Dual-task interference is greater in delayed grasping than in visually guided grasping

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Previous kinematic research suggests that visually guided grasping employs an accurate real-time control system in the dorsal stream, whereas delayed grasping relies on less accurate stored information derived by the perceptual system in the ventral stream. We explored these ideas in two experiments combining visually guided and delayed grasping with auditory tasks involving perception-based imagery and semantic memory. In both experiments, participants were cued to grasp three-dimensional objects of varying sizes. During visually guided trials, objects were visible during the interval between the cue and movement onset. During delayed trials, objects were occluded at the time of the cue. In Experiment 1, the second task required participants to listen to object names and vocally respond if the objects were of a particular shape. In Experiment 2, participants studied a paired-associates list prior to testing and then performed cued recall while grasping. The results of these experiments showed that there was reciprocal interference on both tasks, which was consistently greater during delayed grasping. Experiment 2 showed that the introduction of the second task resulted in larger grip apertures during delayed grasping. This supports the idea that delayed grasping involves processing of stored perception-based information that shares resources with cross-modal tasks involving imagery and memory.

Keywords: grasping, memory, vision, perception, dual task

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Introduction

Reaching out and grasping a visible object is an everyday behavior that requires the brain to rapidly process accurate information about the size, shape, position, and orientation of the intended goal object. There is a large body of converging evidence suggesting that visually guided grasping is under the control of mechanisms in the posterior parietal cortex of the dorsal visual stream (Binkofski et al., 1998; Culham et al., 2003; Goodale, Milner, Jakobson, & Carey, 1991; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). Another common behavior is reaching out and grasping an object that is no longer visible, such as grasping the handle of a bedroom door after the lights have been turned off. It has been argued that this kind of grasping relies on stored perceptual information provided by the ventral visual stream (Goodale & Milner, 1992). This also suggests that in certain circumstances, there is a strong relationship between motor performance and memory (Klatzky, Pellegrino, McCloskey, & Lederman, 1993). This idea has received support from studies of the visual-form agnosia patient D.F., who has bilateral ventral-stream lesions but an intact dorsal stream. D.F. has no problem grasping a visible object but cannot scale her grip aperture properly when she has to grasp an object that was removed from view 2 s earlier (Goodale, Jakobson, & Keillor, 1994). This result shows that D.F. had no memory of the size and shape of the goal object, presumably because her damaged ventral stream prevented the processing of vital perceptual information about the target in the first place (Goodale et al., 1994). Additional work with the optic ataxia patient I.G., who has bilateral damage

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in the posterior parietal cortex but an intact ventral stream, has shown that although she is unable to scale her grip when she attempts to grasp visible objects, her grip scaling improves significantly when she pantomimes a grasping movement to an object viewed 5 s earlier (Milner et al., 2001). Taken together, these two studies provide compelling evidence that delayed grasping actions rely on stored perceptual information initially processed by mechanisms in the ventral visual stream and raise the possibility that the dorsal stream may not even be necessary for delayed grasping (Goodale, Westwood, & Milner, 2004).

Additional support for this idea comes from studies of normal participants showing that delayed grasping has different kinematics from those seen in real-time grasping. For example, when a target object is occluded from view prior to movement onset, the movements are slower and the hand trajectory is more curvilinear than in full-vision conditions (Goodale et al., 1994). Furthermore, when participants grasp targets that are no longer in view, the scaling of their grip aperture remains correlated with target size but is larger compared with full-vision conditions (Grosskopf & Kuhtz-Buschbeck, 2006; Hu, Eagleson, & Goodale, 1999). Presumably, when the target is occluded prior to the movement, information about the object available in memory is less precise than the information available in real time, when the object is still visible.

The most compelling evidence that delayed grasping depends on earlier perceptual processing comes from studies showing that such movements are more sensitive to perceptual illusions than are visually guided grasping movements (Westwood, Chapman, & Roy, 2000; Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2001). In one such study (Hu & Goodale, 2000), participants were presented with target blocks that were adjacent to "companion" blocks of differing size. The presence of the companion blocks induced an illusion in which a target accompanied by a smaller companion block was perceived to be larger than a target of the same size accompanied by a larger companion. When the participants were asked to reach out and grasp the target block with full vision, however, their grip aperture was scaled appropriately to the real size of the target and was not affected by the size-contrast illusion. When a 5-s delay was imposed between seeing the target and initiating the grasping movement, participants opened their hand wider for the target when it was accompanied by a smaller companion object than when it was accompanied by a larger one, suggesting that the scaling of the delayed grasps reflected the earlier perception of the target using the same relative (scene-based) metrics that led to the size-contrast illusion in the first place. However, real-time and delayed grasping trials were run in separate blocks. Thus, participants could have used different strategies in the two conditions. In the delay condition, they could have attended to the scene-based aspects of the target array to store this information in memory and, as a consequence, would have engaged ventral-stream processes although, under other circumstances, they might have stored some sort of motor plan (set up by "encapsulated" visuomotor mechanisms in the dorsal stream) that computed the real size of the target. In the visually guided condition, of course, a scene-based strategy would not have provided any advantage, and participants were better off directly engaging the visuomotor mechanisms in the dorsal stream.

To address this concern, Westwood and Goodale (2003) used the same size-contrast illusion used by Hu and Goodale (2000) but randomly interleaved the visually guided and delayed trials rather than running them in separate blocks. Because participants could not predict which type of trial they would encounter, they could not deploy their attention strategically to different parts of the display. However, even with this interleaved design, the size-contrast illusion produced "perceptual" effects on grip scaling in delayed trials but not in the visually guided trials, just as it had in the earlier study by Hu and Goodale. This result suggests that the brain goes into an "off-line" perceptually driven mode as soon as vision of the target object is removed and that online visuomotor mechanisms are not engaged unless the target remains visible during the programming of the movement. These studies strongly suggest that delayed grasping depends on a memory that is based on earlier perceptual processing, which is later retrieved to calibrate the grasping movement.

