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UNITARY ATTENTION IN CALLOSAL AGENESIS

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The interhemispheric organisation of two specific components of attention was investigated in three patients affected by partial or complete agenesis of the corpus callosum. A visuospatial component of attention was explored using a visual search paradigm in which target and distractors were displayed either unilaterally within a single visual hemifield, or bilaterally across both visual hemifields in light of prior work indicating that split-brain patients were twice as fast to scan bilateral displays compared to unilateral displays. A central component of attention was explored using a psychological refractory period (PRP) paradigm in which two visual stimuli were presented laterally at various stimulus onset asynchronies (SOAs), with each stimulus associated with a different speeded two-alternative choice task. The stimulus–response compatibility in the second task was systematically manipulated in this paradigm, in light of prior work indicating that split-brain patients exhibited a close-to-normal PRP effect (i.e., slowing of the second response as SOA is decreased), with, however, abnormally decreasing effects of the manipulation of the response mapping on the second task speed as SOA was decreased. The present results showed that, although generally slower than normals in carrying out the two tasks, the performance of each of the three acallosal patients was formally equivalent to the performance of a matched control group of normal individuals. In the visual search task, the search rate of the acallosal patients was the same for unilateral and bilateral displays. Furthermore, in the PRP task, there was more mutual interference between the lateralised tasks for the acallosal patients than that evidenced in the performance of the matched control group. It is concluded that the visuospatial component and the central component of attention in agenesis of the corpus callosum are interhemispherically integrated systems.

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INTRODUCTION

The disconnection of the cerebral hemispheres provides neuroscientists with the unique opportunity to study the cortical organisation of mental processes in humans under conditions in which the bandwidth of information transfer between the hemispheres is limited. Insights into the organisation of mental processes have been achieved in this context by channelling lateralised stimulation to each disconnected hemisphere and monitoring if and how the contralateral hemisphere can process the stimulation. Techniques based on lateralised stimulus presentations have been used extensively to study the cerebral organisation of functions in two specific populations of neurological patients characterised by disconnected cerebral hemispheres, namely, patients who have undergone surgical transection of the corpus callosum (so-called split-brains; Sperry, 1968) and individuals affected by congenital agenesis of the corpus callosum (or acallosals; e.g., Lassonde & Jeeves, 1994).

According to Sperry (1968), at least two interdependent factors converge to establish a basic neurophysiological distinction in the cerebral circuitry of split-brains and acallosals. In the majority of cases, the surgical transection of the corpus callosum in split-brains is carried out in adulthood (usually, for treatment of intractable epilepsy), when the degree of neural plasticity is hypothesised to be reduced compared to earlier stages of development. Support for this view has come from studies showing effective compensation for transection of the corpus callosum in participants who have undergone callosal surgery before puberty but poor compensation when the operation was performed after puberty (e.g., Lassonde, Sauerwein, Geoffroy, & Decarie, 1986). Hypotheses concerning the functional compensation for the absence of the corpus callosum in acallosals have concentrated on the likely hyper-development of uncrossed sensory-motor pathways, and on the enhanced transmission of information through noncallosal or midbrain connections (e.g., Jeeves, 1994). Neuropsychologists have demonstrated substantial differences between split-brains and acallosals, using lateralised stimulus presentation techniques, primarily for three aspects of cognitive performance (Lassonde & Jeeves, 1994). First, unlike split-brains, acallosals can cross-match objects held in each hand out of view. Second, acallosals do not seem to experience any particular difficulty in cross-comparing tachistoscopically presented visual stimuli. Finally, acallosals do not report hemialexia for words channelled to the right cerebral hemisphere, nor do they report anomia for real-world stimuli haptically explored using the left hand.

Despite the massive reorganisation of brain structures that is arguably consequent to callosal agenesis, however, deficits of interhemispheric transfer of information in acallosals analogous to the disconnection deficits typically shown by split-brains have been documented. Probably the most compelling demonstration of defective interhemispheric transfer in callosal agenesis is that related to the crossed-uncrossed difference (CUD; Poffenberger, 1912) in speeded manual reaction time (RT) to lateralised visual stimuli. The CUD is hypothesised to estimate interhemispheric transmission time. This estimate has been shown to be in the order of 3 or 4 ms in normals, and in the order of 50 ms or longer in split-brains. Interestingly, the CUD in acallosal patients is closer in magnitude to that of split-brains than to that of normals (e.g., Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993). An additional demonstration of the notable similarity between split-brains and acallosal patients has been reported in a study by Jeeves, Silver, and Jacobson (1988). Like split-brains, acallosal patients tend to fail in tasks requiring the interhemispheric integration of movements of the upper limbs under conditions in which such movements must be coordinated (see also Sauerwein, Lassonde, Cardu, & Geoffroy, 1981). A number of studies have revealed acallosals' deficits also to be comparable to split-brains' deficits when motor learning skills mastered intrahemispherically must be transferred interhemispherically, using either complex tactile stimuli, such as

formboards or kinaesthetic mazes (see, among others, Jeeves, 1979), or simple visual stimuli (Lassonde, Sauerwein, & Lepore, 1995).

In contrast with the many studies reviewed above, much less is known about the neural basis of attention in callosal agenesis. Only one study has focused on this issue and found that attention in acallosal patients is similar to that found in split-brains. Specifically, Hines, Paul, and Brown (2002) cued the location of an upcoming target. The cue was either valid, in that it accurately predicted the location of the target, or it was invalid, in that it predicted another location. Acallosal patients had greater difficulty than normal controls in reorienting attention to an invalidly cued target when the cue and the target were displayed in opposite visual hemifields. Such difficulty was not apparent when the invalidly cued target and the cue were displayed in the same visual hemifield. Notably, this pattern of results resembles that found with split-brains (Corballis, 1995; Gazzaniga, 2000), and suggests that the corpus callosum may be necessary to support an integrated visuospatial attention system that crosses the vertical meridian.

In the present article, we seek to extend the work of Hines et al. (2002) by studying the characteristics of attentional performance in callosal agenesis using tasks designed to reveal different aspects of the attention system of acallosals. These two tasks were the visual search and the psychological refractory period (PRP) tasks. Whereas some work has been performed with each of these tasks with split-brains, no equivalent work has been done with acallosals.

In the visual search task, an observer must scan a visual display, as rapidly as possible, to determine whether a target is present or absent. Usually, the number of nontargets (distractors) in the display is varied. If the target and distractors are structurally similar (e.g., a green "H" target among green "A" distractors), the search time increases linearly as the number of distractors is increased (e.g., Duncan & Humphreys, 1989; Treisman & Gelade, 1980). Luck, Hillyard, Mangun, and Gazzaniga (1989, 1994) studied how split-brains search for a target in this type of task, with the distractors surrounding the target either distributed evenly in both visual hemifields, or confined to a single hemifield. Strikingly, the search time of split-brains was halved when distractors were displayed in both hemifields compared to when the stimuli were all in a single hemifield. That is, the search time of split-brains depended on the number of items within each hemifield rather than on the total number of distractors in the entire visual field (both hemifields), as is typically found with normal observers. These results suggest that independent visuospatial attention mechanisms co-exist in the separate cerebral hemispheres of split-brains—is the same true for acallosals?

In the PRP task, two visual stimuli are presented at various stimulus onset asynchronies (SOAs), typically ranging from 50 ms to 1000 ms or longer. Each stimulus is associated with a different speeded task, and the reaction time (RT) in each task is recorded in each trial. Usually, RTs in the first task are not strongly influenced by SOA. In contrast, RTs in the second task increase sharply as the SOA between the stimuli is reduced. This is the PRP effect. Using lateralised stimuli, Pashler et al. (1994) presented split-brains with two sequential visual stimuli, one stimulus to the right of fixation and one stimulus to the left of fixation, each requiring a speeded binary decision. Like in normals, robust PRP effects were found in split-brains, suggesting that whereas a visuospatial attention component is not a unitary system in split-brains, a later component of attention could not be divided between two successive stimuli requiring independent speeded responses. However, using a paradigm similar to that used by Pashler et al., Ivry, Franz, Kingstone, and Johnston (1998) argued that the locus of the PRP effect in normals and in split-brains differ substantially. Ivry et al. manipulated the spatial compatibility of the stimulus–response mapping in the second task. A single split-brain case was examined in this work. The split-brain tested and controls were required to respond to a lateralised colored disk presented either above or below the horizontal meridian of a computer monitor using two

distinct stimulus–response mappings, namely, a "compatible" mapping (i.e., they pressed the upper button of two vertically aligned buttons to indicate that the disk was above the meridian, and the lower button to indicate that the disk was below the meridian), or the inverse, "incompatible" mapping. Not surprisingly, longer RTs in the second task were observed with the incompatible mapping compared to the compatible mapping. Of greater relevance, this spatial compatibility effect was generally additive with the PRP effect in normal participants, but underadditive in the split-brain (i.e., the spatial compatibility effect decreased as SOA was decreased). Spatial compatibility effects are held to emerge from a longer processing time required for response selection when the response mapping is incompatible. In this context, the underadditive effects of SOA and spatial compatibility in the split-brain have been taken by Ivry et al. to indicate that each of two functionally independent central attention mechanisms is likely to perform response selection, and that these mechanisms coexist in the cerebral hemispheres of split-brains. The results of Ivry et al. were consistent with a locus of interference causing the PRP effect that, unlike in normals, was beyond response selection, at least in the specific case of the split-brain tested in his investigation. Do acallosals show the same apparent ability to carry out two independent response selection operations, one in each hemisphere, as split-brains?

