-Willemse et al. (2005) both used tracking to study attention in attention-deficit hyperactivity disorder in children.

With the advent of single-cell recording, electroencephalography, and functional magnetic resonance imaging (fMRI), neuropsychologists have been able to localize cognitive processes involved in visuomotor tracking in the human brain. Current research has traced the processing stream from visual detection to motor output. Visual representations of the target and the cursor enter the visual system through the retina and are relayed via the lateral geniculate nucleus to the primary visual cortex, area V1 (Merigan & Maunsell, 1993). Motion and spatial signals encoded by the M-cells travel from area V1 to V2, then to area V5 where stimulus motion is analyzed (Oreja-Guevara et al., 2004). The stream then continues to the posterior parietal cortex (PPC) (Wurtz & Kandel, 2000). Integration and processing of visual and motor information takes place in the PPC (Andersen & Buneo, 2002; Battaglia-Mayer et al., 2003). Motor instructions are then formulated in the dorsal premotor and motor areas (Wise, Boussaoud, Johnson, & Caminiti, 1997).

The human homologue of the middle temporal (MT) and middle superior temporal (MST) areas, area V5, is involved in motion perception (Ferrerra & Lisberger, 1997; Watson & Myers, 1993). Cells in that region are tuned to respond to specific directions of movement. They show the highest activation when stimulus movement matches the cell's directional preference. With populations of neurons coding for specific directions of movement, any motion can be encoded in neural signals. In addition to motion perception, Oreja-Guevara et al. (2004) found area V5 to also be involved in motor control. In nine healthy young subjects, the researchers contrasted brain activation during a pursuit task and the replay of the task on screen. Visual replay of the task allowed the brain regions involved in motor control processes to be isolated from those responsible for visual perception. Even though the replay condition was subtracted from the pursuit condition, area V5 still showed significant bilateral activation. Considering that visual processing was already subtracted from the overall cortical activation, the remaining activity in area V5 suggested its involvement in motor control.

Visuomotor integration

The encoded motion and spatial information from area V5 need to be integrated with motor processing to direct motor output. Visual stimuli are initially encoded retinotopically. Since the direction of gaze determines the position of a stimulus on the retina, this system of coordinates also called the gaze-centered coordinates. This spatial mapping is maintained all the way to area MT in monkeys (Wurtz & Kandel, 2000). The processed visual information is then transformed into a reference frame that the motor system can use to instruct muscle contraction. In the case of a simple reaching motion, the amount of hand displacement has to be calculated based on visual feedback about the distance from the hand to the target. The amount of hand displacement is initially encoded in retinotopic space. In order for the arm to reach the target, the visually detected distance between the hand and the target has to be converted into the amount of displacement the arm has to move relative to the torso, i.e., a torso-centered reference frame (Crawford, Medendorp, & Marotta, 2004). Visuomotor integration processes play a crucial role in the conversion between the different coordinate systems.

Visuomotor integration has been a major topic of research. Two main theories are being investigated to explain the visuomotor transformation process (Andersen & Buneo, 2002; Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Buneo, Jarvis, Batista, & Andersen, 2002). Both theories agree on the role of PPC in visuomotor integration and the modulation of neuronal activity by gain fields in areas of PPC. Andersen, Essick, and Siegel (1985) characterized gain fields in area 7a of a monkey’s inferior parietal lobe using a single-cell recording technique. Neurons in area 7a showed a preference for regions in head-centered space through modulation of gaze-centered encoding. The monkeys’ heads were immobilized while they fixated at nine different points on a 3x3 grid. The receptive fields of neurons were first determined as monkeys fixated at the center of the grid. Spatial gain fields were then found by measuring the activity level of these neurons in response to a stimulus consistently positioned in the center of the receptive field in relation to the retinotopic center. Neurons exhibited preferential activation for specific regions of the space. For example, a neuron with a gain field in the upper left quadrant in relation to the head was most active when the eyes rotated to look at that spatial region. The increase in activity was independent of the stimulus location in retinotopic space because the stimulus was continuously presented in the center of the receptive field for each corresponding neuron studied as the monkey viewed various fixation points. Gain fields enabled the convergence of eye rotation signals with information in gaze-centered coordinates by modulating the activity of gaze-centered encoding neurons.

The two theories differ in the mechanics of visuomotor integration. Buneo et al. (2002) argue for the common frame of reference to be gaze-centered. The encoding of the various frames of reference, such as hand- and body-reference frames, can be achieved by modulation of gaze-centered signals through gain fields. The second theory argues against a common frame of reference, and instead, for a dynamic integration of information from different reference frames (Battaglia-Mayer et al., 2003). Battaglia-Mayer and colleagues analyzed neuronal responses in areas V6a, Pec, and 7m. In response to the different phases of a delayed-reaching task, such as reaction to stimulus, movement to target, and holding of target, neurons are most active when the action is within a certain direction, regardless of the action type (Battaglia-Mayer, Ferraina, Genovesio, Marconi, Squatrito, Molinari, et al., 2001). This is called the global tuning field of neurons. Directional selectivity, instead of reference-frame selectivity, is believed to allow matching of actions that have similar movement direction.

Despite the unresolved debate on the neural mechanism of visuomotor integration, research has converged on the engagement of the posterior parietal cortex in visuomotor integration (Connolly, Andersen, & Goodale, 2003; Grefkes, Ritzl, Zilles, & Fink, 2004). Grefkes et al. (2004) designed a simple joystick task in which subjects performed a simple movement to bring a cursor onto a target. The control condition presented the same visual display of a cursor moving to a target, but subjects did not have to direct the cursor movement. Instead, subjects moved the joystick in the cued direction regardless of the target location. In contrast to the control activation, guiding the cursor to the target recruits the medial wall of intraparietal sulcus, which is part of the human parietal reach area (Connolly, Andersen, & Goodale, 2003).

Error correction

Movement contains errors that need to be detected and corrected quickly to reach a goal. Error in performance correlates with activity changes in the rostral cingulate zone (RCZ) in the posterior frontomedian cortex (Klein, Endrass, Kathmann, Neumann, von Cramon, & Ullsperger, 2007; Ullsperger & von Cramon, 2004). Klein et al. (2007) conducted neural imaging on subjects who were instructed to look away from a stimulus. Looking towards a stimulus was counted as an error. In each trial, subjects had to indicate whether they had just made an error in response. It would be an error if subjects looked towards instead of away from the stimulus. During trials in which they committed an error, activation was found in the RCZ, the pre-supplementary motor area, and the insular cortex (Klein et al., 2007). Hill and Raab (2005) monitored performance in pursuit tracking using event-related brain potentials. Both self- and externally generated errors correlated with activity in the central areas of the brain. Researchers believed that the activities were generated from the anterior cingulate. In both of these studies, RCZ activity correlated with the detection of error, regardless of the nature of the error committed.

Error correction follows error detection. Whenever an action is performed, a motor plan is assembled. Error correction mechanisms continuously monitor and adjust the motor plan even after its execution is initiated, allowing the target to be accurately reached. Detection of deviation from the target position is hypothesized to involve forward prediction of limb position as well as the use of sensory and proprioceptive feedback to evaluate prediction error (Desmurget & Grafton, 2000). An error correction loop is believed to be composed of these two mechanisms such that predictive processes provide quick corrective motor commands while the error evaluation components feed the predictors to generate the next set of motor correction instructions.

The intraparietal sulcus (IPS) is thought to participate in the error evaluation loop (Desmurget & Grafton, 2000). Desmurget, Epstein, Turner, Prablanc, Alexander, & Grafton (1999) investigated the role that the IPS plays using a reach-to-target task. Targets either remained stationary or quickly jumped 7.5 degrees away from the original location. Target jump occurred after muscles already received contraction signals, ensuring that correct reaching to the new target location must be caused by online-correction mechanisms. In the control condition, subjects correctly reached the new target location. To test the role of IPS directly, transcranial magnetic stimulation (TMS) was applied to the region during arm movement. TMS applied in the jumped target condition prevented subjects from modifying their original motor plan to adjust for the new location, but response to a stationary target was relatively accurate even under TMS effect. Interruption in IPS activation interfered with online error correction only, but did not affect the original motor plan. Therefore subjects were not able to adjust the motor execution appropriately, but were able to reach the original target position with minimum difficulty.

Ogawa, Inui, & Sugio (2007) also found evidence that activation in the IPS was greater when visual feedback was presented to the subject than when only proprioceptive information was available. Subjects performed a smooth-pursuit tracking task while undergoing fMRI. Compared to the control condition, activation significantly decreased when the curve to be traced was not shown on the screen. Instead, subjects connected the locus of the targets, eliminating any visual target for performance monitoring. With only proprioceptive information available for error processing, IPS activation was significantly less than in the control condition.

Given the hypothesized role that IPS performs in visuomotor integration, it is logical that it is an important part of motor error correction processes. IPS is believed to be the integrating site where different coordinate systems, such as the gaze-centered and shoulder-centered coordinates, converge (Andersen & Buneo, 2002; Battaglia-Mayer et al., 2003). Translating among different coordinate systems is a necessary component in calculating the error between the target and the predicted limb position. If visual feedback is used, for example, the error in gaze-centered coordinates has to be compared with the predicted limb position in shoulder-centered coordinates. The two coordinate systems have to be integrated to enable comparison between the two systems. Further evidence is still needed to pinpoint the role of the IPS in error evaluation. Error evaluation may be performed in IPS or the region may just be a component in the error evaluation mechanism (Desmurget & Grafton, 2000).

Experimental manipulations that prevented subjects from receiving sensory feedback did not interfere with subjects' ability to correct movement errors (Bard et al., 1999), demonstrating the corrective power of a prediction component in the error detection process that does not rely solely on sensory input. The predictive aspect of the error correction processing has been associated with activation in the cerebellum (Bastian, 2006; Desmurget & Grafton, 2000). Morton & Bastian (2006) reported that subjects with damage to the cerebellum did not lose the ability to move, but were unable to make predictive motor responses. A split-belt treadmill was used to measure subjects' reactive and predictive ability to changes in one of the belts. Both normal controls and cerebellar-damaged subjects were able to react to the sudden change in speed for one of the belts, with no significant difference between the two groups. Within a few strides after the belt speed had changed for a single leg, both groups took longer strides on the leg walking on the faster belt. Despite the patients' normal reactive response, they were not able to adapt to the split-belt task while healthy controls quickly learned to adjust their movement to the new task. Having ruled out reactive impairment as the cause for the patients' poor performance, the deficit was believed to be in the predictive component of motor processing. Cerebellar-damaged patients showed similar predictive deficits in other studies involving different tasks such as ball catching (Lang & Bastian, 1999) and grasping objects (Nowak, Hermsdorfer, Rost, Timmann, & Topka, 2004).

Current research has not elucidated the nature of predictive processing in the cerebellum. In the forward model proposed by Desmurget and Grafton (2000), the cerebellum is hypothesized to estimate the future position of a limb based on the motor commands sent to the limb muscles. Forward prediction compensates for the delay in sensory feedback, allowing motor errors to be corrected quickly. In the inverse model, on the other hand, the cerebellum generates the motor command for a certain action by taking the end position and the desired velocity of a limb and conducting calculations in the inverse direction to produce a set of motor instructions based on the motor effect required. The resulting instructions fine-tune the more basic instructions from the motor cortex and the spinal cord (Schweighofer, Arbib, & Kawato, 1998). The two theories are not mutually exclusive. It is also possible that the cerebellum performs both functions.

To summarize, tracking recruits a significant portion of the brain and requires extensive interaction between different brain regions. The visual areas identify stimuli location and movement. The cingulate detects error commission. The parietal regions combine visual information with motor coordinates. The parietal lobes and cerebellum participate in the online error correction mechanism to minimize the error between the target and the cursor. The premotor and motor regions monitor motor execution. Research has provided valuable information on the cognitive roles played by each of these regions, but further research is still needed to understand the mechanics of the individual systems that enable proper tracking behavior.

Dual-task processing

Performing two or more tasks simultaneously is an everyday occurrence. A mother changes a diaper while talking on the phone while also keeping an eye on the boiling soup. A professor delivers a lecture while figuring out what a giggling student is doing behind his laptop. It seems logical that if the professor was delivering the lecture for the first time, the giggling student might distract her from delivering a smooth lecture. Psychologists are interested in whether multi-tasking leads to poorer task performance and they also seek to understand the neurological and cognitive sources of interference.

Worsened performance during dual tasking can be observed in the relative reaction times of the primary task performed alone and in the dual-task condition. When two speeded tasks are performed in sequence, the reaction time for the second task is greater than the reaction time for the same task when it is performed independent of the first task (Pashler, 1994a). More specifically, as the interstimulus interval (ISI) decreases, reaction time (RT) for the second task lengthens. This phenomenon was termed the “psychological refractory period” (PRP) by C.W. Telford (1931) who was the first researcher to demonstrate this phenomenon with simple RT tasks. Creamer (1963) showed the same result with choice RT tasks. Pashler (1990) demonstrated the PRP with tasks involving different response modalities such as manual and vocal.

Two major theories have been proposed to explain the existence of PRP: Bottleneck and Capacity-Sharing (Pashler, 1994a). The Bottleneck model attributes the PRP to a central mechanism that can only process one task at a time. When there are two tasks, tasks I and II, that require the same central process, task II has to wait for task I to be fully processed before the processing for task II can begin. The restriction that a central mechanism can only operate for a single task at any given time becomes a bottleneck in the processing stream, causing the RT for task II (RT2) to increase. The Capacity-Sharing model is similar to the Bottleneck model in the assumption that certain steps in the processing are rate-limiting factors. The difference lies in the central processing step being shared among all of the tasks in the Capacity-Sharing model rather than putting tasks on a queue to be processed individually as proposed in the Bottleneck theory. This model encompasses a broader array of situations than the Bottleneck model because it allows for any percentage of the processing capacity to be shared among all of the tasks at hand. The Bottleneck model can be viewed as a special case of the Capacity-Sharing model in which the capacity for the first task is 100%. Despite its ability to account for the Bottleneck model, the validity of both models is still being investigated.

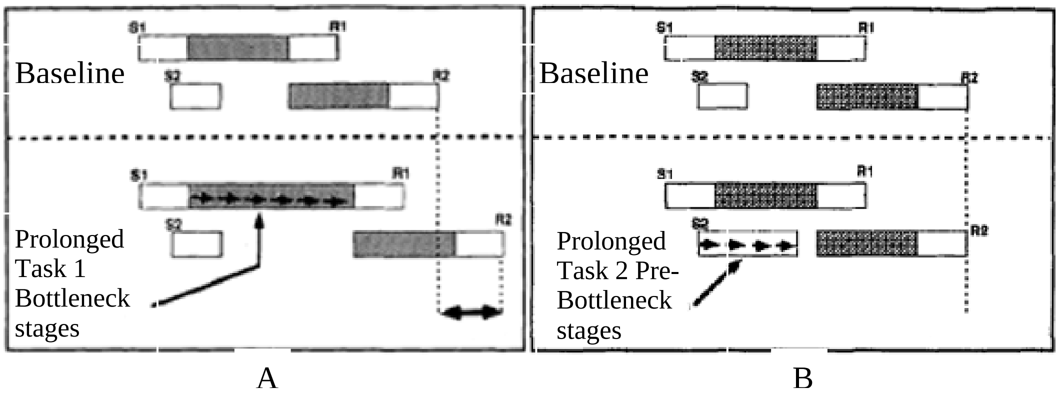

Fig 1. Predictions made by Pashler’s response selection stage bottleneck model. The bottleneck stage is shaded. The arrows show the lengthened stage in the experimental design. (A) When the response processing stage is lengthened, RT2 is also increased. (B) Increasing perceptual processing of task II should have no effect on RT2. S = Stimulus. R = Response. Modified from Pashler (1994a).

