Auditory and Visual Spatial Localization Deficits Following Bilateral Parietal Lobe Lesions in a Patient with Balint’s Syndrome

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Abstract

Lesion and electrophysiological studies indicate that the parietal lobes play a role in visual spatial attention and in computing the spatial coordinates of visual input. Fewer studies have investigated the role of the parietal lobe in auditory spatial processing, and an extensive comparison of visual and auditory spatial processing in humans with parietal lobe lesions has yet to be conducted. We have studied such localization abilities in a Balint’s syndrome patient (RM) who has bilateral parietal lobe lesions. The results indicated that this patient had a significant deficit in both visual and auditory localization relative to age-matched controls. Unlike the controls, however, RM’s auditory localization ability either matched or exceeded his visual localization ability depending on the task. Accordingly, RM exhibited “auditory capture,” but not “visual capture” under conditions where control subjects showed the opposite pattern. These results are consistent with hypotheses that the parietal lobes are involved in creating multiple spatial representations and in shifting from one spatial reference point to another, but suggest that these parietal structures are not necessary for the integration of multiple sensory stimuli resulting in capture effects.

INTRODUCTION

Patients with parietal damage commonly suffer deficits in visual spatial processing including impairments in spatial attention, visual localization, and feature binding (e.g., see Behrmann, 1999; Bernstein & Robertson, 1998; Vallar, 1998; Karnath, 1997; Friedman-Hill, Robertson, & Treisman, 1995; Coslett & Saffran, 1991; Bisiach, Perani, Vallar, & Berti, 1986; Balint, 1909). Studies in humans have focused on the role of the parietal lobe in creating visual spatial representations (e.g., Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997; Behrmann & Moscovitch, 1994; Goodale, Milner, Jakobson, & Carey, 1991) or in directing and shifting spatial attention to visual stimuli (e.g., Corbetta, Shulman, Miezin, & Petersen, 1995; Posner, Walker, Friedrich, & Rafal, 1984; Posner, Walker, Friedrich, & Rafal, 1987). Electrophysiological studies in the behaving monkey have implicated the parietal lobe in attention (e.g., Bushnell, Goldberg, & Robinson, 1981; Lynch, Mountcastle, Talbot, & Yin, 1977), in the preparation of executing motor commands (see Andersen, Snyder, Bradley, & Xing, 1997), and in the coordination of different spatial reference frames (e.g., see Andersen, Snyder, Batista, Buneo, & Cohen, 1998; Colby & Duhamel, 1996). The extent to which the parietal lobes contribute to auditory spatial processing is less clear, although there is evidence of auditory spatial information processing in the parietal lobes of both humans and monkeys (Mazzoni, Bracewell, Barash, & Andersen, 1996; Brotchie, Andersen, Snyder, & Goodman, 1995; Pinek & Brouchen, 1992; De Renzi, Gentilini, & Barbieri, 1989). The primary goal of the present study was to investigate the role of the human parietal lobes in spatial representation by characterizing both the auditory and visual spatial localization abilities in a patient (RM), with bilateral parietal lobe lesions including Brodmann’s areas 7 and 39.

Although visual processing deficits can be profound in patients with unilateral parietal lesions, deficits in auditory spatial processing are less common. This may be due to the bilateral projections of the ascending auditory pathways as compared to the more lateralized visual pathways, and the fact that both ears are usually stimulated by free-field stimuli. The bilateral auditory projections may allow for greater compensation by parietal areas in the intact hemisphere. Previous studies in patients with unilateral parietal damage have shown that some patients do not report hearing a sound presented to the contralesional ear when both ears are stimulated.
(Soroker, Calamaro, Glicksohn, & Myslobodsky, 1997; De Renzi et al., 1989; Heilman & Valenstein, 1972), or have sound localization deficits (Pinek, Duhamel, Cave, & Brouchon, 1989; Ruff, Hersch, & Pribram, 1981). A study of 144 patients by De Renzi, Gentilini, and Patacini (1984) indicated that approximately 50% of unilateral parietal lesioned patients showed signs of auditory deficits, and in a later study of 31 unilateral patients, approximately one quarter showed signs of auditory deficits (De Renzi et al., 1989). In both studies, the auditory deficits were not correlated with visual neglect. In a separate study, all nine patients with right inferior parietal lesions that showed auditory deficits also had both visual and somatesthetic neglect (Heilman & Valenstein, 1972). Thus, the data are mixed as to the degree to which auditory and visual spatial processing rely on parietal structures. A patient with bilateral parietal damage offers a unique opportunity to study the role of the parietal lobes in visual and auditory spatial processing without the possibility of compensation from the intact parietal lobe. Bilateral lesions eliminate concerns of the different lateralization of ascending auditory and visual anatomical projections, and allow the performance on visual and auditory versions of the same tasks to be directly compared.

