Parallel Response Selection after Callosotomy

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Abstract

■ Two studies [Ivry, R. B., Franz, E. A., Kingstone, A., & Johnston, J. C. The psychological refractory period effect following callosotomy: Uncoupling of lateralized response codes. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 463–480, 1998; Pashler, H., Luck, S., Hillyard, S. A., Mangun, G. R., O'Brien, S., & Gazzaniga, M. S. Sequential operation of disconnected hemispheres in split-brain patients. *NeuroReport, 5,* 2381–2384, 1994] reported robust dual-task costs in split-brain patients even when the two tasks were associated with separate cerebral hemispheres. Although the patients failed to demonstrate specific forms of interference observed in control participants, the timing of the two responses suggested that performance was constrained such that the responses could not be initiated independently. Alternatively, the split-brain participants may have adopted a strategy in which the second response was withheld until the first was initiated. The present study revisits this phenomenon using a procedure in which the stimuli for both tasks are presented simultaneously and neither is given priority over the other. Under these conditions, neurologically intact participants show robust dual-task costs that are mediated by compatibility effects between the responses of the two hands. In contrast, the split-brain participants show greatly reduced dual-task costs and compatibility effects. The minimal dual-task costs observed in the current study indicate that previous dual-task costs in split-brain patients may be strategic, reflecting experimental instructions to prioritize one task, rather than reflect fundamental constraints of the cognitive architecture. ■

INTRODUCTION

In many situations, people have great difficulty performing two tasks at the same time. The source of these limitations remains contentious. One widely investigated account holds that the principle constraint reflects a limitation in the selection of actions (McCann & Johnston, 1992; Pashler, 1984). Specifically, it is hypothesized that our behavior is constrained by a response selection bottleneck (RSB) that requires that responses to be selected in a serial manner. This constraint may be due to structural limitations of the cognitive architecture (Ruthruff, Pashler, & Hazeltine, 2003; Pashler, 1994b; Pashler & Johnston, 1989) or it may result from strategies adopted by individuals to insure minimal interference between concurrent task operations (Tombu & Jolicoeur, 2003; Navon & Miller, 2002; Meyer & Kieras, 1997).

Much of the empirical support for the RSB hypothesis comes from experiments using the psychology refractory period (PRP) procedure. In the PRP task, the participant is required to perform two tasks simultaneously. However, one task is assigned a primary role: The stimulus for this task is presented first and the instructions emphasize that priority should be given to responding to this stimulus as fast as possible. The second stimulus is presented after a variable delay, or stimulus-onset asynchrony (SOA). Given the ordering of the stimuli and instructions, reaction times (RTs) on the first task are minimally affected by the second task (but see Hommel, 1998; Ivry, Franz, Kingstone, & Johnston, 1998). However, RTs on the second task are inversely related to the SOA. The increase in RT for short SOAs is attributed to a delay in access to a unitary response selection process for the second task until this operation is completed for the first task (see Pashler, 1994b).

In many dual-task studies, the stimuli are presented in separate visual fields and require responses with the two hands (e.g., Hazeltine, Diedrichsen, Kennerley, & Ivry, 2003; Ivry & Hazeltine, 2000; Logan & Schulkind, 2000; Spijkers, Heuer, Steglich, & Kleinsorge, 2000; Pashler et al., 1994). Under such conditions, a robust PRP effect is observed, consistent with the idea that even when the tasks are, at least to some degree, segregated to different hemispheres, performance is subject to an RSB. Of course, in neurologically healthy individuals, there is substantial sharing of information between the two cerebral hemispheres. Thus, it is not unreasonable to posit that a unitary RSB can influence actions produced by different hands, or in fact, any combination of effectors.

Individuals lacking the anatomical substrate for direct interhemispheric communication have provided a unique opportunity to explore the underlying psychological and neural mechanisms of dual-task costs. Split-brain patients have undergone a callosotomy operation as a treatment for intractable epilepsy. Studies with these patients have investigated the degree to which the two hemispheres can

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operate independently. For example, using a sequential matching task, Holtzman and Gazzaniga (1985) reported that visual information can be encoded in parallel in the two cerebral hemispheres, and that these representations can be independently maintained after callosotomy. However, it is important to note that the participants were only required to produce a single response on each trial. Thus, studies such as this do not address the question of whether the split-brain individual is able to select two responses without being subject to the constraints imposed by an RSB.

This issue has been directly examined in two studies (Ivry et al., 1998; Pashler et al., 1994) that used a PRP procedure in which two responses were required on every trial, one to a stimulus lateralized to the left visual field and a second to a stimulus lateralized to the right visual field. Both studies revealed robust PRP effects in the same split-brain patient tested by Holtzman and Gazzaniga (1985); that is, RT on Task 2 was much longer when the SOA was short compared to when the SOA was long. In fact, the overall magnitude of the PRP effect was similar to that of control subjects. Thus, the callosotomy procedure did not eliminate dual-task costs when two overt, speeded responses were required on each trial. Within the framework of the RSB model, Pashler et al. (1994) proposed that a subcortical mechanism or pathway must play a critical role in the temporal coordination of task operations, limiting response selection to a single task at a time.

However, Ivry et al. (1998) observed that, despite the robust PRP effect, there were significant differences in the manifestation of dual-task costs between the split-brain patient and control participants. In particular, the split-brain patient did not show benefits when the S–R mappings for the two tasks corresponded. In one experiment, both tasks required the participant to judge if a lateralized stimulus (with the first one appearing on the left, and the second on the right) was above or below the horizontal midline. A compatible mapping was always used for the left hand (e.g., response key for responding "above" was farther from the participant than the response key for responding "below"), whereas the mapping for the right hand could either be the same (corresponding) or opposite (noncorresponding, e.g., right hand response key for responding "above" was closer to the participant than the response key for responding "below").

The mapping manipulation had substantial influence on the performance of the control participants. RTs on Task 2 were much larger when the two mappings were noncorresponding and the effect was additive with SOA, consistent with the predictions of an RSB. RTs on Task 1 were also larger for noncorresponding trials, likely reflecting increased demands on working memory to maintain the conflicting mappings (see Duncan, 1979).

In contrast, the split-brain patient's performance on Task 1 was unaffected by whether the two mappings were corresponding. Noncorresponding mappings did lead to longer RTs on Task 2, but, critically, this increase was underadditive with SOA. That is, when the two stimuli were presented very close together in time, the RTs for the corresponding and noncorresponding mappings were similar. This pattern is consistent with the notion that the split-brain patient was able to do the extra response selection work associated with the incompatible mapping while selecting the response for Task 1.

These results suggest that compatibility effects and dual-task costs have distinct sources. Intermanual compatibility effects appear to be dependent on transcallosal interactions between the two hemispheres. For example, in this PRP study, conflict would arise when the S–R mapping for the two hands are noncorresponding. Various lines of evidence using a range of tasks provides further support for the notion that, quite generally, compatibility effects are eliminated or greatly diminished after callosotomy (Diedrichsen, Hazeltine, Nurss, & Ivry, 2003; Ivry & Hazeltine, 2000; Franz, Eliassen, Ivry, & Gazzaniga, 1996).

Nonetheless, the split-brain patient did not perform the two tasks independently in Ivry et al. (1998): RT was substantially slower when the SOA was short (i.e., the classic "PRP" effect). Thus, dual-task costs persisted even in the absence of interference effects related to the degree of correspondence of the two tasks. This cost suggests some form of interaction between the two tasks that limits response selection processes so that they operate on a single task at a time, even when the hemispheres are disconnected.