Using the method devised by Luck et al. (1989, 1994) and a variant of the PRP task close to Ivry et al.'s (1998), we examined visual search performance (Experiment 1) and PRP performance (Experiment 2) in three acallosals. These three individuals represented three distinct points along the spectrum of callosal agenesis in terms of the degree of preservation of connections linking the two hemispheres. Patient A had an incomplete callosal agenesis with sparing of the rostrum and the anterior commissure. This patient was presumably the least likely to have a performance similar to that of split-brains. At the other extreme, Patient C had complete callosal agenesis and agenesis of the anterior commissure. Finally, Patient B represented an intermediate case, having complete callosal agenesis but an intact anterior commissure.

EXPERIMENT 1 (VISUAL SEARCH TASK)

Method

Participants

Patient A is a 40-year old, right-handed male, with 5 years of formal education and an IQ of 89. Callosal agenesis in this patient was first diagnosed when he was 33 years old, after his recovery for an episode of hemicrania. According to MRI (top scan of Figure 1), the agenesis extends from the genu to the splenium of the corpus callosum with sparing of the rostrum and the anterior commissure. The disorder was classified in origin as a Shapiro syndrome, due to some episodes of excessive sweating and disorders in thermoregulation, and treated with clozapine and clonazepam. However, such episodes have always been irregular and infrequent. In the last 7 years, on several occasions he has undergone in-depth neurological examination. In none of these occasions have neurological deficits been discovered. The patient was not on medication during the testing described in the present article.

Patient B is a 32-year-old, left-handed man with 6 years of formal education and an IQ of 75. He started to have absence seizures at the age of 23 years following the installation of a ventroperitoneal derivation for hydrocephaly. An MRI (middle scan in Figure 1) performed at that time revealed complete absence of the corpus callosum with presence of the anterior commissure. The patient has been seizure-free for several years and does not take any medication. His neurological exam is within normal limits. Patient B lives by himself and is gainfully employed.

Patient C is a 31-year-old, right-handed man with 14 years of formal education and an IQ of 107. He was born with various craniofacial malformations such as hypertelorism, cleft lip,

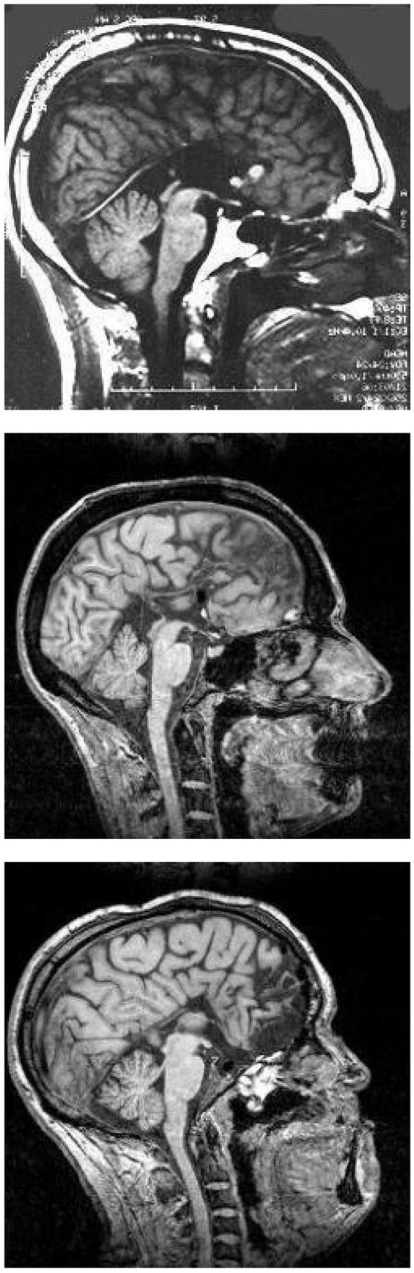

Figure 1. *Magnetic resonance imaging scans (saggital view) of acallosals. From top to bottom, patient A who has a near-complete callosal agenesis but preservation of the rostrum and anterior commissure, Patient B who has a complete callosal agenesis with an intact anterior commissure, and patient C, with agenesis of both the callosal and anterior commissures.*

and cleft palate, which were surgically corrected at the age of 4 months. In addition, a basal transpalatal encephalocele was removed through a bifrontal craniotomy at the age of 18 months. At that time, complete agenesis of the corpus callosum was detected. A subsequent MRI (bottom scan in Figure 1) also showed agenesis of the anterior commissure and discrete bilateral prefrontal atrophy related to the previous surgery. A left hydrocele and two prepalatal fistulas, diagnosed at the age of 4 years, were also surgically corrected. As a consequence of the frontal surgery, he developed hypothyroidism and hypopituitarism, which responded well to hormone therapy. He was not on medication at the time of testing. The patient has a normal neurological exam. He is married and gainfully employed.

The control participants were five healthy adults. They were matched to the acallosals on the basis of age, sex, and education, using the lowest level of education of the three acallosals as the point of reference (5 years).

Patient A and the controls were tested at the Neuropsychological Lab of the S. Anna Hospital in Ferrara, Italy, whereas patients B and C were examined at the Laboratory of the Groupe de Recherche en Neuropsychologie et Cognition of the University of Montreal, Canada.

Apparatus and stimuli

A schematic representation of the spatial configuration of the stimuli on a trial of Experiment 1 is reported in Figure 2 (upper panel).

The display consisted of 2, 4, or 8 items, each composed of a red square above or below a green square to form a vertically oriented rectangle subtending $0.8^\circ \times 0.4^\circ$ at a distance of 50 cm set by a chin-rest. The stimuli were displayed on a black background of a CRT computer monitor controlled by a PC-type computer. Nontarget items were red-above-green rectangles, and target items were green-above-red rectangles. The items were placed at random locations within either or both of two vertically oriented rectangular regions subtending $4^\circ \times 8^\circ$, each centred 4° to the left or to the right of a central fixation point