Another issue under debate is the identity of the specific processing stage. Dual-task interference can occur in the perceptual, decision-making, or response execution stage of task processing. Pashler (1994a) presented evidence against perceptual and response execution interference. He argued that the bottleneck occurs in the response selection stage of information processing, which has been confirmed by various studies (Karlin & Kestenbaum, 1968; Pashler & Christian, 1994; Pashler & Johnston, 1989). The most straightforward prediction from the model is an increase in RT2 when the response selection stage in task I (S1) is lengthened (Fig. 1A). Karlin and Kestenbaum (1968) increased S1 by increasing the number of choices from which subjects had to choose. As predicted by the theory, RT2 increased as more choices were added to task I. Another prediction from the theory stems from the idea that if the bottleneck in the processing of task I is delaying the task II response from being processed, then for short ISIs, increasing the perceptual processing of stimulus II, a non-bottleneck stage, should not affect RT2 (Fig 1B). To increase the amount of perceptual processing in task II, the intensity of stimulus II was weakened in Pashler and Johnston's (1989) study. Their results followed the predictions derived from Pashler's theory. They found that for weak stimulus intensity, there was a significantly smaller increase in RT2 when the ISI was short than when it was long.

While many studies have found evidence in support of Pashler's theory, other studies have not. According to the Response-selection Bottleneck theory, varying ISI should not affect RT for task I (RTI) since processing for task I should already be completed before task II is processed. At all levels of ISI, RTI should be the same. However, Tombu & Jolicoeur (2002) found the opposite result. The researchers analyzed RTI instead of following the usual PRP paradigm where the analyses concentrate on RTII. They found that as the two stimuli are presented closer in time, RTI increases significantly, thus supporting the Capacity Sharing model.

Pashler (1994b) conducted a study to test predictions from the Capacity Sharing model. Based on his results, he concluded that the Capacity Sharing model is refuted in support of the Bottleneck model. Pashler's experiment differed from the previous experiment by Tombu & Jolicoeur (2002). A 0 ms ISI was included such that two stimuli were presented simultaneously. The smallest ISI in Tombu & Jolicoeur's study was 50 ms. Pashler argued that at 0 ms ISI, if the Capacity Sharing model is correct, the processing capacity should be randomly distributed between the two tasks such that there can be any amount of time between the two responses. The two tasks should have a wide distribution of inter-response interval (IRI). He added that there should be a tendency for subjects to group the responses, resulting in a mean of 0 IRI for the distribution. However, subjects' IRI either followed a bimodal distribution or a complete grouping of responses where IRI was 0 ms. The lack of a distributed set of IRIs convinced Pashler that the observed results could only be predicted by the Bottleneck model and thus weakened the plausibility of the Shared Capacity model.

Unfortunately, Tombu & Jolicoeur's (2002) study did not include a 0 ms ISI, which makes comparison of the results between the two studies difficult. The only comparison that can be made is the RTI for levels of the ISI. Similar to the results found by Tombu & Jolicoeur, Pashler also reported increasing RTI as ISI shortened, which is not predicted by the Bottleneck theory. Pashler did not discuss this aspect of the data, however. To resolve the differences between the two models, future research has to address the issues raised by the two studies, and develop a model that explains the observed results.

Despite the disagreement between the two models, dual-task interference is a widely recognized phenomenon. FMRI studies have been performed to locate neural correlates of dual-task coordination and interference (Herath, Klingberg, Young, Amunts, & Roland, 2001; Marois, Larson, Chun, & Shima, 2006; Stelzel, Schumacher, Schubert, & D'Esposito, 2006; Szameitat, Lepsien, von Cramon, Sterr, & Schubert, 2006). Szameitat et al. (2006) examined areas that are correlated with the amount of dual-task coordination required. Their rationale was based on the observation that subjects tend to expect the same task order as in the previous trial of a given task. When task order is different from a previous trial, areas involved in coordinating task priorities were hypothesized to exhibit greater activation. By comparing activation during different-order trials versus same-order trials, activity in the lateral prefrontal cortex (LPFC) correlated with task-order, which agrees with the role of prefrontal cortex in executive functions.

Other fMRI studies that examined dual-task interference reported that areas of the frontal lobe were most active during dual tasking. Marois et al. (2006) showed dorsal pre-motor cortex and parts of LPFC, specifically in the inferior frontal cortex, to be involved in response selection, which is the stage of information processing believed to be interrupted in dual-task interference. They used a parametric design to locate brain regions that correlated positively with increasing number of alternative choices. Their paradigm was based on the logic that changes in the number of possible choices increase the demand on the response selection process, resulting in greater activation in brain regions involved in response selection. Herath et al. (2001) further localized the right inferior frontal cortex to be involved in dual-task interference. They employed a different approach from Marois' team. Instead of manipulating the number of alternative choices, they contrasted activations found in long versus short ISIs. Interference was only found for the short ISI condition while interference was not observed for the long ISI condition. Based on the conclusion made by subtracting long ISI from short ISI, the researchers reasoned that brain regions activated when dual-task interference occurs could be isolated. Schubert and Szameitat (2003) presented the most convincing evidence for inferior frontal cortex activation in dual tasking. They compared activations during two different choice RT tasks performed separately with activation during the dual-task condition. Brain regions not active in the single-task conditions were areas involved in managing and resolving contradicting information from the two simultaneous tasks. The greatest amount of activation was observed in the left inferior frontal sulcus.

Research has demonstrated that performance on dual-task paradigms is vulnerable to interruption. The nature of the interruption is hypothesized to be either a complete bottleneck, in which processing for the first task must be completed before processing for the second task can proceed, or a partial bottleneck such that processing for both tasks can share different proportions of the processing capacity. Some studies have showed the bottleneck to occur during response selection while others demonstrated response programming to be the bottleneck stage. Both questions require further research. In terms of brain regions, LPFC participates in dual-task *coordination*, while the inferior frontal cortex and the dorsal pre-motor cortex were found to be involved in dual-task *interference*.

Dual-task interference in a continuous-tracking task

Tracking has been used in dual-task paradigms since the mid 1950’s (Poulton, 1974). Early dual task tracking experiments aimed to investigate the effect of dual task on subject performance (Garvey, 1960; Griew, 1959; Monty & Ruby, 1965). Griew (1959) tested subjects on pursuit tracking concurrent with an auditory RT task. Subjects tracked with their left hands while responding to buzzes with their right hands. Griew found a significant decrement in tracking performance as well as in RT relative to the corresponding measures in the single-task conditions. Monty and Ruby (1965) also found performance decrements in both tasks when compensatory tracking was executed simultaneously with a visual motor task.

Researchers took advantage of the continuous demand that tracking places on cognitive processing in order to study other cognitive processes. Power (1986) used tracking to measure processing demands during speech. He asked subjects to give either a descriptive or discussion speech while performing tracking. By analyzing tracking performance, Power pinpointed the time line of processing for complete clauses.

Netick and Klapp (1994) used tracking to quantify processing in dual tasking. The researchers examined the behavioral effect of a go-no-go distracter task on continuous pursuit tracking. The experimental design aimed to tease out the exact processing stage that is vulnerable to dual-task interference. For each distracter trial, two tones were presented. The first tone was a cue that signaled if a response was required (go) or not (no-go). For go trials, subjects made a response when the second tone was presented. In addition to tracking error, the researchers quantified the amount of hesitations in the subjects' tracking movement. A hesitation was characterized by minimal joystick movement of no more than 0.05° and for a minimum duration of 0.33 s. The authors reasoned that hesitations constitute halting of processing for task II in the PRP paradigm. The number of hesitations during the go condition was contrasted with the no-go condition. There were significantly less hesitations in the no-go condition than in the go condition. Since both conditions require the same steps from visual processing to response selection, the additional processes present in the go condition but not in the no-go condition were response programming and response execution. Based on behavioral data, the onset of hesitations occurs before response onset. The authors concluded that the interrupted stage cannot be response execution. Instead, dual tasking causes interference specifically in the response programming stage. Netick and Klapp's conclusion diverged from Pashler's Response Selection Bottleneck theory, which hypothesized response selection to be the bottleneck stage rather than response programming.

Tracking has been used in dual-task paradigms in a number of behavioral studies. A major advantage of using tracking in dual-task designs is its ability to quantify cognitive demands. It is a valuable tool for cognition research.

Summary

Much is known about online motor error correction and dual tasking. Although both topics have been studied extensively for the last few decades, there are still questions to be answered by future research.

Motor Error Correction

Online error processing enables movement to be performed accurately and smoothly. Desmurget & Grafton (2000) proposed a model with a prediction and an error evaluation component that continuously monitors and corrects a motor plan even after the hand, for example, has initiated movement. According to the model, the cerebellum predicts the future location of the limb based on the motor instructions given, whereas IPS evaluates prediction error by comparing the predicted location with the actual hand location. IPS is also the site where information encoded in different reference frames is integrated (Grefkes et al., 2004). Its role in error processing may be the transformation of retinotopically encoded tracking error into the hand reference frame in order to generate motor commands.

Ogawa, Inui, & Sugio (2007) correlated brain activation with tracking error to locate brain regions involved in online error correction. This analysis led to ambiguous results. Neural regions associated with online error correction may have positive or negative correlation with tracking error. If an increase in tracking error triggers activation of error correction regions, then activation should correlate positively with tracking error, meaning the greater the tracking error, the more activated the error processes become. Conversely, increase in error can be a result of decreased activation in the error processes, in which case the correlation should be negative. A better measure should be chosen to eliminate the ambiguity and locate the regions involved in online error processing.

Dual-tasking

Dual-task interference is hypothesized to originate from limitation in the processing capacity of a common stage between the two tasks. The identity of the bottleneck stage is believed to be either the response selection or the response programming stage of information processing (Pashler, 1994). Pashler presented evidence for the response selection bottleneck, but Netick and Klapp (1994) showed that the interference, measured by hesitations in tracking, occurs during response programming stage.

Netick and Klapp's study cleverly utilized the continuous nature of tracking as a measuring tool for dual-task interference. Any interruption in processing is readily observable. Their behavioral analysis was able to illustrate a temporal relationship between dual-task interruption in tracking processes and responses to the second task. However, a neural correlate of hesitation has not been shown. Brain areas that correlate with hesitations are most vulnerable to dual-task interference. An fMRI study is needed to further explore the hesitations shown in Netick and Klapp's study.

Potential applications

The current study was developed to study the Multi-Attribute Task Battery (MATB) using neuroimaging. Dual-task tracking research is beneficial to learning about the nature of dual-task interference such that jobs requiring multi-tasking can be better designed and made safer for operation. In particular, driving and piloting contain risks derived from the need to multi-task. Understanding the stage of processing interrupted by dual tasking enables improvements to be made on vehicle design and operator training.

Current Study

The current study employed a dual-task paradigm consisting of compensatory tracking and a speeded go-no-go task. Measurements were made behaviorally and using neuroimaging with BOLD fMRI. Subjects were tested with two conditions: single-task, in which only tracking was performed, and dual-task. For motor error correction analyses, activation was taken from the single-task condition, while for the dual-task interference analyses, the activation differences between the two conditions were analyzed.

Motor Error correction

The first topic of interest was the areas associated with online correction of motor activity. Because only the tracking error is evident in the screen display, compensatory tracking has the advantage of eliciting only mechanisms that correct the error whereas pursuit tracking require additional mechanisms for calculating the target movement with respect to time. Therefore, compensatory tracking was used in the current study. Furthermore, to assess the relationship between tracking error and the activation of error correcting regions, instead of cursor-to-target distance, brain activation was correlated with joystick velocity. Joystick movement directly reflects the output of the motor error correction mechanism. Activation in areas involved in error correction should correlate positively with joystick velocity, assuming most joystick movements minimize the tracking error.

Dual-task Interference

The second goal was to identify the cognitive processes and brain regions associated with changes in motor error correction mechanism under dual-task conditions. The number of hesitations is a measure used in motor tasks to assess dual-task interference. The current study used joystick velocity in tracking to quantify dual-task interference instead of counting individual instances of hesitations. Joystick velocity was able to characterize a greater array of phenomena. A full hesitation equated to a joystick velocity of zero, and a full tracking motion resulted in the highest joystick velocity. Joystick velocity was examined in time bins relative to both secondary stimulus onset and response to observe the time course of dual-task effect. Neuroimaging analyses compared dual- and single-task conditions to localize brain regions the activity of which changes in motor functions under dual-tasking.

If interference was in the perceptual stages, then joystick velocity would decrease following stimulus presentation, and brain activity should be less for targets than non-targets in regions associated with perception such as visual cortex and area V5, which was known for motion detection. Alternatively, if interference occurs in motor stages, then decrease in joystick velocity should be time-locked to response, and brain activity should decrease in targets in motor areas such as M1.

METHODS

Two groups of subjects were included in the study. Both groups were tested under the same conditions, but the second group participated in a sleep-deprivation study. Behavioral and imaging data for the second group were acquired before subjects were sleep-deprived.

Participants

All subjects were right-handed and carefully screened to ensure that they had no history of medical, psychiatric, neurological, sleep disorder, or color-blindness. In group 1, 26 subjects were recruited with one subject excluded due to MR artifact, one subject due to poor performance (mean tracking error at maximum value), and two subjects due to equipment failure, resulting in a total of 22 subjects used in the analyses. Subjects ranged in age 20 – 33 years old (mean = 26.4 ± 3.4 years). In group 2, 34 out of 37 participants were included in the analyses and they ranged in age from 18-34 years (mean = 23.1 ± 3.1years). Three subjects were excluded for poor behavioral performance: two subjects did not perform the tracking task and one subject responded to secondary task in the single-task condition.

Behavioral tasks

All subjects were tested in two conditions: single- and dual-task. Only visuomotor tracking (VT) was performed in the single-task condition. The dual-task condition consisted of tracking and a speeded go-no-go color-matching task (GNG).

Visuomotor tracking

The visuomotor tracking task employed was compensatory tracking. A cross was placed in the center of the screen. A small circular cursor was displaced from the center by random perturbation. Subjects controlled a joystick with the right hand to maintain the cursor position on top of the cross by counteracting the perturbing force.

Go-no-go color-matching task

Stimuli for the GNG consisted of four circles arranged one in each of the four corners of the screen. Each circle could be of any four possible colors (red, green, blue, or yellow). Subjects pressed a button with the left index finger whenever diagonally opposite circles matched in color (“target”). The appearance of unmatched diagonal colors was termed “non-target” events. Six targets were presented on every trial. Mean ITI for targets was 19.3 ± 10.0 s, which remained on screen for 8 sec. Mean ITI for non-targets was 3.86 ± 2.44 s.

Testing procedure

Subjects received titration and training. Subject performance was titrated, for 16 min, to a median tracking error of 15 pixels from the center by varying the magnitude of perturbation. Titration standardized baseline subject performance. Subjects were trained for 27.4 min on 6 trials of single- and of dual-task conditions separately. For group 1, titration and training were performed on the same day as testing whereas group 2 subjects were titrated and trained two weeks prior to testing in accordance with the protocol of the larger study.

Subjects were tested in three blocks, each lasting for 11.87 min each block. Single- and dual-task conditions were presented twice in each block for two minutes each trial. ITI for each trial was 40 s. The order of trials was randomized across blocks and subjects.

Behavioral data were recorded every 60 ms. For tracking, the data included tracking error (RMS), joystick displacement, thrust, cursor position, wind factor, and, for circle changes, the times of targets, non-targets, and the subjects’ responses.

fMRI data acquisition

During each block of testing, 285 T2*-weighted images, which are BOLD images (Ogawa, Menon, Tank, Kim, Merkle, Elelrmann, et al., 1993), were acquired with an Intera 1.5-T Phillips MR scanner equipped with a 6-channel SENSE head coil (Pruessmann, Weiger, Scheidegger, & Boesiger, 1999), using a gradient echo echo-planar (GE-EPI) sequence (time echo/time repetition [TE/TR] = 50 ms/2500 ms; flip angle = 90°; 80 x 80 matrix, in-plane voxel size = 3.124 mm x 3.124 mm; slice thickness = 6 mm [no gap]; 25 trans-axial slices per volume). Four additional GE-EPI excitations were performed before the task began, at the beginning of each block, to allow transverse magnetization immediately after radio-frequency excitation to approach its steady-state value; the image data for these excitations were discarded. A T1-weighted spoiled gradient image was also acquired from each subject for spatial normalization purposes (TE/TR = 3 ms/ 25 ms; flip angle = 45°, 256 x 256 matrix; in-plane voxel size = 0.781 mm x 0.781 mm; slice thickness = 1.5 mm [no gap]; 124 trans-axial slices per volume).