The two-stream perception–action model of Goodale and Milner (1992) has been challenged on the basis that not all studies have found dissociations between perceptual judgments and real-time grip scaling with pictorial illusions. Some studies have shown that when a more "traditional" measure of perception (an adjustment task) is used, these perceptual reports are no more sensitive to pictorial illusions (typically, the Ebbinghaus illusion) than visually guided grasping (Franz, 2001, 2003; Franz, Bülthoff, & Fahle, 2003; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000). Although the results of these studies provide a challenge for the two-stream perception–action model of Goodale and Milner, it is important to note that they do not directly challenge the work examining the nature of delayed grasping or its relationship with the perceptual system.

In this study, we designed a paradigm to further test whether delayed grasping uses a perception-based memory system that engages the same perception-based cognitive mechanisms that mediate other tasks that rely more explicitly on perceptual "imagery" and working memory. Therefore, in this study, we employed a dual-task paradigm, in which we asked participants to make real-time or delayed grasps while performing a second task that taxed their imagery, working memory, or both. This paradigm has been used to study the putative role of cognitive processing in grasping functional objects, such as tools, where a particular posture has to be adopted, in addition to any metrical computations that might be demanded by the disposition of the tool in respect to the hand. Using this paradigm, Creem and Proffitt (2001) showed that when participants are required to perform an auditory paired-associate task while they are grasping tools, they make functional but not basic visuomotor errors, presumably because their cognitive system is overloaded by the other task.

In this study, we carried out two dual-task experiments that were designed to further investigate the specific nature of the memory processes that are engaged during delayed grasping. In both experiments, we employed the same interleaved arrangement of visually guided and delayed grasping trials used by Westwood and Goodale (2003). In Experiment 1, we paired both visually guided and delayed grasping with a semantic shape discrimination task, which was presented auditorily. This task was primarily a familiarity–recognition task requiring declarative memory. We reasoned that this shape task, in which participants had to decide whether or not a named object was "round", would engage the same perception-based cognitive systems that drive delayed grasping. Therefore, we predicted that delayed grasping and shape discrimination would show mutual interference. In contrast, we predicted that real-time grasping would not show such interference because it is mediated by dedicated bottom–up visuomotor mechanisms. Specifically, we hypothesized that the kinematic behavior of the delayed grasping trials would be more affected by the introduction of the shape task than the visually guided grasping trials in the form of (a) overall movement time (MT) of the grasps and (b) the maximum grip aperture of the grasps. Furthermore, from the other side of things, we hypothesized that the delayed grasping trials would interfere more with the shape task performance in the form of vocal reaction time (RT) compared with the visually guided trials. In Experiment 2, we also used a dual-task paradigm, but this time, the secondary task was a more explicit "memory" task. In this experiment, real-time and delayed grasping trials were each paired with an auditory paired-associates working memory task. This task was primarily a recall task requiring more reinstatement of the encoded event compared with the shape task employed in Experiment 1 (Haist, Shimamura, & Squire, 1992). Here, we reasoned that the interference imposed by the paired-associates task on the delayed grasping task might be even greater than that seen in Experiment 1 because the paired-associate task would put even more demands on specific memory-retrieval systems that are shared between the two tasks.

Experiment 1

Methods

Participants

Twelve right-handed volunteers (8 men, mean age = 25.4 years) participated in Experiment 1. All had normal or corrected-to-normal vision and normal hearing, and all participants gave informed consent. The experimental procedures were in accordance with the Code of Ethics Declaration of the World Medical Association (Helsinki, 1964).

Grasping task

The participants were comfortably seated in front of a table on which the target for a grasping movement was presented approximately 40 cm away. Three square target objects were presented in a randomized order (small object = 40 × 40 × 5 mm, medium object = 45 × 45 × 5 mm, and large object = 50 × 50 × 5 mm), and their position was jittered slightly from trial to trial. The *x*-, *y*-, and *z*-axes were defined as follows: *x* = left to right from the participants' point of view on the plane of the table, *y* = back to front from the participants' point of view on the plane of the table, and *z* = table surface to ceiling. The participants were instructed to grasp the objects using the thumb and forefinger of their right hand along the *y*-axis (Cartesian space) of the object and pick it up. Vision was controlled using liquid crystal shutter goggles (PLATO Translucent Technologies, Toronto, ON, Canada). The participants previewed the target for 500 ms and initiated their grasping movement when they heard a 50-ms auditory tone delivered over a loudspeaker immediately after the preview period. Two types of trials were randomly interleaved in equal numbers for each target size. Visually guided (VIS) trials provided vision of the target from the onset of the preview period until the hand began to move; delayed (DEL) trials provided vision from the onset of the preview period until the presentation of the auditory tone (Figure 1). Thus, in