One goal of this study was to better characterize the role of the parietal lobe in spatial processing by examining this patient’s relative and egocentric localization abilities in both the auditory and visual modalities. If the lesioned regions process spatial information across sensory modalities, similar deficits should be observed in both visual and auditory spatial localization, whereas different performance would imply differential involvement of these parietal regions in auditory and visual localization. A second goal of this study was to investigate the role of the parietal lobes in aligning sensory input from different modalities into a common coordinate system, as suggested by Andersen et al. (1998). To address this, we examined the effects of unattended stimuli in one modality on the localization of stimuli in the other modality.\(^1\)

RESULTS

A 61-year-old male subject with bilateral parietal damage (RM), five age- and gender-matched controls (AM1–AM5), and three younger controls (Y1–Y3) served as subjects. Experiments were conducted to test relative localization ability (Experiments 1–3), egocentric spatial representation (Experiment 4), and interactions between auditory and visual stimuli (Experiment 5).

Relative Localization Ability

Two different relative localization paradigms (Experiments 1 and 2) required subjects to compare the location of a second stimulus (S2) relative to the location of a preceding stimulus (S1) that was always presented 12° below fixation and aligned with the subject’s midline. The general result from these experiments was that compared to control subjects, RM showed a large deficit in visual localization ability, particularly within the right hemifield, whereas there was a much smaller and symmetrical deficit in his auditory localization ability.

Experiment 1: Implicit Relative Localization

This experiment required the detection of a change in spatial location, but not explicit knowledge of the location. Each trial consisted of three to eight stimulus presentations from 0° (directly ahead), and a final presentation that could change to a different location (Figure 1A). Subjects were required to depress a button to start each trial, and release the button when the stimulus changed location.

Figure 1B plots the results from the visual task. Control subjects showed few errors (thin line of Figure 1B). In contrast, RM rarely detected a change in location when the S2 stimulus was presented in the right visual field (heavy line). The arrows point to locations where RM’s response rate fell outside of the 95% confidence interval based on the age-matched controls (see Subjects and Methods). Control subjects showed no difference in their hit rate as a function of the hemifield (paired t test, \(p > .05\) for all subjects), but RM showed greater localization ability in the left hemifield than in the right (\(p < .05\)).

One possible explanation for these results is that RM could not see these small visual stimuli, potentially due to his inability to shift his attention away from the visual fixation point. To assess this, RM performed a control task in which he made a button response whenever he perceived any visual stimulus other than the fixation point. The same visual stimuli were randomly presented at each of the 15 tested locations (five trials each; 75 total trials). He made only one error (7/75 correct; no response for one stimulus at −8°) indicating that he could perceive all of these visual stimuli. In separate sessions, the same task as shown in Figure 1A was run in which the fixation point was replaced with a 420-Hz tone at the same location. In this condition, his performance on the visual trials was not altered (dashed line of Figure 1B).

A second potential explanation for these results is that RM had a stricter criterion for responding to stimuli in the right visual field compared to those presented in the left visual field or was more hesitant to respond than controls. This is unlikely given that RM had a higher false-positive rate (4.8%) than either the age-matched (0.88 ± 0.62%) or younger (1.15 ± 0.28%) control subjects, indicating that he was more likely to make a response during this task than were the control subjects. The results from Experiments 2 and 3 (see below) also indicate that RM did not have a stricter criterion for responding to right hemifield stimuli. We therefore
conclude that RM was capable of detecting these visual stimuli, but was impaired in his ability to localize them.

Figure 1C shows the data from RM (heavy and dashed lines) and the control subjects (thin line) for the same task using auditory stimuli. As in the visual task, there was no difference between the age-matched and younger control groups, nor in the hit rate between stimuli presented in the left and right hemifields (all \( p \) values > .05). RM showed a statistically significant difference in the hit rate between his left and right hemifields for stimuli of the same eccentricity (paired \( t \) test; \( p < .05 \)), and was significantly different from controls at all rightward locations, and 2/5 leftward locations (arrows). Control experiments in which the auditory fixation stimulus replaced the visual fixation stimulus showed little difference in performance (dashed line).

