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Sequential operation of disconnected cerebral hemispheres in split-brain patients

Harold Pashler,[1,CA] Steven J. Luck,[2] Steven A. Hillyard,[2] George R. Mangun,[3] Shannon O'Brien[1] and Michael S. Gazzaniga[3]

[1]Department of Psychology, 0109, University of California, San Diego, La Jolla, CA 92093-0109; [2]Department of Neurosciences, 0608, University of California, San Diego, La Jolla, CA 92093-0608; [3]Center for Neuroscience, University of California, Davis, CA 95616, USA

[CA] Corresponding Author

WHEN two concurrent sensorimotor tasks require separate responses, selection of the first response generally delays selection of the second. Dual-task performance was examined in four patients who had undergone surgical transection of the forebrain commissures including the corpus callosum. One light flash was presented to each visual field in succession, and patients made a choice response to each stimulus with the ipsilateral hand, thereby confining the tasks to separate hemispheres. All four showed dual-task interference very similar to that found with normal individuals. Therefore, still-intact subcortical structures must play a critical role in sequencing response selection processes (the 'dual-task bottleneck'), confirming the distinction between the attentional limitations involved in planning actions and those involved in perceptual analysis.

Key words: Attention; Brain-pathophysiology; Cerebral hemispheres; Dual-task interference; Psychological refractory effect; Reaction times; Visual fields

Introduction

The present experiment employed a variant of the 'psychological refractory period' paradigm, in which two stimuli are presented in succession and independent responses are required for each stimulus (see Fig. 1).[1-5] Decreasing the delay between the two stimuli in this paradigm leads to increases in the response latency for the second stimulus, even if there is no perceptual interference between the two tasks.[6] Several studies have shown that this dual-task interference occurs because the selection of the second response is forced to wait until the selection of the first response has been completed.[7,8] This delay in the second response, sometimes called a 'central bottleneck', may be observed in normal individuals even if the two tasks involve seemingly 'easy' tasks or engage different cerebral hemispheres.[9] The present study investigated the neural substrates of this interhemispheric interference. If the interference depends upon direct cortico–cortical connections between the two hemispheres, then this form of dual-task interference should be eliminated in patients who have undergone surgical transection of the forebrain commissures. Conversely, the presence of response delays in these 'split-brain' patients would provide evidence that subcortical structures play a critical role in the coordination and sequencing of cognitive processing.

Materials and Methods

Commissurotomy patients J.W., N.G., V.P. and L.B., whose neurological status has been described elsewhere,[10,11] performed 300–400 trials each (per ses-