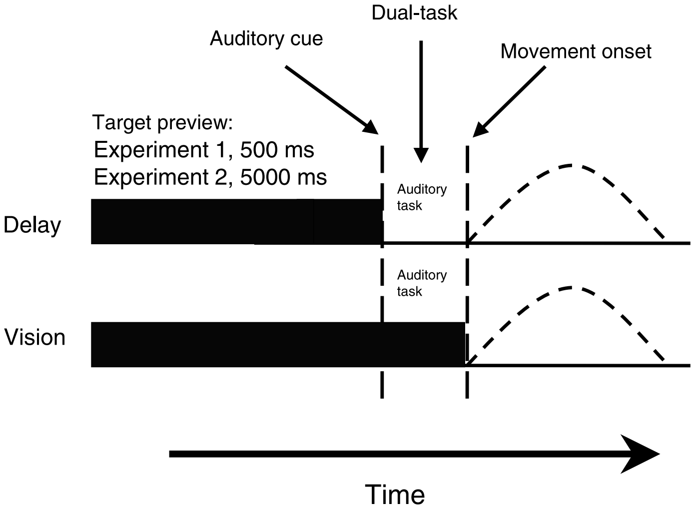

Figure 1. Event sequences for the DEL and VIS grasping tasks. In the VIS conditions, the target was visible in the interval between the auditory cue and movement onset. Experiment 1 employed a 500-ms target preview time, and Experiment 2 employed a 5,000-ms target preview time.

the VIS trials, vision of the target was available during the programming of the required movement, whereas in the DEL trials, participants had to rely entirely on the preview period for their information about the target.

The grasping movements were measured with an OPTOTRAK 3020 system. Data were recorded at 200 Hz from infrared emitting diodes (IREDs) attached to the index finger, thumb, and wrist (opposite the styloid process) of the right hand. RT was measured from the onset of the auditory tone until the initiation of the grasp movement. Trials with RTs less than 150 ms were marked as anticipatory and were excluded from analysis. The dependent measures, RT, total MT, and maximum peak grip aperture (vector distance between the IREDs on the thumb and index finger), were analyzed by repeated measures analysis of variance (ANOVA). These dependent measures were chosen for analysis because they have been studied in other experiments investigating delayed and visually guided grasping. This allows for comparisons to be made between our study and previous work.

Shape discrimination task

Participants were also required to perform a memory-based shape discrimination task while they were grasping the targets. In this task (SHAPE), object names were presented to the participants via headphones. The participant was required to say "yes" if the object named was round (e.g., ball). The participants were required to be silent if the object was not round (e.g., brick). The names of round objects made up 20% of the trials. The words were controlled for word frequency (Francis & Kucera, 1982) to prevent any familiarity–recognition effects (Mandler, Goodman, & Wilkes-Gibbs, 1982; see the Appendix for word list). In the dual-task conditions, the word was presented on each grasping trial, immediately after the onset of the auditory movement cue (see Figure 1). Vocal RT was recorded by a small microphone attached to the participant's chin and was defined as the time from word presentation onset to vocal response onset. Task accuracy data were also collected. In both the auditory-task-alone and dual-task conditions, each trial was initiated by an auditory cue.

Design and procedure

Prior to the experiment, participants were given 10 practice trials on the primary grasping task and 10 practice trials on the dual task, which paired the grasping task and the shape discrimination task. There were three conditions in this experiment: (a) a grasping-alone condition (GRASP-ALONE) consisting of two blocks of 36 interleaved VIS and DEL grasping trials, (b) a dual-task condition (DUAL) consisting of two blocks of 36 randomly interleaved VIS + Shape and DEL + Shape grasping trials done in conjunction with the auditory shape discrimination task, and finally, (c) a shape-discrimination-task-alone condition (SHAPE-ALONE) consisting of two blocks of 36 trials of the auditory shape discrimination task presented in the absence of the grasping task. The participants were instructed to respond as quickly as possible on both tasks, with the grasping task serving as the primary task. The three conditions were presented in counterbalanced order between participants. The dependent measures were analyzed by a series of different repeated measures ANOVA. Planned contrasts were carried out according to our predictions that we would observe task performance differences between the single- and dual-task conditions and between the VIS and DEL trials. The contrasts were corrected for family-wise error with the modified Bonferroni approach (Keppel, 1991).

Results

Vocal RT

The vocal RT data are shown in Figure 2A. There was a significant main effect of condition on vocal RT, $F(2, 22) = 21.71$, $p < .0001$. Planned contrasts revealed that vocal RT was slowed between the SHAPE-ALONE and VIS + Shape tasks ($p < .004$) and between the VIS + Shape and DEL + Shape tasks ($p < .001$), showing that the grasping task added a processing load to the shape discrimination task and that the DEL trials added more load than the VIS trials. The vocal accuracy data were equivalent across all conditions (95%).

Manual RT

The manual RT data are shown in Figure 2B. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) ANOVA revealed that there was a main effect of condition, $F(1, 11) = 49.32$, $p < .0001$, where the introduction of the shape discrimination task significantly slowed RT compared with the GRASP-ALONE condition. There was no interaction between condition and trial type (VIS and DEL).

Movement time

The MT data are shown in Figure 3. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) ANOVA revealed that there was a main effect of condition, $F(1, 11) = 11.15$, $p < .02$, where the introduction of the shape discrimination task significantly slowed MT compared with the GRASP-ALONE condition. Furthermore, there was a significant interaction between condition and trial type, $F(1, 11) = 5.02$, $p < .04$, where the difference between the two trial types (VIS vs. DEL) was greater in the DUAL condition than in the GRASP-ALONE condition ($p = .02$).