One complication in interpreting these data relates to the task instructions. The PRP instructions gave priority to one task, and the split-brain patient complied with these instructions by delaying responses to the second task until after the first response had been emitted. Indeed, Meyer and Kieras (1997) have proposed that such strategic factors might underlie much of the costs observed in dual-task studies, reflecting the operation of a flexible control system. The task structure and instructions used in PRP studies may encourage participants to adopt a conservative strategy that effectively imposes an RSB even when participants could simultaneously select two responses. To examine this issue, Schumacher, Seymour, Glass, Kieras, and Meyer (2001) trained participants to perform two tasks but presented the stimuli simultaneously and provided instructions that did not prioritize one task at the expense of the other. With a moderate degree of practice, participants were able to perform the two tasks with little evidence of any dual-task costs (see also Hazeltine, Teague, & Ivry, 2002). However, when the instructions were modified to be similar to those given in PRP tasks (e.g., prioritize one task over the other), a robust PRP effect was observed.

The PRP instructions can be implemented by adopting a strategy that will ensure the response for Task 2 does not precede the response for Task 1. An optimal strategy results in the largest increases in Task 2 RT occurring for short SOAs; as SOA increases, the likelihood that the first response has occurred increases, and the participant need not guard against prematurely responding to the second stimulus. There are several reasons to believe that the patterns of behavior observed in PRP studies with neurologically healthy individuals do not arise solely from strategic considerations (Ruthruff et al., 2003; Levy & Pashler, 2001; Ruthruff & Pashler, 2001; Carrier & Pashler, 1995). For instance, even when both tasks are given equal priority and the two stimuli are presented simultaneously, participants with little training show robust dual-task costs that generally fall in line with the quantitative predictions of the bottleneck model (Ruthruff & Pashler, 2001; see also, Hazeltine et al., 2003; Schumacher et al., 2001).

Nonetheless, a prioritization strategy could be the source of the effect for the split-brain patient. Subcortical communication between the two hemispheres should be sufficient for signaling the occurrence of the first response (e.g., Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002; Forster & Corballis, 2000; Funnell, Corballis, & Gazzaniga, 2000; Gazzaniga, 2000; Corballis, 1995; Iacoboni & Zaidel, 1995; Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995; Marzi, Bisiacchi, & Nicoletti, 1991), even if the contents of that response (or stimulus) do not influence performance on the second task.

THE PRESENT STUDY

The present study re-examines dual-task costs and compatibility effects in a split-brain individual to determine whether the bisected brain faces dual-task limitations like those confronted by the intact brain. Rather than using the PRP procedure employed in previous experiments, we adopted a procedure in which neither task was prioritized and the lateralized stimuli for the two tasks were presented simultaneously. The patient was simply instructed to respond to the stimuli as quickly as possible. We examine the degree of interaction between the two tasks under these less-constrained conditions to assess the degree to which strategic factors may underlie persistent dual-task costs observed in previous PRP studies.

EXPERIMENT 1

Methods

Participants

J.W., 46 years old at the time of testing, was the same participant studied in the previous studies of the PRP effect in a split-brain patient (Ivry et al., 1998; Pashler et al., 1994; for a full case history, see Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981). He completed two 1-hr sessions of the experiment on consecutive days. Five age-matched controls with no history of neurological disorders completed the experiment using an identical protocol as J.W. All of the participants received monetary compensation for performing the experiment. The study was conducted in accordance with the guidelines of Committee for the Protection of Human Subjects at University of California, Berkeley.

Apparatus and Stimuli

The stimuli were white presented against a black background. A central fixation cross subtending 0.5° of visual angle remained present on the screen throughout each block. At the start of each trial, schematic pictures of the left and right hands appeared centered 6° to the left and right of fixation, respectively. Each hand picture subtended 4° and was drawn in a mirror symmetric fashion to match the anatomy of the two hands. Red ovals, varying in size to almost fill the corresponding digit, indicated the appropriate keypresses (Figure 1A). The ovals were presented until the participant responded, whereas the hands and fixation cross remained on the screen for the entire experimental block. On unimanual trials,

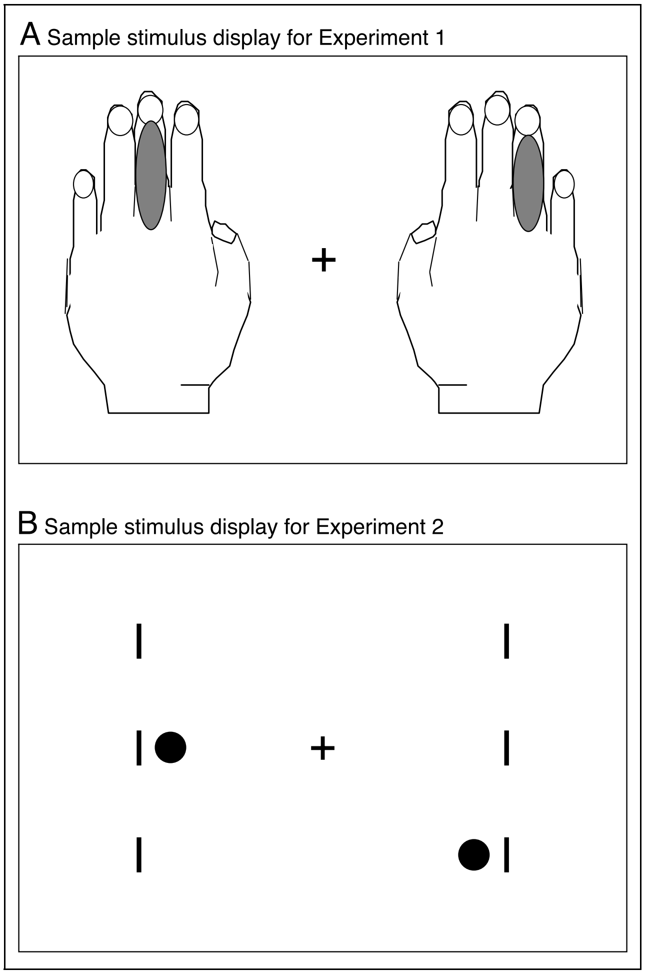


Figure 1. Stimulus displays used in Experiment 1 (top panel) and Experiment 2 (bottom panel). The actual stimuli were white on black rather than black on white. Participants responded to the stimulus on the left side of fixation with their left hands and the stimulus on the right side of fixation with their right hands.

a stimulus was presented on one side and a single response was required with the corresponding hand. On bimanual trials, the two stimuli appeared simultaneously, one on the left side and one on the right side. There was never more than one stimulus presented on a side. Although the hands depicted in the display had thumbs, thumb responses were never signaled.

Procedure

Participants were informed of the compatible S–R mapping and were instructed to respond to either the single stimulus or both stimuli as quickly and accurately as possible. Sample stimuli were presented on the screen and participants practiced responding until they felt comfortable with the task.

At the beginning of each trial, the fixation cross blinked for 100 msec, serving as a warning signal. After 500 msec, one (on unimanual trials) or two (on bimanual trials) red ovals appeared over the static pictures of the hands. Participants had up to 3 sec to respond, after which the trial was terminated and no responses were recorded. The ovals disappeared when either a response was recorded or 3 sec elapsed. There was a 1-sec interval between consecutive trials. No feedback was given for correct or incorrect responses.