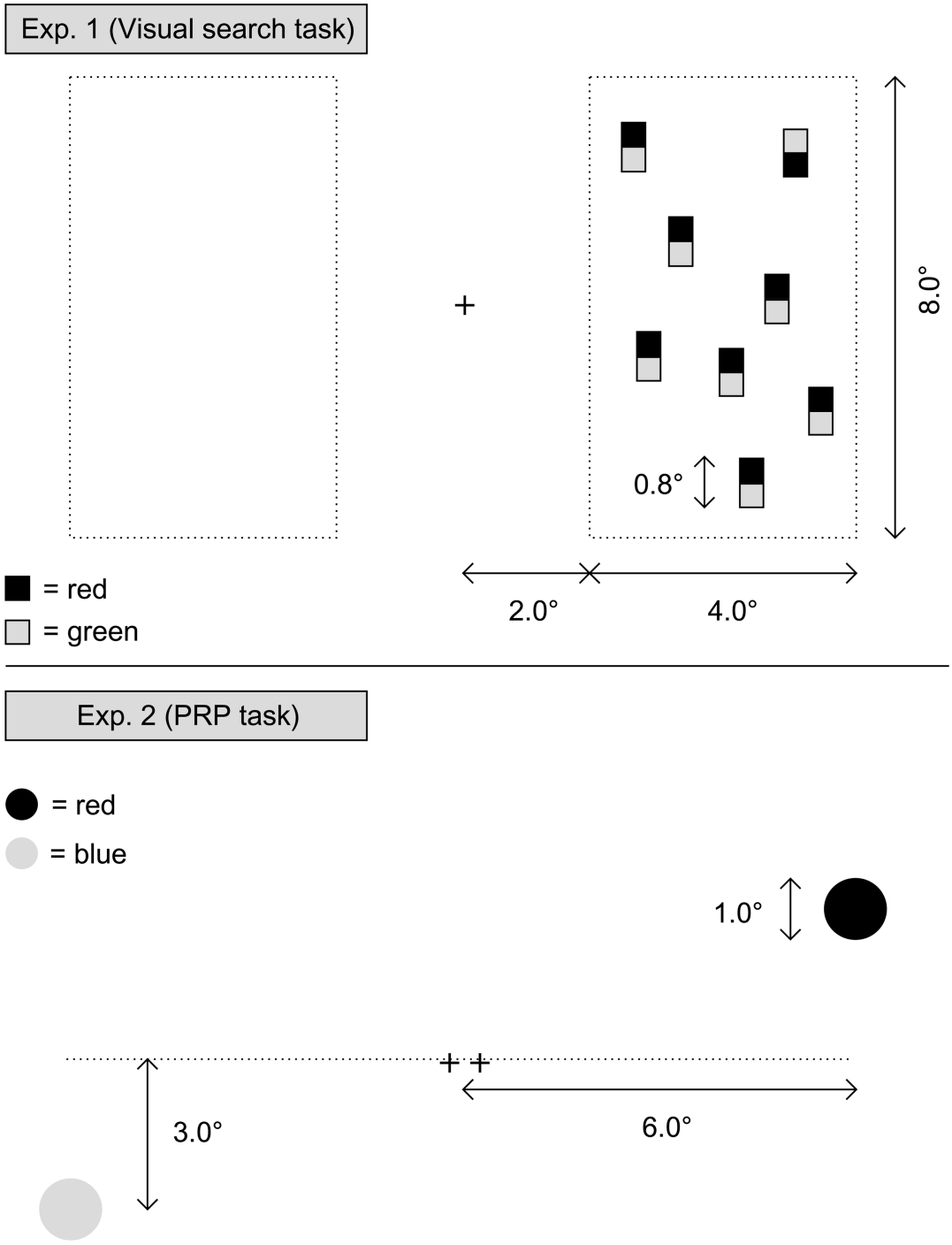

Figure 2. *Examples of the spatial configuration of the stimuli used in the visual search task (Experiment 1; upper panel) and in the PRP task (Experiment 2; lower panel).*

marked by a plus sign. In half of the trials, the items were confined to a single hemifield (equally often left and right). In the other half of the trials, the stimuli were equally divided between the two hemifields. Half of each type of trial contained a target (target-present trials) and half contained only distractors (target-absent trials). Only one target was presented in any given target-present trial.

Control for eye movements

The algorithm adopted for the control of eye movements differed between the two settings (Italy and Canada). For Patient A and for each of the adults included in the control group, horizontal eye movements were detected through three Ag/AgCl electrodes. Two electrodes were placed on the left and right lateral canthii, and a ground electrode was placed in the centre of the forehead. The EOG was amplified using a Colbourn amplifier, whose gain and band-pass filter were set to 5000 and 0.016–100 Hz, respectively. The EOG was sampled at 400 Hz by means of a National Instruments 12-bit DAQCard-1200 card. Before the beginning of the experimental session, each participant performed in an eye calibration phase consisting of 30 eye movements (15 to the left and 15 to the right) from the central fixation point to the centre of the rectangular regions (i.e., 4°), within which stimuli were later presented (see Figure 2). This distance was chosen because of the inherent low signal-to-noise ratio of the single-trial EOG recorded with the present apparatus, and because only variations in the EOG clearly exceeding 12 microV (i.e., 2°) could be related with confidence to the production of an eye movement. Each participant also made 30 analogous eye movements from the central fixation point to the outer boundary of the two rectangular regions (i.e., 6°). Measurements obtained during the calibration phase were used to establish an EOG amplitude threshold for eye movements of 4° or greater. For each trial, an EOG epoch of 1000 ms post-stimulus was selected and the mean EOG amplitude recorded 250 ms pre-stimulus (baseline) was subtracted. Following the display onset in each trial, the latency of the first eye movement exceeding the threshold was then computed.

For patients B and C, lateral eye movements were monitored during each trial by means of a video camera (VHS AG-190 Panasonic) connected to a colour video monitor (Sony Trinitron PMV-1910Q). The camera was centred on one of the patient's eyes that covered the entire monitor. A set of grid lines (1 cm = 1°) overlayed on the video monitor allowed the experimenter to detect any movements of the eyes. A central dot on the grid indicated the eye position when the participant looked at the fixation point. Any trial in which there was eye movement prior to the response were flagged by the experimenter and later excluded from statistical analyses of the data. The rejection criterion was quite severe; absolutely no deviation of the eyes was allowed during stimulus presentation.

Procedure

Each participant participated in four experimental sessions, scheduled on two different days with two consecutive sessions per day. Each trial began with the presentation of a fixation point displayed at the centre of the monitor. The fixation point was exposed for 1000 ms, and followed by a blank field exposed for 800 ms. At the end of the blank field exposure, the items were displayed on the monitor for a maximum duration of 2500 ms. In the two sessions on one day, participants were instructed to press one button with the index finger of the right hand on target-present trials, or a different button with the index finger of the left hand on target-absent trials. In the other two sessions on the different day, this response mapping was reversed. The acallosals and three control participants started with two sessions in which right-hand responses had to be produced on target-present trials, and left-hand responses had to be produced on target-absent trials, followed by two sessions with the other hand–response pairings. Two control participants began with left-hand responses on target-present trials, and right-hand

responses on target-absent trials, followed by two sessions with the other pairings. Both speed and accuracy were emphasised at the beginning of each session. A blank field was presented for 2000 ms after the participant made a response, following which the fixation point for the next trial was presented. The fixation point provided feedback on response accuracy. A plus sign indicated a correct response and a minus sign indicated an error. Each session was divided into eight blocks of 24 trials each. The trials in one block were a randomised cycle through each possible factorial combination of the levels of number of items in the display (set size: 2, 4, or 8), spatial layout (unilateral or bilateral), target presence/absence, unilateral display hemifield (left or right). Each participant contributed 768 experimental responses. The first session on each day was preceded by a training phase composed of two blocks of 24 trials each.

Results

Only trials in which the target was displayed in the hemifield ipsilateral to the hand used for target-present responses were considered in the analyses. These trials were screened for eye movements, and only trials free of eye movements were considered in the analyses. Eye movement filtering resulted in the loss of 17.3% of the acallosals' trials, and 16.1% of the trials in the control group. The analyses concentrated on correct RTs and error rates. Correct RTs were screened for outliers using an adaptation of the procedure described by Van Selst and Jolicoeur (1994). When an outlier or an error was found, the entire trial was excluded from the analyses. The application of the outlier elimination procedure on the present data set resulted in a loss of 3.0% of correct RTs for the acallosals, and 2.0% of correct RTs for the control participants. The results were analysed using an analysis of variance (ANOVA), in which set size (2 vs 4 vs 8 visual items) and spatial layout (unilateral vs. bilateral) were treated as within-participant factors. In the separate single-case analyses of the acallosals, session (total = 4) was treated as random factor.

Control group

A graphical summary of the results of the control group in Experiment 1 is reported in Figure 3 (right lower panel). The RT analysis indicated a significant effect of set size, $F(2, 8) = 20.8$, $MSe = 7573$, $p < .001$, and no effect of spatial layout ($F < 1$), or of the interaction between set size and spatial layout ($F < 1$). The analysis performed on the mean percentage of correct responses revealed a significant effect of set size, $F(2, 8) = 9.4$, $MSe = 0.0087$, $p < .008$, in which the percentage of correct responses tended to decrease (from 95% to 78%) as set size increased. It also revealed a significant effect of the spatial layout. $F(1, 4) = 36.3$, $MSe = 0.0019$, $p < .004$, indicating a slightly higher accuracy of the control group with bilateral arrays than with unilateral arrays (91% vs 83%, respectively). Neither the effect of the spatial layout, nor the effect of the interaction between set size and spatial layout, were significant in this analysis (both Fs < 1). The analyses performed on the parameters of the best-fitting linear regression equations indicated that neither the slopes nor the intercepts of unilateral vs bilateral linear equations differed significantly: slope, $F < 1$; intercept, $F(1, 4) = 2.8$, $MSe = 63$, $p > .10$.