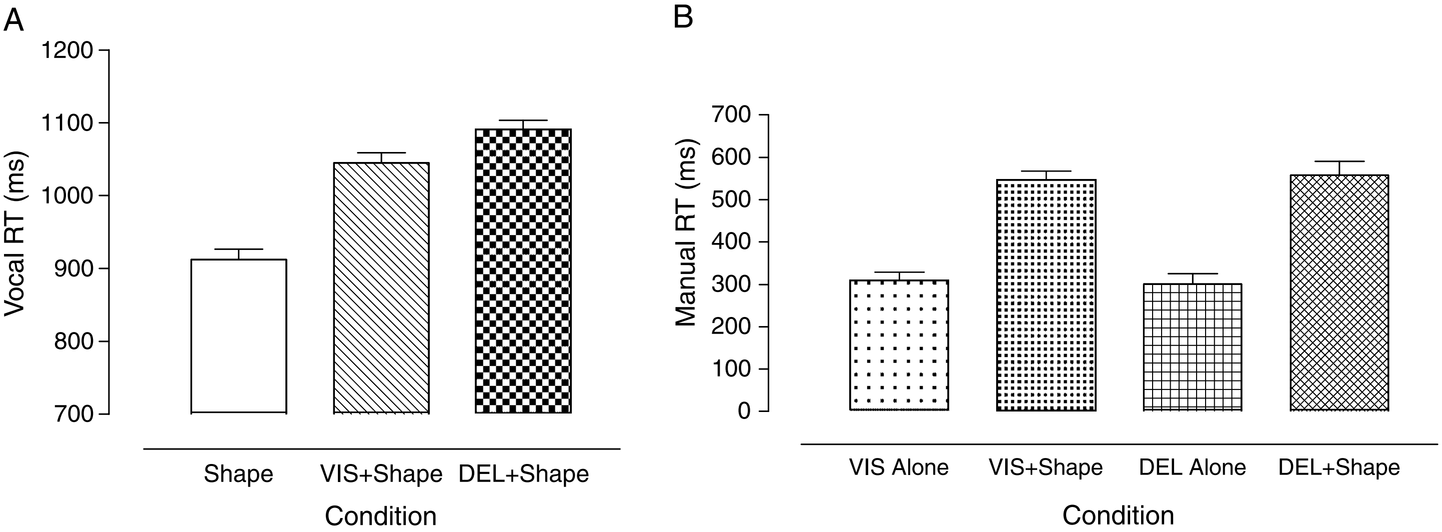

Figure 2. (A) Vocal RT from Experiment 1. (B) Manual RT from Experiment 1. Shape = auditory task alone. Dual conditions are as follows: VIS + Shape = visually guided grasping + auditory task; DEL + Shape = delayed grasping + auditory task. Grasping-alone conditions are as follows: VIS Alone = visually guided grasping alone; DEL Alone = delayed grasping alone. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

Peak grip aperture

Peak grip aperture data are presented in Figure 4. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) × 3 (target size) ANOVA revealed that peak grip aperture increased as the target object size increased, $F(2, 22) = 31.92$, $p < .0001$, was greater for DEL trials compared with VIS trials, $F(1, 11) = 51.09$, $p < .0001$, and was greater for the DUAL condition compared with the GRASP-ALONE condition, $F(1, 11) = 6.75$, $p < .02$.

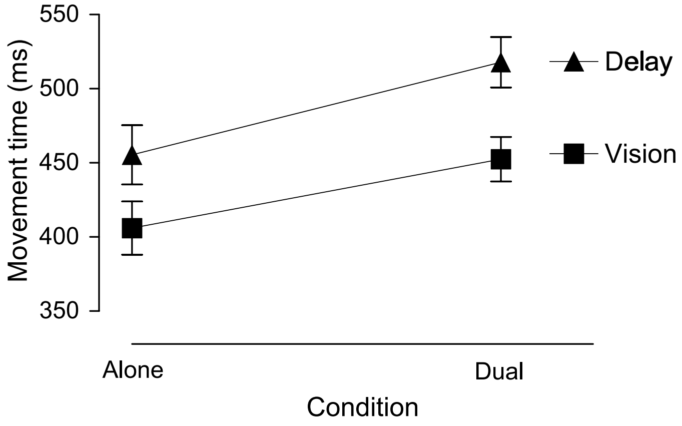

Figure 3. MT data from Experiment 1 showing visually guided (Vision) and delayed grasping (Delay) trials in both grasping-alone and dual-task conditions. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

Discussion

Experiment 1 was designed to investigate the differences between visually guided and delayed grasping by probing these two conditions with an auditory shape discrimination task in a dual-task paradigm. The results of this experiment show that grasping an object and performing a shape discrimination task interfere with one another, presumably because the two tasks share some

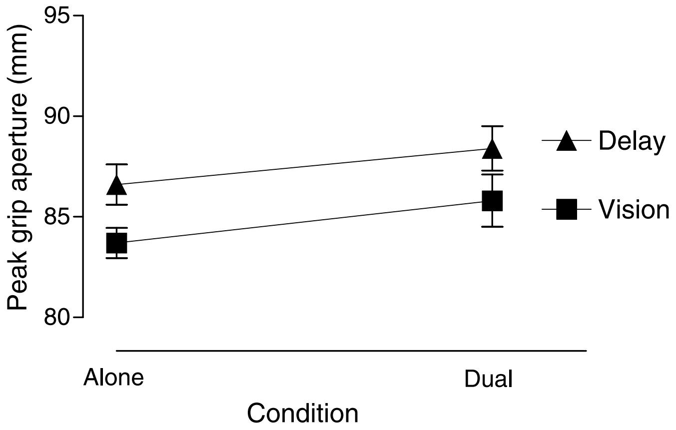

Figure 4. Mean peak grip aperture from Experiment 1 collapsed across all three target object sizes for visually guided (Vision) and delayed grasping (Delay) trials in both grasping-alone and dual-task conditions. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

processing in common. In particular, the manual RT to initiate visually guided or delayed grasping movements was equally slowed by the simultaneous performance of the shape discrimination task. This slowing of RT likely reflects the increased attentional load that was imposed in the dual-task condition (Lavie, 2005; Rohrer & Pashler, 2003) as well as the scheduling trade-offs between the tasks (Shin & Rosenbaum, 2002), which, at the premovement stage of the task, were equivalent between the two types of grasping trials. This load effect was also evident from the slowed vocal RT in the shape discrimination task. Importantly, however, the slowing of vocal RT was significantly greater in the DEL trials as opposed to the VIS trials. The fact that there was greater interference on DEL than on VIS trials suggests that the cognitive resources required for the shape discrimination task had more in common with the programming of movements based on memory of the target object than they did with the programming of movements that used current visual input about the shape, size, and position of the target.