Each experimental block consisted of 96 trials. Of these, 48 were unimanual trials, consisting of six repetitions of each of the eight fingers of the two hands. The remaining 48 trials were bimanual trials, consisting of three repetitions of each of the possible 16 bimanual responses formed by the factorial combination of the four possible responses for each hand. The bimanual trials were further divided into three categories. Bimanual trials that required responses with the same digit of each hand (e.g., left ring finger and right ring finger) were classified as anatomically compatible trials. Bimanual trials that required responses with digits having the same relative position from left to right (e.g., left ring finger and right middle finger) were classified as spatially compatible trials. The remaining combinations were classified as incompatible trials.[1] Thus, in each block, participants performed 24 left-hand only trials, 24 right-hand only trials, 12 anatomically compatible trials, 12 spatially compatible trials, and 24 incompatible trials. Participants completed six experimental blocks in each of two sessions.

Results and Discussion

The first block of the experiment was treated as practice and not analyzed. For each participant, RTs more than 2.5 standard deviations from the mean of that trial-type were excluded from the analysis. This procedure eliminated 3.1% of the data for J.W. and less than 2.0% for each of the other participants. Only correct responses were used in the RT analysis.

Response Grouping

The RTs for the two hands on the bimanual trials are plotted against each other in Figure 2. The participants, including the split-brain patient, produced responses that were temporally coupled, with the correlation between the RTs for the two hands highly reliable for all participants, all ts > 251, ps $< .0001$. For four of the five controls, the correlations between the responses for the two hands were nearly perfect, with correlation coefficients (r) ranging between .996 and .998. For the remaining control (S.R.), the correlation coefficient was .93. Thus, although not instructed to respond in a particular manner, the control participants synchronized their responses.

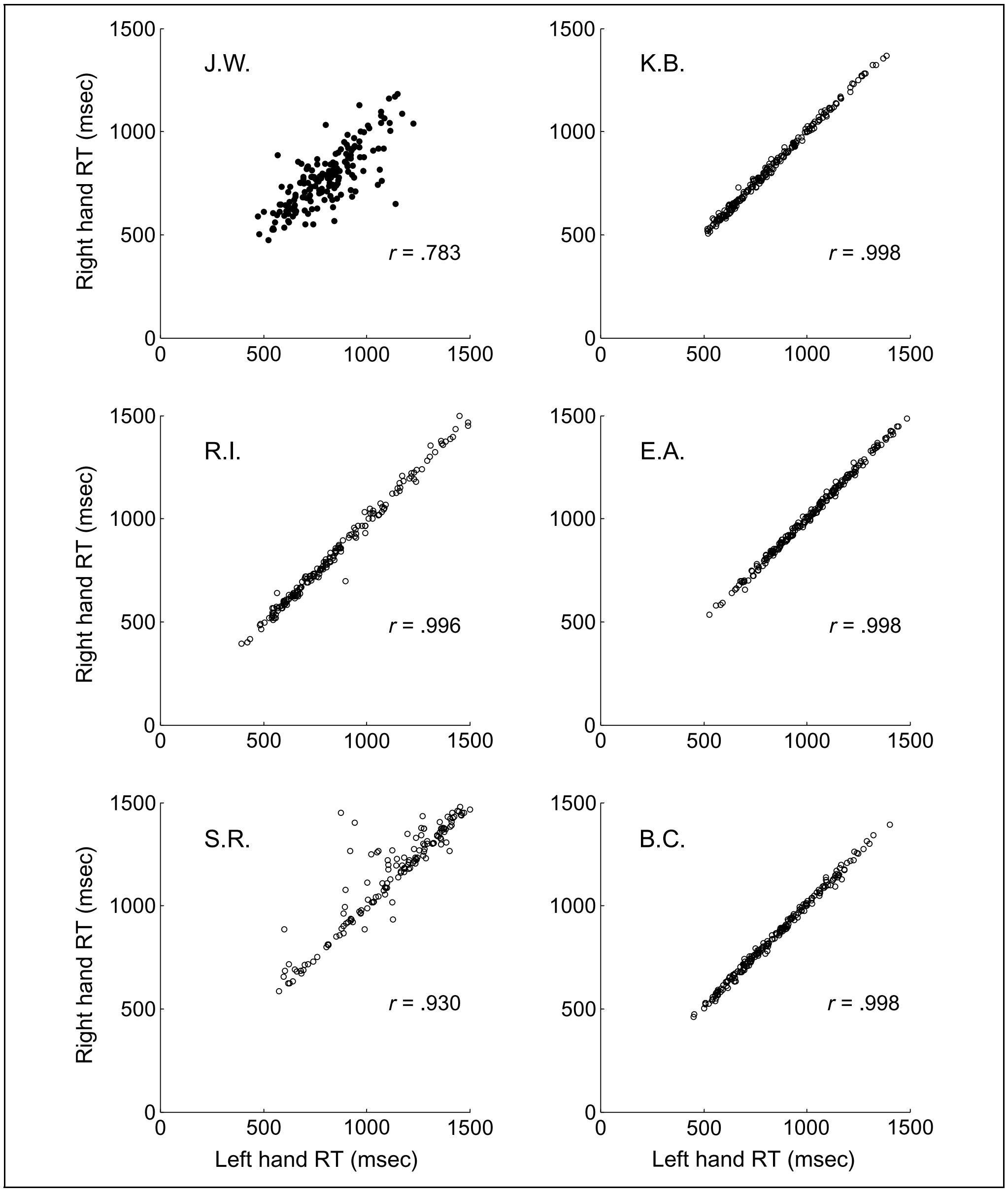
For the controls who consistently grouped their responses, the left and right responses were produced within 50 msec of each other on 99% of the trials. For S.R., the left and right responses were produced within 50 msec of each other on 75% of the trials. These "uncoupled" responses did not appear to be evenly distributed across the three bimanual trial types. Responses were produced within 50 msec of each other on 89% of anatomically compatible trials, 61% of spatially compatible trials, and 71% of incompatible trials. These differences were marginally different from what would be expected by chance, $\chi^2 = 2.40$, $p = .07$.

A different pattern of coupling was apparent for J.W. As evident in Figure 1, the correlation between the two hands was positive ($r = .78$), however, J.W.'s responses were not as strongly coupled as the controls. Responses were produced within 50 msec of each other on only 48% of the trials. As with participant S.R., the proportion of grouped responses were not the same for the three types of bimanual trials: Anatomically compatible responses were produced within 50 msec of each other on 66% of trials, spatially compatible responses were produced within 50 msec on 47% of trials, and incompatible responses were produced within 50 msec on 39% of trials. This distribution of grouped responses significantly differed from chance, $\chi^2 = 4.52$, $p = .03$, indicating that J.W. was more likely to group his responses when they were anatomically compatible.[2]

Dual-task Costs

When the responses are grouped, dual-task costs may be distributed across the two tasks, making their measurement less straightforward than with the standard PRP procedure where dual-task costs are generally restricted to Task 2. Nonetheless, as a starting point, the RTs on single-task trials can be used to estimate the distribution of grouped bimanual RTs. The difference between this expected distribution and the observed grouped bimanual RTs can serve as a measure of dual-task costs. Although the difference is uninformative with regard to which hand is the source of the dual-task costs, we

Figure 2. RTs on bimanual trials in Experiment 1 with the left-hand RT plotted on the *x*-axis and the right-hand RT plotted on the *y*-axis.



are not testing whether interference relates to graded sharing of central capacity or an all-or-none bottleneck. Rather, we are examining whether the patient performed similar to controls under conditions designed to favor independent performance on the two tasks.

The mean RTs revealed a clear difference between the controls and J.W. (Figure 3). For the controls, there was an advantage for the unimanual and anatomically compatible trials compared to the spatially compatible and incompatible trials. In contrast, J.W. showed little difference in RT across the four trial types.