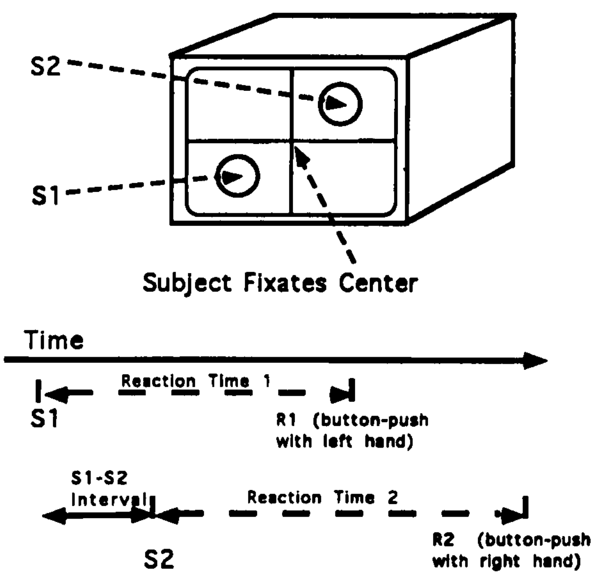

FIG. 1. Stimulus configuration and timing. At the beginning of each trial, a large cross appeared, dividing the video monitor into four quadrants and providing a fixation point; this cross remained present for the entire duration of the trial. One second after the onset of the cross, a disk was presented in the upper or lower left quadrant (S1) and this was followed by a second disk in the upper or lower right quadrant (S2). The disks were solid white on a black background, subtending about 2.4° of visual angle (based on an approximate 60 cm viewing distance). The center of the disk was 4.5° from the vertical meridian and 6.3° from the horizontal. The duration of each disk was 100 ms, and the interval between the onset of the first and second disks was 50, 150, 500, or 1000 ms, varied at random within trial blocks. Subjects responded to the upper and lower disk (S1) with the left middle or index finger (R1), respectively, and responded to the upper and lower right disk (S2) with the same fingers of the right hand (R2). The spatial configuration of the response buttons was similar to the spatial configuration of the stimuli, thus eliminating any stimulus-response incompatibilities. Subjects were instructed to respond both quickly and accurately, while minimizing any delays of the first response. Trials with incorrect responses or responses with latencies below 150 ms or greater than 2 s were discarded.