To clarify whether RM’s impairment only consisted of a reduced response rate, we conducted a test of dispersion (see Subjects and Methods) to compare the variability in RM’s response function to that of the controls. Analysis of the pattern of RM’s responses revealed significant differences from both the age-matched \( [F(90, 651) = 1.47, \ p < .05] \) and the younger \( [F(90, 707) = 1.42, \ p < .05] \) controls, indicating that RM not only had a reduced hit rate, but also that his pattern of responding across locations was broader than that of the controls (Figure 1G). Comparisons between the visual and auditory tasks showed that the hit rates for visual stimuli were higher than those for auditory stimuli across stimulus locations for all control subjects (paired one-tailed \( t \) test; \( p < .05 \)). In contrast, for RM, there was no difference between the hit rates for auditory and visual trials in the left hemifield, but his hit rates were significantly higher for auditory stimuli in the right hemifield than for visual stimuli (\( p < .05 \)).

**Experiment 2: Explicit Relative Localization**

The above result suggests that the parietal lobe regions damaged in this patient normally influence both visual and auditory localization. To extend these findings, the same subjects were tested on a task that required them to explicitly indicate the direction of a location change by verbally stating whether the second stimulus (S2) of a two-stimulus sequence was presented to the left, right, or at the same location as the first stimulus (S1; Figure 2A). The data from RM performing the visual task are shown in Figure 2B, where the percentage of Left (triangles), Same (diamonds) and Right (squares) responses are plotted for each S2 location. RM made many more Right responses (50.8%) than Same (30.8%) or Left (18.45%). These data were pooled and assigned numerical values to calculate a normalized response value at each S2 location (−1: all Left; +1: all Right; see Subjects and Methods). RM consistently responded that he perceived the second stimulus to be located to the right of the first, even on trials where the S2 stimulus was in the
left hemifield (Figure 2C). Control subjects showed very few errors and had much steeper normalized response functions (Figure 2D). Control subjects made each of the three responses with equal probability (mean: 33.1%, 33.7%, and 33.2% for Left, Same, and Right responses, respectively). Analysis of the difference between the normalized functions and the expected result for perfect performance (thin line of Figure 2C,D) indicated that there was no difference in the errors made between hemispheres in any control subject (all p values > .05), but RM did have a significant difference between hemispheres from ideal performance (p < .05) with greater errors for stimuli to the left of midline than the right.

Data from RM on the auditory task were comparable to both the age-matched and younger controls (Figure 3). The distribution of responses (Figure 3A) followed the expected shape for each of the three response categories, and the normalized response function also showed the expected shape with the y-intercept near the S2 location of 0° (dashed line of Figure 3B). The data from the age-matched (Figure 3C) and younger controls (Figure 3D) were significantly different from each other and are shown separately. RM again had a greater tendency to respond Right (36.6%, 18.5%, and 43.9% for Left, Same, and Right responses, respectively), although not to the same degree as on the visual trials. The control subjects’ responses were more evenly distributed, although there was greater between-subject variability among age-matched controls (means: 37.3%, 31.4%, and 31.4% for Left, Same, and Right, respectively) than among younger controls (33.2%, 34.0%, and 32.8% for Left, Same, and Right responses, respectively).

This tendency of RM to make a Right response may be due to either a response bias or that he incorrectly perceived most of the stimuli to appear to the right of the S1 stimulus. A response bias for right stimuli would be inconsistent with the concern raised in Experiment 1 that RM might have had a stricter criterion for responding to stimuli in the right hemifield. Thus, it seems more likely that RM’s apparent bias to respond Right was not the result of some strategy or preferred response, but rather to a shifted perception of these stimuli, consistent with the results of Experiments 3 and 4 (see below).

In summary, both the implicit and explicit relative localization tasks showed that RM had a greater deficit localizing visual stimuli than auditory stimuli compared to control subjects, and his auditory localization ability was superior to his visual localization ability. These data suggest that the parietal areas lesioned in this patient influence spatial processing of auditory stimuli, but to a lesser extent than for visual stimuli.

**Localization Based on External or Egocentric Reference Frames**

The preceding experiments required subjects to make a relative localization judgment based on the location...
of the S1 stimulus, which was presented directly below the fixation point and at the same location (0°) throughout the session. It is possible that RM compared the S2 stimulus location to either the externally provided S1 reference (as instructed), or to some internal egocentric reference created by the repeated presentations of the S1 stimulus at 0°, or to one or the other of these cues for the different stimulus modalities. To distinguish between these possibilities, subjects performed a task with an S1 stimulus that varied in location between trials (Experiment 3), and another task, which measured the perceived location of the body midline (Experiment 4). The general result was that RM’s estimation of his body midline was altered for both stimulus modalities.