To evaluate these differences, the mean RTs for each of the trial types were compared for each hand and each participant and *t* tests were performed on the means from each block. The results (Table 1) confirm that dual-task costs are observed for the controls and that these costs are smaller or nonexistent for J.W. With one exception (K.B.: unimanual right hand vs. anatomically compatible), the controls were significantly slower on bimanual trials compared to unimanual trials. The mean increase in RT on bimanual trials for the controls across the trial types was 430 msec for the left hand and 416 msec for the right hand. For J.W., the overall mean RT for the left hand was actually 27 msec faster on bimanual trials compared to unimanual trials. For the right hand, J.W. was faster on unimanual trials by 83 msec compared to the overall mean on bimanual trials. These differences are 5.4 and 4.2 standard deviations less than the mean of the distribution defined by the controls, indicating that J.W. shows considerably reduced dual-task costs compared to the controls.

Given that participants grouped their responses, the greater RTs for the bimanual trials might reflect strategic delays. If controls delayed one of the keypresses in order

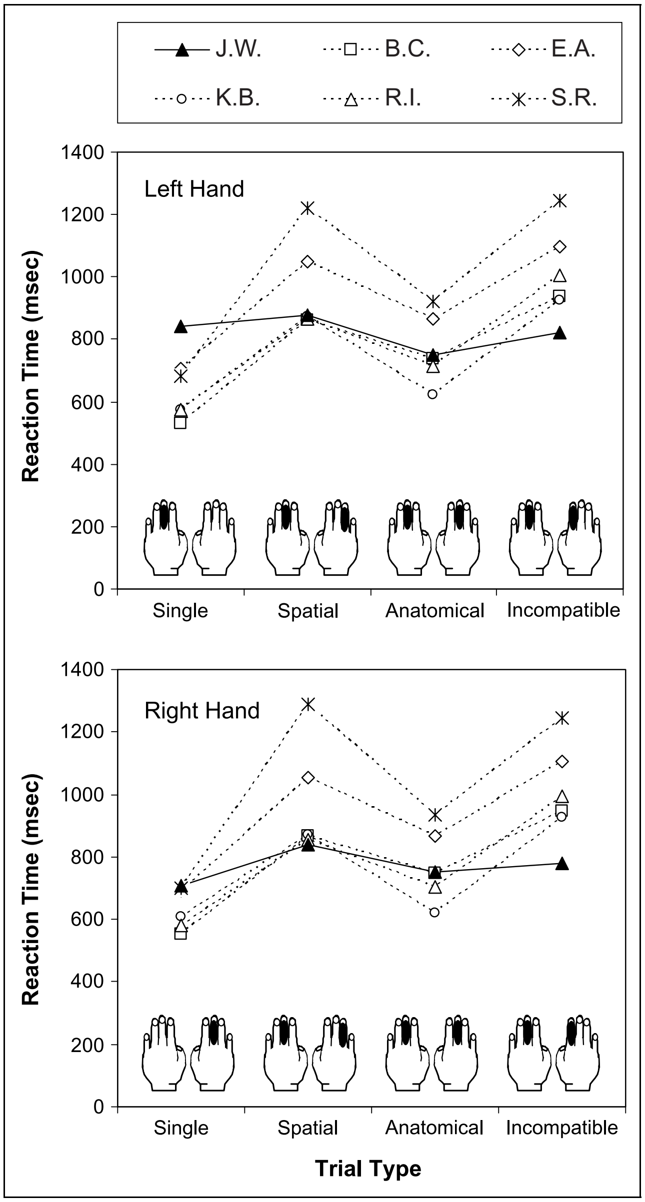


Figure 3. Mean RTs in Experiment 1 for the left (left panel) and right hand (right panel) for the four trial types. Sample stimuli are depicted underneath each category on the *x*-axis.

to produce a grouped response, then RTs in the bimanual conditions should be slower than the unimanual RTs. That is, the bimanual RT would be constrained to be equal to the slower of two unimanual RTs. In addition, bimanual trials might require an additional process to determine when the two responses are ready; this delay would be a form of a dual-task cost.

To assess this possibility, we used the unimanual trials in each block to predict the distribution of bimanual RTs if they simply resulted from delays associated with waiting for response selection to be complete for each hand. Each of the left hand unimanual RTs were paired with each of the right hand unimanual RTs. The larger of the two RTs was used in the estimate of the expected bimanual RT. The distribution across all combinations of left and right unimanual trials was divided into three distributions depending on whether the combination would form an anatomically compatible, spatially compatible, or incompatible response.

The differences between the estimates of the bimanual RTs based on the unimanual distributions and the actual bimanual RTs are shown in Figure 4. Because the results strongly indicated that the control participants grouped their responses, we averaged the left- and right-hand RTs when computing the actual bimanual RTs. All of the controls showed reliable costs for all of the bimanual trial types, ts > 4.91, ps $< .01$, except K.B. and R.I., who did not show reliable costs for the anatomically compatible trials [K.B.: $t(4) = -2.35, p = .08$ (trend is in the wrong direction); R.I.: $t(4) = 2.14, p = .10$]. With these exceptions, the dual-task costs observed in the controls do not stem solely from delays imposed by the slower of the two responses when coupled with a grouping constraint. Rather, additional dual-task costs are present.

We examined J.W.'s dual-task costs in two ways. First, as with controls, we computed his dual-task costs using the expected distribution based on the slower of the left- and right-hand RTs (i.e., grouped). Second, we used the average of the two RTs rather than maximum because, although the RTs for the two hands were correlated on bimanual trials, the correlation was weaker than that observed in the controls (i.e., ungrouped). This method provides a more traditional measure of dual-task costs because it simply reflects the difference between the mean single-task and mean dual-task RTs, ignoring any delays associated with coordinating the responses. Together, these two measures can be viewed as providing a range of the possible dual-task costs depending on the role grouping plays in the bimanual RTs.

The results from both methods reinforce the conclusion that J.W. showed much smaller dual-task costs than the controls, and in fact, may not exhibit any dual-task cost. For the incompatible trials, J.W.'s dual-task costs were −44 msec assuming grouping and 44 msec assuming no grouping. These values were over 4 standard deviations from the mean of the dual-task costs for the controls. Similar patterns are observed for the anatomically and spatially compatible trials, although, given the inconsistent dual-task costs observed in the controls for anatomically compatible trials, the differences were less pronounced. Nonetheless, given the range defined by the two estimates of dual-task costs, it is unclear whether J.W. is slowed at all when having to make two manual responses compared to a single unimanual response.

Compatibility Effects

All of the controls showed significantly faster RTs for anatomically compatible responses compared to the incompatible responses (Table 1). The difference between these two trial types was at least 200 msec for all of the

Table 1. Unimanual Reaction Times and Difference in Reaction Time between Trial Types in Experiment 1

Subject	*Uni. RT*	*Inc.–Uni.*	*Spat.–Uni*	*Anat.–Uni*	*Inc.–Spat.*	*Inc.–Anat.*
Left Hand						
J.W.	843	**−20**	**35**	**−92*****	−55	**72****
B.C.	529	410***	331***	210***	79*	200***
E.A.	705	394***	343***	161***	50	233***
K.B.	573	352***	298***	49**	54	304***
R.I.	575	437***	292***	137**	145*	300***
S.R.	681	553***	541***	242***	12	312***
Right Hand						
J.W.	707	**72***	134**	44	−62	**28**
B.C.	552	395***	316***	195***	78	200**
E.A.	692	413***	362***	173***	51	240***
K.B.	610	316***	263***	11	53	305***
R.I.	581	413***	276***	122*	137	291***
S.R.	699	540***	589***	235***	−49	305***

Uni. = Unimanual; Inc. = Incompatible; Anat. = Anatomically compatible; Spat. = Spatially compatible. **Bold** values for J.W. represent values that are more than 3 standard deviations from the mean of the controls.

