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Temporal discrimination in the split brain

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Abstract

Divided visual field studies of neurologically normal adults indicate that the left hemisphere is superior to the right in making temporal judgments. Some neuroimaging and neuropsychological studies, however, have suggested a role for the right hemisphere in temporal processing. We tested the divided hemispheres of a split-brain patient in two tasks requiring temporal judgments about visually presented stimuli. In one task, the patient judged whether two circles presented to one visual field appeared for the same or different durations. In the second task, the patient judged whether the temporal gaps in two circles occurred simultaneously or sequentially. In both tasks, the performance of the right hemisphere was superior to that of the left. This suggests that the right hemisphere plays an important role in making temporal judgments about visually presented stimuli.

1. Introduction

Over the past four decades a growing body of literature has reported a left-hemisphere advantage for tasks involving fine temporal discriminations (see Elias, Bulman-Fleming, & McManus, 1999, for a recent review). Several authors have suggested that this superior ability to discriminate rapidly presented stimuli might underlie the left hemisphere's specialization for processing verbal material (Efron, 1963b; Tallal & Newcombe, 1978; Tallal, Stark, & Mellits, 1985). Efron (1963b) offered some confirmation of this possibility. They found that the degree of asymmetry in a visual inspection time task correlates significantly with a measure of linguistic lateralization obtained from a dichotic listening task.

The first models proposed to account for the left-hemisphere temporal advantage were based on experiments in which stimuli were presented bilaterally and observers were required to make a temporal order judgement. For example, Efron (1963a) asked observers to judge whether bilateral visual or tactile stimuli occurred simultaneously or sequentially. For both modalities Efron found lower simultaneity thresholds when the right stimulus was presented before the left, but not vice versa (though see Brown & Sainsbury, 2000, for a failure to find any hemispheric asymmetry for tactile simultaneity judgement). To account for these results, as well as a similar finding with bilateral auditory stimulation, Mills and Rollman (1980) proposed a model in which judgement of temporal order was computed exclusively in the left hemisphere.

This model accounts for bilateral stimulation, but predicts no asymmetry when the stimuli are presented to a single hemisphere since the task would always be solved by the left hemisphere. An alternative is that both hemispheres are capable of making temporal judgements, but the left hemisphere is superior to the right, so completes this task more efficiently (e.g., Allen, 1983). This possibility was rejected by Mills and Rollman, but is favored by Nicholls (1994), who found a right visual field (and, by extension, left hemisphere) advantage for both the threshold of fusion for two flashes of light and the discrimination of successive vs. simultaneous visual events. Similarly, Brown and Nicholls (1997) have reported a right-ear (and thus left hemisphere) advantage for detecting a short (2–8 ms) gap in the middle of a white noise burst.

The overwhelming majority of studies reporting this left-hemisphere advantage have relied on asymmetric performance by neurologically normal observers in lateralized tasks. These studies rely on the (sometimes implicit) assumption that more efficient processing of stimuli presented to one side of space is the result of more efficient processing in the contralateral cerebral hemisphere. Although this assumption seems to be generally valid, some authors have cautioned against

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inferring hemispheric specialization from behavioral asymmetries (e.g., Efron, 1990). A number of studies have been conducted to address to roles of the two hemispheres in temporal processing more directly by studying either patients with brain lesions or measures of brain activation recorded during temporal tasks. These studies offer qualified support for the hypothesis that the left hemisphere is superior for some aspects of temporal processing, but also suggest that temporal processing is not monolithic, and has some aspects that are processed better by the right hemisphere. For example, previous examinations of simultaneity discrimination in split-brain patients reveal a right hemisphere advantage in conditions conducive to the perception of apparent motion (i.e., longish SOAs; Forster, Corballis, & Corballis, 2000), but left-hemisphere advantage for shorter SOAs for which there is no percept of apparent motion (Corballis, 1996; Corballis, Boyd, Schulze, & Rutherford, 1998)

In support of the left-hemisphere-advantage hypothesis, Nicholls, Schier, Stough, and Box (1999) reported increased power in the beta band of the electroencephalogram over the left temporal region, but not the right, during an auditory gap detection task. Supporting evidence has also come from studies of patients with unilateral brain damage. For example, Peretz (1990) found that patients with damage to the left temporal lobe were unable to discriminate rhythms, whereas patients with equivalent damage to the right hemisphere were unimpaired on this task. Likewise, von Steinbuchel, Wittmann, Strasburger, and Szelag (1999) found that patients with damage to posterior regions of the left temporal lobe were more impaired on temporal order judgements than patients with other focal lesions.