**Experiment 3: Relative Localization with Interleaved Reference Stimuli**

This task used the same stimuli and instructions as Experiment 2, but included S1 locations that were located at −12°, 0°, or +12° on randomly interleaved trials. The results from a control subject showed that different starting locations did not affect performance (Figure 4A), whereas RM’s performance was greatly reduced in both the visual (Figure 4B,C) and auditory (Figure 4D) tasks. For each S1 location for both stimulus modalities, the responses by RM better reflected the location of the S2 stimulus relative to his midline than the location of the S1 stimulus. The presence of a visual fixation point did not influence his performance, as the data on sessions with either a visual (Figure 4B) or auditory (420 Hz tone) fixation stimulus (Figure 4C) were not significantly different (paired t test; p > .05). These control data, as in Experiment 1, showed that the use of a fixation LED had little effect on RM’s perception of these stimulus locations. Comparison between stimulus modalities showed that there was no difference between RM’s performance on the visual and auditory tasks (paired t test; p > .05), and there was also no difference between hemifields for each stimulus modality.

One concern with such a result was that the patient was unable to understand the instructions to judge the S2 stimulus relative to the S1 stimulus and not to his own body. To verify that this was not the case RM performed two different sessions in which the visual S1 stimulus was only presented at either −12° or +12° for all trials (Figure 5). These data showed that RM did understand the instructions to respond to the location of the S2 stimulus relative to the S1 stimulus location, and not to his body midline or the fixation stimulus. Immediately following these two sessions, RM was tested again on the visual task using interleaved S1 locations, and in this session, the data were consistent with that shown in Figure 4B. This control session, and his reports that he did understand the
task (although he found it very difficult), indicated that a simple misunderstanding of the instructions
cannot account for the data shown in Figure 4.

The results from Experiment 3 indicated that RM
was unable to shift the point of reference to judge
the spatial location of these stimuli from trial to trial.
This suggests that RM used a default egocentric
reference frame when there was no spatially constant
reference point, resulting in equivalent performance in
auditory and visual tasks. When a constant reference
point was available (Experiment 2), he may have
relied on this default egocentric reference frame to
a greater extent in the visual task than in the auditory
task resulting in poorer visual localization. This is
consistent with a role for the parietal lobes in creating
multiple representations of space that may be body-
centered (Karnath, Fetter, & Niemeier, 1998), object-
centered (Behrmann & Moscovitch, 1994; Behrmann
1999) or axis-based (Driver, Baylis, Goodrich, & Rafal,
1994).

**Experiment 4: Estimates of Egocentric Midline**

This experiment was designed to measure the ability
of subjects to estimate their egocentric midline in
absolute space. Subjects were instructed to respond
when they perceived stimuli aligned with their body
midline and to withhold responses to all other stimuli
(Figure 6A). The data from the age-matched and the
younger controls did not differ on the visual task and
were averaged (Figure 6B: thin line). For RM (heavy

![Figure 4](image-url)

**Figure 4.** Auditory and visual localization was similar when different S1 locations were presented on interleaved trials. (A) Three separate normalized response curves (as in Figure 2C,D) from a representative younger control subject for S1 stimulus locations of $-12^\circ$ (circles), $0^\circ$ (triangles), and $+12^\circ$ (squares). Thin lines depict the pattern expected for perfect performance, and the dashed line indicates a normalized score of zero. (B) Visual task data from RM. (C) Visual task data from RM using an auditory fixation stimulus. (D) Auditory task data from RM.

![Figure 5](image-url)

**Figure 5.** A control experiment verified that RM did understand the task. RM's performance on two separate sessions of the visual explicit relative localization task in which the S1 stimuli were blocked at either $-12^\circ$ (circles) or $+12^\circ$ (squares). Thin lines depict perfect performance. The dotted line depicts the pattern expected if judgments were based on the body midline.
line), it was necessary to extend the range of tested locations to the left in order to fully define his midline response function. These data were fitted by a gaussian to determine the mean midline estimate, which was shifted $-10.6^\circ$ in RM, compared to $+0.94^\circ$ for the controls.

In the auditory task, there was a difference between the younger controls, age-matched controls, and RM (Figure 6C). The age-matched controls were less precise than the younger controls, indicated by the broader gaussian function. The mean location of estimates of the control subjects were similar (age-matched: $+1.2^\circ$; younger: $+3.5^\circ$), but clearly different from RM ($-16.5^\circ$). Figure 7 shows the results from the control experiments that indicate no difference in RM’s responses on the visual (7A) and on the auditory (7B) task when there was either an auditory (thin line) or visual (thick line) fixation stimulus.