Patients' group

The results obtained by each of the three acallosal patients are also displayed in Figure 2. From the outset, it can be seen that all three patients showed longer RTs than the controls. A detailed analysis of each patient's performance is presented below.

Patient A (partial callosal agenesis, intact rostrum, and anterior commissure). A graphical summary of the RT results of Patient A in Experiment 1 is reported in Figure 3 (upper left panel). The ANOVA for the RT results indicated a significant effect of set size, $F(2, 6) = 11.3$, $MSe = 34144$, $p < .009$, but no effect of the spatial layout ($F < 1$), and no interaction between set size and spatial layout ($F < 1$). The analysis performed on the mean percentage of correct

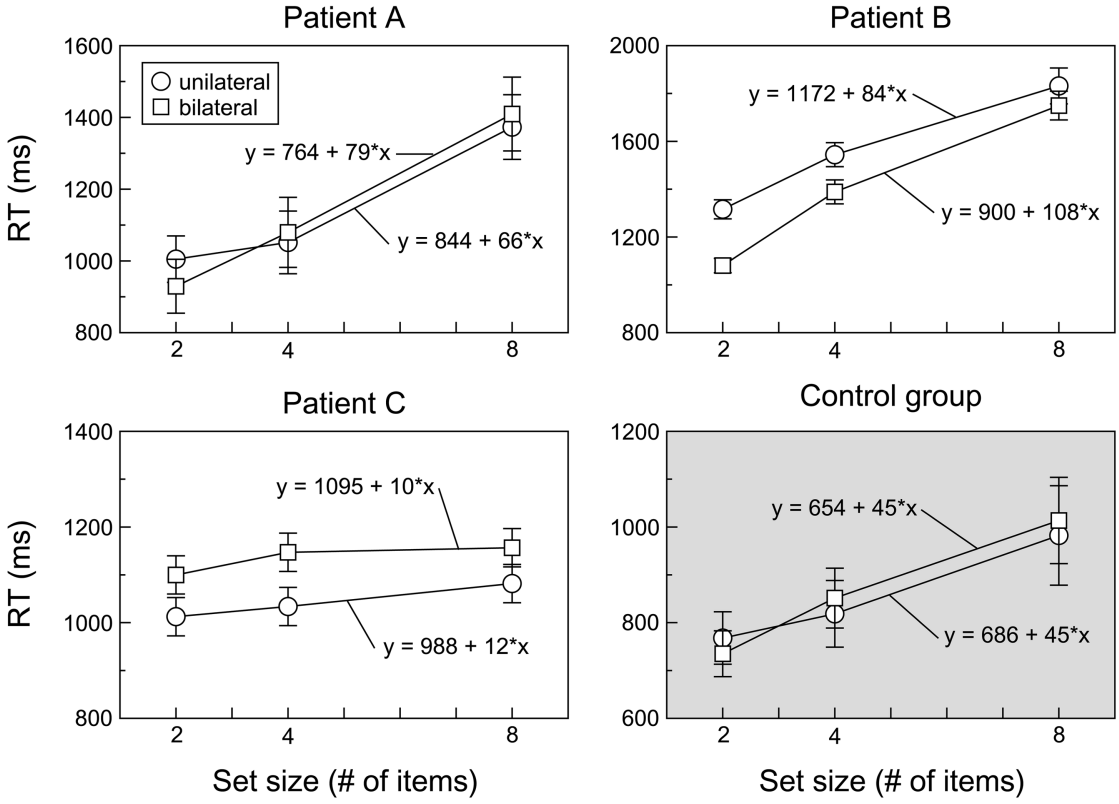

Figure 3. *Visual search task RTs and standard error bars for the acallosals and the control group. The best-fitting linear equations for each RT function across set size are reported within the graphs (graphs are on different scales).*

responses revealed a marginally significant effect of set size, $F(2, 6) = 4.9$, $MSe = 0.005$, $p < .06$, reflecting a trend for the percentage of correct responses to decrease (from 98% to 89%) as set size increased. Neither the effect of spatial layout, nor the effect of the interaction between set size and spatial layout, were significant in this analysis (both Fs < 1). An analysis was also performed on the parameters (i.e., slope and intercept) of the best-fitting linear regression equations describing the RT functions associated with the unilateral and bilateral spatial layouts. These analyses indicated that neither the slopes nor the intercepts of the two linear equations differed significantly: slope, $F < 1$; intercept, $F(1, 3) = 1.3$, $MSe = 9606$, $p > .33$.

Patient B (complete callosal agenesis, intact anterior commissure). A graphical summary of the RT results of Patient B in Experiment 1 is reported in Figure 3 (upper right panel). The ANOVA for the RT results indicated a significant effect of set size, $F(2, 6) = 227.5$, $MSe = 3093$, $p < .001$, a significant effect of the spatial layout, $F(1, 3) = 40.9$, $MSe = 3651$, $p < .008$, and no interaction between set size and spatial layout, $F(2, 6) = 1.2$, $p > .33$. The analysis performed on the mean percentage of correct responses revealed a significant effect of set size, $F(2, 6) = 24.1$, $MSe = 0.003$, $p < .005$, with the percentage of correct responses decreasing from 94% to 80% as set size increased. Neither the effect of spatial layout, nor the effect of the

interaction between set size and the spatial layout, were significant in this analysis (both Fs < 1). The analysis performed on the parameters of the best-fitting linear regression equations indicated a significant difference in slope between unilateral and bilateral RT functions, $F(1, 3) = 1399.6$, $MSe = 0.85$, $p < .001$ (note that this difference is in the direction opposite than found for split-brains, as discussed below), and a significant difference in intercept between these functions, $F(1, 3) = 96.0$, $MSe = 1542$, $p < .003$.

Patient C (complete callosal agenesis, agenesis of anterior commissure). A graphical summary of the RT results of Patient C in Experiment 1 is reported in Figure 3 (lower left panel). The ANOVA for the RT results indicated a marginally significant effect of set size, $F(2, 6) = 3.9$, $MSe = 2074$, $p < .08$, a significant effect of the spatial layout, $F(1, 3) = 19.2$, $MSe = 2637$, $p < .03$, and no interaction between set size and spatial layout, $F(2, 6) = 1.4$, $p > .32$. The analysis performed on the mean percentage of correct responses revealed a significant effect of set size, $F(2, 6) = 32.7$, $MSe = 0.005$, $p < .001$, with the percentage of correct responses decreasing (from 89% to 64%) as set size increased. Neither the effect of spatial layout, nor the effect of the interaction between set size and the spatial layout, were significant in this analysis, $F < 1$ and $F(2, 6) = 1.2$, respectively, both ps $> .40$. The analysis performed on the parameters of the best-fitting linear regression equations indicated no significant difference in the slope of unilateral and bilateral RT functions, $F(1, 3) = 2.7$, $p > .2$, and a significant difference in intercept between these functions, $F(1, 3) = 12.8$, $MSe = 1780$, $p < .04$.

Group analyses

In two separate ANOVAs, the group of acallosals was compared directly with the control group. In this set of analyses, in addition to the factors considered in the individual analyses, the factor group (acallosals vs controls) was considered as a between-subject factor, and only effects related to this factor are discussed in this section. Acallosals were generally slower than controls in detecting targets, $F(1, 6) = 7.7$, $MSe = 208271$, $p < .04$. No other effect involving the factor group emerged as significant in the RT analysis (all Fs < 1). No effects involving the factor group emerged as significant in the analysis of accuracy data (all Fs < 1).

Discussion

The most important results in Experiment 1 were that the spatial layout of the items (unilateral vs bilateral) made either no difference to the rate of visual search for the acallosals and the control group, or, when it did (Patients B and C), the pattern of RTs produced by this factor was not convergent with the typical pattern shown by split-brains (i.e., search rate halved when scanning a bilateral display). In the case of Patient B, the search rate for bilateral displays was actually slower than the search rate for unilateral displays. In the case of Patient C, the search rate for bilateral displays was slower than for unilateral displays, but the difference between search rates was minimal. Furthermore, in none of these cases did the pattern of errors suggest an effective modulatory role of the spatial layout in the present task involving either the patients or the control group. A comment concerning Patient C's visual search performance is in order in the present context. As is clear from Figure 3, Patient C showed search rates that were rather shallow compared to the control group and the other patients. It is not entirely clear why this occurred. One indication might come from the particularly pronounced increase in errors for Patient C as set size increased, which might be suggestive of a general predisposition of Patient C to trade speed for accuracy on a larger proportion of trials compared to the other participants tested.