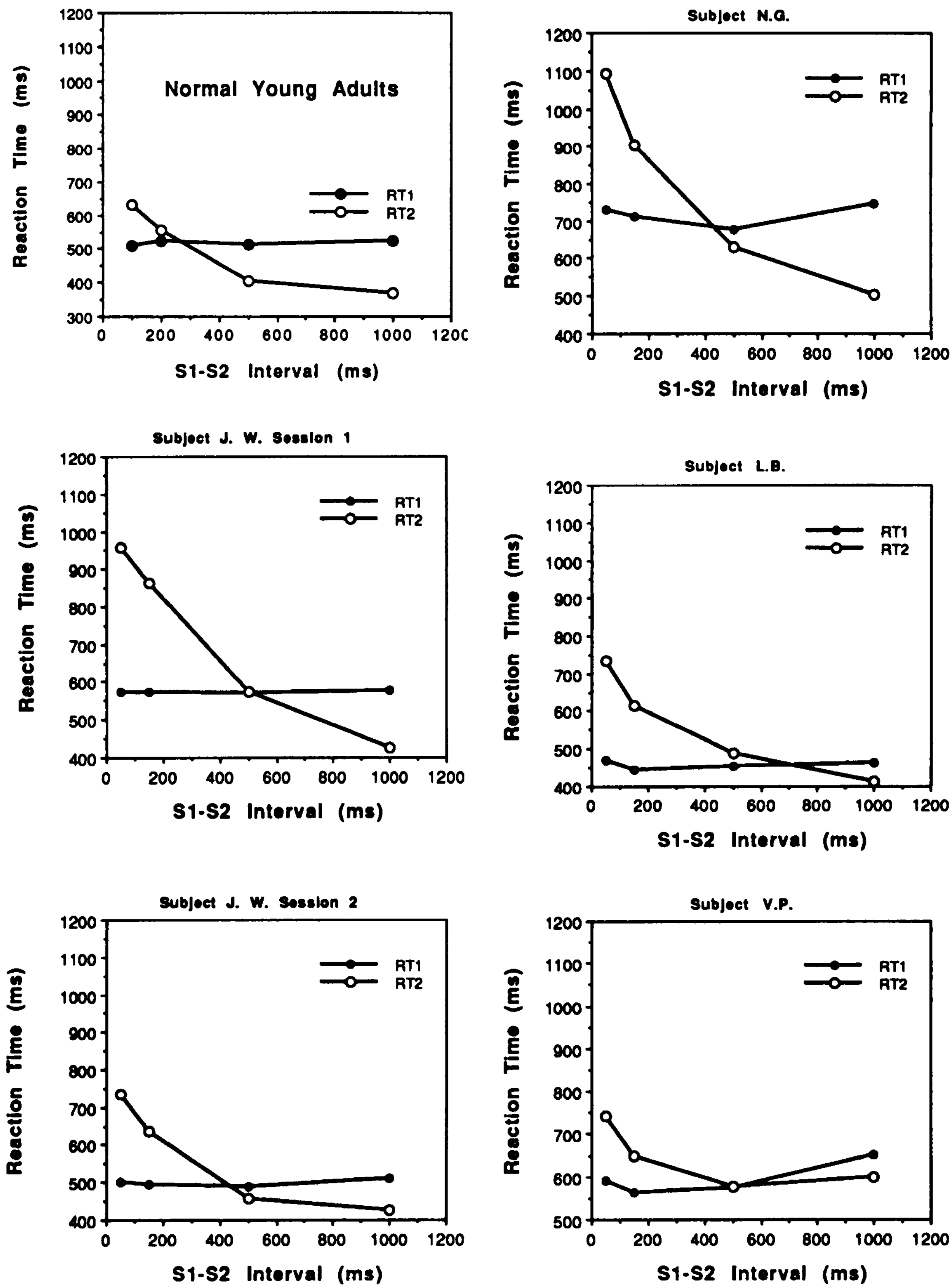

FIG. 2. Reaction time as a function of S1–S2 interval for the first task (filled circles) and the second task (open circles), presented for the average of the normal group[a] (A) and for each individual split-brain patient (B). Reaction times for S1 remained fairly constant as the S1–S2 interval is reduced, while responses to S2 became substantially slower, indicating that the selection of R2 was delayed until the selection of R1 was complete. This pattern can be seen in both the split-brain and normal groups and was clearly evident for every individual split-brain patient (although reaction times were generally longer for both tasks in the split-brain group).

sion) in this experiment, and previously reported data collected from 12 neurologically normal young adults in this task[9] was used for comparison. While fixating a control point, subjects were presented with a sequence of two stimuli, first a disk in the upper left or lower left quadrant (S1) and then a disk in the upper right or lower right quadrant (S2). The delay between S1 and S2 was varied within trial blocks with values of 50, 150, 500, or 1000 ms (see Fig. 1 for details). Subjects responded with the left hand (R1) to indicate the position of S1 and with the right hand (R2) to indicate the position of S2. Thus, the input and output for the first task (S1/R1) were confined to the right hemisphere and the input and output for the second task (S2/R2) were confined to the left hemisphere. Fixation was monitored via a high magnification video camera in patients J.W., V.P. and L.B. in order to ensure that S1 and S2 were presented to the appropriate visual hemifields on virtually all trials.

Results

Figure 2 shows that the performance of the split-brain subjects was highly similar to that of the normal control group. In controls, the reaction time for S2 (RT2) increased progressively as the S1–S2 delay was shortened, while the reaction time for S1 (RT1) remained essentially constant (Fig. 2A). The same pattern of interference was observed in each of the four split-brain patients (Fig. 2B); the effect of S1–S2 delay on RT2 was significant at the 0.001 level for each individual patient (analysis of variance using blocks as the unit of replication). The magnitude of task-2 slowing appears somewhat greater for the patients, especially N.G. and J.W. Session 1 (as assessed, for example, by the total effect of S1–S2 delay). However, note that task 1 was also completed more slowly by the patients, a ubiquitous finding with brain-injured individuals. This slower completion of the critical portions of task 1 could account for much or all of the apparent increase in interference. Patients L.B. and J.W. Session 2 showed interference fairly similar to that exhibited by controls. Thus, the results provide little reason to suspect that commissurotomy fundamentally changes the nature of dual-task processing limitations.