In summary, these results showed that RM had a severe deficit in judging the location of a sensory stimulus, either visual or auditory, with respect to his body midline. The data revealed a leftward shift of RM’s perceived midline, on the order of $10^\circ$ for visual stimuli, and approximately $16^\circ$ for auditory stimuli, consistent with a shifted, or rotated, representation of extrapersonal space (see Karnath, 1997). This shift is consistent with RM’s high number of Right responses in the explicit relative localization task (Figure 3), as the location directly in front of him and up to $10-16^\circ$ to the left were perceived to be toward the right in this patient.

**Visual and Auditory Stimulus Interactions**

RM’s similar midline shifts and localization deficits in auditory and visual tasks are consistent with the hypothesis that the parietal lobes function to align the inputs of different stimulus modalities (and/or features) in order to create a unified spatial representation of real-world objects that contain multiple stimulus attributes (e.g., see Andersen et al., 1997, 1998; Robertson et al., 1997). Such a parietal-dependent spatial representation could ultimately resolve conflicts between the perceived location of objects within different sensory modalities, e.g., between the normally less precise auditory spatial representations and the more precise visual spatial representations. This could account for such phenomena as visual capture, the ventriloquist effect, and the McGurk effect (see Recanzone, 1998; Driver, 1996; Welch & Warren, 1980; McGurk & MacDonald, 1976; Pick, Warren, & Hay, 1969). One hypothesis to account for inter-stimulus interactions is the “Modality Appropriateness Hypothesis” in which the sensory modality that best represents the stimulus feature to be judged (in our case, spatial location) will dominate the percept when two sensory modalities provide discor-

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**Figure 6.** RM had a shifted perception of his midline for visual and auditory stimuli. (A) Task Design. Subjects were required to make a response whenever they perceived a stimulus to be aligned with their body midline. (B) Visual task results for the data pooled across control subjects (thin line) and for RM (heavy line). Symbols denote means (controls) and measured values (RM). (C) Audiory task results from RM (heavy line, solid circles) age-matched (thin line, shaded squares) and the younger controls (dashed line, open squares).
Figure 7. The fixation stimulus did not affect midline localization in RM. Data from RM on the Visual (A) and Auditory (B) Midline task with either a visual (heavy line) or auditory (thin line) fixation. Response functions show the percent responses for each stimulus location and are not normalized.

dant information (see Welch & Warren, 1980). The auditory spatial acuity in RM is equivalent to the visual spatial acuity for objects to the left of midline, and appears better for objects to the right of midline (see above), predicting auditory capture for stimuli to the right. In order to test this prediction, we had the same subjects localize stimuli of one modality in the presence of unattended, or distracter stimuli of another modality.

Experiment 5: Relative Localization in the Presence of Unattended Distracters

This task required subjects to indicate whether the stimulus of the attended modality changed location (but not the direction of change), as in Experiment 1. Except for baseline trials, auditory and visual stimuli were presented simultaneously in space, but not necessarily in time. The subject was instructed before each session to detect a change in location of either the auditory or the visual stimuli and to ignore stimuli of the other modality. Initially, stimuli of both modalities were presented from 0° (S1), then both the target and distracter S2 stimuli could appear at the same peripheral location (Both-Move), both could remain at 0° (catch trials), the attended stimulus could change location while the distracter remained at 0° (Attended-Moves), or vice versa (Unattended-Moves).

Results from the sessions where the subjects were instructed to attend to the visual stimuli are shown in Figure 8. Diamonds show hit rates on trials when no auditory stimulus was presented (Baseline; see inset), squares show results from trials when both S2 stimuli were presented from the same nonzero location (Both-Move), and triangles show results from trials where the attended visual stimulus moved to a new location while the auditory stimulus remained at 0° (Attended-Moves). For the controls (Figure 8A and B), there was very little effect of the auditory distracter whether it was presented at the same location as the visual stimulus (Both-Move) or did not move (Attended-Moves), as these subjects performed with essentially no errors on this task (SDs are shown as dashed lines at the bottom of the plots).

For RM (Figure 8C), there was also no influence of the auditory distracter on the localization of visual stimuli to the left of the midline. For stimuli presented to the right of the midline, however, there was a marked increase in the hit rate when the auditory stimulus moved to the same location as the visual stimulus (Both-Move trials, squares) compared to both visual Baseline (diamonds) and trials where only the visual target changed location (Attended-Moves, triangles). Chi-square analyses indicated that there was a significant increase in hit rate on the Both-Move trials as compared to Baseline trials at the most peripheral locations in the right hemifield (indicated by filled squares), as well as a significant decrease in hit rate on the Attended-Moves trials near the midline in the right hemifield (filled triangles). In the Both-Move condition, RM’s visual localization in the right hemifield was not significantly different than in the left hemifield (paired t test; p < .05), although there was a deficit relative to the control subjects.
The results from sessions where subjects were instructed to attend to and localize the auditory stimuli and to ignore the visual stimuli are shown in Figure 9. For the auditory Baseline task (diamonds), both the age-matched (Figure 9A) and younger controls (Figure 9B) showed results consistent with the those described earlier on a similar paradigm (compare with Figure 1C). On the Attended-Moves trials where the auditory target changed location (triangles), the performance for all control subjects was similar to the Baseline trials, indicating that these subjects were able to effectively ignore the stationary visual distracter. All control subjects also showed a consistent increase in their hit rates on trials where the visual distracter was presented at the same location as the auditory target for locations near the midline as compared to the auditory Baseline trials (filled squares: $\chi^2, p < .05$). This finding is consistent with the ventriloquism effect (see Recanzone, 1998).