The kinematic data confirmed previous findings that delayed grasping is associated with larger grip apertures and slower movements than visually guided grasping (Hu et al., 1999). At the same time, grip aperture and MT were also affected in both trial types by the performance of a competing shape discrimination task. But there was an important interaction in one of these measures: MT was slowed more in the dual-task condition for delayed than for visually guided grasps. This again suggests that the resources required for the shape discrimination task overlapped those used to program grasping movements based on memory of the target object than they did those used to program movements based on direct visual input. Taken together, these findings of reciprocal interference between the shape discrimination task and the delayed grasping suggest that there are shared processing resources between the two tasks.

A central assumption in our experiment was that mutual interference in the dual-task condition is evidence of shared processing resources (Wickens, 1976). In the shape discrimination task, participants presumably had to create a mental representation of the named object based on auditory input and then make a cognitive judgment about the object's shape. To do this, they would have had to recover the information from long-term memory and then make use of that information in some sort of short-term working memory buffer. It was almost certainly the engagement of these processes that led to the mutual interference between the shape discrimination task and the delayed grasping trials, which presumably also had to make use of information about the just-viewed object with the use of short-term working memory processes. Another point of interest from this experiment is that we did not observe any performance differences associated with the category of the word presented in the auditory task. For example, a word describing a graspable object such as "coin" did not have any more effect than a nongraspable word such as "moon".

There are two additional issues, however, that have to be addressed. First, as already discussed, the discrimination task would have made use of long-term memory representations of the named objects, whereas the delayed grasping task would be using information that was just encoded in memory and was presumably still present in short-term memory. This begs the question of what would happen if the short-term memory load of the competing task also primarily engaged short-term memory and did not rely as much on long-term memories. Would there be even greater mutual interference between delayed grasping and the competing task? A second issue revolves around the time available in the preview period for the DEL and VIS grasping trials. For instance, the target preview period in both delayed and visually guided conditions was 500 ms. Thus, the total target-viewing time for the VIS trials was 500 ms plus the ~300 ms RT, allowing the participants an additional 60% of target encoding time (see Figure 1). This was increased by an additional 120% in the dual-task conditions because of the increased RT (~600 ms). Thus, one cannot rule out the possibility that the differences between delayed and visually guided grasping were due to differences in available target-viewing times and that the potentiation of this effect in the dual-task condition reflected the even greater increase in viewing time available in the visually guided condition. To address the first issue, we designed a second experiment in which we used a paired-associates recall task as the competing task on the assumption that, because such a task would more fully engage short-term memory, it would result in even greater interference with the DEL grasping trials than the interference we observed in Experiment 1. To address the second issue, we extended the target preview time to 5,000 ms to minimize the overall difference in total target-viewing time between the memory-guided and VIS grasping trials.

Experiment 2

Methods

Participants

Twenty right-handed volunteers (12 men, mean age = 23.8 years) participated in Experiment 2. All had normal or corrected-to-normal vision and normal hearing, and all participants gave informed consent.

Grasping task

The grasping task was identical to that used in Experiment 1 except that the target preview period was increased to 5,000 ms (Figure 1).

Auditory paired-associates memory task

Prior to the experimental session, participants were visually presented with a paired-associates word list to study. They were then tested by having the first word of each pair presented via headphones and required to say the corresponding word out loud (see the Appendix for word list). There were 44 word pairs in the list. Participants were required to perform at 80% accuracy to advance to the experimental session. Nineteen participants met this criterion without additional study time, and one participant required a second study session. The pairs consisted of words from the same general semantic category (Creem & Proffitt, 2001), and the target word of each pair was balanced for word frequency (Francis & Kucera, 1982) as in Experiment 1 (see the Appendix for word list). During the experiment, the first words of the paired associates were presented in random order, and the first four and last four word pairs from the training session were dropped to control for serial position effects.

Design and procedure

Prior to the experiment, participants were given 10 practice trials on the primary grasping task. There were three conditions in this experiment: (a) GRASP-ALONE consisted of one block of 36 interleaved VIS and DEL grasping trials. (b) DUAL consisted of one block of 36 interleaved VIS and DEL grasping trials done in conjunction with the auditory short-term memory task (RECALL). (c) The auditory task alone (RECALL-ALONE) consisted of one block of 36 trials of the auditory short-term memory task presented in the absence of the grasping task. The three conditions were presented in counterbalanced order between participants. All dependent measures were analyzed by repeated measures ANOVA.

Results

Vocal RT

The vocal RT data are shown in Figure 5A. There was a significant main effect of condition on vocal RT, $F(2, 38) = 11.72$, $p < .0001$. Planned contrasts revealed that vocal RT was slower for VIS + RECALL versus RECALL ($p < .03$) and for DEL + RECALL versus VIS + RECALL ($p < .002$), showing (a) that the grasping task added a processing load to the auditory task and (b) that the DEL grasping trials added more load than the VIS grasping trials. The vocal accuracy data were equivalent across all conditions (86%).

Manual RT

The manual RT data are shown in Figure 5B. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) ANOVA revealed that there was a main effect of condition, $F(1, 19) = 86.10$, $p < .0001$, where the introduction of the auditory memory task significantly slowed RT compared with the GRASP-ALONE conditions. There was no interaction between condition and trial type (VIS and DEL).