Task stimuli were back-projected onto a screen located at the foot of the MRI bed using an LCD projector. Stimuli subtended 10.5º by 10.5º visual angle on the screen. Subjects viewed the screen via a mirror system located in the head coil. All subjects had vision corrected to as normal as needed using MR compatible glasses (manufactured by Safe Vision, LLC. Webster Groves, MO). Tracking control was performed with an MR-compatible joystick (Resonance Technology) placed to the right of the thighs. GNG responses were made on a LUMItouch response system (Photon Control Company) with the response paddle placed to the left of the thighs. Task onset was electronically synchronized with the MRI acquisition computer. Task administration and data collection were controlled using REALbasic. A Carnegie Mellon Button Box (New Micros, Inc. Dallas, TX) provided digital input-output for the response system and synchronization with the MRI acquisition computer, as well as millisecond accurate timing of responses.

Behavioral data analysis

Tracking Error

Root-mean-square (RMS) of the tracking error was calculated using the formula $\text{sqrt}(\text{mean}(x^2+y^2))$. X and y were the horizontal and vertical cursor distances, respectively, from the center of the screen in pixels. Screen size was approximately 82 pixels per inch.

Joystick Velocity

Joystick velocity between two time points (t_1, t_2) was calculated by $\text{sqrt}[(jx_2-jx_1)^2 + (jy_2-jy_1)^2]/(t_2-t_1)$ with jx and jy being the joystick's horizontal and vertical distance, respectively, from the joystick's neutral position. Joystick velocity was then low-pass filtered with 101th order finite impulse response function with a cut-off frequency of 0.2. The order and cut-off frequency were selected to filter out high frequency changes while preserving the trend in joystick movement. Low-pass filtering joystick velocity was necessary to simulate the slower metabolic change in the brain in relation to movement.

Repeated-measures ANOVA on trial means

Repeated-measures ANOVAs were conducted separately for RMS tracking error, joystick velocity, reaction time to GNG target, number of hits (correct response to GNG target), and number of false alarms. Each ANOVA consisted of 2 conditions (single/dual-task) x 3 blocks x 2 trials with group (1 and 2) as the between-subjects factor. P-values for factors that did not satisfy the sphericity assumption were corrected using the Huynh-Feldt correction.

Repeated-measures ANOVA on binned time-series

The goal of performing ANOVA on binned time-series was to test the changes in RMS tracking error and joystick velocity around stimulus presentation and response for the GNG task. Targets lasted 8 s, therefore, time series from 8 s before to 8 s after the event of interest. Two sets of twenty-five 640 ms bins were created. The 640 ms bin width was selected based on the sampling period of approximately 60 ms and the neat division of 1600 ms into 25 bins. The first set of bins centered at GNG stimulus presentation and the second set centered on stimulus response. For stimulus presentation, RMS tracking error and joystick velocity were averaged in each bin separately for targets and non-targets within each of the single- and dual-task conditions, resulting in 4 sets of binned time-series for each variable. Non-targets only included circle color changes that did not overlap with a target. The response-locked bin set contained binned means only for targets in the dual-task condition because these are the only stimuli that elicited responses. Thus, the ANOVA design consisted of 2 conditions x 2 stimulus types x 25 bins x 2 groups for the stimulus presentation bin set and 25 bins with group as the between-subject factor for the stimulus response bin set. Each design was performed on RMS tracking error and joystick velocity separately for a total of 4 repeated-measures ANOVAs on binned time-series data. A priori contrast analyses were performed by comparing each bin mean to the grand mean of the 25 bins.

Netick and Klapp (1994) found that joystick movement began to change at about 180 msec before response onset. To find this pre-response effect, a zoomed-in set of response-locked bins were also generated for bins of 100 ms in duration from 1500 ms before and after response. This allowed examination of bin mean-centered at 200 ms and 100 ms before response onset. Bin means were calculated for joystick velocity only because Netick &

Klapp’s study measured hesitation in joystick movement. Post hoc contrasts were performed to compare each bin mean to the baseline bin mean. The first bin mean was used as the baseline instead of the grand mean because the grand mean for a 3000 ms window around the event of interest was not wide enough to provide a good baseline measure. Because this is a post hoc test, the p-value was adjusted with Bonferroni correction to the number of bins used in the analysis, resulting in a p-value of 0.0016 (0.05/31bins). Same bin interval was used for stimulus-locked data for dual-task targets, but the window used was 650 ms before to 1850 ms after stimulus onset. This window was chosen based on the 640 ms binned time-series analyses for a window around the most changes observed. The p-value used was 0.0020 (0.05/25bins).

fMRI statistical analysis

Preprocessing

All image preprocessing and analysis were implemented using the SPM5 program (Wellcome Department of Cognitive Neurology) and other code written in MATLAB 7.1 (Mathworks, Natick, MA). The following procedures were used for each subject’s GE-EPI data set. Data were temporally shifted to correct for the order of slice acquisition, using the first slice acquired in the TR as the reference. All GE-EPI images were realigned to the first volume of the first session and then coregistered to the T_1-weighted (structural) image using the mutual information coregistration algorithm implemented in SPM5. The high-resolution image was then used to determine parameters (7 x 8 x 7 nonlinear basis functions) for transformation into a Talairach standard space (Talairach & Tournoux, 1988) defined by the Montreal Neurologic Institute template brain supplied with SPM5. This transformation was then applied to the GE-EPI data, which were resliced using sinc-interpolation to 2 mm x 2 mm x 2 mm and then spatially smoothed with an 8mm FWHM kernel.

Time-series modeling

The fMRI data analysis comprised 2 levels of voxel-wise GLMs (Holmes & Friston, 1998): the first-level GLM is a time-series analysis that yields summary measures to be used in the second-level GLM, which affords statistical inference at the population level. In the (subject-separable) first-level GLM, the GE-EPI time series were modeled with regressors representing the expected BOLD fMRI response (implicitly, relative to the blank intervals) to each condition (single- and dual-task) and to target and non-target stimulus presentations in each condition for each of three blocks, totaling to 18 regressors (3 blocks x [2 conditions + 2 x 2 stimulus types]) plus a regressor representing the instruction screens for each block (18 + 3 = 21 regressors) and additional regressors for false alarms. In addition, in each block, both condition regressors were multiplied by the corresponding joystick velocity to locate brain regions that correlate with joystick velocity. This added six regressors to the time-series model for a total of at least 27 regressors in each subject’s model. The regressors were constructed by convolutions of an indicator sequence (i.e., a train of discrete-time delta functions) representing tracking and GNG trial component onsets, an assumed BOLD impulse response function (as represented by default in SPM5), and a rectangular function of duration dictated by the duration of the assumed neural response (Zarahn, 2000). In particular, hits regressors were modeled with event durations equaling to the respective reaction time.

In order to minimize the correlation between predictors in the time-series model, the non-target predictors were orthogonalized with respect to the tracking predictor. The tracking block predictor contained the mean activation of the entire trial, which included not only activity related to tracking, but also any activity that persisted for most of the trial. Since non-targets occurred fairly frequently throughout the trial, it was unavoidable that the tracking block contained some variability associated with non-targets. For the non-target predictor, orthogonalization only removed the mean from the predictor and still corresponded to the time-varying signal change associated with the non-target event onsets, enabling valid interpretation of this predictor after orthogonalization. The contrast estimate images were then used as the dependent variable in a second-level GLM.

Group analyses

Six group GLMs were performed: two examined brain activity related to visuomotor tracking and four analyses compared dual- and single-task performance. For each model, two types of analyses were conducted: multivariate linear modeling (MLM) (see Zarahn et al., 2005 for details of the method) and univariate *statistical parametric modeling* (SPM: Friston, 2007). MLM enabled tests of replication in the overall spatial network activated by the two groups of subjects while SPM analyses examined localized effects in each analysis.

Multivariate linear modeling. Multidimensional contrasts (e.g. F-test contrasts) were constructed in each model consisting of two levels: groups 1 and 2. Latent root testing was used to assess the number of latent spatial patterns needed to summarize the brain images for each dimension in the F-contrast (Worsley et al., 1997; Zarahn et al., 2005). The latent predictor weights for each significant latent spatial pattern were examined to determine if the weights were significantly different from zero and were similar across groups using one- and two-sample t-tests, respectively. Successful replication between the two groups would be a significant latent spatial pattern shared by the two groups that accounts for a majority of variance in the data. A common pattern activated by the two groups would support a similar network of brain regions being activated, and therefore, would suggest successful replication of results in group 2.

SPM analysis. Voxel-wise SPM comparisons were performed to localize regions with the effects of interest. Contrasts of the parameter estimates from single-subject models were entered into random-effects analyses (repeated-measures ANOVA). Group identity was entered as the between-group factor in each model. Except where mentioned, results were corrected for multiple comparisons across the whole brain using the Bonferroni correction for the number of resolution elements (Worsley, Marrett, Neelin, Vandal, Friston, & Evans, 1996), using an extent threshold of 10 voxels. Likely cytoarchitectonic labels for cluster maxima in these thresholded patterns were obtained using Talairach daemon software (Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, et al., 2000).

Effects of interest. MLM and SPM analyses were performed on the six effects of interest. The first two effects examined regions associated with visuomotor tracking: single-task tracking and joystick velocity. The single-task tracking contrast compared the tracking trials in the single-task condition to the rest condition while the single-task joystick velocity analysis localized any regions that showed correlated activity with joystick velocity, which was intended to identify areas associated with online motor error correction. The other four analyses tested dual-task interference. Dual- vs. single-task tracking compared tracking trials between dual- and single-task conditions. Dual- vs. single-task joystick velocity could locate any differences in regions that correlate with joystick velocity. Targets vs. non-targets in the dual-task condition addressed the question of which additional areas are recruited to respond to the secondary task. The last analysis contrasted non-targets in single- and in dual-task conditions to determine which brain regions were engaged by non-targets in the dual-task condition but not in the single-task condition.

RESULTS

Behavioral data

ANOVA results for the independent variables and their interactions are presented first to clarify the effects of experimental manipulations. Then temporal changes with respect to the secondary stimulus onset and response are presented followed by analyses with higher temporal resolution (smaller time-bins) to further dissect the time course of tracking performance in relation to the secondary task. Group differences are also discussed.

Trial means analyses

Tracking variables. The overall mean tracking error was 22.89 ± .938 pixels. The dual-task condition was more difficult than the single-task condition, as shown by the increase in error across conditions in Figure 2, $F(1,50) = 4.262$, $p < 0.05$. Block interaction effects are plotted in Figures 3 and 4 for tracking error. Across blocks, tracking error remained constant across conditions but in the dual-task condition tracking error decreased from blocks 1 to 3, $F(2,100) = 3.728$, $p < 0.05$. Across trials, block 1 error decreased but in blocks 2 and 3, error increased from trial 1 to 2 ($F(2,100) = 4.069$, $p < 0.05$). All other main effects and interactions were not significant.

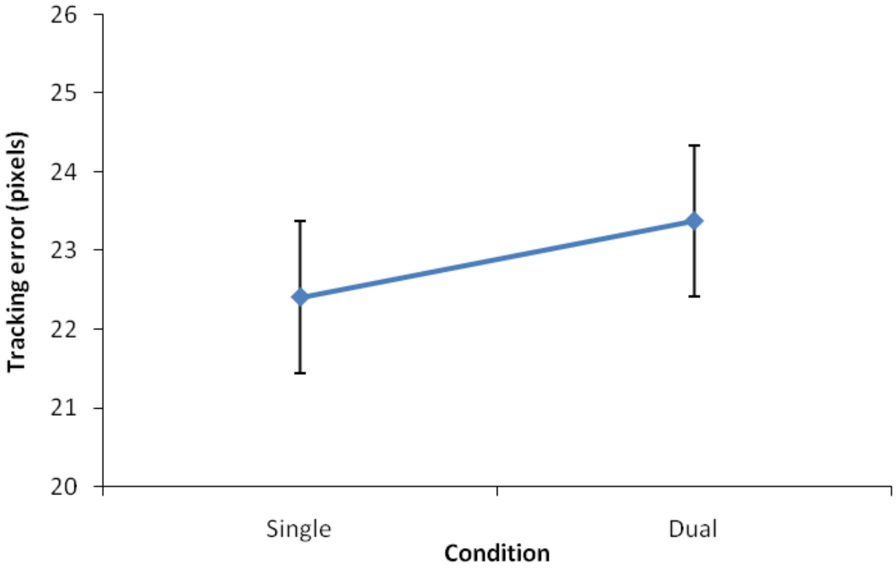

Fig. 2. Mean (± SE) for tracking error for each condition.

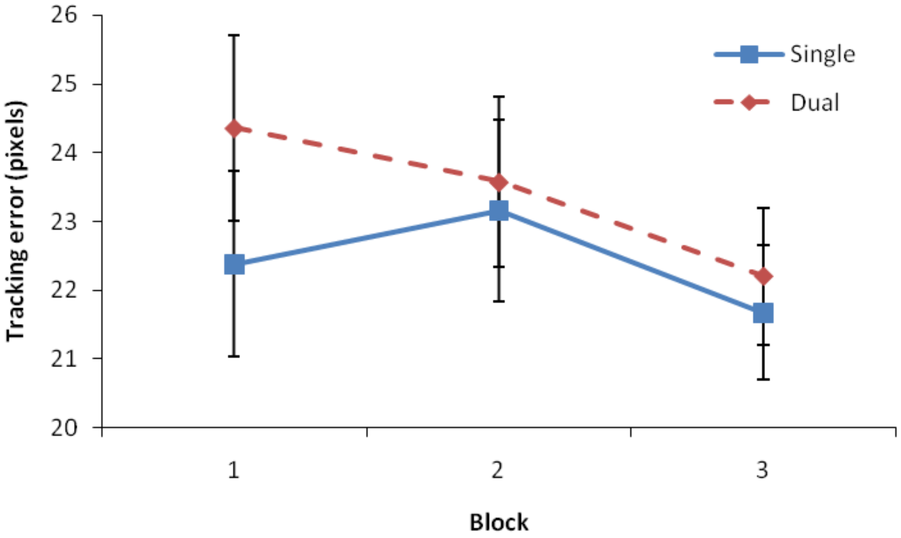

Fig. 3. Mean (± SE) for tracking error for each condition in each block.

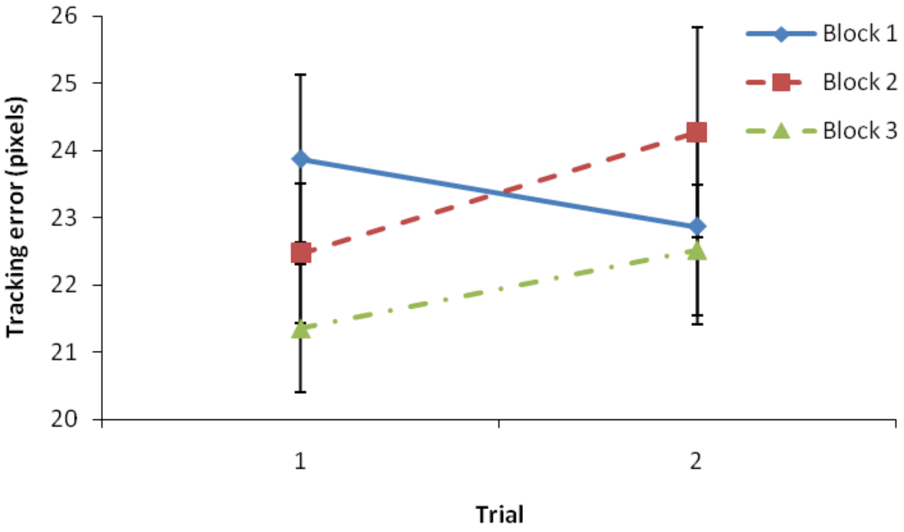

Fig. 4. Mean (± SE) for tracking error for each block across trials.