The data from RM showed the highest hit rates for the auditory Baseline task (diamonds, Figure 9C), and did not show a significant increase when a visual stimulus was presented at the same S2 location as the auditory target, except in one case where a small but significant increase was observed at $-4^\circ$ (filled square of Figure 9C). For the Attended-Moves trials, in which the auditory target was presented from a new location and the visual distracter remained at the midline, there was a significant effect of the stationary visual distracter on auditory localization at the most peripheral locations in both hemifields ($\chi^2, p < .05$, filled triangles). Further analysis of these data indicated that the hit rate was decreased more for auditory stimuli presented in the left than in the right hemifield (paired $t$ test; $p < .05$). Thus, for RM, the visual distracter only captured auditory stimuli when it remained near the midline and the auditory target was presented in the periphery. The fact that the peripheral visual distracters did not affect RM’s auditory localization is consistent with RM’s reduced spatial acuity for visual stimuli.

In order to further analyze these stimulus interactions, we measured the effect of the distracter when it was presented from a different location and the target stimulus remained at the starting location (Figure 10). For the control subjects, there was very little effect of the movement of the auditory stimulus on their ability to detect that the location of the visual stimulus had not changed. This minimal effect is shown as the mean error rate (solid thin line) plus one standard deviation (thin dashed line) in Figure 10A. The same error data from RM, however, indicated that his perception of the stationary visual stimulus was disrupted by the change in location of the auditory distracter. This was particularly true for the auditory distracters in the right hemifield, which also showed the greatest effect on the Both-Move trials when both stimuli were presented at the same S2 location (Figure 9C). The error rate for RM was significantly different from both the age-matched

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Figure 8. Influence of unattended auditory stimuli on visual localization. (A) Results from age-matched control subjects for each of the three trial types (see inset). Dashed lines show the SD of the mean across subjects. (B) Results from the younger control subjects. (C) Results from RM. Thin line shows perfect performance. Filled symbols show locations that were significantly different from baseline trials (see Subjects and Methods). Inset shows each of the trial types. Stars: visual stimuli; open rectangles: auditory stimuli.
Figure 9. Influence of unattended visual stimuli on auditory localization. Results from age-matched (A), younger controls (B), and RM (C). Conventions as in Figure 8.

Figure 10. Error rates when the attended stimulus did not move. (A) Results from control subjects (thin line: mean; dashed line: mean + 1 SD) and RM (heavy line) when subjects were instructed to attend to the visual stimulus, which was presented from 0° and the auditory stimulus moved to a location shown on the x-axis. (B) Results from the sessions where the subjects were instructed to attend to the auditory stimulus and the visual stimulus changed location. The error rates for RM were within 1 SD of the control subjects.
[F(1,42) = 69.9; p < .01] and younger controls [F(1,42) = 17.87; p < .01]. There was no difference between the two control groups [F(1,62) < 1]. These significant differences were also observed when the overall response rate of the individual subjects was taken into account by calculating the difference between the error rate on the Unattended-Moves trials and the false alarm rate on catch trials where neither stimulus changed location (Difference scores: RM = 0.032; AM1–AM3 = 0.007, 0.000, 0.000, respectively; Y1–Y3 = 0.020, 0.00, 0.00, respectively). These data indicate that there was a clear influence of the auditory distractor stimulus on RM’s visual localization in the right hemifield, and are consistent with the notion that auditory stimuli in the right hemifield were able to capture the less well-localized visual stimuli in this patient, in contrast to the results observed in the control subjects.

Analysis of the errors made on trials in which the attended auditory stimulus remained at the midline while the visual distracter moved are shown in Figure 10B. There was considerable variability between both sets of control subjects, as indicated by the large standard deviations (dotted lines) relative to the mean (thin line). RM’s error rates fell well within the range of ±1 standard deviation of the control subjects, indicating that for all subjects, there was some influence of a visual distracter that moved when the auditory target remained at the midline. Statistical analysis of the error rates indicated no difference between RM and the controls [F(1,41) < 1 for age-matched and younger controls]. This suggests that visual capture was no different under these circumstances between subjects.