Some studies, however, suggest a right-hemisphere advantage for at least some aspects of temporal processing. For example, Harrington, Haaland, and Knight (1998) found that right-hemisphere lesions disrupted both a duration-perception task and a frequency discrimination task more than similar lesions in the left hemisphere. They concluded that a right-hemisphere prefrontal/inferior parietal network is critical in temporal processing, possibly because of the involvement of these areas in time-dependent working memory and attentional processes. This conclusion was supported by Rao, Mayer, and Harrington (2001), who investigated temporal processing with event-related fMRI. They found a network of cortical and subcortical areas involved in temporal processing, including an area in the right prefrontal cortex associated with the encoding of brief time intervals, and a later activation in the right dorsolateral prefrontal cortex associated with the comparison of time intervals. These findings suggest that temporal processing is heterogeneous, and that some aspects are lateralized to the right, rather than the left hemisphere.

In the present study, we investigated temporal processing in the divided hemispheres of a callosotomy ("split-brain") patient, in whom the corpus callosum has been resected to relieve pharmacologically intractable epilepsy. A consequence of this surgery is that the two hemispheres are effectively isolated at the cortical level, which allows us to investigate the abilities of each hemisphere independently. We employed two tasks, both of which we expected to be performed better by the left hemisphere. In the first task, two circles appeared simultaneously in one visual field, and the patient was required to judge whether their offset was simultaneous or whether one circle disappeared before the other. In the second task, the patient was required to determine whether brief gaps in the presentation of two circles occurred simultaneously or sequentially. Based on previous research, we expected the left hemisphere to outperform the right in both tasks.

2. Methods

2.1. Observer

The observer for these experiments was patient J.W., who underwent two-stage callosotomy in 1979 for relief of intractable epilepsy. Complete resection of the corpus callosum was confirmed by post-surgical MRI (Gazzaniga, Holzman, Deck, & Lee, 1985). J.W. is a right-handed male who was 48 years old at the time of testing. He has been tested extensively and a complete case history can be found in Gazzaniga, Nass, Reeves, and Roberts (1984a). Patterns of cerebral lateralization of function revealed in patient J.W. are consistent with those found in neurologically normal right-handed adults (e.g., language: Gazzaniga, Smylie, Baynes, Hirst, & McClearly, 1984b; emotion: Stone, Nisenson, Eliassen, & Gazzaniga, 1996; visuospatial: Funnell, Corballis, & Gazzaniga, 1999; face processing: Gazzaniga & Smylie, 1983) suggesting that findings from this patient are relevant to theories of hemispheric specialization in the intact brain.

2.2. Experiment 1

All stimuli for both experiments were presented on an Apple Macintosh G4 personal computer using the PsyScope program. The stimuli were pairs of black circles presented simultaneously one above the other. The circles subtended 2° of visual angle. In half of the trials, the two circles remained on the screen for the same amount of time, and in the other half of the trials, the two circles remained visible for different durations. When the duration was the same, the two circles were on the screen for 200 ms. When the duration was different, one circle remained on the screen for 200 ms and the other remained on the screen for less than 200 ms by these amounts: 24, 36, 48, 60, and 72 ms. There were 240 trials in the set, with 120 trials in each visual field. Of these 120 trials, 60 were same duration and 60 were different duration, with 12 trials for each of the five duration differences. J.W. completed five sets with at least a one-week interval between sets.