If selection of the second response is postponed until processing in the first task has been completed, then faster RT1s will be associated with faster RT2s when the S1–S2 interval is short. As the interval is lengthened, however, the probability that task 2 waits for task 1 should be reduced, thereby weakening the association between RT1 and RT2. Figure 3 shows data confirming this predicted pattern: for the commissurotomy patients (as for normal controls),[9] trial-to-trial variations in RT1 were strongly associated with variation in RT2, with the effect becoming weaker at shorter S1–S2 intervals (confirmed by a significant interaction of S1–S2 interval and relative speed of RT1,

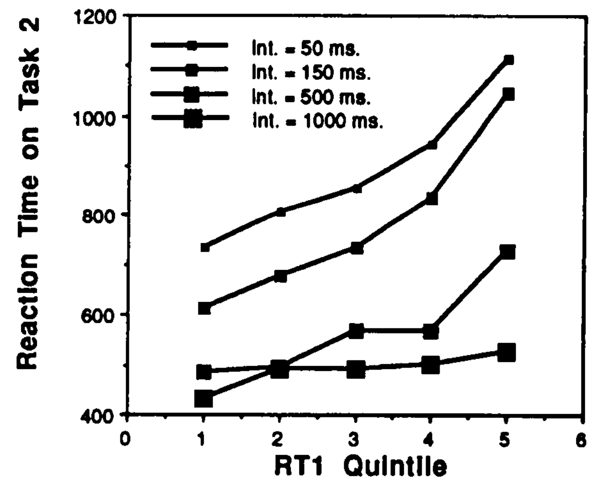

FIG. 3. Reaction time for the second task (RT2) as a function of reaction time for the first task (RT1). Each trial was assigned to a quintile on the basis of RT1, and the corresponding RT2 values were then averaged for each of these quintiles. At short S1–S2 intervals (SOAs), longer reaction times for S1 were associated with longer reaction times for S2, as would be expected if the selection of R2 began immediately after the selection of R1 was complete. At long S1–S2 intervals, however, variations in RT1 did not lead to variations in RT2, as would be expected if the selection of R1 was already complete before the presentation of S2. This pattern was observed for both the split-brain and control groups, providing additional evidence for the presence of similar response selection interference mechanisms in both groups.

defined in terms of quintiles as described in Figure 3 caption). These results clearly demonstrate interference between the separated hemispheres, with response selection in one hemisphere delaying the response selection made by the other hemisphere. Thus, even after commissurotomy the left and right cerebral hemispheres appear to be incapable of selecting motor actions independently and simultaneously.

Discussion

The present results suggest a framework for interpreting the divergent results obtained in prior studies of concurrent sensorimotor performance in split-brain patients. In a number of these experiments, it was found that each hemisphere could carry out a task quite independently of whether or not the opposite hemisphere was similarly engaged in task performance.[12–14] This independence was most striking when the task involved perceptual judgements with minimal motor demands, such as the search for a target among distractor items divided between the two visual fields.[15] In another set of studies, however, the imposition of task demands on one hemisphere interfered with the performance of the other. These interhemispheric interactions were most evident in tasks that required timed intermanual coordination,[16,17] imposed complex response requirements,[18,19] or involved the cued preparation for making rapid choice responses.[20,21] While this latter set of studies generally placed greater response requirements on the subjects, they did not reveal the exact processing stage at which interhemispheric interference occurs. The present design, however, allows this interference to be assigned specifically to the stage of response selection.[7,8] Thus, several studies now support the hypothesis that split-brain patients exhibit dual-task interference during response selection but not during perceptual analysis. This accords with the recent proposal that these two types of competition stem from functionally separate attentional systems—a proposal based on evidence from behavioral studies of normal individuals.[5]

Conclusions

The present observations support the view that intact subcortical structures mediate important aspects of behavioral integration in callosum-sectioned patients.[22–27] In particular, these data indicate that subcortical pathways do not merely allow the transfer of coarse sensory and semantic information between the hemispheres, but also participate in coordinating multiple streams of sensorimotor performance. The nature of this coordination remains to be elucidated, but the present results argue that it is not likely to consist merely of scheduling the inputs to cortical circuitry carrying out response-selection, because task 2 evidently waits for *completion* of the task-1 decision-making. Whatever the exact role of subcortical structures in scheduling stimulus-response sequences, it seems reasonable to suspect that this role may be critical for the remarkable intactness of bilaterally coordinated behaviors in the everyday lives of commissurotomy patients.

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