Joystick velocity measured the rate at which subjects corrected tracking errors. Mean joystick velocity was 7.305 ± .564 pixels per second. The rate of error correction was similar in the two conditions, $F(1, 50) = .148$, $p > 0.05$, but it increased across blocks (see Figure 5), $F(2, 100) = 5.492$, $p < 0.05$. All other main effects and interactions did not reach significance.

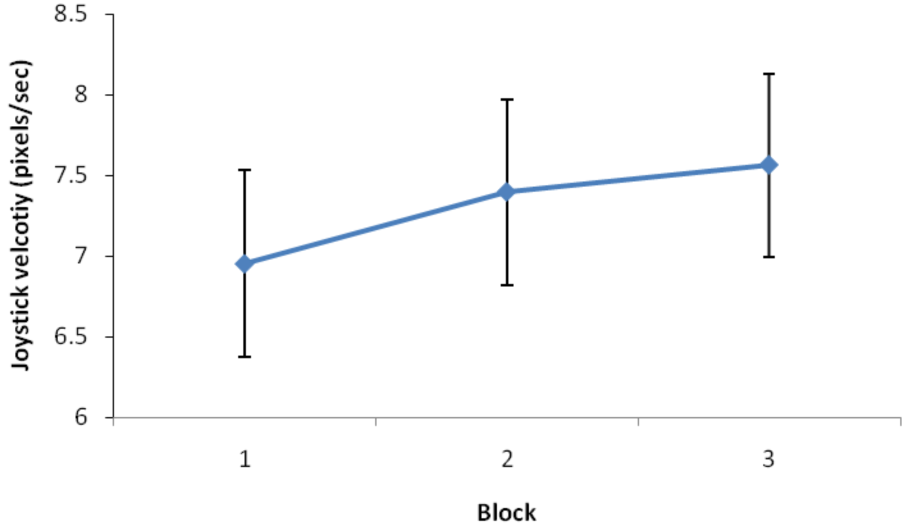

Fig. 5. Mean (± SE) for joystick velocity for each block.

Efficiency in tracking describes the accuracy of each joystick movement in correcting tracking errors. Greater tracking error in the dual- than in the single-task condition with constant joystick velocity showed less efficient tracking when subjects had to perform two simultaneous tasks as opposed to performing only one task. Increasing joystick velocity and decreasing tracking error across blocks in the dual-task conditoin suggest subjects performed tracking more efficiently as the study progressed. Perhaps the gap between training and testing was too long, resulting in a small learning effect during testing.

GNG variables. Subjects performed the GNG task very well. The overall mean number of hits was 5.643 ± 0.051 out of 6 possible targets per trial. None of the effects tested in the hits analysis reached significance. Mean reaction time to targets was 1094 ± 33.67 ms. Subjects became slower to react to the GNG task as testing proceeded. Reaction time increased across blocks (shown in Figure 6), $F(2, 100) = 4.809$, $p < 0.05$. All other effects with reaction time were not significant. On average, subjects had 0.900 ± 0.162 false alarms per trial. There were more false alarms in the dual- than in the single-task condition, $F(1,50)$

= 41.69, *p* < 0.001. Across blocks, Figure 7 shows the number of false alarms that remained the same in the single-task condition but decreased in dual-task, *F*(2, 100) = 4.459, *p* < 0.05, with the corresponding main effects of block (*F*(2, 100) = 4.470, *p* < 0.05).

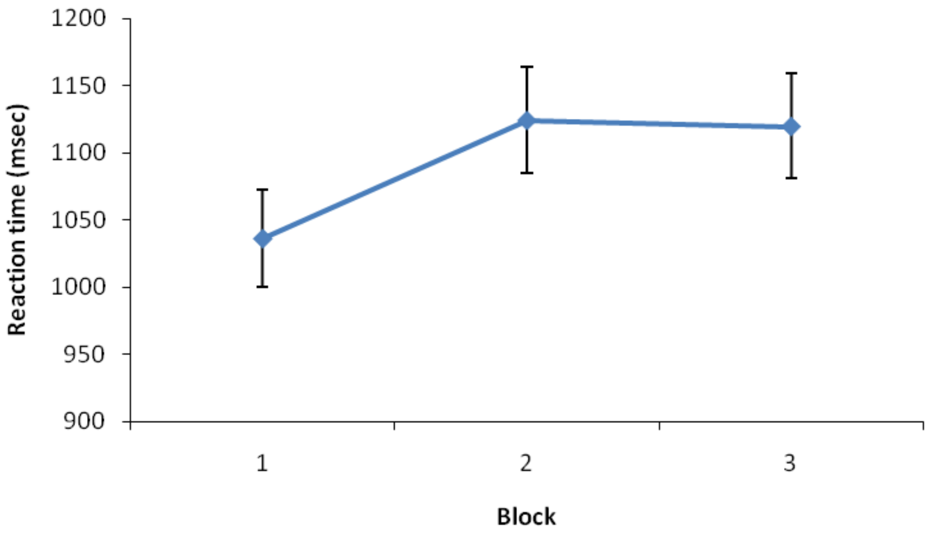

Fig. 6. Mean (± SE) for reaction time for each block.

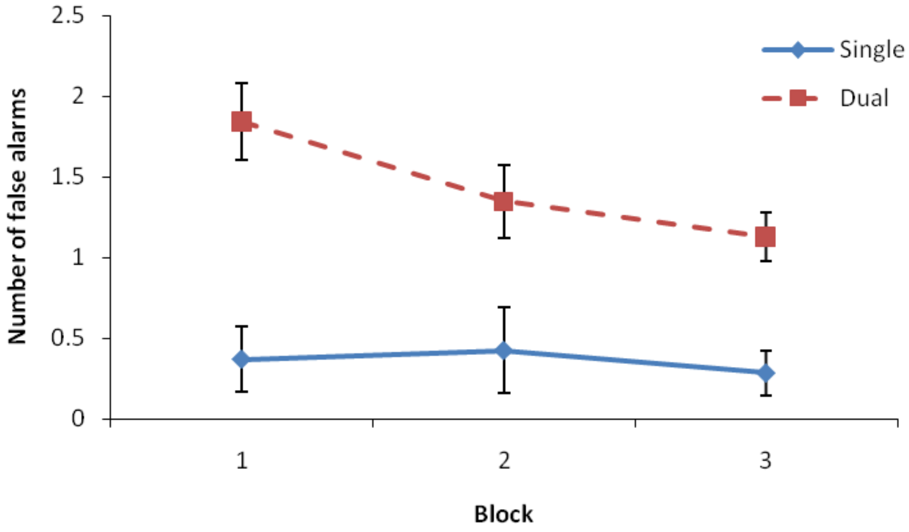

Fig. 7. Mean (± SE) for the number of false alarms for each condition in each block.

Binned time-series analyses

Stimulus-locked 640 ms bin set. Figures 8 and 9 show the binned tracking error means for non-targets and targets in single- and dual-task conditions. Both tracking error and joystick velocity remained constant across bins for non-targets in both single- and dual-task conditions and for non-targets in the dual-task condition, suggesting tracking was not interrupted by non-targets in the dual-task condition. A significant interaction was found for condition, stimulus type, and bin in the tracking error analysis, $F(24, 1296) = 3.325$, $p < 0.05$, and in the joystick velocity analysis, $F(24, 1296) = 5.369$, $p < 0.001$. Most of the corresponding interactions and main effects for both variables were also significant. Between condition and bin, significance was found for tracking error, $F(24, 1296) = 3.227$, p < 0.05, and for joystick velocity, $F(24, 1296) = 3.558$, $p < 0.001$. The stimulus type and bin interaction was significant for both tracking error, $F(24, 1296) = 4.700$, $p < 0.001$ and joystick velocity, $F(24, 1296) = 3.632$, $p < 0.001$. Condition and stimulus type interaction was significant for tracking error only, $F(1, 54) = 5.129$, $p < 0.05$. Both variables showed significant bin main effects: tracking error: $F(24, 1296) = 4.099$, $p < 0.001$; joystick velocity: $F(24, 1296) = 5.369$, $p < 0.001$.

Deviation contrast analyses located bins with significant change from the grand mean. As shown in Figures 10 and 11, relative to GNG target presentation in the dual-task condition, tracking error was greater than the grand mean from 1.28 to 2.56 s after stimulus onset while joystick velocity showed significant changes 0.64, 1.28, 2.56, 3.40, and 4.48 ms bins after stimulus onset. The corresponding F statistics are shown in Tables 1 and 2 in the condition by stimulus type by bin interaction. Joystick velocity showed dual-task interference one bin (640 ms) earlier than tracking error did, suggesting that joystick velocity was more sensitive to detecting interruption in tracking than tracking error.

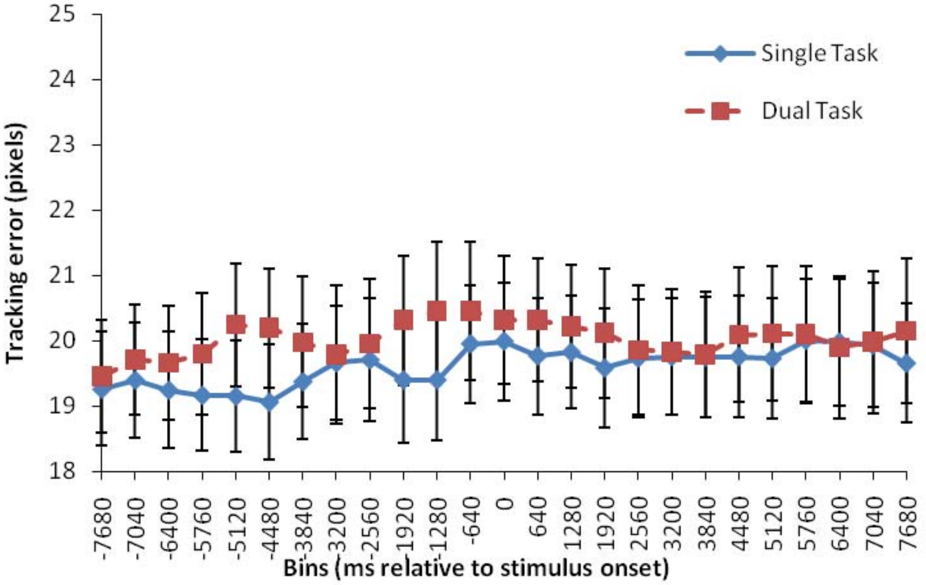

Fig. 8. Mean (± SE) tracking error in each bin and condition for non-targets.

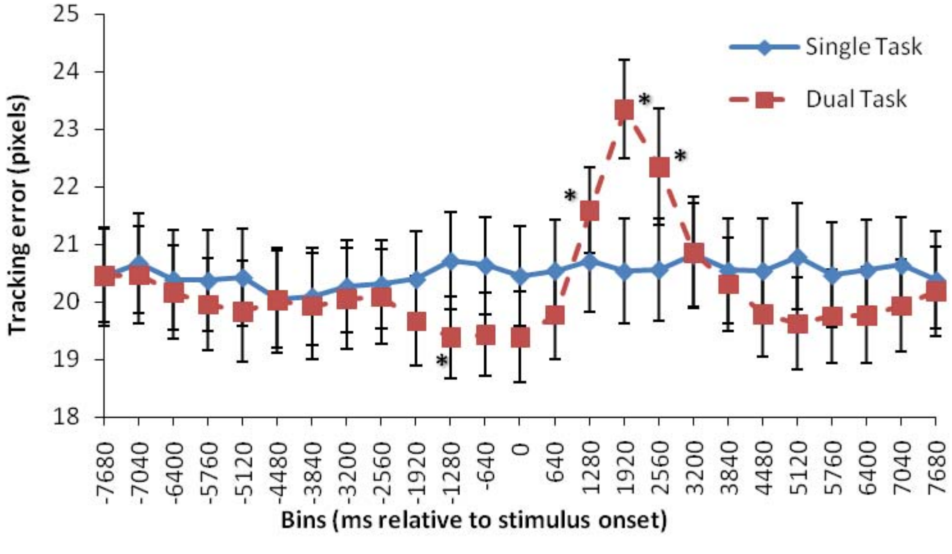

Fig. 9. Mean (± SE) tracking error in each bin and condition for targets. Asterisks mark the bins with significant difference from the grand mean.

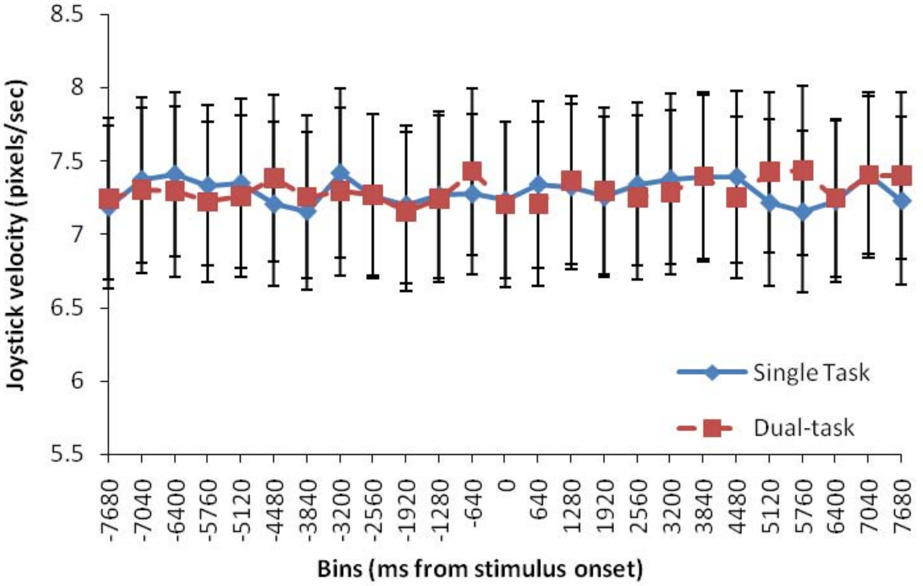

Fig. 10. Mean (± SE) joystick velocity in each bin and condition for non-targets.

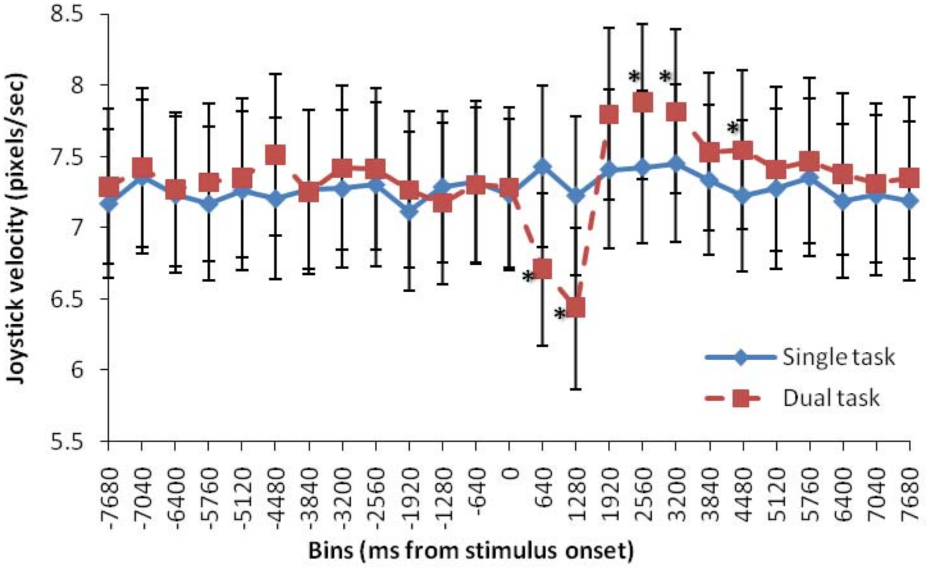

Fig. 11. Mean (± SE) joystick velocity in each bin and condition for targets. Asterisks mark the bins with significant difference from the grand mean.