EXPERIMENT 2 (PRP TASK)

Method

Participants

The participants were the same as in Experiment 1.

Apparatus and stimuli

A schematic representation of the spatial configuration of the stimuli on a trial of Experiment 2 is shown in Figure 2 (lower panel). The visual stimuli were red or blue disks, with a diameter of 1.0°, displayed on the black background of the same monitor as that used in Experiment 1. On each trial of Experiment 2, one red disk and one blue disk were presented in succession, with the red disk 6° to the right of fixation and the blue disk 6° to the left of two small fixation symbols (plus signs in Figure 2). Each disk could appear 3.0° above or below the fixation location.

Control for eye movements

The procedure and parameters for the control of horizontal eye movements were the same as those used in Experiment 1. In the present experiment, two stimuli were presented sequentially on each trial, and the latencies of the first two eye movements following the onset of the first stimulus were computed, for control participants and for Patient A. For Patients B and C, the procedure for eye monitoring used in Experiment 1 was also used in the present experiment.

Procedure

Each participant participated in four experimental sessions, scheduled on two different days with two sessions per day. Throughout an experimental session, participants rested the index and middle fingers of the left hand on the "Z" and "A" keys of the computer keyboard, and the index and middle fingers of the right hand on the "M" and "K" keys of the computer keyboard, respectively. These particular keys were selected because the slight tilt in the layout of "Z/A" and "K/M" key pairings on the computer keyboard assisted in making their correspondence with disk above/below the horizontal midline either spatially compatible (upper disk mapped to the upper key) or spatially incompatible (upper disk mapped to the lower key).

Each trial began with the presentation of two fixation symbols displayed at the centre of the monitor. The symbols were exposed for 1000 ms, and followed by a blank field exposed for 800 ms. At the end of the 800 ms blank field, a first coloured disk was exposed for 80 ms on one side of fixation, followed, after a stimulus onset asynchrony (SOA) of either 100, 340, or 1000 ms, by a second coloured disk exposed for 80 ms on the opposite side of fixation. Participants produced two independent responses on each trial, a first response to the first disk that appeared, and a second response to the second disk, always using the hand ipsilateral to the respective disk. The fixation symbols also provided accuracy feedback for the previous trial. The left symbol indicated accuracy of the first response, and the right symbol indicated accuracy of the second response. A plus sign signalled a correct response whereas a minus sign signalled an error. Each response had to be produced as quickly as possible, while keeping errors to a minimum. The instructions emphasised both speed and accuracy.

Each session was composed of two blocks of 48 trials each, representing four randomised cycles through each possible factorial combination of the levels of SOA (100, 340, or 1000 ms), spatial position of first disk (above or below), and spatial position of the second disk (above or below). In the first block of trials of each of two consecutive sessions, participants were informed that the first disk to appear was always the red disk (right of fixation), followed by the blue disk (left of fixation). Participants pressed the "A" key with the left middle finger if the red disk was above the horizontal meridian, or the "Z" key if the red disk was below the horizontal meridian. Participants then pressed the "K" key with the right middle finger if the blue disk was above the horizontal meridian, or the "M" key if the blue disk was below the horizontal meridian. The stimulus–response mapping for both disk in this block of trials was spatially compatible, in that the fingers closer to the body (i.e., the index fingers) were mapped to disks appearing below the horizontal meridian, and fingers farther from the body were mapped to disks appearing above the horizontal meridian.

In the second block of trials within the same session, the stimulus–response mapping for the first task remained constant whereas the stimulus–response mapping for the second task was reversed, generating an incompatible mapping for the second response. In this block, participants pressed the "K" key with the right middle finger if the blue disk was below the horizontal meridian, or the "M" key if the blue disk was above the horizontal meridian. In each of the two other consecutive sessions, the order of disks presentation was reversed. Participants were informed that the first stimulus to appear was the blue disk to the right of fixation, which was followed by the red disk to the left of fixation. In the first block of trials within each of these sessions, participants produced a compatible response to each disk using the ipsilateral hands. In the other block of trials, the stimulus-response mapping for the second task was reversed. Thus, the first response always involved a compatible stimulus–response mapping, whereas the second response could either involve a compatible or an incompatible stimulus–response mapping. In this way, we manipulated the compatibility of the stimulus–response mapping in Task 2 of the PRP paradigm (e.g., McCann & Johnston, 1992).

Patients A and C and two control participants started with two sessions in which the red disk was displayed first, followed by two sessions in which the blue disk was displayed first. Patient B and the other two control participants started with two sessions in which the blue disk was displayed first, followed by two sessions in which the red disk was displayed first. Each participant contributed 384 responses to the first disk, and 384 responses to the second disk. Each block of trials was preceded by a practice block composed of 12 trials resulting from one cycle through each possible combination of the levels of SOAs, and spatial positions of first and second disk.

Results

Trials were screened for eye movements, and only trials free of eye movements (for Patients A, B, C, and the control group) or trials in which the latency of an eye movement was longer than the recorded RT in either task of the present paradigm (for Patient A and the control group only) were considered in the analyses. Eye movement filtering resulted in the loss of 16.1% of the trials from the acallosal patients, and 16.3% of the trials from participants in the control group. The analyses concentrated on correct RTs and error rates in each task. Correct RTs were screened for outliers using the procedure used in Experiment 1. When an outlier or an error was found in either task, the entire trial was excluded from further analysis. The outlier procedure rejected 2.0% of correct RTs for the acallosals, and 2.2% of correct RTs for the control participants. The screened results were analysed using ANOVAs, in which SOA and Task 2 stimulus–response mapping compatibility in the second task were treated as within-participant factors. In the separate single-case analyses of the acallosals, session (total = 4) was treated as the random factor.

Task 1

Control group. Figure 4 (lower right panel) shows the RT performance of the control group. Task 1 RTs are plotted using dashed lines. As can be seen, there was a significant effect of Task 2 mapping compatibility, $F(1, 4) = 26.3$, $MSe = 2276$, $p < .007$. However, neither the effect of SOA, $F(2, 8) = 2.81$, $MSe = 1479$, $p > .11$, nor the interaction between SOA and compatibility, $F(2, 8) = 2.2$, $MSe = 820$, $p > .16$, were significant. The mean percentage of correct responses in Task 1 was 94%. None of the factors was significant (all Fs < 1) in an analysis performed on the mean percentage of correct responses in Task 1.

Patient A (partial callosal agenesis, intact rostrum, and anterior commissure). Figure 4 (upper left panel) shows the RT performance of Patient A. Task 1 RTs are plotted using dashed lines. RTs increased slightly as SOA was reduced, $F(2, 6) = 23.8$, $MSe = 2248$, $p < .002$. There was also a significant effect of Task 2 mapping compatibility, $F(1, 3) = 37.6$, $MSe = 4663$, $p < .001$. However, there was no interaction between these two factors ($F < 1$). The mean percentage