Movement time

The MT data are shown in Figure 6. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) ANOVA revealed that there was a significant

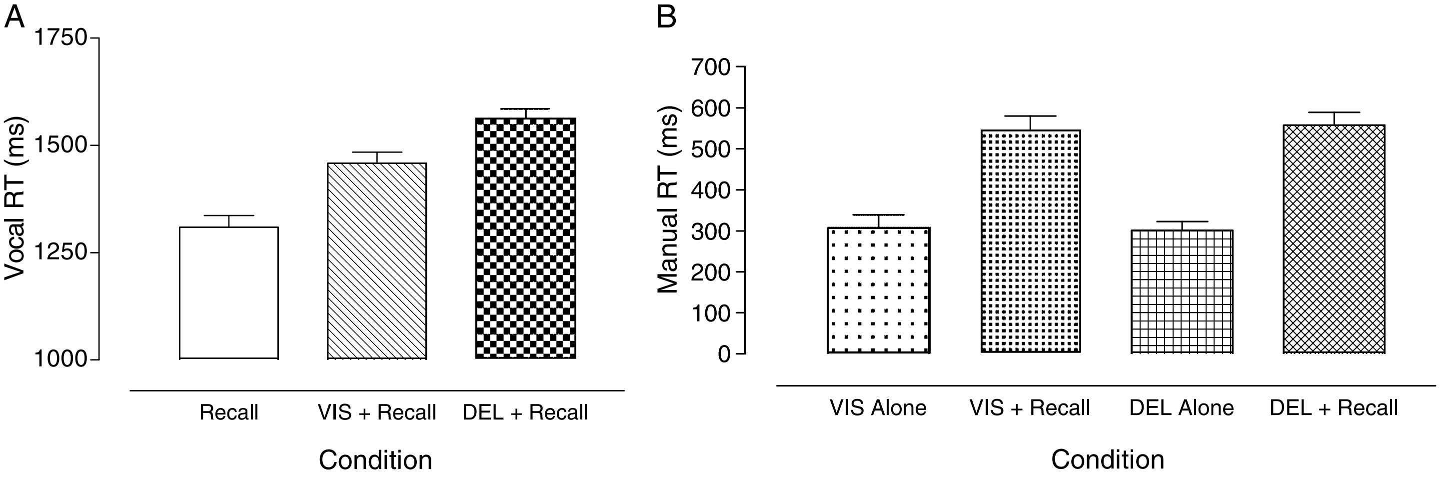

Figure 5. (A) Vocal RT from Experiment 2. (B) Manual RT from Experiment 2. Recall = auditory task alone. Dual conditions: VIS + Recall = visually guided grasping + auditory task; DEL + Recall = delayed grasping + auditory task. Grasping-alone conditions: VIS Alone = visually guided grasping alone; DEL Alone = delayed grasping alone. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

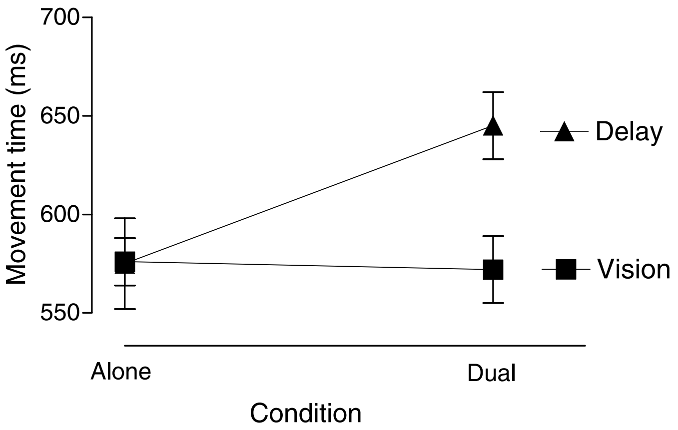

Figure 6. MT data from Experiment 2 showing visually guided (Vision) and delayed grasping (Delay) trials in both grasping-alone and dual-task conditions. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

interaction, $F(1, 16) = 6.67$, $p < .01$, where the MT for the DEL trials was longer than that for the VIS trials in the DUAL condition ($p = .02$) but not in the GRASP-ALONE condition.

Peak grip aperture

The peak grip aperture data are shown in Figure 7. A 2 (condition: GRASP-ALONE vs. DUAL) × 2 (trial type: VIS vs. DEL) × 3 (target size) ANOVA revealed that peak grip aperture increased as the target object size increased, $F(2, 38) = 9.67$, $p < .0001$, and was greater for DEL as compared with VIS trials, $F(1, 19) = 24.61$, $p < .0001$. In addition, peak grip aperture overall was larger in the DUAL condition than in the GRASP-ALONE condition, $F(1, 19) = 58.24$, $p < .001$. Furthermore, there was a significant two-way interaction between condition and trial type, $F(1, 19) = 11.96$, $p < .005$, showing that DEL grip aperture was increased more by the introduction of the auditory short-term memory task than was VIS grip aperture.

Discussion

Experiment 2 was designed to further investigate the differences between delayed and visually guided grasping observed in Experiment 1 by probing these two conditions with an auditory short-term memory paired-associates task and increasing the target preview time of the grasping task to 5,000 ms. As we found in Experiment 1, manual RT was slowed by the introduction of a second task, but again, there was no difference between the effects of that task on the DEL and VIS trials. Furthermore, in Experiment 1, the vocal RT was slowed by the simultaneous performance of a grasping task. But again, as we found in Experiment 1, DEL grasping trials slowed vocal RT more than VIS grasping trials did. Finally, it should be noted that the overall RT effect was greater in magnitude for the paired-associates short-term memory task compared with the shape discrimination task used in Experiment 1, reflecting its increased difficulty.