Table 1.

F statistics for stimulus-locked 640 ms bin analysis for tracking error.

msec from stimulus onset	Bin	Bin x Group	Cond x Bin	Cond x Bin x Group	Stim Type x Bin	Stim Type x Bin x Group	Cond x Stim Type x Bin	Cond x Stim Type x Bin x Group
-5120	ns	ns	ns	ns	ns	4.98	ns	ns
-4480	ns	ns	ns	ns	ns	5.525	ns	ns
-3840	ns	ns	ns	ns	ns	ns	ns	ns
-3200	ns	ns	ns	ns	ns	ns	ns	ns
-2560	ns	ns	ns	ns	ns	ns	ns	ns
-1920	ns	ns	ns	5.446	ns	ns	ns	ns
-1280	ns	ns	ns	8.905	ns	ns	13.595	ns
-640	ns	ns	ns	5.81	4.972	ns	ns	ns
0	ns	ns	ns	ns	9.276	ns	ns	ns
640	ns	ns	ns	ns	5.15	ns	ns	ns
1280	20.44	ns	5.176	ns	7.752	ns	6.166	ns
1920	46.95	ns	45.567	ns	43.38	ns	30.984	ns
2560	17.62	ns	9.006	ns	19.027	ns	17.729	ns
3200	ns	ns	ns	ns	ns	ns	ns	ns
3840	ns	ns	ns	ns	ns	ns	ns	ns
4480	ns	ns	ns	ns	ns	ns	ns	ns
5120	ns	ns	ns	ns	ns	ns	ns	ns
5760	ns	ns	ns	ns	4.577	ns	ns	ns
6400	ns	ns	4.801	ns	ns	ns	ns	ns
7040	ns	ns	ns	ns	ns	ns	ns	ns
7680	ns	ns	ns	ns	ns	ns	ns	ns

Note. Degrees of freedom are 1 for numerator and 54 for denominator. Presented F statistics have $p < 0.05$. ns = not significant.

Table 2.

F statistics for stimulus-locked 640 ms bin analysis for joystick velocity.

msec from stimulus onset	Bin	Bin x Group	Cond x Bin	Cond x Bin x Group	Stim Type x Bin	Stim Type x Bin x Group	Cond x Stim Type x Bin	Cond x Stim Type x Bin x Group
-5120	ns	ns	ns	ns	ns	ns	ns	ns
-4480	ns	ns	5.486	ns	ns	ns	ns	ns
-3840	ns	ns	ns	ns	ns	ns	ns	ns
-3200	ns	ns	ns	ns	ns	ns	ns	ns
-2560	ns	ns	ns	ns	ns	ns	ns	ns
-1920	10.77	4.241	ns	ns	ns	ns	ns	ns
-1280	ns	ns	ns	ns	ns	ns	ns	ns
-640	ns	ns	ns	ns	ns	ns	ns	ns
0	ns	4.989	ns	ns	ns	ns	ns	ns
640	10.99	ns	22.139	ns	5.383	ns	13.948	ns
1280	19.76	ns	13.742	ns	27.731	ns	18.449	ns
1920	8.732	ns	ns	ns	10.083	ns	ns	ns
2560	20.26	5.161	ns	ns	22.142	6.152	12.139	ns
3200	15.69	ns	ns	ns	13.718	9.503	9.007	10.571
3840	8.74	ns	ns	ns	ns	ns	ns	ns
4480	ns	ns	ns	ns	ns	ns	6.987	ns
5120	ns	ns	ns	ns	ns	ns	ns	ns
5760	ns	ns	4.273	4.917	ns	ns	ns	ns
6400	ns	ns	ns	ns	ns	ns	ns	ns
7040	ns	ns	ns	ns	8.055	6.266	ns	ns
7680	ns	ns	ns	ns	ns	ns	ns	6.504

Note. Degrees of freedom are 1 for numerator and 54 for denominator. Provided F statistics have p < 0.05. ns = not significant.

Response-locked 640 ms bin set. As observed in the stimulus-locked bin analysis, joystick velocity changed earlier than tracking error. Figures 12 and 13 show the bin means for the two measures. Tracking error peaked at 0.64 s after response and decreased to lower than baseline until 5.12 s after response. Joystick velocity was the lowest at time of secondary response and exceded baseline, peaking at 1.28 s after response. Effect of bin was significant for both tracking error, $F(24, 1296) = 12.63$, $p < 0.001$ and joystick velocity, $F(24, 1296) = 19.98$, $p < 0.001$. Only joystick velocity showed an interaction between bin and group, F(24,1296) = 2.03, p = 0.013. Table 3 shows the F statistics for deviation contrasts confirming the differences presented.

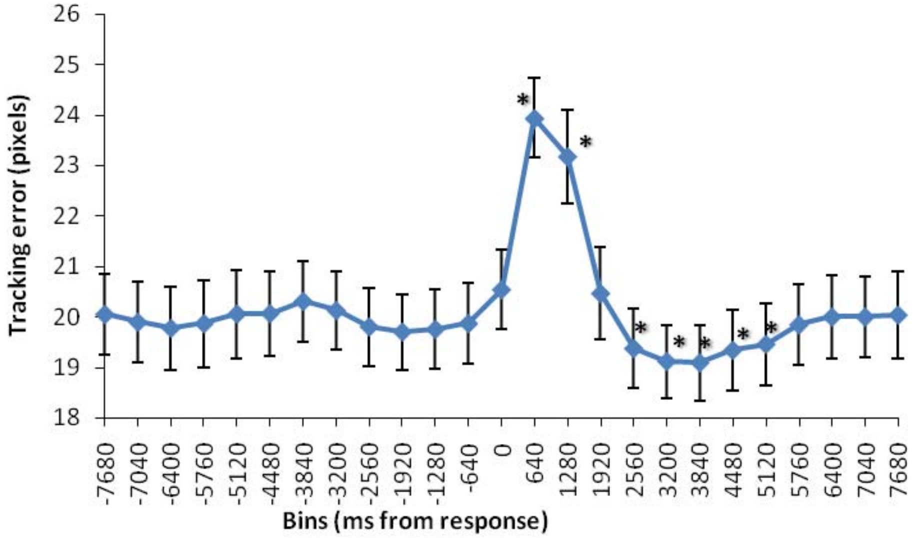

Fig. 12. Mean (± SE) Tracking error in each bin relative to response. Asterisks point to bins with significant contrast.

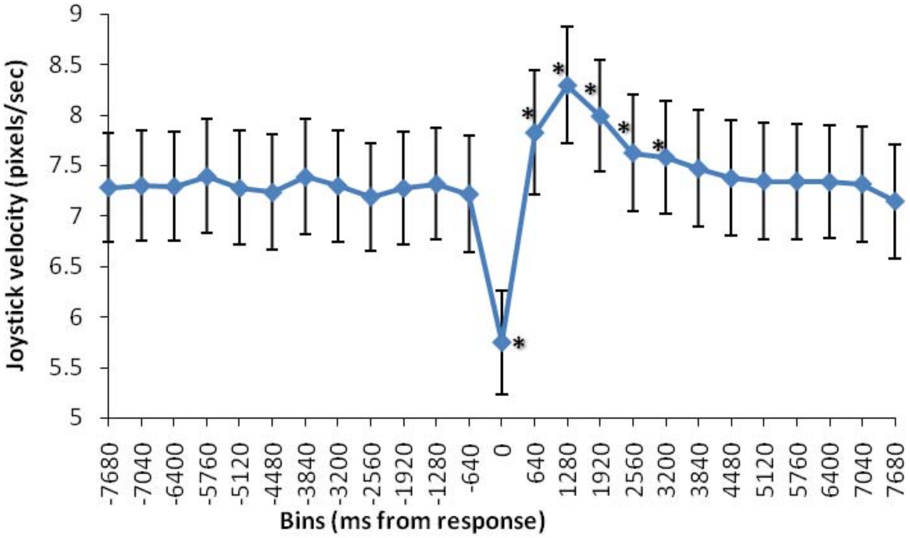

Fig. 13. Mean (± SE) joystick velocity in each bin relative to response. Asterisks point to bins with significant contrast.

Table 3.
F statistics for response-locked 640 ms binanalysis.

	Tracking Error		Joystick Velocity	
ms from response	Bin	Bin x Group	Bin	Bin x Group
0	ns	ns	75.979	ns
640	104.348	ns	9.814	ns
1280	65.699	ns	69.338	6.093
1920	ns	ns	39.021	13.909
2560	5.119	ns	7.628	ns
3200	7.939	ns	8.65	ns
3840	11.816	ns	ns	ns
4480	6.159	ns	ns	ns
5120	4.413	ns	ns	ns
7680	ns	ns	5.65	ns

Note. Degrees of freedom are 1 for numerator and 54 for denominator. Presented F statistics have $p < 0.05$. ns = not significant.

Response-locked 100 ms bin set. The 640 ms bin analyses showed that joystick velocity was the lowest at secondary task response, but it was unclear whether joystick velocity began to decrease before or after response. In order to examine the temporal change more closely, the bins were further decreased to 100 ms. Figures 14 and 15 show the bin means for stimulus onset- and response-locked analyses. Comparison of the two analyses suggested the joystick velocity change was more closely related to response than to stimulus onset. Bin effect was found for both stimulus onset- and response-locked (stimulus onset: $F(4.923, 265.9) = 13.60$, $p < 0.001$; response: $F(30, 1620) = 43.25$, $p < 0.001$). The interaction between bin and group was not significant for both sets of analyses. As was shown by Netick & Klapp (1994), joystick velocity began to decrease in the 200 ms bin before response. The decreasing trend lasted until 400 ms post response, after which compensation resulted in greater joystick velocity than at baseline. Tables 4 and 5 show the significant F values for the contrasts.

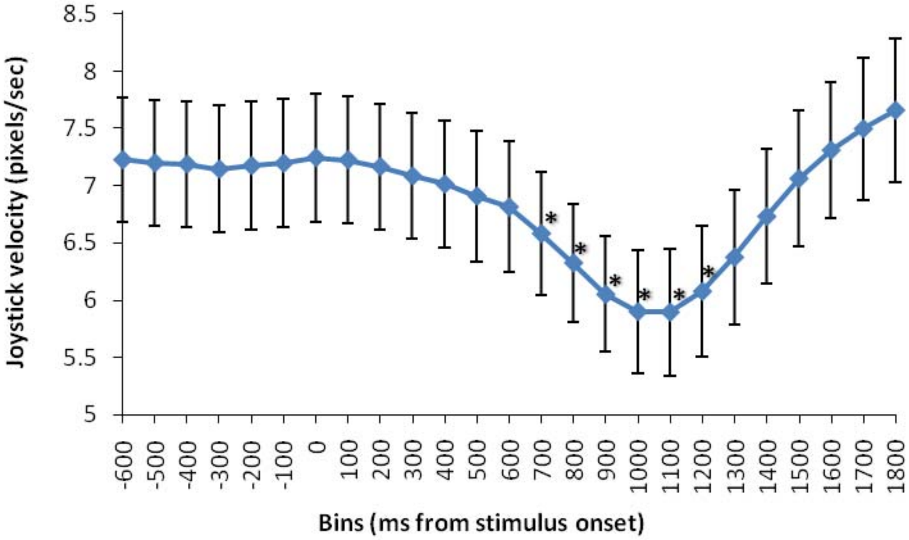

Fig. 14. Mean (± SE) joystick velocity in each bin relative to stimulus onset. Asterisks point to bins with significant contrast.

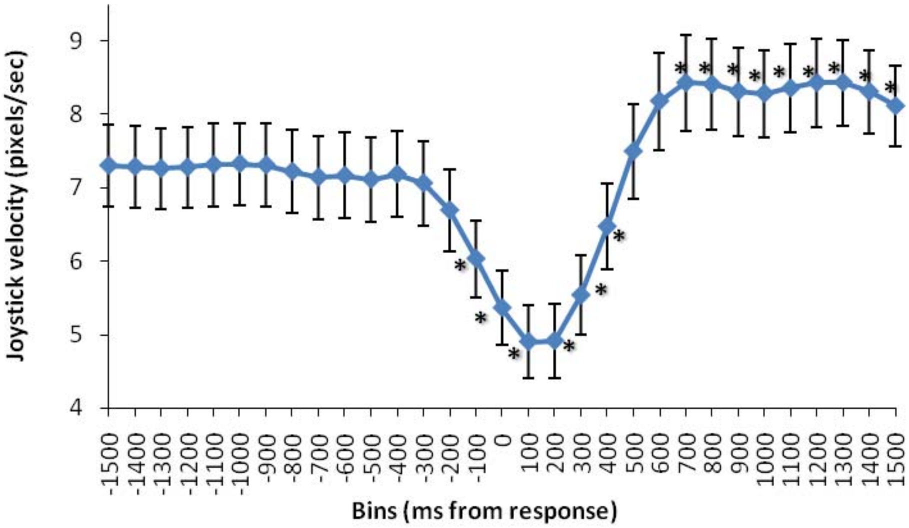

Fig. 15. Mean (± SE) joystick velocity in each bin relative to response. Asterisks point to bins with significant contrast.

Table 4.
F statistics for stimulus-locked 100 ms bin means.

ms from stimulus onset	Stimulus onset
700	11.564
800	21.416
900	30.658
1000	30.362
1100	27.337
1200	19.216

Note. Degrees of freedom are 1 for numerator and 54 for denominator. Presented F statistics have p < 0.002.

Table 5.
F statistics for response-locked100 ms bin means.

ms from response	Response
-100	28.275
0	50.961
100	69.498
200	75.575
300	48.912
400	11.804
500	ns
600	ns
700	18.855
800	25.271
900	25.798
1000	26.543
1100	33.967
1200	40.834
1300	37.649
1400	29.353
1500	21.241

Note. Degrees of freedom are 1 for numerator and 54 for denominator. Presented F statistics have p < 0.0016. ns= not significant.

Group differences. As shown in Figures 16 and 17, group 2 subjects improved their performance as measured by decreased tracking error while group 1's performance did not change as the experiment progressed across blocks, $F(2,100) = 3.727$, $p < 0.05$. Within each block, group 1 tracking error increased slightly while group 2 error remained the same, $F(1,50) = 5.282$, $p < 0.05$. Group 1 subjects had less false alarms than subjects in group 2, $F(1, 50) = 15.14$, $p < 0.001$. The two groups also differed in the trend across conditions for false alarms with greater increase in false alarms in the dual- than in the single-task condition for group 2 (see Figure 18), $F(1, 50) = 17.18$, $p < 0.001$. Due to the larger lapse in group 2 training, tracking error showed a learning effect for this group, but subjects also experienced greater fatigue as a result of the heavier testing load required by the sleep deprivation protocol, thus contributing to a greater number of false alarms. Furthermore, the fatigue affected dual-task performance more than in the single-task condition.

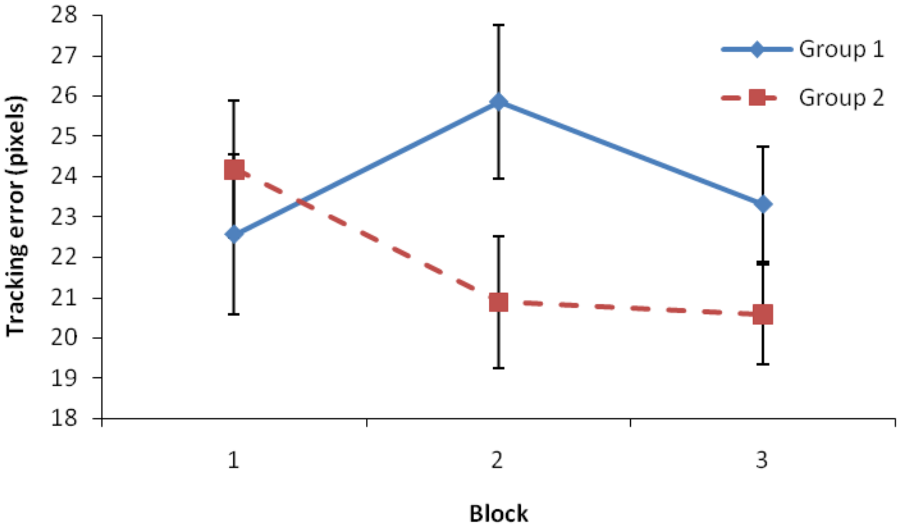

Fig. 16. Mean (± SE) for tracking error for each group in each block.