*$p < .05$.

**$p < .005$.

***$p < .0005$.

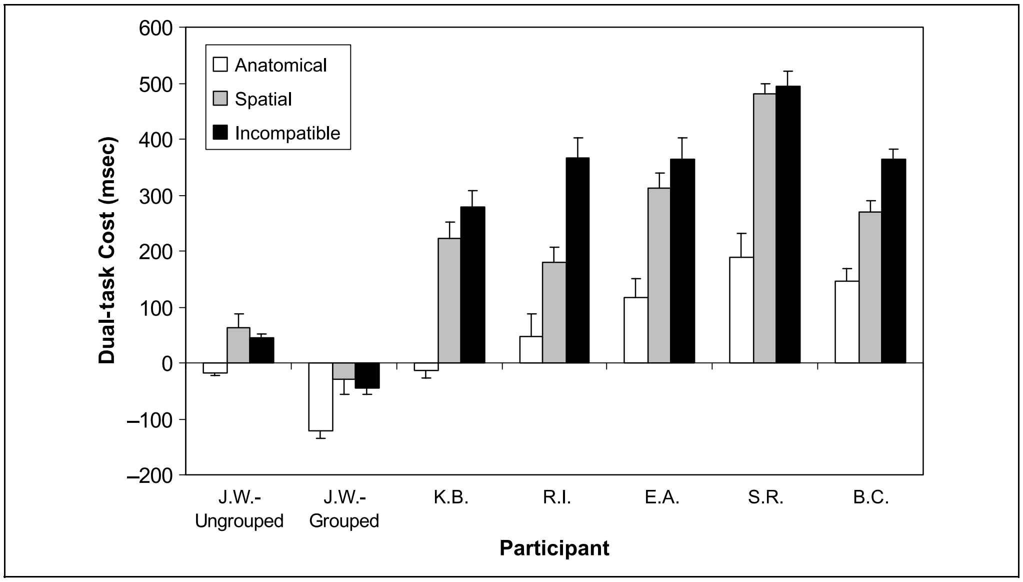


Figure 4. Difference between observed increase in RT on bimanual trials and estimated increase in RT if the slowing on bimanual trials resulted from a delay associated with withholding a grouped response until the slower response was ready. Positive values indicate dual-task costs beyond that associated with a delay strategy (see text). Because it was unclear whether the split-brain patient J.W. was grouping his responses or not (Figure 1), dual-task costs were computed in two ways. First, it was assumed that the responses were independent (first set of bars); second, it was assumed that the responses were grouped (second set of bars). For the control participants, we assumed that the responses were grouped in estimating the dual-task costs.

control participants. In contrast, J.W. showed comparatively small differences between the anatomically compatible and incompatible trials. With his left-hand, J.W. was 20 msec *faster* on incompatible trials than anatomical trials, indicating no evidence of any compatibility effect. With his right-hand, J.W. was 72 msec slower on incompatible trials than anatomically compatible ones. Although this difference was reliable [$t(19) = 3.50$, $p < .005$], this cost is 3.9 standard deviations below the mean of the costs demonstrated by the controls.

Differences in performance between the spatially compatible and incompatible trials were much smaller than those between anatomically compatible and incompatible trials. On average, controls were 68 msec faster on spatially compatible trials with their left hands and 54 msec faster with their left hands, although these differences were reliable only for two participants and only for their left hands (Table 1). J.W. showed no evidence of any benefit from spatial compatibility, with mean RTs faster on the incompatible trials for both hands.

Accuracy

The proportions of correct responses are presented in Table 2. These data were submitted to paired *t* tests for each subject and each hand separately. For J.W., none of the conditions differed from each other for either hand, all $t\text{s} < 1.51$, $p\text{s} > .20$. The overall mean accuracy for incompatible responses with the left hand was 7% lower than the average of the other response types. However, this nonsignificant effect was confined to two of the experimental blocks; his accuracy on incompatible trials on the remaining experimental blocks was slightly higher than the other responses. Critically, the pattern of RTs was identical for blocks with low accuracy on incompatible trials compared to blocks with higher accuracy on these trials.

For the controls, the effects on accuracy mimicked those observed in the RT data. Accuracy was lowest for incompatible trials (79%) and differed significantly from accuracy on unimanual trials in every comparison except one (the right hand for K.B.), all $t\text{s} > 3.47$, $p\text{s} < .05$. Accuracy on anatomically compatible trials (97%) was nearly identical to that observed on unimanual trials (97%), with no significant differences between the two scores for any of the participants. Spatially compatible trials (87%) produced intermediate accuracies. In short, the accuracy data are consistent with the RT data and do not suggest that speed–accuracy tradeoffs play a role in the pattern of effects.

Table 2. Proportion of Correct Responses for the Four Trial Types in Experiment 1

Subject	*Uni.*	*Spat.*	*Anat.*	*Inc.*
Left Hand				
J.W.	0.87	0.85	0.87	0.79
B.C.	0.97	0.95	0.97	0.79*
E.A.	0.98	0.90	0.98	0.86*
K.B.	0.98	0.97	0.98	0.89*
R.I.	0.98	0.83**	0.97	0.74*
S.R.	0.98	0.67**	0.95	0.59***
Right Hand				
J.W.	0.94	0.88	0.85	0.91
B.C.	0.97	0.95	0.98	0.85*
E.A.	0.98	0.92*	0.98	0.87*
K.B.	0.98	1.00	0.98	0.93
R.I.	0.93	0.85*	0.95	0.77*
S.R.	0.98	0.62*	0.90	0.59***

Abbreviations as in Table 1. Asterisks indicate a statistical significant difference from the unimanual condition, $^*p < .05$; $^{**}p < .005$; $^{***}p < .0005$.

EXPERIMENT 2

The results of Experiment 1 indicate that response selection can occur in parallel for the hands after resection of the corpus callosum. Thus, we failed to obtain support for the hypothesis that subcortical circuits impose some sort of processing bottleneck for response selection. However, one concern with this interpretation stems from the fact the visual stimuli were relatively complex, and, as such, may have overloaded perceptual processing. Given that split-brain individuals can deploy attention across the two visual hemifields more quickly than neurologically intact individuals (Luck, Hillyard, Mangun, & Gazzaniga, 1989, 1994), it is possible that the advantage observed in J.W. relates to differences in perceptual processing rather than in response selection per se.[3] Although some additional assumptions are necessary to account for the fact that perceptual limitations are not apparent on anatomically compatible trials, the perceptual complexity of the stimuli is different from those of previous studies, and it is possible that this contributes to the pattern of costs. To address this possibility, we ran a second experiment with reduced perceptual demands. Moreover, we tested a different split-brain individual to assess the generalizability of the effects.

Methods

Participants

V.P., 56 years old at the time of testing, underwent a callosotomy operation in 1979 (for a full report, see Sidtis et al., 1981) and has participated in many psychophysical studies over the past 25 years, including some that assessed dual-task performance (e.g., Ivry & Hazeltine, 2000). She was tested in two sessions on consecutive days. Four age-matched controls (50–65 years old, 3 women) with no history of neurological disorders completed the experiment using an identical protocol as V.P. All participants received monetary compensation.

Apparatus and Stimuli

A central fixation cross subtending 0.5° of visual angle remained present on the screen throughout each block. At the start of each trial, two sets of three vertically arranged dashes appeared on the left and right sides of the display (Figure 1B). A circle (unimanual trials) or two circles (bimanual trials), one on each side indicating the appropriate response(s), were presented for 200 msec. As in Experiment 1, there was never more than one stimulus presented on a side.