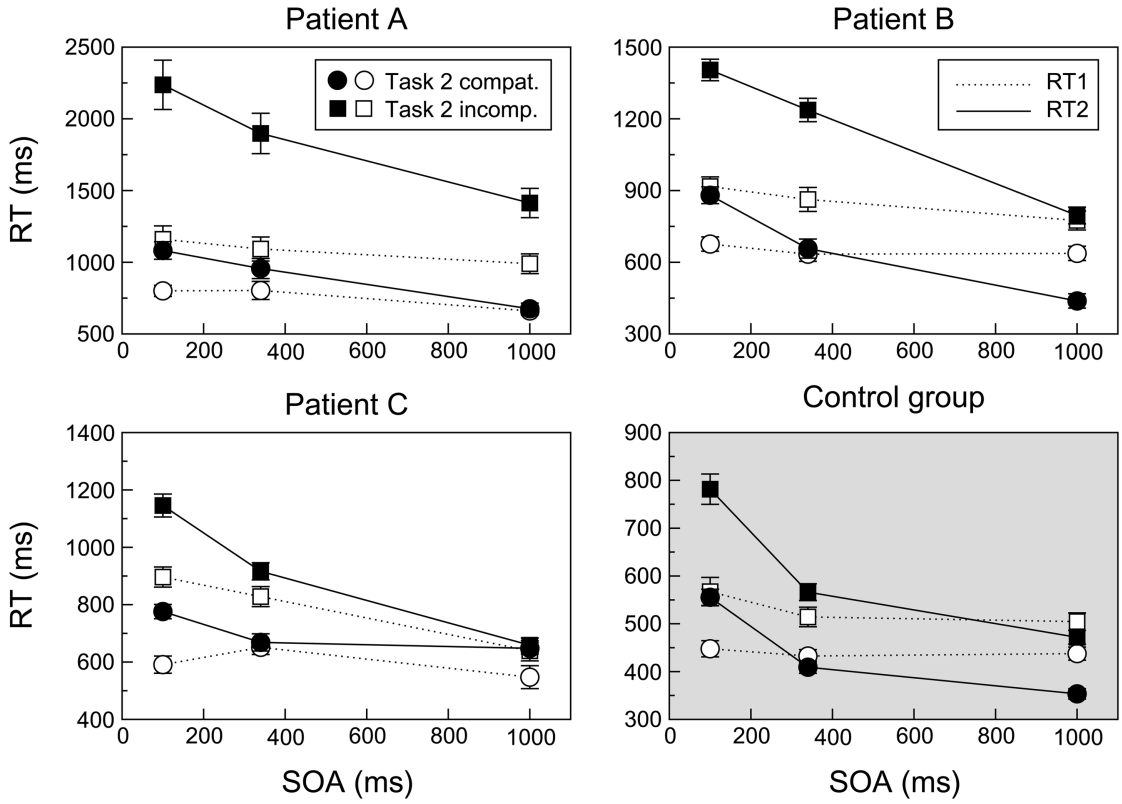

Figure 4. *PRP task RTs and standard error bars for the acallosals and the control group. Note that response–mapping compatibility (compatible vs. incompatible) was manipulated in Task 2 only (graphs are on different scales).*

of correct responses in Task 1 was 88%. None of the factors was significant (all Fs < 1) in an analysis performed on this variable.

Patient B (complete callosal agenesis, intact anterior commissure). Figure 4 (upper right panel) shows the RT performance of Patient B. Task 1 RTs are plotted using dashed lines. RTs tended to increase as SOA was reduced, $F(2, 6) = 4.6$, $MSe = 3589$, $p < .07$. There was also a marginally significant effect of Task 2 mapping compatibility, $F(1, 3) = 8.0$, $MSe = 29641$, $p < .07$. The interaction between these factors was not significant, $F(2, 6) = 1.9$, $p > .22$. The mean percentage of correct responses in Task 1 was 89%. None of the factors was significant (all Fs < 1) in an analysis performed on this variable.

Patient C (complete callosal agenesis and agenesis of anterior commissure). Figure 4 (lower left panel) shows the RT performance of Patient C. Task 1 RTs are plotted using dashed lines. RTs increased as SOA was reduced, $F(2, 6) = 7.6$, $MSe = 7733$, $p < .03$. There was also a significant effect of Task 2 mapping compatibility, $F(1, 3) = 270.6$, $MSe = 812$, $p < .001$, and a significant interaction between the two factors, $F(2, 6) = 71.8$, $MSe = 321$, $p < .001$. The mean percentage of correct responses in Task 1 was 88%. The analysis on this variable revealed a significant effect of Task 2 mapping compatibility, $F(1, 3) = 12.1$, $MSe = 0.004$, $p < .05$, with more errors when Task 2 mapping was incompatible (11%) than compatible (2%), and a significant interactions between SOA and Task 2 mapping

compatibility, $F(2, 6) = 388.0$, $MSe = 0.001$, $p < .001$. There was a substantial trend of compatibility effects on accuracy to be particularly pronounced at long and short SOAs (12% and 11%, respectively) compared to the middle SOA (4%).

Task 2

Control group. The mean RT in Task 2 is shown using solid lines in the lower right panel of Figure 4. As expected, RT increased as SOA was reduced, $F(2, 8) = 111.2$, $MSe = 1556$, $p < .001$, and RT was longer for the incompatible mapping than for the compatible mapping, $F(1, 4) = 74.6$, $MSe = 2809$, $p < .001$. Furthermore, the effect of compatibility increased as SOA was reduced, producing an overadditive interaction between compatibility and decreasing SOA, $F(2, 8) = 19.6$, $MSe = 380$, $p < .001$. The mean percentage of correct responses in Task 2 was 92%. None of the factors was significant (all Fs < 1) in an analysis performed on this variable.

Patient A (partial callosal agenesis, intact rostrum and anterior commissure). Task 2 RTs are plotted using solid lines in the upper left panel of Figure 4. The analysis revealed a significant effect of SOA, $F(2, 6) = 499.0$, $MSe = 1544$, $p < .001$, a significant effect of Task 2 mapping compatibility, $F(1, 3) = 674.1$, $MSe = 2002$, $p < .001$. There was also a significant interaction between these two factors, $F(2, 6) = 52.3$, $MSe = 1665$, $p < .001$, reflecting an increase in the effect of compatibility as SOA decreased (from 736 ms at the longest SOA to 1155 at the shortest SOA). The mean percentage of correct responses in Task 2 was 93%. An analysis performed on this variable revealed a significant effect of Task 2 mapping compatibility, $F(2, 6) = 37.3$, $MSe = 0.0003$, $p < .001$, reflecting more errors with the incompatible Task 2 mapping than with the compatible Task 2 mapping (21% vs 3%, respectively). There was also a significant interaction between SOA and Task 2 mapping compatibility, $F(2, 6) = 9.0$, $MSe = 0.0009$, $p < .02$, indicating an increase in the effect of Task 2 mapping compatibility on errors as SOA decreased (from 13% at the longest SOA to 26% at the shortest SOA).

Patient B (complete callosal agenesis, intact anterior commissure). Task 2 RTs are plotted using solid lines in the upper right panel of Figure 4. The analysis revealed a significant effect of SOA, $F(2, 6) = 44.4$, $MSe = 12717$, $p < .001$, a significant effect of Task 2 mapping compatibility, $F(1, 3) = 16.37$, $MSe = 86940$, $p < .001$, and no significant interaction between these factors, $F(2, 6) = 1.1$, $p > .4$. The mean percentage of correct responses in Task 2 was 93%. An analysis performed on this variable revealed a significant effect of Task 2 mapping compatibility, $F(2, 6) = 37.3$, $MSe = 0.0003$, $p < .001$, reflecting more errors with the incompatible Task 2 mapping than with the compatible Task 2 mapping (2% vs 10%, respectively). SOA and the interaction between SOA and Task 2 mapping compatibility factors did not produce significant effects (all Fs < 1).

Patient C (complete callosal agenesis, agenesis of anterior commissure). Task 2 RTs are plotted using solid lines in the lower left panel of Figure 4. The analysis revealed a significant effect of SOA, $F(2, 6) = 16.5$, $MSe = 11522$, $p < .004$, a significant effect of Task 2 mapping compatibility, $F(1, 3) = 57.4$, $MSe = 4591$, $p < .005$, and a significant interaction between these two factors, $F(2, 6) = 13.3$, $MSe = 4992$, $p < .007$, reflecting the evident oveadditive interaction between Task 2 mapping compatibility and decreasing SOA. The mean percentage of correct responses in Task 2 was 92%. An analysis performed on this variable revealed a marginally significant effect of Task 2 mapping compatibility, $F(1, 3) = 8.6$, $MSe = 0.007$, $p < .07$, reflecting the trend of more errors with the incompatible Task 2 mapping (11%) than with the compatible Task 2 mapping (3%). SOA and the interaction between SOA and Task 2 mapping compatibility did not produce significant effects, $F(2, 6) = 2.0$, $p > .21$, and $F(2, 6) = 2.8$, $p > .15$, respectively.

Group analyses

In a set of separate ANOVAs, the group of acallosals was compared directly with the control group. In this set of analyses, in addition to the factors considered in the individual analyses, the factor group (acallosals vs controls) was considered as a between-subject factor, and only effects related to this factor are discussed in this section. Consider first the results for the first response. Acallosals were slower than controls in producing the first response, $F(1, 6) = 30.8$, $MSe = 33374$, $p < .01$, and the SOA effect on RT1 was larger for acallosals for controls, $F(2, 12) = 8.0$, $MSe = 1518$, $p < .01$. Furthermore, acallosals showed a greater compatibility effect (i.e., slower RT1 for incompatible responses in Task 2) compared to controls, $F(1, 6) = 14.7$, $MSe = 4317$, $p < .02$.