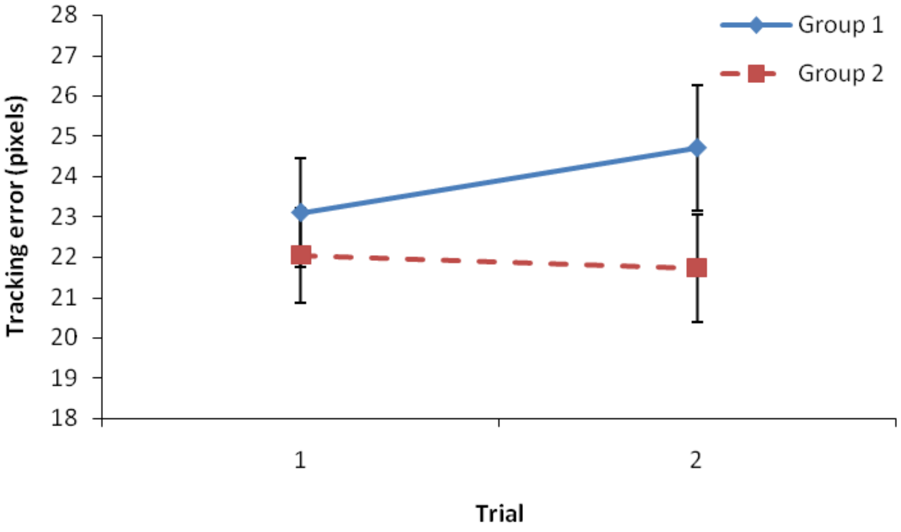

Fig. 17. Mean (± SE) for tracking error for each group in each trial.

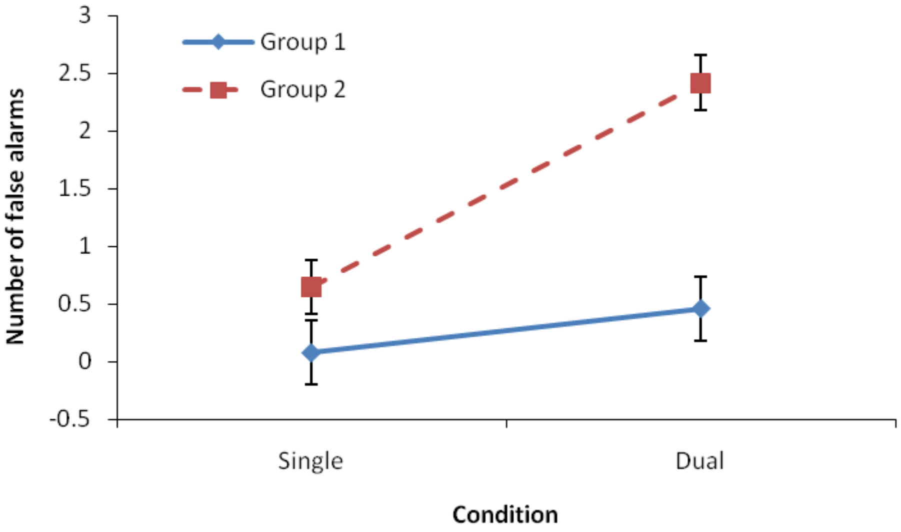

Fig. 18 . Mean (± SE) for the number of false alarms for each group in each condition.

Various bins showed significant differences in the deviation contrasts for interactions involving the group factor (see Tables 1 to 3), but these differences did not show any remarkable trend with respect to stimulus-onset and response. As Figures 19 to 22 illustrate, both groups followed the same overall trend relative to stimulus presentation and stimulus response for both tracking error and joystick velocity. Thus, it is likely that the significant differences found were spurious effects.

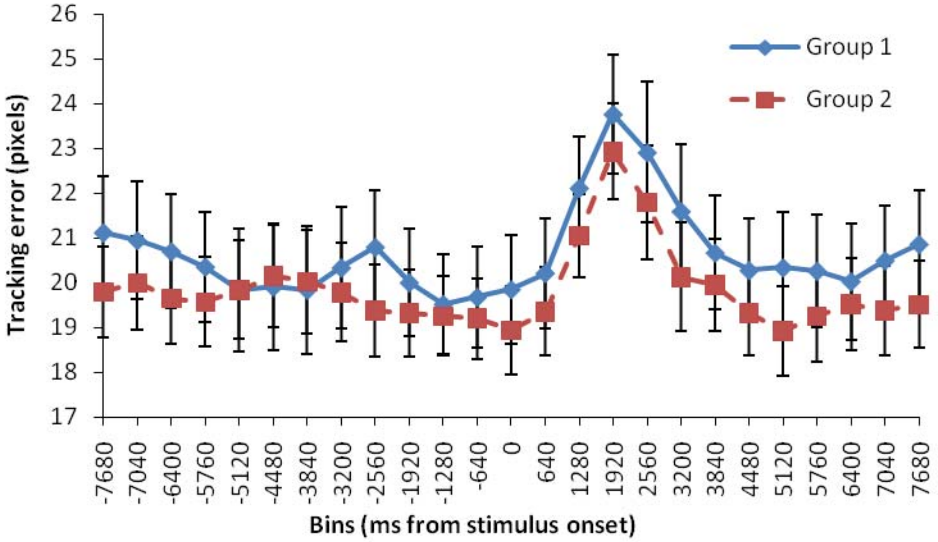

Fig. 19. Mean (± SE) tracking error in each bin relative to stimulus onset for each group.

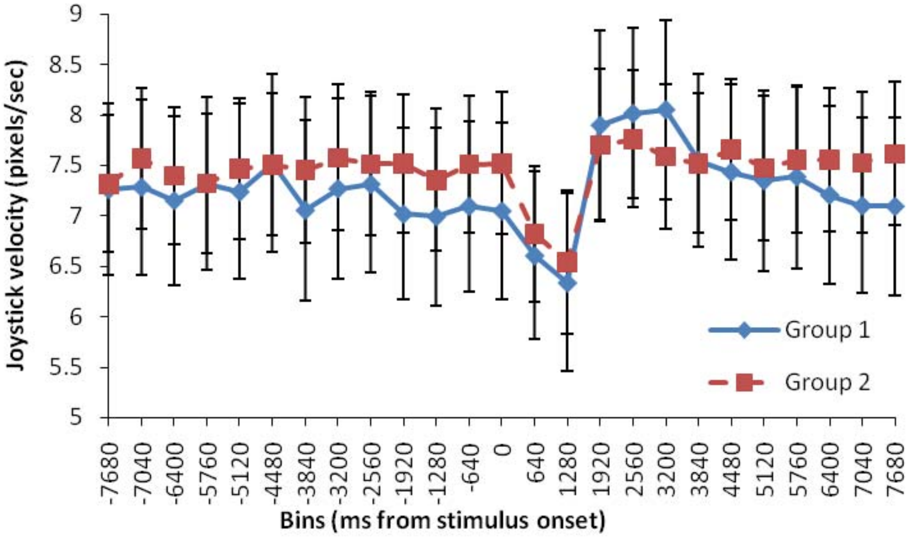

Fig. 20. Mean (± SE) joystick velocity in each bin relative to stimulus onset for each group.

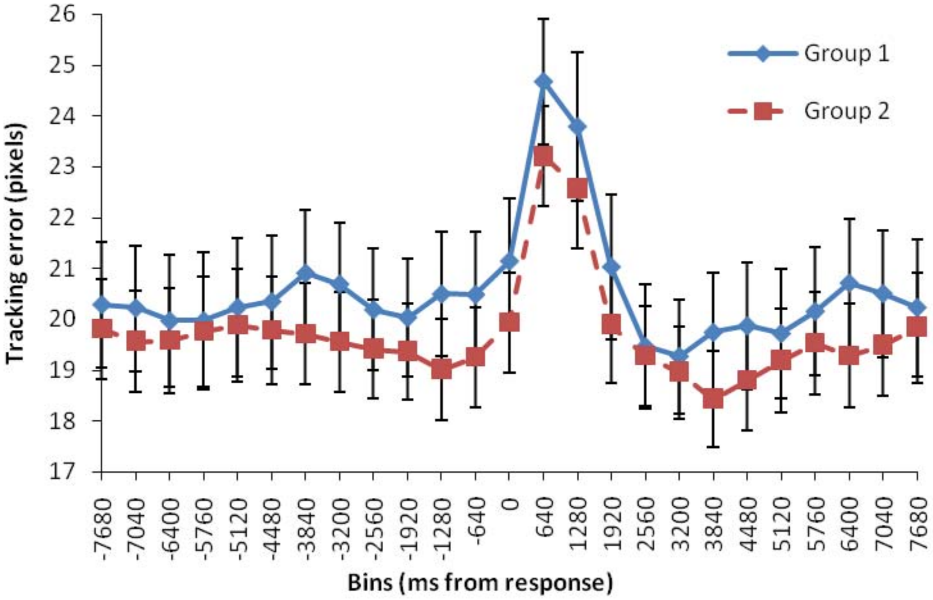

Fig. 21. Mean (± SE) tracking error in each bin relative to response for each group.

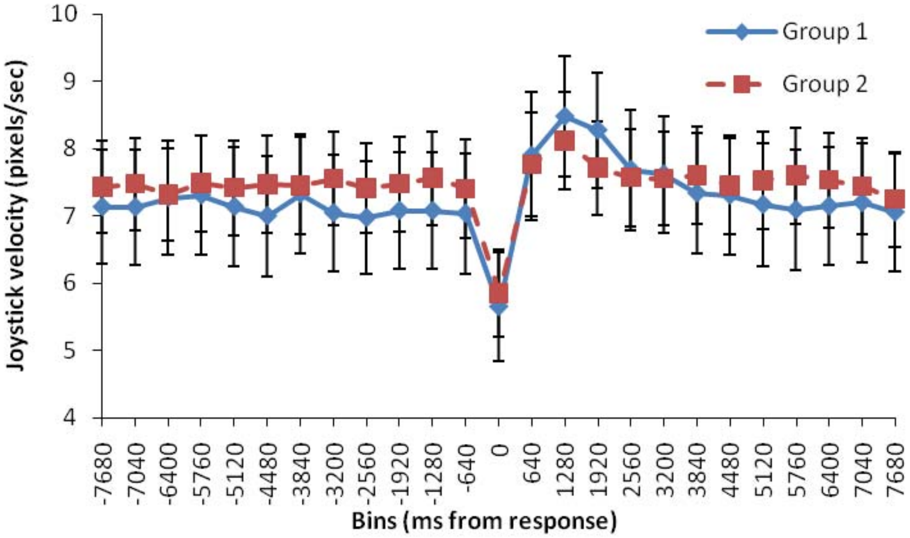

Fig. 22. Mean (± SE) joystick velocity in each bin relative to response for each group.

Neuroimaging

Results for the test of replication are presented first. The SPM analyses for the primary task in the single-task condition are then reported followed by analyses comparing dual- and single-task activations.

Global tests of replication with MLM

MLM analyses showed that group 2 results spatially replicated the imaging results from group 1. For four of the six MLM analyses comparing groups 1 and 2, one network was common to both groups, accounting for more than 71% of the total variance. Tables 6 and 7 list the relevant statistics for networks 1 and 2. MLMs on single-task tracking and dual- vs. single-task tracking revealed two networks each, but the first network accounted for 92% of the total variance in both analyses. Individual expressions of each primary network in the six analyses were not significantly different from each other. This indicates the two groups activated similar regions in each analysis and to a similar degree. Because the two groups showed similar activations, group differences in SPM models are not reported.

Table 6.
Statistics forMLM analylses for the first network.

Statistics	Single Track	Dual-Single Track	Single Jvel	Dual-Single Jvel	Hit-NTCC	Dual-Single NTCC
Numerator df	795	1029	848	1055	1207	1141
Denominator df	9936	12427	10394	12868	14589	13876
F	7.6793	10.7816	2.2891	1.085	5.0419	2.8611
% variance	92.309	92.141	82.178	71.350	89.464	84.144
Group 1 Mean	0.533	0.638	0.353	0.220	0.484	0.334
Group 1 SE	0.058	0.069	0.067	0.050	0.075	0.054
Group 2 Mean	0.499	0.579	0.134	0.097	0.360	0.275
Group 2 SE	0.057	0.039	0.071	0.058	0.046	0.038

Note. All analyses presented have $p < 0.05$. df = degrees of freedom. Grp = group. Subj = subject. SE = standard error.

Table 7.
Statistics forMLM analylses for the second network.

Statistics	Single Track	Dual-Single Track
Numerator df	398	514
Denominator df	6642	8302
F	1.1813	1.6947
% variance	0.077	0.079
Grp 1 Subj Exp Mean	0.190	0.253
Grp 1 Subj Exp SE	0.034	0.046
Grp 2 Subj Exp Mean	-0.117	-0.125
Grp 2 Subj Exp SE	-0.020	-0.021

Note. All analyses presented have $p < 0.05$. df = degrees of freedom. Grp = group. Subj = subject. SE = standard error.

Localized tests for effects of interest with SPM

Single-task tracking. Tables 8, 9, and Figure 23 show the brain regions activated in this anaylsis. Since the activations were very strong, the t-threshold was corrected by the most stringent threshold, family-wise error correction, at $p < 0.05$ and an extent threshold of 50 contiguous voxels. Compensatory visuomotor tracking in the single-task condition positively activated bilateral primary motor cortex, premotor cortex, supplementary motor area (SMA), inferior parietal cortex, primary somatosensory cortex, extrastriate cortex including area V5 (MT), and cerebellum, in particular the right culmen and the declive (lobules V & VI). Tracking was associated with decreased activation relative to baseline in the bilateral extrastriate cortex.

Table 8.

Major anatomical loci in single-task tracking analysis for positive activations.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Precentral	L	4	-38	-24	58	13.99	Inf	0.00	5470
Precentral	L	6	-30	-11	54	10.39	7.66	0.00	---
Parietal_Inf	L	3	-53	-21	40	9.47	7.24	0.00	---
Cerebelum_6	R	37	18	-53	-18	9.99	7.49	0.00	1682
Vermis	6	0	6	-63	-14	8.39	6.69	0.00	---
Vermis	8	0	4	-67	-27	6.40	5.49	0.00	---
Occipital_Mid	L	37	-44	-68	3	8.40	6.69	0.00	219
Temporal_Mid	R	37	46	-64	7	8.08	6.51	0.00	324
Parietal_Inf	R	40	36	-38	50	7.00	5.88	0.00	363
Parietal_Sup	R	5	34	-44	56	6.55	5.59	0.00	---
Occipital_Inf	R	18	32	-86	-1	6.95	5.85	0.00	92
SupraMarginal	R	3	55	-21	40	6.88	5.80	0.00	138
SupraMarginal	R	40	51	-27	47	5.34	4.76	0.00	---
Cerebelum_6	L	0	-24	-57	-22	6.41	5.50	0.00	175
Cerebelum_6	L	0	-16	-63	-20	6.37	5.48	0.00	---
Temporal_Sup	R	42	59	-32	18	6.13	5.32	0.00	61

Note. Dashes in column k indicate regions that are part of the previous cluster listed. Lat = laterality. BA = Brodmann's area. Tal = Talairach coordinate. k = cluster size.