Procedure

The two response boxes were arranged such that, with the elbows flexed, the hands could rest comfortably on the response keys in a mirror-symmetric fashion. With this configuration, the upper display locations corresponded spatially with the keys under the ring fingers, the middle locations corresponded with the keys under the middle fingers, and the lower locations corresponded with the keys under the index fingers. The participants were instructed to use this compatible S–R mapping and respond to either the single stimulus or both stimuli as quickly and accurately as possible. Sample stimuli were presented on the screen and participants practiced responding until they felt comfortable with the task.

At the beginning of each trial, the dashes and fixation cross blinked for 100 msec, serving as a warning signal. After 1000 msec, one or two circles appeared. On unimanual trials, a single circle appeared in one of the six locations and was extinguished after 200 msec. On bimanual trials, two circles appeared with the onset of the two circles separated by one of three SOAs. For the −50 SOA, the left-side stimulus appeared 50 msec before the right-side stimulus; for the 0 SOA, the two stimuli were simultaneous; for the +50 SOA, the right-side stimulus appeared 50 msec before the left-side stimulus. We varied SOA as a further probe of temporal coupling. Participants were not informed of this manipulation. Participants had up to 3 sec to respond and there was a 1-sec interval between trials. No feedback was given until the block was completed.

Each experimental block consisted of 45 trials. Of these, 18 were unimanual trials, consisting of three repetitions of each of the six fingers of the two hands. The remaining 27 trials were bimanual trials, consisting of three repetitions of each of the possible nine bimanual responses formed by the factorial combination of the three possible responses for each hand. Each set of three repetitions involved one of each possible SOA so that every possible combination of left- and right-hand stimulus and SOA occurred once in each block. Note that because the hands were positioned in a mirror-symmetric manner, spatial compatibility and anatomical compatibility were identical; that is, spatially compatible trials required movements of homologous effectors. Thus, there were only two categories of bimanual trials: compatible (3 of the 9 possible bimanual combinations) and incompatible trials (6 of the 9 combinations).

V.P. was tested in two sessions composed of 10 experimental blocks each. Her performance was quite poor in the first session with low accuracy (<50%) and slow RTs (>1000 msec) for the first several blocks. Near the end of this session, she spontaneously announced that she now understood the task (which was corroborated by her data). Thus, although our plan was to only count the first few blocks as practice, we tested her in a complete second session the next day and it is these data that are reported in the analyses. To match this procedure, the controls were also tested in two separate sessions, only the second of which is reported here, even though their performance was quite similar across the two sessions.

Results and Discussion

The first two blocks of the second session were treated as practice. For each participant, RTs more than 2.5 standard deviations from the mean of that trial-type were excluded from the analysis. This procedure eliminated less the 1.5% of the data for all of the participants. Only correct responses were used in the RT analysis.

Response Grouping

The RTs for the two hands on the bimanual trials are plotted against each other in Figure 5. We show the raw data in this format for V.P. and one control participant, L.T. L.T.'s mean RTs closely matched V.P.'s on the single and compatible trials, and the overall pattern is highly representative of the other controls' data. V.P.'s data are quite distinct from the controls. First, the RTs for the two hands are much less strongly correlated for V.P. than for the controls, similar to what was observed in Experiment 1. Second, there is a clear effect of SOA on the relationship between the two RTs for the control participants, whereas the effect of SOA is much more subtle for V.P. In particular, the controls maintained tight synchronization of the two responses such that the temporal relationship remained the same regardless of SOA. The mean interresponse interval (IRI) did not significantly differ for the −50 and +50 SOA for any of the controls (D.B.: 12 vs. 8, $t < 1$; M.P.: 18 vs. 7, $p > .15$, $t =$ 1.46; L.T.: 17 vs. 18; $t < 1$. P.O.: −18 vs. −27, $p > .15$, $t =$

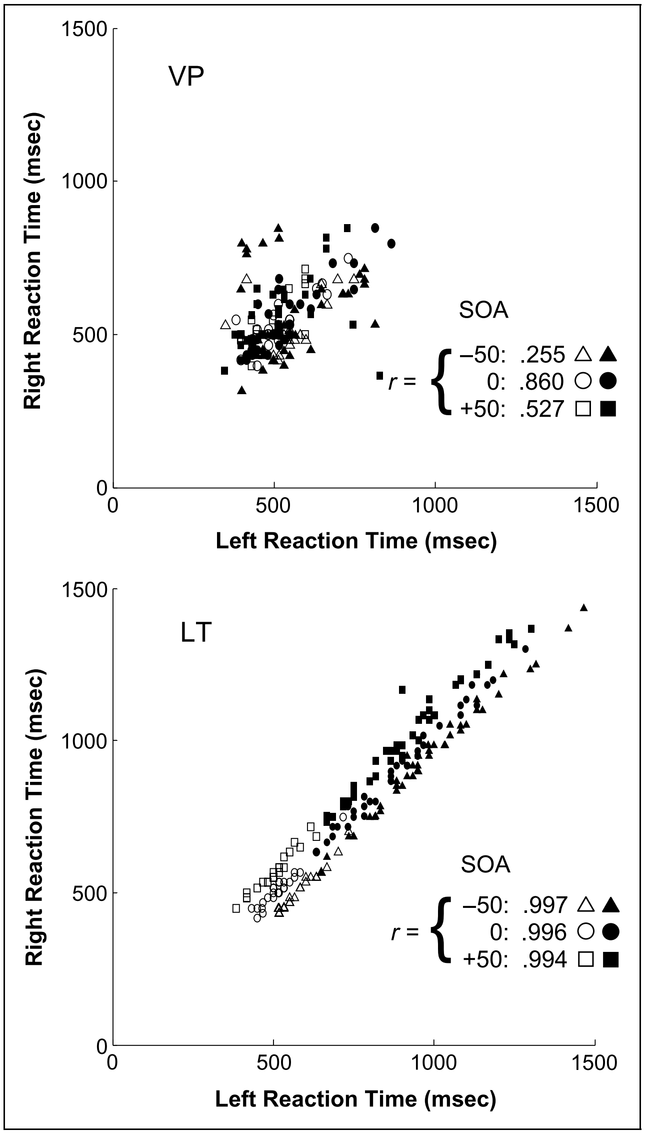


Figure 5. RTs on bimanual trials in Experiment 2 with the left-hand RT plotted on the *x*-axis and the right-hand RT plotted on the *y*-axis. Open symbols indicate compatible trials; filled symbols indicate incompatible trials. The three SOAs are indicated by different symbols.

1.46). In contrast, the mean IRI for V.P. differed significantly for the −50 and +50 SOA (83 vs. −28, $t = 4.03$, $p < .005$), with the 0 SOA condition falling between the two (11 msec). The fact that the magnitude of the response asynchronies approximated the magnitude of the stimulus asynchronies indicates that V.P. produced the two responses with greater independence.

Because the control participants synchronized their responses, we calculated separate correlation coefficients for each SOA. For the controls, the correlations between the responses for the two hands were strong, but not quite as strong as in Experiment 1, with correlation coefficients (*r*) ranging between .912 and .997. SOA did no affect the correlation between the two responses. Thus, as in Experiment 1, the control participants clearly responded in a coupled manner, in the absence of any instructions to do so. In contrast, V.P.'s responses were less strongly correlated, and the correlation was strongest at 0 msec SOA (see Figure 5). This latter finding suggests that VP was sensitive to the simultaneity of the stimuli, which did affect the synchronization of task operations.