Consider now the results for the second response. Acallosals were slower than controls, $F(1, 6) = 14.4$, $MSe = 199286$, $p < .01$, and showed a greater PRP effect compared to controls, $F(2, 12) = 10.4$, $MSe = 5760$, $p < .01$. There was also a three-way interaction involving group, SOA, and response compatibility, $F(2, 12) = 9.5$, $MSe = 1255$, $p < .03$. Although both groups tended to show an overadditive effect of compatibility with decreasing SOA (i.e., greater compatibility effects at short vs long SOA), this interaction was larger for acallosals than for controls. The factor group did not produce significant effects on Task 1 or Task 2 accuracy (all Fs < 1).

Discussion

The most important results of the present experiment were that none of the three acallosals produced underadditive effects of Task 2 stimulus–response compatibility with decreasing SOA. One of them (Patient B) produced additive effects, whereas the other two (A, C) produced clearly overadditive effects. Results from the control group were also overadditive, but to a lesser degree on average. In contrast, Ivry et al. (1998) found that the effects of stimulus–response compatibility in Task 2 of a PRP experiment were underadditive with decreasing SOA in a split-brain, in contrast with an overadditive effect found with their control participants. The results from our acallosals were thus more similar to those of normal control participants than to those found with Ivry et al.'s split-brain. The underadditive effect found with the split-brain suggests that this patient was able to overlap the mental operations required to perform the response selection in Task 2 concurrently with those required to perform response selection in Task 1 (see McCann & Johnston, 1992; Pashler, 1994; Van Selst & Jolicoeur, 1997). Like normal participants, the acallosals were unable to perform response selection operation in Task 2 in parallel with the concurrent response selection required to perform Task 1. As such, the pattern of behaviour exhibited by all three acallosals was functionally more similar to that of normal controls than that of Ivry et al.'s split-brain.

We note that all three acallosals were more strongly affected by the stimulus–response compatibility manipulation than were the control participants. Callosal agenesis is known to result in a reduction of cortical cells that normally receive commissural input (Shoumura, Ando, & Kato, 1975). This in turn could alter the attentional control capacities of each hemisphere, thus leading to deficits in disengagement under the incompatible condition. Nevertheless, the fact that all three acallosals showed a pattern of behaviour similar to that of the controls points to a coupling between the response selection operations required to respond with each of the two hands. Again, this result is consistent with the hypothesis that there is a single central attentional control system—carrying out response selection operations under the present testing conditions—in acallosals, unlike what has been hypothesized to be the case for the split-brain tested by Ivry et al. (1998).

GENERAL DISCUSSION

Recent developments in neuroscience suggest that attention is not a unitary function of the brain

(e.g., Parasumaran, 1998). Rather, several neurophysiological studies (some reviewed in Motter, 1998) argue for a fractionation of attention into multiple components, each engaging a finite set of cerebral circuits distributed across several brain loci. The present work examined two distinct components of attention in three patients with different forms of agenesis of the corpus callosum, with and without presence of the anterior commissure. A visuospatial component of attention was examined in Experiment 1 using a variant of a visual search paradigm apt to provide a direct estimate of the degree of functional independence of the cerebral hemispheres in scanning the visual field for the presence of a specified target. A central component of attention was examined in Experiment 2 using a dual-task (psychological refractory period, PRP) paradigm, which has been hypothesised to reflect central attention limitations (e.g., Jolicoeur, 1999; Pashler, 1994). Importantly for the present purposes, both these paradigms reveal disconnection symptoms when administered to commissurotomised, split-brain patients.

Each of the present experiments generated results that were clear-cut in showing no sign of disconnection symptoms in callosal agenesis. In the visual search paradigm, the reaction times (RTs) of acallosals and control participants were modulated by the number of items displayed in the visual field, independent of whether the items were displayed unilaterally or bilaterally. This pattern is clearly different from what has been observed in split-brains, for whom search slopes decrease when items are displayed bilaterally (Luck et al., 1989, 1994). The results of Experiment 1 suggest a different picture of the cerebral organisation of the visuospatial attention system in callosal agenesis than Hines et al. (2002) have advocated based on results obtained with a spatial cuing paradigm (see Introduction). Although the results of Hines et al. are congruent with the principle that a callosum-mediated visual integration process is demanded whenever the focus of attention crosses the subjective vertical meridian, the results of Experiment 1 support the notion that the visuospatial attention system is interhemispherically integrated in the present acallosals, conceivably by virtue of the subcortical structures that are preserved in these patients. The fact that one of our acallosals (C) also lacked the anterior commissure suggests that this structure is not necessary for this type of integration. The apparent incongruence between the present study and the study of Hines and colleagues is all the more interesting in light of previous suggestions for a functional analogy of the attention mechanisms mediating visual search and those mediating spatial shifts of attention induced by spatial cues (e.g., Luck & Girelli, 1998). An analogy also exists at a neuroanatomical level between the brain areas involved in these tasks. It has indeed been shown that posterior parietal areas play a major role in both visual search and cuing tasks (Ashbridge, Walsh, & Cowey, 1997), with the posterior part of the corpus callosum representing the specialised support for an interhemispheric connection between these areas (e.g., Reuter-Lorenz & Fendrich, 1990).

Concerning the difference between the present visual search findings and the results reported in the study by Hines and colleagues and mentioned in the Introduction, some have argued (e.g., Lepore, Lassonde, Poirier, Schiavetto, & Villette, 1994) that the impairment described by Hines and colleagues stems from a deficit in integrating visual information in the proximity of the vertical meridian, namely, a problem due to the small eccentricity of the stimuli acallosals had to respond to. It is, however, important to note that the difference between the Hines study (finding increased costs of invalid cross-field cueing in acallosals) and the present study cannot be explained in terms of stimulus eccentricity. The stimuli in the study by Hines et al. were centred 3.5° left and right of fixation, which is a similar distance to the centre of the search fields in the present study (i.e., 4°). This makes eccentricity unlikely to be a discriminant factor between these studies. The difference between the Hines et al. study and the present work may rather be that the invalid cueing condition in the spatial cueing experiments required stimulus-driven reorienting of attention between hemifields,

which was not (or less) required in the current search task. Stimulus-driven reorienting (or "circuit breaking") processes, involving the temporoparietal junction area (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Friedrich, Egly, Rafal, & Beck, 1998), seem to rely on an intact splenium (Pollmann, Maertens, & Von-Cramon, 2004). The Hines et al. data suggest that acallosal patients may lack an efficient interhemispheric pathway for these signals. The top-down controlled serial search processes required in the present visual search task, involving rather superior parietal structures (e.g., Muller, Donner, Bartelt, Brandt, Villringer, & Kleinschmidt, 2003), may instead be connected via subcortical commissures.[1]

In the PRP paradigm implementing the manipulation of stimulus–response (SR) mapping compatibility in the second task (Experiment 2), both controls and the acallosals showed a substantial cross-talk between tasks, in the form of an effect of the Task 2 manipulation on response times in Task 1. This in turn may have contributed to the overadditive interaction between the mapping manipulation and the manipulation of the degree of temporal overlap (i.e., stimulus onset asynchrony, SOA) between the concurrent tasks. Ivry et al. (1998) have shown that one split-brain observer exhibited a rather different response pattern: In the second task of the PRP paradigm, they revealed an effect of the mapping manipulation that was underadditive with decreasing SOA, suggesting a locus of dual-task interaction that was beyond response selection, possibly at a stage of motor initiation required to maintain well-coordinated motor behaviour. Although it is quite possible that the lack of a known replication of Ivry's finding in the literature may weaken the conclusions drawn from his study, which was based on results obtained from a single split-brain patient, the crucial evidence obtained in the present experimental context is suggestive of mechanisms mediating the interaction between response compatibility effects and SOA effects in acallosals that are interhemispherically connected.