Table 9.

Major anatomical loci in single-task tracking analysis for negative activations.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Lingual	L	30	-20	-62	7	7.31	6.07	0.00	449
Lingual	L	19	-18	-66	-2	6.87	5.80	0.00	---
Calcarine	L	31	-18	-61	16	6.16	5.34	0.00	---
Cuneus	L	18	-4	-88	19	7.16	5.98	0.00	357
Cuneus	R	19	4	-80	33	7.02	5.89	0.00	---
Cuneus	R	18	6	-88	19	6.93	5.84	0.00	---
Lingual	R	18	14	-74	6	6.80	5.76	0.00	479
Calcarine	R	30	18	-58	8	6.67	5.67	0.00	---
Lingual	R	19	24	-56	-1	5.30	4.73	0.00	---

Note. Dashes in column k indicate regions that are part of the previous cluster listed. Lat = laterality. BA = Brodmann's area. Tal = Talairach coordinate. k = cluster size.

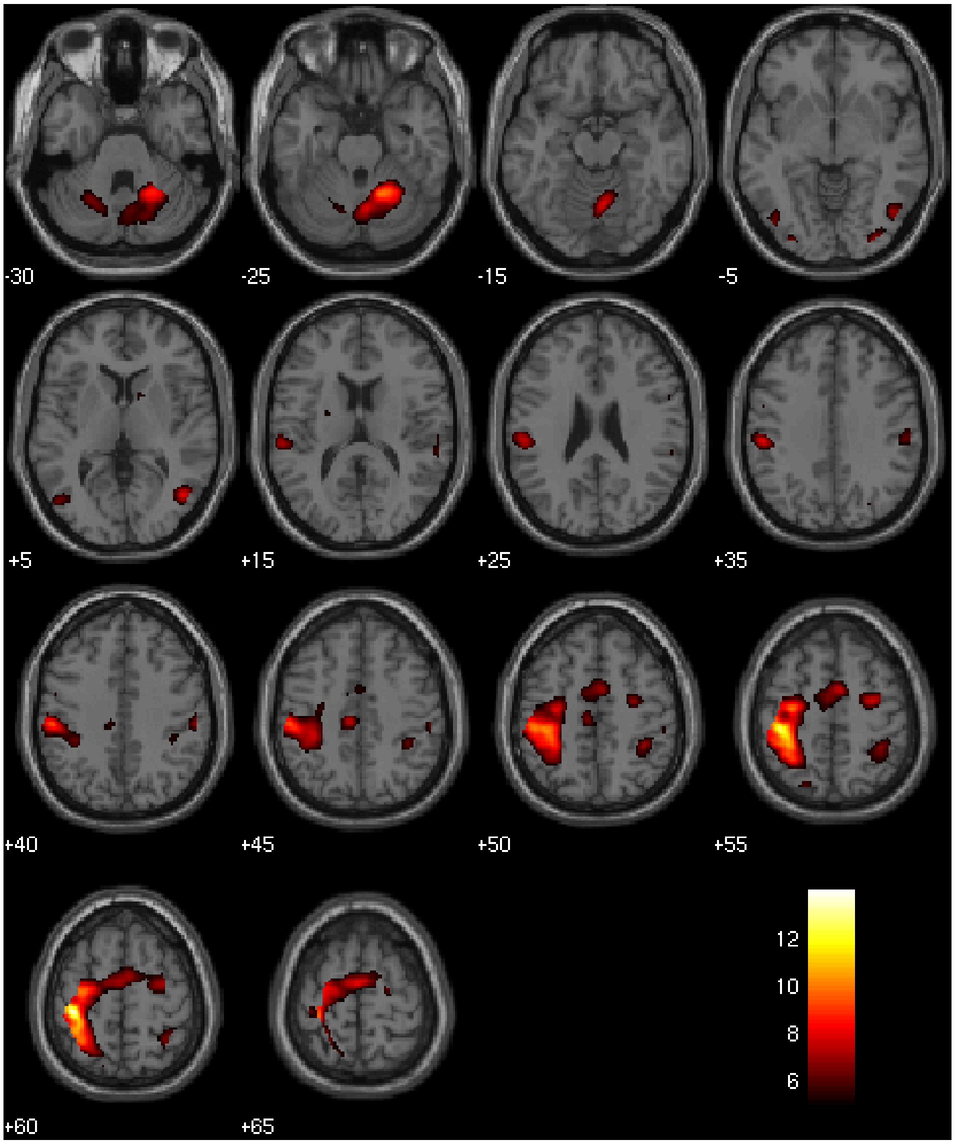

Fig. 23. Brain regions activated in single-task tracking. Shown at $t > 5$. Yellow to orange represent positively activated areas.

Single-task regressed with joystick velocity. The postcentral gyrus was found to be positively correlated with joystick velocity at the locus with talairach coordinate [-46, -26, 55], which was BA 2 in the left hemisphere. The t-value at the locus was 4.48 with $p < 0.05$. The absence of activations hypothesized to be associated with motor activity was likely due to the orthogonalization performed by SPM with respect to the main tracking trials. This point is further developed in the Discussion section.

Dual- versus single-task tracking. Brain areas associated with greater activation in the dual- versus single-task condition were bilateral extrastriate cortex and left superior parietal lobe (Table 10, Figure 24). There were no regions that showed greater activation in single- as compared to dual-task tracking.

Table 10.
Major anatomical loci for areas with greater activation in dual- than single-task tracking.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Fusiform	L	19	-28	-75	-14	5.04	4.55	0.00	59
Occipital_Mid	R	19	28	-84	19	4.61	4.21	0.00	11
Parietal_Inf	L	7	-25	-48	40	4.57	4.18	0.00	15

Note. Dashes in column k indicate regions that are part of the previous cluster listed. Lat = laterality. BA = Brodmann's area. Tal = Talairach coordinate. k = cluster size.

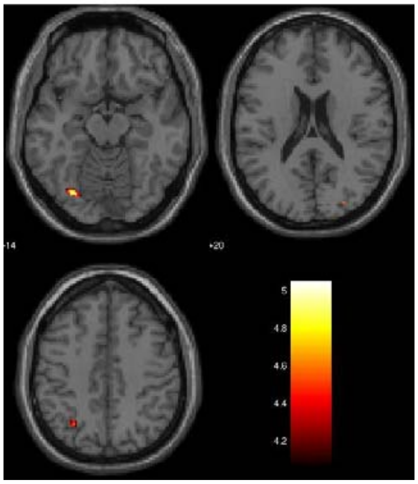

Fig. 24. Brain regions with greater activation in dual- than in single-task tracking. Shown at $t > 4.06$.

Dual- versus single-task regressed with joystick velocity. No difference was found in the correlation between brain activity and joystick velocity for single- versus dual-task conditions.

Target versus non-target in dual-task condition. Comparison between targets and non-targets was intended to reveal brain areas associated with response to a secondary task. Table 11 and Figure 25 show the activated regions. Greater activation was found for hits than for non-targets in the right primary motor cortex, somatosensory cortex, thalamus, bilateral cingulate gyrus, inferior frontal gyrus, and insula, and declive in the left cerebellum. Interestingly, the left primary motor and somatosensory cortices showed greater activation to non-targets than to targets, further supporting the hypothesis that dual-task interference in visuomotor tracking occurs in the motor output stages. See Table 12 and Figure 26 for specific results.

Table 11.

Major anatomical loci for areas with greater activation to targets than to non-targets in dual-task condition.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Postcentral	R	3	42	-24	56	11.60	Inf	0.00	1230
Postcentral	R	3	46	-21	51	10.57	7.74	0.00	---
Precentral	R	4	34	-22	60	10.16	7.56	0.00	---
Rolandic_Oper	R	43	50	-19	18	8.96	6.98	0.00	349
Insula	R	47	36	31	-2	6.85	5.79	0.00	883
Frontal_Inf_Orb	R	47	36	25	-6	6.74	5.71	0.00	---
Insula	R	48	46	8	3	6.24	5.39	0.00	---
Cerebelum_6	L	0	-18	-51	-16	6.76	5.73	0.00	979
Cerebelum_6	L	0	-4	-61	-14	6.04	5.26	0.00	---
Cerebelum_6	L	0	-6	-60	-4	5.64	4.98	0.00	---
Cingulum_Mid	R	32	4	23	36	6.36	5.47	0.00	1397
Frontal_Sup_Medial	L	6	-10	27	34	5.41	4.82	0.00	---
Cingulum_Mid	R	24	6	6	37	5.27	4.71	0.00	---
Lingual	R	30	10	-43	4	5.44	4.84	0.00	207
Calcarine	R	30	16	-62	9	4.62	4.22	0.00	---
Lingual	R	30	16	-54	6	4.62	4.22	0.00	---
Insula	L	48	-46	4	2	5.30	4.74	0.00	197
Insula	L	48	-42	12	-1	5.16	4.63	0.00	---
Thalamus	R	0	16	-19	6	5.27	4.71	0.00	205
Thalamus	R	0	14	-10	2	4.77	4.33	0.00	---
SupraMarginal	L	40	-61	-31	35	5.25	4.70	0.00	130
Parietal_Inf	L	40	-57	-45	37	4.94	4.47	0.00	---
SupraMarginal	L	48	-61	-37	30	4.52	4.14	0.00	---
Frontal_Inf_Orb	L	47	-28	25	-11	5.24	4.69	0.00	69
Frontal_Inf_Orb	L	47	-30	31	-5	4.83	4.38	0.00	---
Insula	R	48	40	-12	1	4.99	4.51	0.00	37
Lingual	L	30	-10	-43	0	4.71	4.29	0.00	29
Cingulum_Mid	R	31	6	-21	45	4.50	4.13	0.00	28

Note. Dashes in column k indicate regions that are part of the previous cluster listed.

Lat = laterality. BA = Brodmann’s area. Tal = Talairach coordinate. k = cluster size.

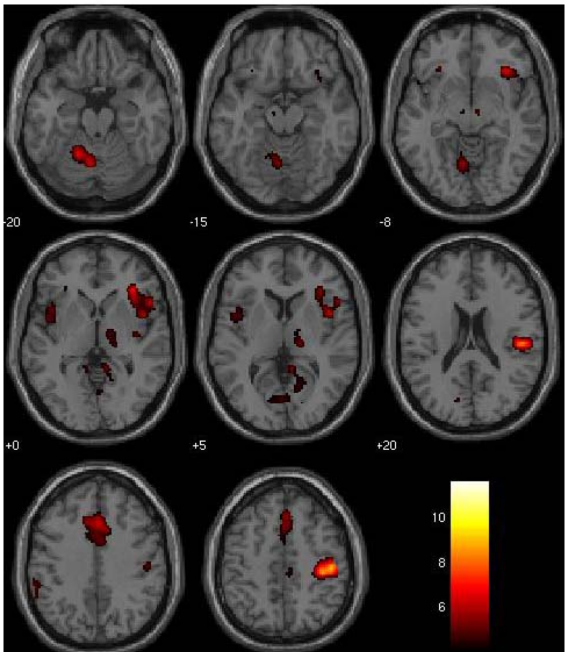

Fig. 25. Brain regions with greater activation to targets than to non-targets. Shown at $t >$ 4.11.

Table 12.

Major anatomical loci for areas with greater activation to non-targets than to targets in dual-task condition.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Postcentral	L	3	-30	-30	63	5.19	4.65	0.00	71
Precentral	L	4	-38	-26	62	5.15	4.62	0.00	---
Postcentral	L	4	-30	-17	43	4.35	4.01	0.00	---

Note. Dashes in column k indicate regions that are part of the previous cluster listed. Lat = laterality. BA = Brodmann’s area. Tal = Talairach coordinate. k = cluster size.

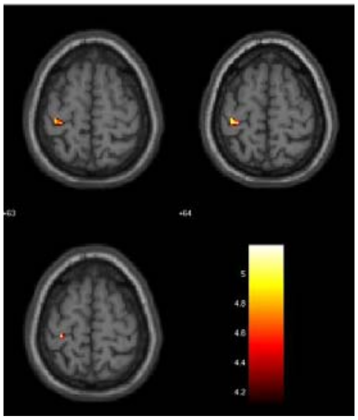

Fig. 26. Brain regions with greater activation to non-targets than to targets. Shown at $t > 4.11$.

Dual- versus single-task NTCC. The goal of comparing brain activity to non-targets in the dual- and single-task conditions was to identify areas associated with response inhibition. Table 13 and Figure 27 show the activated areas. Regions with greater activity in the dual- than single-task condition in this analysis were bilateral extrastriate cortex, right superior parietal lobe, and left inferior frontal lobe.

Table 13.

Major anatomical loci for areas with greater activation to non-targets in the dual- versus single-task condition.

			Tal						
Region	**Lat**	**BA**	**x**	**y**	**z**	**T**	**Z**	**p**	**k**
Calcarine	R	17	12	-81	10	7.19	6.00	0.00	2240
Occipital_Mid	L	19	-28	-74	33	6.01	5.24	0.00	---
Lingual	R	18	10	-70	-2	5.58	4.93	0.00	---
Occipital_Mid	R	19	30	-68	37	6.35	5.46	0.00	380
Occipital_Mid	R	19	34	-79	21	4.93	4.46	0.00	---
Occipital_Sup	R	7	28	-62	47	4.69	4.28	0.00	---
Frontal_Inf_Oper	L	9	-38	11	22	5.05	4.55	0.00	36
Precuneus	R	7	12	-56	51	4.77	4.34	0.00	21
Lingual	L	30	-20	-52	1	4.23	3.92	0.00	11

Note. Dashes in column k indicate regions that are part of the previous cluster listed. Lat = laterality. BA = Brodmann’s area. Tal = Talairach coordinate. k = cluster size.

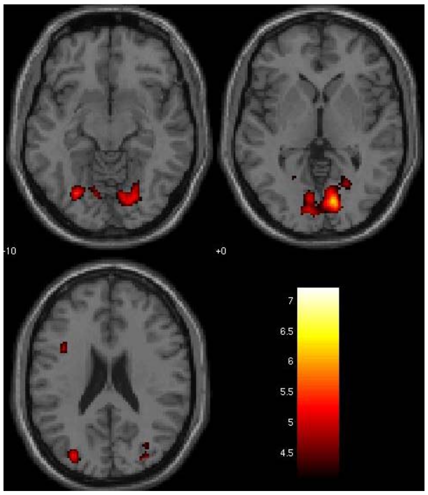

Fig. 27. Brain regions with greater activation to non-targets in dual- versus single-task condition. Shown at $t > 4.09$.

DISCUSSION

This study aimed to understand the stages of processing affected by dual-task compensatory tracking compared to the single-task condition. Dual-task interference was investigated by comparing tracking activity during dual-task condition with tracking activity in the single-task condition. Interference was measured with joystick velocity and was expected to occur during motor stages of the secondary task such that joystick velocity should be the lowest when subjects made a motor response to the secondary task.

Compensatory tracking in the single-task condition was also used to localize motor error correction processes, which were hypothesized to consist of activation in the cerebellum and the inferior parietal lobule. In addition, joystick velocity was correlated with brain activation during single-task tracking to find regions associated with the direct output of motor error correction processes.

Replication

Both imaging and behavioral results showed successful replication between experiments 1 & 2. MLM enabled examination of replication in spatial relationship among voxels in the brain images. MLM showed that the same network was activated in both groups with most of the variance accounted for. A common network shared by both experimental groups pointed to similar regions being activated by task events. Behavioral results were also replicated in the two experiments for all of the overall mean analyses performed except false alarms and for all of the binned time-series analyses. The two experimental groups did not show mean differences across experimental conditions for RMS tracking error, joystick velocity, number of hits, and reaction time, and interaction between the bin and group factors were not found in any of the binned time-series analyses. Replication in the two experiments showed the robustness of the results and that type I and II errors were unlikely to be committed. Because of this replication, we will dispense with distinctions between experiments from here on.