The pattern of results observed in the kinematic data replicated and extended the findings of Experiment 1. In fact, in the grasping-alone conditions, the data were almost identical between the two experiments. The introduction of a second competing task had a larger effect on total MT in delayed grasping than it did on visually guided grasping, confirming the earlier finding. Furthermore, the introduction of the competing task increased the maximum grip aperture, as it did in Experiment 1, but this time, we observed a bigger effect of this task on grip aperture in DEL trials than in VIS trials. In other words, when participants were performing the paired-associates task, they opened their hand wider when they were relying on their memory of the target than when they were allowed to use vision to program their grasp. Of course, it has been shown previously that delayed grasping shows larger grip scaling than visually guided grasping does, perhaps because it relies on less accurate "perceptual" representations of the target object stored in memory (Hu et al., 1999). Here, we present a further interactive effect of a competing memory-demanding task on grip aperture when the scaling of that grip aperture also depends on memory. In other words, the level of uncertainty regarding the size of the target, which was already increased by having participants rely on their memory of the target, was further increased by the addition of additional memory load from performing the paired-associates task. This effect strongly supports the idea that

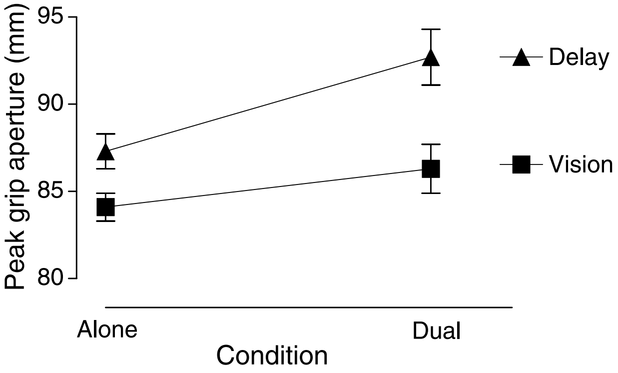

Figure 7. Mean peak grip aperture from Experiment 2 collapsed across all three target object sizes for visually guided (Vision) and delayed grasping (Delay) trials in both the grasping-alone and dual-task conditions. Error bars show standard error of the mean and are appropriate for within-subjects comparisons (Loftus & Masson, 1994).

delayed grasping utilizes perceptual information about the target that is stored in some sort of general working-memory buffer, which shares resources with auditory semantic memory.

The concern raised in Experiment 1 that the memory-guided trials had less total target-viewing time than the VIS trials was addressed in Experiment 2 by increasing the initial target preview time to 5,000 ms. This dramatic increase in available viewing time had no effect on manual RT, which was the same as that obtained in Experiment 1 (~300 ms for ALONE and ~600 ms for DUAL), but nevertheless meant that there was very little difference between the total viewing time for DEL and VIS trials. This observation, coupled with the fact that the grasping kinematics in Experiment 2 closely followed those already observed in Experiment 1, strongly suggests that the differences between DEL and VIS trials were due to the absence of visual information during movement programming and not to any difference in total viewing time.

General discussion

Dual-task interference studies have been used for many years to make inferences regarding the nature of processing resources utilized in the performance of various tasks. Here, we have presented the results of two dual-task experiments that show reciprocal interference between delayed grasping and auditory tasks involving perception and memory, and we make the assumption that the interference was due to the overlapping nature of the processing resources required by each task.

The observed pattern of interference between the competing tasks suggests that the visually guided grasping trials had some commonality with the auditory tasks, likely involving some general attention-related limits. However, the interference effects of the auditory tasks on the DEL grasping trials were significantly greater, suggesting that these trial types had more in common with the auditory memory tasks. The results of our two experiments support the idea that memory processes involved in semantic recognition and recall are also utilized in delayed grasping. This is in agreement with previous studies suggesting that perceptual mechanisms in the ventral stream are invoked for memory-guided action. The random interleaving of DEL and VIS grasping trials prevented the participants from allocating more attention to the target features in the DEL trials because they were indistinguishable from the VIS trials, until the very moment the grasp was initiated. In other words, participants could not predict whether or not they would have to rely on memory until the cue to initiate the movement was given. Nevertheless, it is possible that participants could have consciously tried to store information about the target during the preview period because they knew there was a 50% probability that they would have to use this information later to program their grasping movements. Indeed, the deployment of this strategy could explain why performance of a second memory-demanding task slowed RT for the VIS and the DEL trials. However, this explanation cannot account for the differential effect of the competing task on DEL trials as opposed to VIS trials. Here, the greater memory load required on DEL trials affected vocal RT on the competing semantic task and also influenced the actual kinematics of the grasp itself. Visually guided tasks presumably escaped this influence much more because, on these trials, participants could make use of direct visual information to program their grasping movements. Finally, the possibility that any memory-based strategy used on VIS trials might have benefited from the longer overall viewing time in Experiment 1 is unlikely because the same pattern of results was obtained in both experiments although, in Experiment 2, the preview period was extended to 5,000 ms, minimizing any difference in total target-viewing time between trial types.

A further assumption in this study was that the nature of the interfering tasks was different in the two experiments. For instance, the shape task in Experiment 1 was primarily a familiarity-recognition task, and the paired-associates task in Experiment 2 was a recall task. It has been argued that recall tasks are more difficult than recognition tasks because recall requires a more substantial reinstatement of the encoded event (Haist et al., 1992). Thus, the pattern of interference we observed in the two experiments suggests three additional points: (a) The paired-associates (recall) task in Experiment 2 led to an increased level of interference because of more overlap between explicit recollection processes required for both the auditory and delayed grasping tasks, (b) this recollection is less important for visually guided grasping, and (c) explicit recollection is not as strong a characteristic of the shape (recognition) task we employed in Experiment 1 and, thus, did not lead to the same level of interference as observed in Experiment 2.