The combined analyses of the results of Experiments 1 and 2 revealed further important details that may be critical in the interpretation of the present findings, and in the understanding of the cerebral organisation of attention processes in callosal agenesis. Namely, in Experiment 1, the search rate for the acallosals was lower than that of controls, and there was a tendency of the intercept of the regression equation for the acallosals to be more elevated than the intercept for controls. In addition, in Experiment 2, the size of the mapping manipulation effect and the size of the PRP effect in the second task were both more pronounced in the acallosals than in the matched control group, as were also the overadditive effects of compatibility and SOA. Several studies have indicated an increase in response times in acallosals during processing of visual stimuli presented either intra- or interhemispherically (e.g., Lassonde, 1994). These results have been interpreted within the context of a facilitatory influence exerted by the corpus callosum on perceptual processing. The present findings suggest that this interpretation may extend to attentional capacities. At the anatomical level, callosal agenesis has been found to result in the loss of cortical cells that are normally receiving a callosal input (Shoumura et al., 1975). This loss of callosally recipient cells could in turn lead to reduced cortical activation, thus inducing central attentional limitations. In this context, the important compatibility effects observed in all three acallosal patients may reflect greater deficits in attention disengagement.

The analogy between the overall patterns of results in acallosals and controls is entirely consistent with an organisation of visuospatial attention systems and of central-attention systems in acallosals that are functionally equivalent to those of normal controls, but that function less efficiently in acallosals. The differences between the performance of acallosals and that of split-brains

[1] We are indebted to one anonymous reviewer for suggesting this insightful explanation of the difference between the results in the present work and the work by Hines et al. (2002).

provide interesting contrasts and suggest that the absence of the corpus callosum early in development does not prevent the elaboration of a normal organisation of attention subsystems. In contrast, the loss of the corpus callosum later in life, when brain plasticity is reduced, is more likely to produce disruptions in attentional organisation. Although more work will be required to determine whether the patterns of results we found in these acallosals generalise to all cases of callosal agenesis, our results suggest that the structure of the functional architecture of spatial attention and central attention can be normal (although perhaps less efficient) even in the complete absence of the corpus callosum and of the anterior commissure, provided the absence of these structures occurs early in development.

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REFERENCES

Aglioti, S., Berlucchi, G., Pallini, R., Rossi, G. F., & Tassinari, G. (1993). Hemispheric control of unilateral and bilateral responses to lateralized light stimuli after callosotomy and in callosal agenesis. *Experimental Brain Research*, *95*, 151–165.

Ashbridge, E., Walsh, V., & Cowey, A. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, *35*, 1121–1131.

Conti, F., & Manzoni, T. (1994). The neurotransmitters and postsynaptic action of callosally projecting neurons. *Behavioural Brain Research*, *64*, 37–53.

Corballis, M. C. (1995). Visual integration in the split brain. *Neuropsychologia*, *33*, 937–959.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.

Friedrich, F. J., Egly, R., Rafal, R. D., & Beck, D. (1998). Spatial attention deficits in humans: A comparison of superior parietal and temporo-parietal junction lesions. *Neuropsychology*, *12*, 193–207.

Gazzaniga, M. (2000). Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain*, *123*, 1293–1326.

Hines, R. J., Paul, L. K., & Brown, W. S. (2002). Spatial attention in agenesis of the corpus callosum: Shifting attention between visual fields. *Neuropsychologia*, *40*, 1804–1814.

Ivry, R. B., Franz, E. A., Kingstone, A., & Johnston, J. C. (1998). The psychological refractory period effect following callosotomy: Uncoupling of lateralized response codes. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 463–480.

Jeeves, M. A. (1979). Some limits to interhemispheric integration in cases of callosal agenesis and partial commissurotomy. In I. S. Russel, M. W. van Hof, & G. Berlucchi (Eds.), *Structure and function of cerebral commissures* (pp. 449–474). London: MacMillan Press.

Jeeves, M. A. (1994). Callosal agenesis—a natural split brain: Overview. In M. Lassonde & M. A. Jeeves (Eds.), *Callosal agenesis—a natural split brain?* (pp. 285–299). New York: Plenum Press.

Jeeves, M. A., Silver, P. H., & Jacobson, I. (1988). Bimanual coordination in callosal agenesis and partial commissurotomy. *Neuropsychologia*, *26*, 833–850.

Jolicoeur, P. (1999). Dual-task interference and visual encoding. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 596–616.

Lassonde, M. (1994). The facilitatory influence of the corpus callosum. In M. Lassonde & M. A. Jeeves (Eds.), *Callosal agenesis—a natural split brain?* (pp. 275–284). New York: Plenum Press.

Lassonde, M., & Jeeves, M. A. (1994). *Callosal agenesis—a natural split brain?* New York: Plenum Press.

Lassonde, M., Sauerwein, H. C., & Lepore, F. (1995). Extent and limits of callosal plasticity: Presence of disconnection symptoms in callosal agenesis. *Neuropsychologia*, *33*, 989–1007.

Lassonde, M., Sauerwein, H. C., Geoffroy, G., & Decarie, M. (1986). Effects of early and late transection of the corpus callosum in children. *Brain*, *109*, 953–967.

Lepore, F., Lassonde, M., Poirier, P., Schiavetto, A., & Villette, N. (1994). Midline sensory integration in callosal agenesis. In M. Lassonde & M. A. Jeeves (Eds). *Callosal agenesis—a natural split brain?* (pp. 155–160). New York: Plenum Press.

Luck, S. J., & Girelli, M. (1998). Electrophysiological approaches to the study of selective attention in the human brain. In R. Parasuraman (Ed). *The attentive brain* (pp. 71–94). Cambridge, MA: MIT Press.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature*, *342*, 543–545.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1994). Independent attentional scanning in the separated hemispheres of split-brain patients. *Journal of Cognitive Neuroscience*, *6*, 84–91.

McCann, R. S., & Johnston, J. C. (1992). Locus of the single-channel bottleneck in dual-task interference. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 471–484.

Miller, J. (2004). Exaggerated redundancy gain in the split brain: A hemispheric coactivation account. *Cognitive Psychology*, *49*, 118–154.

Motter, B. C. (1998). Neurophysiology of visual attention. In R. Parasuraman (Ed.), *The attentive brain* (pp. 51–70). Cambridge, MA: MIT Press.

Muller, N. G., Donner, T. H., Bartelt, O. A., Brandt, S. A., Villringer, A., & Kleinschmidt, A. (2003). The functional neuroanatomy of visual conjunction search: A parametric fMRI study. *Neuroimage*, *20*, 1578–1590.

Parasuraman, R. (1998). *The attentive brain*. Cambridge, MA: MIT Press.

Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin*, *116*, 220–244.

Pashler, H., Luck, S. J., Hillyard, S. A., Mangun, G. R., O'Brien, S., & Gazzaniga, M. S. (1994). Sequential operation of disconnected cerebral hemispheres in split-brain patients. *Neuroreport*, *5*, 2381–2384.

Poffenberger, A. T. (1912). Reaction time to retinal stimulation with special reference to the time lost in conduction through nervous centers. *Archives of Psychology*, *23*, 1–73.

Pollmann, S., Maertens, M., & Von-Cramon, D. Y. (2004). Splenial lesions lead to supramodal target detection deficits. *Neuropsychology*, *18*, 710–718.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.

Reuter-Lorenz, P. A., & Fendrich, R. (1990). Orienting attention across the vertical meridian: Evidence from callosotomy patients. *Journal of Cognitive Neuroscience*, *2*, 232–238.

Sauerwein, H. C., Lassonde, M., Cardu, B., & Geoffroy, G. (1981). Interhemispheric integration of sensory and motor functions in agenesis of the corpus callosum. *Neuropsychologia*, *19*, 445–454.

Shoumura, K., Ando, T., & Kato, K. (1975). Structural organization of callosal Obg in human corpus callosum agenesis. *Brain Research*, *93*, 241–252.

Sperry, R. W. (1968). Plasticity of neural maturation. *Developmental Biology*, *2* (suppl.), 306–327.

Treisman, A. M., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology*, *12*, 97–136.

VanRullen, R., Reddy, L., & Koch, C. (2004). Visual search and dual-tasks reveal two distinct attentional resources. *Journal of Cognitive Neuroscience*, *16*, 4–14.

Van Selst, M., & Jolicoeur, P. (1994). A solution to the effect of sample size on outlier elimination. *Quarterly Journal of Experimental Psychology*, *47A*, 631–650.

Van Selst, M., & Jolicoeur, P. (1997). Decision and response in dual-task interference. *Cognitive Psychology*, *33*, 266–307.