Compensatory tracking

Inferior parietal activation associated with single-task tracking coincided with regions found by Ogawa et al. (2007) in which tracking error was correlated with brain activity. Ogawa et al. believed that the inferior parietal activation was associated with evaluation of visuomotor error. Activation in the current study was consistent with this interpretation since in compensatory tracking, only the tracking error was displayed, which meant that the main perceptual task was error evaluation. However, other interpretations are also possible. For example, the posterior parietal lobe has been associated with the integration between different coordinate systems (Battaglia-Mayer, Archambault, & Caminiti, 2006). Thus, inferior parietal lobule's involvement in visuomotor error may also be the integration of error in visual distance with the hand's position to generate the next set of motor commands.

In a different part of the study, the temporal parietal junction, was found to be significant in the single-task tracking condition in the current study. This area was correlated with the amount of delay in subject's control of the cursor movement in Ogawa et al. (2007). The delay in the visual feedback was believed to induce greater activation in the state estimation mechanism by delaying the visual feedback. The cursor control used in the current study was acceleration control, which delayed the effect of joystick movement on the cursor position. Joystick movement didn't affect the cursor position immediately, but instead, was delayed because changes in joystick movement caused changes in acceleration, which then changed velocity, and finally affected the cursor position. This sequence of events led to inherent delay in changes made by the joystick movement to be reflected in the cursor position. Subjects didn’t receive visual feedback until the cursor position was changed. The delay in visual feedback under acceleration control is therefore similar to the delay built into Ogawa et al.’s task. Thus the activation of the temporal parietal junction in the current study is consistent with Ogawa et al.’s interpretation of this area’s role in tracking.

Both the inferior parietal cortex and the cerebellum were activated in the single-task tracking trials, but were not correlated with joystick velocity. The two regions were hypothesized to correlate with joystick velocity because it is thought that they are activated during online error correction mechanisms. The null result was most likely due to technical issues. Both of these regions were highly active during the single-task tracking trials. The joystick velocity regressor was intended to extract any variable activity in addition to the activations in the tracking trials. In other words, the regressor should identify areas with activity that correlated with changes in joystick velocity such that if an area is already activated for the entire tracking trial, it has to also show variation in its activation that correlated with joystick velocity in order to show significance in the joystick velocity analysis. Areas that maintained a consistent level of activity would only be significant in the tracking trial analysis and not in the joystick velocity analysis. Therefore, since both the inferior parietal lobule and the cerebellum were highly significant in the tracking trials, it is possible that the online error correction mechanisms did not show any variable activity for different amounts of error correction. A second possibility is that the frequency of variability in these regions did not match well with the frequency of the joystick velocity regressor used, in which case a better filter should be used in future research to simulate the variability in these regions. As with all null results, a third possibility is the lack of power to detect the effect.

Dual-task interference

Dual-task tracking enabled the localization of the processing stage that is shared between tracking and a secondary task and that also has limited capacity, which resulted in interference in the dual-task condition. For the purposes of analyses and discussion, continuous tracking can be broken into a repeating series of events in which a complete trial starts with perception of cursor and target locations, then movement of joystick has to be chosen in order to minimize tracking error, then the chosen movement is executed. For GNG, ‘go’ trials start with perceptual processing circle colors and decide whether a match has been created, then response selection, then motor processing. ‘No-go’ trials follow the same stages as ‘go’ trials but the processes terminate before initiation of motor stages such that as soon as the perceptual processing has determined the stimulus to be a ‘no-go’ signal, processing terminates for that trial (De Jong, 1993; Pashler, 1994a). Thus, for ‘go’ trials, overlap between the two tasks could occur in any of the three processing stages: perceptual, response selection, and motor response, but interference between ‘no-go’ trials and tracking would be limited to perceptual and response selection.

Researchers debate the existence of a motor bottleneck. Pashler (1994a) strongly argued against a motor bottleneck and in favor of a response selection bottleneck. However, other studies found evidence for bottlenecks in perceptual and motor stages (Karlin and Kestenbaun, 1968; De Jong, 1993; Ulrich, Fernandez, Jentzsch, Rolke, Schroter, & Leuthold, 2006; Bratzke, Ulrich, Rolke, Schroter, Jentzsch, & Leuthold, 2007). Karlin and Kestenbaum (1968) first reported PRP effect in simple reaction time tasks. Because simple reaction time tasks require minimum response selection, the authors inferred that the PRP must be due to motor interference. Later studies did not find consistent motor interference in various pairings of tasks. De Jong (1993) presented an extended bottleneck model which included bottlenecks in other stages besides response selection. De Jong’s model was able to resolve conflicting results from previous studies by taking into consideration the interaction between two bottlenecks. According to the dual-bottleneck model, if response selection processing was minimal, as in Karlin and Kestenbaum’s study, then the brief period of motor interference could be observed. Inversely, motor interference may not be observed when it is absorbed by the longer perceptual or response selection stages, such as in choice reaction time tasks. As shown in Figure 28, the motor refractory period does not delay motor response in task 2 because the response selection stage extends pass the motor refractory period. De Jong attributed the difference between studies that found motor interference and those that did not to be a function of the duration of the first bottleneck: the motor interference was observed only if the first response selection bottleneck was very short. Thus, bottleneck can occur in any of the processing stages, and is not just limited to response selection.

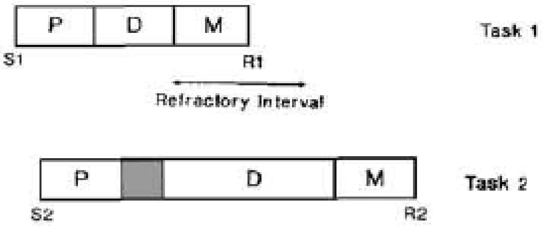

Figure 28. Interaction between two tasks in the dual-bottleneck model. Boxes show the sequential stages: perceptual (P), decisional (D), and motor (M). The gray area shows refractory period in the decisional stage in task 2. Even though motor refractory period in task 1 is there, it is absorbed by the long decisional stage. Modified from De Jong (1993).

Dual-task interference was found between tracking and GNG. Significant increase in tracking error combined with decreased joystick velocity after GNG target presentation in the dual-task condition suggested interruption in tracking processes due to secondary task activation. Furthermore, interruption in tracking was only observed for target presentations but not for non-target presentations, and only in the dual-task condition.

Based on the behavioral and imaging results, interference in the perceptual stages was not likely. Stimulus processing was necessary during presentation of secondary task stimuli in the dual-task condition, but not in the single-task condition. During the dual-task condition, subjects had to determine whether the secondary stimuli were ‘go’ or ‘no-go’ signals. Secondary task stimuli required color discrimination and spatial localization to ensure the circles were diagonally opposite each other. This was supported by greater activation found in the visual and parietal cortices to non-targets in the dual-task condition than in the single-task condition. Given that stimulus processes were activated for non-targets in the dual- but not in the single-task condition, interference during stimulus processing should have been revealed by changes in joystick velocity following presentation of non-targets in the dual-task condition. As was shown in the binned time-series data for joystick velocity, no difference was found in response to non-targets in the dual-task condition. In fact, joystick velocity during non-target presentation was similar to joystick velocity during the single-task condition, further suggesting dual-task interference was not found in the stimulus perceptual stages.

Behavioral and imaging results provided evidence for motor response interference instead. Joystick velocity was a good measure for temporally locating the interference in tracking in relationship to the secondary task events (stimulus onset and response). The point at which joystick velocity started to decrease marked the beginning of secondary task interference. Binned time-series analyses showed that the decrease in joystick velocity was much closer in time to stimulus response than to stimulus onset, beginning at less than 200 ms before stimulus response but more than 700 ms after stimulus onset. This result alone could not differentiate between the perceptual, response selection, and motor response bottlenecks because a bottleneck in either of the first two stages could still result in joystick velocity changes occurring close to stimulus response due to the sequential nature of the processing stages.

When behavioral results were combined with neural imaging results, however, the evidence for motor response interference was strengthened. Comparison between target and non-target in dual-task condition showed decreased activation in the left primary motor and somatosensory cortices. Activation for the right hand motor control, which operated the joystick, was reduced when subjects had to respond to the secondary task stimulus with their left hand than when they did not have to make a left-hand response. This finding suggested that left-hand responses, which should have only affected right motor cortex activation, were associated with decreased activation of the right hand area. Thus, with joystick velocity decrease occurring within 200 msec of response and decreased activation in the left motor cortex in response to left hand movement, dual-task interference in tracking was most likely due to a bottleneck in the motor output stages. Furthermore, based on the high temporal resolution binned time-series analysis on joystick velocity, the decrease occurred 200 ms before secondary task response, suggesting the interference exists in the motor preparation stage rather than in motor execution stage.

Role of the inferior frontal cortex

Greater inferior frontal activation was found for targets than non-targets in the dual-task condition. The inferior frontal gyrus has been associated with executive functions in numerous studies (for example: Derrfuss, Brass, & von Cramon, 2004; Szameitat, Lepsien, von Cramon, Sterr, and Schubert, 2006; Zysset, Müller, Lohmann, & von Cramon, 2001). Inferior frontal activation to targets suggests an executive control processing involved in dual-task tracking. According to the Bottleneck theory, on the other hand, additional regions are not necessary to coordinate the two tasks. The bottleneck occurs because the sharing of a common neural region prevents the second task from accessing the same region. A region involved in executive control in targets condition points away from Bottleneck theory and towards additional processes associated with task coordination.

Derrfuss et al. (2004) found common activation in the inferior frontal gyrus in three different tasks: task-switching, manual Stroop task, and verbal *n*-back task. All three tasks share the characteristic of requiring coordination between conflicting cognitive processes. Derfuss and colleagues' finding was consistent with that found in Zysset et al. (2001), in which regions around the inferior frontal sulcus showed increased activation in incongruent trials relative to congruent trials in the Stroop task. Incongruent trials contained color words printed in a different color from the color described by the word. For example, "red" might be printed in green ink. Response to incongruent trials required resolving conflicting response tendencies in order to suppress the word description and identifying the color of the ink used. Szameitat, Lepsien, von Cramon, Sterr, and Schubert (2006) also found greater left inferior frontal activation for task-switching. The researchers compared trials preceded by a different task with trials preceded by the same task. Trials that required task-switching differed from no-switch trials in the amount of task coordination needed, further supporting the role of the inferior frontal sulcus in cognitive coordination.

Based on the above studies, the role of inferior frontal sulcus activation in the current study was likely coordination of two competing tasks. As was discussed, tracking movement had to be halted while GNG response was made. Interruption in the primary task as a result of secondary task activation may have been caused by a passive process, or the interruption may have been actively coordinated by an executive control process that directed the resources to meet the top priority goal.

Passive queuing, postulates that competing processes are handled on a first-come-first-serve basis (Pashler, 1994a), without the need of a coordinating process to supervise task ordering. For example, while the bottleneck stage in task 1 takes place, the same stage in task 2 just waits because the processor that it needs is not yet available. Salvucci and Taatgen (2008) implemented a computer model to understand the operation of a passive system and to evaluate the validity of this system. Independent tasks share the same resource by following a set of rules defining which task receives priority access to a limited-capacity process. According to this model, concurrent tasks are performed according to a set of rules that define the order of execution. When conflict arises, processes follow specified rules for deciding which process is handled first. This model suggests that a coordinating agent is not a necessary component of multi-task management. However, the evaluation of rules still has to be performed, either by encoding into neural connections or by a specialized brain area. For example, one of their rules is:

> IF the goal buffer contains a dual task
> THEN add a goal to perform the choice task
> and add a goal to perform the secondary task.

In order to follow this rule, an agent has to evaluate the IF statement and direct action according to the evaluation. If task coordination is a passive process, then a possible role for the inferior frontal gyrus is the evaluation of conditions.

Active coordination of tasks requires a process that exerts executive control over lower processes. Koechlin, Ody, and Kouneiher (2003) proposed a cascade model in which the level of control increases in the anterior direction starting from the premotor cortex. More specifically, the premotor cortex coordinates response based on stimulus identity. Anterior to the motor cortex, the inferior frontal gyrus manages contextual information such as the type of task to be performed in a particular trial. Then the middle frontal gyrus exerts episodic control over tasks. The authors performed an fMRI study involving stimulus, context, and episodic manipulations and obtained results consistent with their model. This model attributes an active executive role in task ordering and scheduling to the frontal brain regions. It differs from Salvucci and Taatgen’s model in that control over competing processes is not necessarily induced by a deficit in processing resource. Rather, coordination can be activated by a lack of processing capacity as well as by a purposeful switch from one task to another according to priority or task demand (e.g. context or stimulus).

Limitations and future directions

The correlation analysis between joystick velocity and brain activation did not show meaningful result. The problem was attributed to the high correlation between the tracking predictor and the joystick velocity vector. As was explained previously, the joystick velocity regressor was automatically orthogonalized with respect to the main tracking predictor. The high dependence between the tracking and joystick velocity predictors might have led to most of the variance being placed on the main tracking predictor and only residualized variance being left in the joystick velocity predictor. Ogawa et al. (2007) may not have encountered this problem because they had an event-related predictor for the tracking trials rather than block-design for the tracking predictor. The correlation between an event-related tracking predictor and the tracking error predictor may not have been as high as with a block-design tracking predictor.

A limitation in the experimental design was the lack of control conditions that would have enabled examination of more precise localization of brain regions associated with specific mechanisms. The visuomotor analyses would benefit from additional control conditions to isolate activation associated with visual motion by presenting a video of the tracking cursor moving on its own. Subtracting areas activated during visual presentation from activation due to regular tracking will reveal areas activated by motoric processes. A second control condition is to isolate purely motoric components by asking subjects to move the joystick without visual guidance but with an auditory command. This control condition would isolate motor processes related to visuomotor integration from those involved in purely muscular control.

Other control conditions will improve the dual-task interference paradigm. A condition with only the GNG task will enable understanding of the secondary task with and without dual-task interference. In the current design, only interference in tracking can be observed because single-task tracking performance was compared with dual-task tracking performance. By the same logic, if a single-task GNG was included in the design, performance in this control condition could be compared with performance in the dual-task design. The design would also allow comparison of single-task activation in the primary and secondary tasks with activation in the dual-task condition to study regions activated by dual-tasking and not by either of the tasks individually. Without the GNG control condition, regions with greater activation in dual-task condition than in single-task tracking could have been associated with GNG or with dual-task processing independent of the individual tasks involved.

The study can be further improved with additional measurements to quantify perceptual and motor output variables. Eye-tracking should be included in all task conditions. Keeping track of eye position will enable not only better control of resting eye position by ensuring subjects do maintain gaze on the screen, but will also allow examination of whether dual-task interference was caused by visual processing of the secondary task stimuli, which prevented primary task stimuli from being analyzed. Since both tracking and GNG stimuli were presented visually, subjects had to shift gaze from tracking to GNG stimuli to identify targets and non-targets. It is possible that targets cause longer evaluation processing than non-targets, and this results in interference during dual-tasking. A second device to be added to future studies is electromyography (EMG). EMG provides the exact time point at which muscle contraction is initiated, which will further improve the temporal resolution in dual-task interference analyses. The initiation of muscle contraction for GNG response relative to tracking performance will enable more precise localization of dual-task interference than was possible in the current study. Muscle contraction initiation marks the end of motor preparation. With EMG, decrease in joystick velocity can be precisely located relative to motor preparation. This will resolve the question of whether motor preparation or motor execution was the dual-task bottleneck in tracking and GNG.

Conclusion

Compensatory tracking located a network of regions involved in motor error processing and correction. In addition to the cerebellum and the inferior parietal lobule, the network included basic perceptual and motor regions such as the extrastriate and the primary motor cortices.

Dual-task interference in continuous visuomotor tracking due to a speeded task was found to occur in the motor output stages. Neuroimaging showed decreased activation in the motor area for the tracking hand, thus further illustrating the interference occurring at motor output stages. Since the decrease in joystick velocity began to decrease before response to a secondary task, the specific interrupted stage is most likely motor preparation.

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