J.W. was instructed to maintain fixation on a central crosshair that was present throughout the experiment. In each trial, a pair of circles was presented to one visual field and J.W. responded via keypress with the hand ipsilateral to the field of presentation. His hands were positioned on a standard keyboard such that the middle finger of each hand was above the index finger (left hand: s and x, right hand: k and m). If the two circles appeared for the same amount of time, he responded "yes" by pressing the upper key (s or k), and if they did not appear for the same amount of time, he responded "no" by pressing the lower key (x or m).

2.3. Experiment 2

As in the previous experiment, the stimuli were pairs of black circles that subtended 2° of visual angle each and were presented simultaneously one above the other. The onset and offset of both circles were the same and the circles were on the screen for 250 ms. During the presentation time, each circle disappeared for 50 ms. In half of the trials, these gaps occurred simultaneously in the two circles. In the other half of the trials, the gaps were temporally offset in the two circles by 35, 47, or 59 ms. There were 120 trials in the set, with 60 trials in the left visual field (LVF) and 60 in the right visual field (RVF). Of these 60 trials, 30 were same duration and 30 were different duration, with 10 trials at each of three gap offsets. J.W. completed 24 sets over a three-month period.

The procedure was the same as in the previous experiment. In each trial, J.W. maintained fixation on a central crosshair while a pair of circles was presented to one visual field. J.W. responded with the hand ipsilateral to the field of presentation and pressed the upper key for "yes" if the gaps occurred simultaneously and the lower key for "no" if they did not.

3. Results

3.1. Experiment 1

J.W.'s responses were analyzed using a hierarchical-χ^2 test (Winer, Brown, & Michels, 1991) in which the factors were RESPONSE ("yes" vs "no"), CONDITION (same duration vs. different duration), DURATION DIFFERENCE (24, 36, 48, 60, and 72 ms), and FIELD (LVF vs. RVF). This analysis was designed to reveal the effects of DURATION and FIELD (and the interaction between them) on RESPONSE and CONDITION.

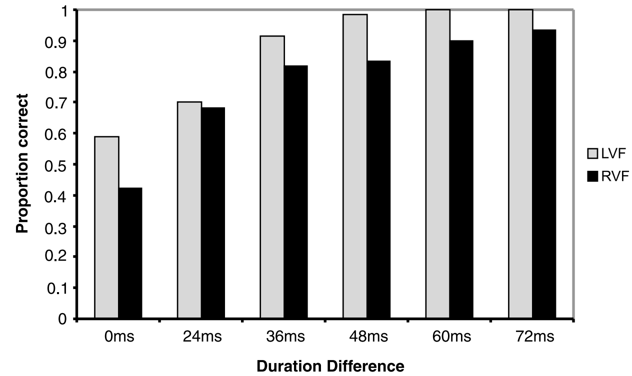

Fig. 1. Data from Experiment 1. The proportion of correct responses for each hemisphere when the circles were the same duration (0 ms difference) and when the circles differed in duration (24, 36, 48, 60, and 72 ms).

J.W.'s performance on this task is depicted in Fig. 1. There was significant effect of DURATION DIFFERENCE ($\chi^2(4) = 11.03,\ p < .05$). This indicates that the amount by which the duration of the two circles differed influenced J.W.'s performance. He was more accurate in responding to larger differences in duration. There was also a significant effect of FIELD ($\chi^2(1) = 15.73$, $p < .01$), with the right hemisphere more accurate than the left (RH/LVF = .755, LH/RVF = .628). The interaction between DURATION DIFFERENCE and FIELD was not significant, indicating that performance in both hemispheres was affected by the difference in duration between the two circles.

3.2. Experiment 2

Data were again analyzed using a hierarchical-χ^2 test in which the factors were RESPONSE ("yes" vs "no"),

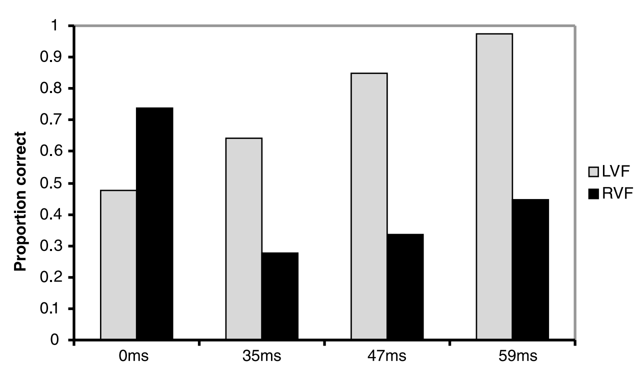

Fig. 2. Data from Experiment 2. The proportion of correct responses for each hemisphere when the gaps in the circles were simultaneous (0 ms) and when the gaps were offset in time (35, 47, and 59 ms).