According to the two-visual-systems proposal of Goodale and Milner (1992), real-time visually guided actions, such as grasping, are mediated by encapsulated visuomotor modules in the dorsal stream. Actions initiated after a delay, however, are thought to depend on stored perceptual information about the target that is initially processed by perceptual networks in the ventral stream—which is why the patient D.F., who has ventral-stream damage, does so poorly on delayed grasping tasks (Goodale et al., 1994). The idea that delayed actions depend on ventral-stream mechanisms also receives support from other neuropsychological studies (e.g., Milner et al., 2001) showing that patients with bilateral parietal damage, who are unable to grasp objects in real time, can often do so after a brief delay, presumably using their intact ventral stream. However, these latter studies also make the point that the dorsal stream may not be required for the programming and/or controlling of these memory-driven actions. The ventral stream, as well as the associated cognitive/memory networks, appears to be sufficient. But where and how is information stored about the target in a delayed grasping task encoded? There is evidence from single-unit recording studies in macaques showing that dorsal stream areas in the parietal cortex remain active during brief delay periods in action paradigms (Murata, Gallese, Kaseda, & Sakata, 1996; Snyder, Batista, & Andersen, 1997). But whether this delay activity in parietal cortex reflects the storage of the necessary information and/or the planning of the movement based on ventral-stream perceptual input remains an unsettled issue, particularly when set alongside the neuropsychological evidence that patients with parietal damage can still perform delayed actions. Recent evidence from two fMRI studies in neurologically intact participants shows that areas in both the dorsal and the ventral streams and the prefrontal regions are active during the delay phase (Culham, 2004; Singhal, Kaufman, Valyear, & Culham, 2006). One implication from these imaging studies is that delayed grasping relies strongly on object recognition areas in the ventral stream, which are reactivated at the end of the delay period, prior to hand action, and in the absence of the reappearance of visual stimuli. But again, it would seem that the information may be stored elsewhere and simply "replayed" in these ventral-stream areas. The fact that memory-guided grasping in this study showed greater mutual interference in the dual-task paradigm than visually guided grasping suggests that wherever such memories are laid down, the memory networks that are involved are also invoked by other more explicitly "cognitive" tasks, such as the shape discrimination and paired-associate tasks employed in our experiments.

Another interesting characteristic of delayed as opposed to real-time grasping is that maximum grip aperture is typically larger (Hu et al., 1999; Westwood & Goodale, 2003). This increase in grip aperture when participants are relying on memory rather than on current visual input presumably reflects their uncertainty regarding the size of the target, its location, or both. In this regard, it is interesting to note that Westwood and Goodale (2003) observed that as the delay increased, grip aperture also increased, perhaps because the memory became less reliable as time went on. Our data are also consistent with this line of argument. Delayed grasping showed larger grip apertures overall as compared with real-time visually guided grasping, and the introduction of a competing task that put increased demands on working memory further increased this maximum grip aperture on memory-driven (but not on visually guided) trials. This latter result converges on a number of studies showing that response uncertainty, reflected in costs in performance, is commonly associated with increasing memory load (Gopher & Donchin, 1986; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Sternberg, 1966, 1998). In summary, we have provided evidence that delayed grasping depends on stored memory of earlier visual information and that the retrieval of this information shares processing resources with other cognitively demanding tasks. The question of how the control of memory-guided actions integrates the stored perceptual information with the programming of the action awaits further research.

Appendix A

Shape discrimination word list from Experiment 1

Target words

Apple
Ball
Balloon
Bubble
Button
Coin
Cookie
Drum
Frisbee
Globe
Marble
Moon
Pie
Plate
Puck
Ring
Saucer
Snowball
Sun
Tire
Washer
Wheel

Nontarget words

Bicycle
Bird
Book
Bottle
Brick
Broom
Brush
Canoe
Car
Cat
Chair
Chimney
Coat
Computer
Cow
Crayon
Dog
Fish
Flag
Flag
Flute
Folder
Foot
Fork
Frog
Glove
Guitar
Hammer
Hand
Hanger
Horse
House
Kayak
Key
Keyboard
Knife
Ladder
Lamp
Leaf
Lion
Magazine
Mouse
Moustache
Nail
Nose
Oven
Pencil
Radio
Rake
Rat
Rifle
Roof
Sandal
Scarf
Scissors
Scooter
Screw
Shark
Shirt
Shoe
Skate
Sock
Stair
Stove
Sweater
Sword
Tiger
Table
Toaster
Tooth
Tractor
Tree
Truck
Trumpet
Violin
Wagon
Wallet
Wire
Wrench

Paired-associates word list from Experiment 2

Onion–Peach
Ball–Frisbee
Frog–Bird
House–Phone
Coat–Glove
Wheel–Tire
Rat–Shark
Chimney–Roof
Nose–Foot
Window–Vase
Toaster–Stove
Stair–Door
Mouse–Horse
Skunk–Penguin
Scissors–Knife
Lion–Cow
Book–Magazine
Chair–Lamp
Fork–Hammer
Carrot–Celery
Tooth–Hand
Car–Bicycle
Dog–Fish
Banana–Pear
Crayon–Pencil
Flute–Drum
Leaf–Tree
Glasses–Hat
Pillow–Blanket
Rake–Broom
Coin–Wallet
Tiger–Cat
Guitar–Trumpet
Scooter–Truck
Wrench–Brush
Tractor–Wagon
Scarf–Shirt
Screw–Nail
Moon–Sun
Canoe–Kayak
Oven–Radio
Teacher–Doctor
Cheese–Bread
Cracker–Melon

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