Direct comparison between the performance on visual and auditory Baseline trials, where only one stimulus modality was presented in a session, showed that RM had better auditory localization performance than visual localization performance (one-tailed t test; p < .05). Separating the hit rates by hemifield revealed no difference between his visual and auditory localization ability in the left hemifield, but superior auditory localization ability in the right hemifield (p < .05), consistent with the data from Experiment 1. Tests within each modality showed no difference between the right and left hemifields for auditory stimuli, but better localization for visual stimuli in the left hemifield compared the right (p < .05).

In summary, the data from Experiment 5 showed that stimulus interactions were present in RM, and suggested that the stimulus with better spatial acuity captured the stimulus with lower spatial acuity. Given RM’s better auditory spatial acuity, this resulted in auditory capture of visual stimuli in the right hemifield, and little or no visual capture when visual stimuli were presented at nonzero locations.

**GENERAL DISCUSSION**

These experiments were designed to measure the extent that the parietal regions damaged in RM (Brodman’s areas 7 and 39) affected auditory and visual localization abilities and to provide some insight into the normal function of these areas. Relative localization tasks revealed a severe deficit in visual spatial processing, and a significant but less severe deficit in auditory spatial processing (Table 1). However, when localization performance was tested either with changing reference locations, or based on explicit egocentric coordinates, equivalent impairments in localization ability were observed in both modalities. Experiments in which both auditory and visual stimuli were presented simultaneously revealed that stimulus interactions remained intact in RM, and were consistent with the modality appropriateness hypothesis (see Welch & Warren, 1980) where the stimulus that is better represented along the dimension to be judged dominates the perception when discordant stimuli are presented. These results indicate that the parietal regions lesioned in this patient normally perform a limited role in relative auditory spatial processing and mainly serve to create spatial representations centered on particular reference points. This suggests that other cortical or subcortical areas serve to register the spatial information of stimuli based on different sensory attributes (at least visual and auditory) giving rise to the phenomenon of visual capture in normal individuals and auditory capture in RM.

**Table 1. Summary of RM’s Performance Across Experiments 1–4**

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Type</th>
<th>Level of impairment</th>
<th>Intended Reference Location</th>
<th>Alternative Effective Location</th>
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<td>Egocentric Midline</td>
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The intended reference location indicates the reference that subjects were instructed to use, while the alternative reference indicates other effective references that may have been utilized. Number of + symbols indicates the level of impairment.
Auditory and Visual Spatial Localization

Auditory localization ability has been shown to be affected by lesions within the superior regions of the temporal lobe in humans and monkeys (Heffner & Heffner, 1990; Sanchez-Longo & Forster, 1958). These regions were spared in RM, who showed relatively minor deficits on the relative auditory localization tasks compared to our controls. In addition, midbrain structures, which are known to process sound location information, were also intact in this patient and could have contributed to his localization ability (e.g., see Cohen & Knudsen, 1999; Wallace & Stein, 1996). Nonetheless, these results are consistent with previous documentation of auditory deficits following unilateral parietal lesions (e.g., Soroker, Calamaro, & Myslobodsky, 1995a; Soroker, Calamaro, & Myslobodsky, 1995b; Soroker et al., 1997; De Renzi et al., 1989; Ruff et al., 1981). In RM, the greatest auditory localization deficit was observed when he was asked to detect that a stimulus was presented in alignment with his body midline. These results indicate that the parietal lobe areas lesioned in this patient are likely normally involved in auditory spatial processing, but play a more significant role in assigning either absolute or relative locations of stimuli based on an egocentric frame of reference.

Visual localization performance was severely disrupted in patient RM, consistent with spatial processing deficits described following unilateral parietal lobe lesions in humans (Behrmann, 1999; Vallar, 1998; Goodale et al., 1991; Posner et al., 1984; Holmes, 1918). This deficit seems to be restricted to spatial processing, as RM had normal visual acuity, and could ‘see’ all of the stimuli presented in this and previous studies (Robertson et al., 1997; Friedman-Hill et al., 1995; Baylis, Driver, Baylis, & Ralff, 1994). The results from these experiments are consistent with previous studies indicating that the parietal lobes are involved in representing spatial relations (Ungerleider & Haxby, 1994).