CONDITION (gaps simultaneous vs. offset), GAP OFFSET (35, 47, and 59 ms), and FIELD (LVF vs. RVF). J.W.'s pattern of performance was similar to that found in Experiment 1 (see Fig. 2). There was a significant effect of GAP OFFSET ($\chi^2(2) = 29.59$, $p < .01$). This indicates that performance was affected by the gap offset, with J.W. more likely to report a difference with greater gap offsets. There was also a significant effect of FIELD ($\chi^2(1) = 385.73$, $p < .01$), with the right hemisphere more accurate than the left. The interaction between GAP OFFSET and FIELD was not significant, indicating that performance in both hemispheres was affected by the gap offsets.

4. Discussion

The results of both experiments indicate that J.W.'s right hemisphere performs duration and gap comparisons better than his left hemisphere. This finding is unexpected, and is strikingly at odds with the results of previous studies using similar tasks (Elias et al., 1999). It is also inconsistent with the models proposed to account for those results. The absolute-specialization model of Mills and Rollman (1980) predicts that only the left hemisphere should be able to perform our tasks at all. More recent studies have suggested that both hemispheres are capable of making temporal judgements, but that the left is superior to the right (e.g., Nicholls, 1994). Neither of these perspectives can account for the finding that the right hemisphere performs our tasks better.

The motivation for examining temporal processing in the split brain was that the logical link between asymmetries in performance and hemispheric asymmetry is stronger than in divided-visual-field studies with normal observers. Nevertheless, we fully expected to replicate the findings from studies with normal observers particularly since decades of research have provided evidence that J.W.'s pattern of cerebral lateralization is consistent with that of neurologically normal right-handed adults (Funnell et al., 1999; Gazzaniga et al., 1984a; Gazzaniga & Smylie, 1983; Stone et al., 1996). Why are our results incompatible with the bulk of the literature? One possibility might be the visual nature of the tasks used to assess temporal processing. In our experimental tasks, and many other tasks used to study temporal processing, there is a visuospatial component in addition to the temporal demands of the task. It is well established that the right hemisphere in split-brain patients is superior to the left for fine-grained visuospatial discriminations (Corballis, Funnell, & Gazzaniga, 1999, 2002; Funnell et al., 1999). When the callosal connection is severed, the left hemisphere no longer has access to the superior visuospatial representations of the right. Because performance in these tasks relies on both visuospatial and temporal processes, the left hemisphere's overall performance may suffer due to lack of input from the right. If this interpretation is correct, the left hemisphere may be superior to the right in temporal processing but this superiority may only be apparent when the left hemisphere receives adequate visuospatial input from the right hemisphere.

An alternate, albeit related, possibility is that the hemispheric difference we found is the result of the attentional demands of the task. It has been demonstrated that attentional resources in the brain are limited, and that the hemispheres, even when divided, compete for these resources (Holzman & Gazzaniga, 1982). The visuospatial nature of our experimental tasks may have resulted in the right hemisphere appropriating the bulk of the attentional resources because of its specialization for this type of processing. This would leave the left hemisphere with fewer resources available, and this may have negatively impacted its ability to make temporal discriminations.

Although one or both of these explanations may in part account for the pattern of results we found in our experimental tasks, our data indicate that temporal processing is not the exclusive domain of the left hemisphere. Neuroimaging and neuropsychological data are consistent with this idea, suggesting that the right hemisphere plays a role in temporal processing possibly because of its involvement in time-dependent working memory and attentional processes (Harrington et al., 1998; Rao et al., 2001). The two hemispheres may make differential contributions to temporal processing depending on the nature of the task.

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