Dual-task Costs

As in Experiment 1, the mean RTs revealed a clear difference between the controls and V.P. (Figure 6). To simplify the analysis and facilitate comparisons with Experiment 1, we focus on the RTs from the 0 SOA condition. Note that the effects of SOA on RT are small compared to the dual-task cost. To evaluate dual-task costs, the mean RTs for each of the trial types were compared for each hand and

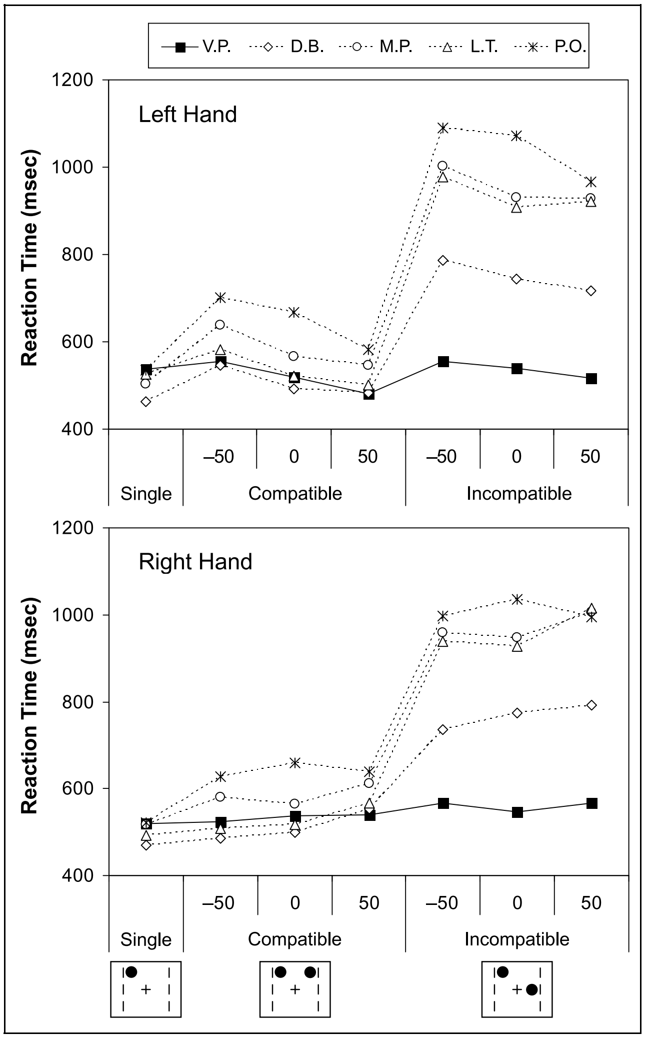


Figure 6. Mean RTs in Experiment 2 for the left hand (top panel) and right hand (bottom panel) for the seven trial types. −50 indicates that the left stimulus was presented 50 msec before the right stimulus, 0 indicates that the two stimuli were presented simultaneously, and +50 indicates that the right stimulus was presented 50 msec before the left stimulus. Sample stimuli are depicted on the *x*-axis.

each participant. t Tests were performed on the means from each block. The results (Table 3) confirm that dual-task costs are observed for the controls and that these costs are smaller or nonexistent for V.P. With one exception (L.T.: left-hand unimanual vs. compatible), the controls were significantly slower on compatible, bimanual trials compared to unimanual trials. The mean increase from unimanual to compatible RT across hands for the controls is 58 msec. The differences between the unimanual and incompatible trials were more dramatic. Each control showed highly significant differences between these two conditions (all ts > 10, ps $< .001$), and the mean across hands was 412 msec.

For V.P., there were no significant differences between bimanual conditions and the unimanual condition for either hand (all ts < 1.7, ps $> .15$). In sum, the mean RTs showed no evidence of a dual-task cost for the split-brain patient.

As in Experiment 1, we used the unimanual trials in each block to predict the distribution of bimanual RTs if they simply resulted from delays associated with waiting for response selection to be complete for each hand. The differences between the estimates of the bimanual RTs based on the unimanual distributions and the actual bimanual RTs provide a conservative measure of dual-task costs. The results for the controls are similar to the direct comparisons of the actual RTs. The costs associated with the compatible trials are small (mean = 21 msec) and statistically significant for only one of the controls (P.O.: $t = 3.38$, $p < .05$). In contrast, the costs associated with incompatible trials are robust (mean = 376 msec) and significant for all controls (all ts > 10, ps $< .001$).

V.P., like J.W. in Experiment 1, showed less evidence of response grouping, so two different models were used to estimate the expected distribution of bimanual RTs based on the unimanual RTs. Neither model indicated any significant dual-task cost for V.P.: For the maximum RT model, the observed bimanual RTs were *shorter* than the expected RTs, with the difference being significant for the compatible trials (43 msec, $t = 2.84$, $p < .05$), but not for the incompatible trials (32 msec, $t = 1.48$, $p = .18$). For the average RT model, the observed bimanual RTs were slightly longer than the expected RTs (compatible: 4 msec, incompatible: 19 msec), but neither difference was significant (ts < 1). In sum, control participants showed robust dual-task costs; V.P. did not.

Compatibility Effects

All of the controls showed significantly faster RTs for compatible responses compared to the incompatible responses (Table 3). Across the two hands and three SOAs, the difference between these two trial types was at least 200 msec for all of the controls (mean = 355 msec). In contrast, V.P. showed comparatively small differences between the compatible and incompatible trials. With her left-hand, V.P. was 20 msec *faster* on compatible trials compared to incompatible trials; with her right hand, this difference was 9 msec. Neither value was significant. Moreover, averaged over the two hands, V.P. performed at

Table 3. Unimanual Reaction Times, Bimanual Reaction Times as a Function of SOA, and Differences in Reaction Time between Trial Types in Experiment 2

Subject	*Uni.*	*Com. −50*	*Com 0*	*Com +50*	*Inc. −50*	*Inc. 0*	*Inc. +50*	*Com.–Uni.*	*Inc.–Com.*	*SOA*
Left Hand										
V.P.	537	554	519	481	**555**	539	**516**	−19	**20**	56*
D.B.	464	546	492	482	787	744	717	28*	252***	67**
M.P.	504	639	565	546	1002	931	927	61*	366***	84*
L.T.	525	582	521	501	978	908	922	−4	388***	69*
P.O.	534	702	667	583	1090	1072	966	133**	405***	121*
Right Hand										
V.P.	519	523	538	539	**567**	**546**	**567**	18	**9**	−8
D.B.	470	485	499	553	736	774	792	29*	276***	−62*
M.P.	518	581	564	611	958	948	1006	46*	384***	−39*
L.T.	493	508	517	567	939	926	1016	24*	409***	−68*
P.O.	521	628	659	640	998	1035	996	137**	376***	−5

Uni. = Unimanual; Com. = Compatible; Inc. = Incompatible; −50 = left-hand stimulus appeared 50 msec before right-hand stimulus; 0 = the two stimuli appeared at the same time; +50 = right-hand stimulus appeared 50 before the left-hand stimulus. Asterisks in the final three columns indicate that value was significantly different from 0, *$p < .05$; **$p < .005$; ***$p < .0005$. **Bold** values for V.P. represent values that are more than 3 standard deviations from the mean of the controls.

Table 4. Proportion of Correct Responses in Experiment 2

Subject	*Uni.*	*Com. −50*	*Com. 0*	*Com. +50*	*Inc. −50*	*Inc. 0*	*Inc. +50*
Left Hand							
V.P.	**0.89**	**0.96**	1.00	**0.83**	0.98	0.94	**0.77**
D.B.	1.00	1.00	1.00	1.00	0.96	0.98	0.98
M.P.	0.99	1.00	1.00	1.00	0.96	0.98	0.96
L.T.	0.96	1.00	1.00	1.00	1.00	1.00	1.00
P.O.	0.97	1.00	0.92	1.00	0.96	0.94	0.92
Right Hand							
V.P.	**0.86**	**0.79**	0.92	**0.79**	0.79	0.79	0.85
D.B.	1.00	1.00	1.00	1.00	0.92	0.90	0.96
M.P.	1.00	1.00	1.00	1.00	0.98	1.00	0.98
L.T.	1.00	1.00	1.00	1.00	1.00	0.96	0.98
P.O.	1.00	1.00	0.92	1.00	0.88*	0.90	0.85*

Abbreviations as in Table 3. Asterisks indicate a statistical significant difference from the unimanual condition, $*p < .05$. **Bold** values for V.P. represent values that are more than 3 standard deviations from the mean of the controls.

essentially the same speed on compatible trials compared to unimanual trials.

Accuracy

The proportions of correct responses are presented in Table 4. As is evident, all of the participants were able to perform the tasks reasonably well, although V.P. responded less accurately (.91 for the left-hand;.83 for the right hand) than the controls (.98 for either hand). To evaluate whether dual-task performance affected accuracy, each of the six bimanual conditions (2 levels of compatibility × 3 SOAs) were compared to the unimanual condition for each hand. None of these comparisons revealed any significant differences for V.P., suggesting that the two selection operations did not affect one another. Although there was a trend for the controls to be less accurate in the bimanual conditions, particularly when the responses were incompatible, this difference was significant only for one of participants at two of the SOAs. In sum, the accuracy data are consistent with the RT data and there is no evidence of a speed–accuracy tradeoff.

GENERAL DISCUSSION

The present experiments provide strong evidence that split-brain patients are able to simultaneously select responses for the two hands. The robust dual-task cost observed by Ivry et al. (1998) and Pashler et al. (1994) appear to result from the use of the PRP procedure, which prioritizes one of the tasks over the other and encourages participants to make their responses in a particular order. When such instructions are absent, the patients exhibited much smaller dual-task costs than the controls and, in fact, little evidence of any increase in RT when making two responses compared to one response.

The data do not indicate whether performance in neurologically intact individuals is limited by a strategic or structural bottleneck. Rather, they suggest that the findings of robust bottleneck limitations in split-brain individuals may stem from strategies they adopt to conform to the PRP instructions. Moreover, the present study, in conjunction with previous PRP studies, demonstrates that PRP instructions can cause individuals to exhibit behavior consistent with a processing bottleneck when, in fact, such limitations are abolished under slightly different experimental conditions (see also Schumacher et al., 2001).

Given that the corpus callosum consists of white matter, it might be argued that the present findings suggest that the bottleneck, whether strategic or structural, does not stem from competition for access to a single neural region. If a single neural structure was required by all response selection tasks, and competition for this structure resulted in a processing bottleneck, it is difficult to see how such competition would be assuaged by callosotomy. However, it is possible that in order to minimize interference, diverse regions are either inhibited or entrained to represent components of a same S–R mapping at a given time. In this way, a processing bottleneck might arise without competition for a single neural structure. Disconnecting the two hemispheres would disrupt this inhibition or entraining process and alleviate the bottleneck, consistent with the present findings.

Response Initiation Bottleneck?

As noted in the Introduction, Ivry et al. (1998) reported that the effects of S–R compatibility were underadditive with SOA for J.W. but additive for the controls. This difference could be explained by a shift in the locus of the bottleneck: For controls, the bottleneck is associated with response selection, but for the split-brain patient, the bottleneck arises at response initiation (see Pashler, 1994a; McCann & Johnston, 1992). This idea is consistent with the proposal of De Jong (1993) that, when two manual responses are required in a dual-task study, there are two bottlenecks, one associated with central processing (e.g., response selection) and one associated with the initiation of the manual responses. The split-brain patient would only be subject to limitations imposed by the second bottleneck. Note that a pattern of RTs consistent with a response initiation bottleneck could also stem from a strategy in which participants attempt to maintain a certain temporal interval between their responses.

In the present study, participants generally emitted their responses at the same time, making a response initiation bottleneck hard to detect (see De Jong, 1993). However, some aspects of the data are not consistent with the presence of a late bottleneck. The split-brain patients' responses were less temporally synchronized than controls, with only 46% of J.W.'s responses on bimanual trials being produced within 50 msec of each other in Experiment 1 and 59% of V.P.'s responses in Experiment 2. In contrast, 94% of the controls' responses were within 50 msec of each other in Experiment 1, and 86% were within 50 msec in Experiment 2. The decreased coupling of the split-brain patients' responses should make the effects of a response initiation bottleneck more apparent. Nonetheless, they did not show increased dual-task costs.[4]

Relationship between Dual-task Costs and Compatibility Effects

Hazeltine et al. (2003) proposed that dual-task costs and cross-task compatibility effects observed in many studies of bimanual coordination have a common source. According to this hypothesis, dual-task costs and compatibility effects reflect the degree of overlap of conceptual codes associated with the actions produced by the two hands (see also Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003). When two simultaneously performed tasks are unrelated, dual-task costs are always high and compatibility effects are low because there is little overlap between the central operations associated with the two tasks. When the tasks are more similar, compatibility effects are high because, on compatible trials, central operations performed for one of the tasks can be applied to the other task and the dual-task costs are smaller. In essence, cross-task compatibility effects simply reflect a reduction in dual-task costs due to savings in central operations.

The findings of Ivry et al. (1998) appeared to be inconsistent with this proposal because they suggested that compatibility effects and dual-task costs had distinct loci. That is, the split-brain patient showed no between task (i.e., between hand) compatibility effects but robust dual-task costs. However, the present findings indicate that the dual-task costs observed in split-brain patients do not stem from processing limitations. Instead, it appears that these costs reflect the instructional demands of the task. When these constraints are removed, both dual-task costs and intertask compatibility effects are dramatically reduced after callosotomy. Thus, the present findings support the hypothesis that dual-task costs and intertask compatibility effects stem from a common source.

Summary

The study of split-brain patients has provided valuable insight into the cognitive architecture of the intact human brain. In the present case, the results emphasize that dual-task performance is highly sensitive to task instructions. In contrast to previous studies, response selection for the two hands occurred essentially independently in the split-brain patients, consistent with the proposal that these operations are performed predominantly by cortical regions. Although subcortical structures are sufficient to support the temporal coordination of bimanual actions (Franz, Waldie, & Smith, 2000; Ivry & Hazeltine, 1999; Franz et al., 1996; Pashler et al., 1994), they do not impose the same limits on performance as observed in neurologically intact individuals.

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Notes

1. Changes in RT stemming from the correspondence or noncorrespondence of the responses of the two hands are referred to as both "compatibility effects" and "congruency effects." In the present article, we have chosen the former term to indicate the benefit of corresponding responses, whereas Ivry et al. (1998) used the latter.
2. A related analysis can be performed using the interresponse intervals (IRIs) rather than proportions of grouped trials. The results of the IRI analysis were highly similar to those of the analysis of grouping. Because it is less sensitive to outliers, we prefer the grouping analysis to the IRI analysis.

3. We are grateful to Hal Pashler for pointing out this alternative explanation.

4. The distribution of IRIs for the split-brain patients (and the control participants) did not show any evidence of bimodality. A bimodal distribution of IRIs is predicted by a response initiation bottleneck assuming some refractory period after the production of the first response.

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