The Role of the Parietal Lobe in Spatial Processing

It has previously been demonstrated that single neurons within parietal areas in monkeys respond to the spatial location of auditory stimuli, visual stimuli, or planned motor movements (Andersen et al., 1997, 1998; Colby & Duhamel, 1996; Mazzoni et al., 1996; Stricanne, Andersen, & Mazzoni, 1996; Brothier et al., 1995). The results from our experiments suggest that although limited spatial localization of both visual and auditory stimuli can still be accomplished, the parietal structures lesioned in this patient enhance visual spatial processing and may select a frame of reference in which to judge the location of different stimuli based on the stimulus modality and center of gaze. The equivalent localization of visual and auditory stimuli in RM suggests that visual localization ability is served by the same (or similar) neuronal structures used in auditory spatial processing. There are many candidate structures for such processing, including the frontal cortex (e.g., see Graziano & Gross, 1998) and the superior colliculus (Wallace & Stein, 1996).

An alternative interpretation is that the parietal lobes function to direct spatial attention (see Vallar, 1998; Posner et al. 1984, 1987 for reviews). This interpretation is based on patients with unilateral lesions, which has been proposed to result in an imbalance in the competition between the two hemispheres (Pouget & Sejnowski, 1997; Kinsbourne, 1993). RM has a slightly larger lesion in the left hemisphere (Friedman-Hill et al., 1995) than in the right hemisphere, which would give the right hemisphere a slight competitive advantage and cause the direction of the shift to be toward the left. Although a form of right neglect may be interpreted from the results of Experiment 1, RM had similar hit rates across locations in Experiment 2 and on the Both-Move trials of Experiment 5. Further, the influence of the auditory stimulus on visual localization occurred only in the right hemifield, whereas the influence of the stationary visual stimulus on auditory localization occurred in both hemifields. These observations, as well as a previous study of this patient (Robertson et al., 1997), indicate that a selective attention deficit as described in many unilateral patients can not account for all of the results observed here.

The deficits observed in Experiments 1–4 are best explained by RM having a shifted egocentric reference frame toward the left, consistent with the larger left hemisphere lesion, a greater tendency to use this reference frame when localizing visual stimuli, and a general inability to use a reference point that varied between trials (see Table 1). For both the implicit and explicit localization tasks, the visual localization deficits were greater than the auditory localization deficits when using a spatially constant reference location (0°). However, it would still be possible for RM to use his internal egocentric midline to perform these two tasks. When the reference location varied between trials, there was a much greater and equal deficit in both auditory and visual localization. Finally, when specifically instructed to localize stimuli relative to his body midline, his localization ability also showed equivalent deficits in auditory and visual localization. These results indicate that under the conditions of Experiments 1 and 2, RM likely used his body midline to a greater degree in localizing visual stimuli relative to auditory stimuli, and that when forced to use either this reference location, or a continually changing external reference location, the deficits in localization were equivalent between the two stimulus modalities. This result argues that the parietal lobe regions lesioned in this patient resulted in a shifted egocentric reference frame and an inability to use an external reference point to make spatial judgements if that reference varied between trials. These results are
consistent with previous findings with this patient where it was discovered that despite some ability to localize stimuli with respect to his own body, RM had great difficulties localizing stimuli with respect to a varying reference object (Robertson et al., 1997). It is not clear whether RM’s ability to use a spatially constant external reference point has always remained intact (Figure 5) or results from strategies or reorganization that has taken place over time because previous studies focused on visual localization that was based either on an egocentric reference or an external reference that could vary in position.

Some of the more interesting findings were the interactions between auditory and visual stimuli presented simultaneously (Figures 8–10). Auditory capture was pronounced for stimuli presented to the right, where RM’s visual deficits were greatest. This never occurred in the control subjects. Similarly, visual stimuli that remained at midline could influence his perception of more peripheral auditory stimuli. The reversed pattern of capture effects are consistent with the modality appropriateness hypothesis of inter-stimulus interactions (Welch & Warren, 1980; see also Recanzone, 1998; Driver, 1996; McGurk & MacDonald, 1976; Pick et al., 1969). These results indicate that the combination of spatial information across modalities is not dependent on the parietal structures lesioned in this patient. If these structures were integral in combining this sensory information, lesions would result in an inability to align these stimuli, and certainly would not produce uncommon capture of one stimulus by another. One intriguing implication of this is that visual localization deficits may be ameliorated by teaching parietal patients to avoid using egocentric localization strategies such as attending to objects aligned with the head or body, and to instead focus on stable, external reference points. Pairing auditory stimuli with visual stimuli may be one way of accomplishing this (see Robertson, Mattingley, Rorden, & Driver, 1998).

SUBJECTS AND METHODS
Case History
RM was 61-years old at the time of testing. He had sustained a right hemisphere embolic infarct at the age of 54 in June 1991 and a left hemisphere infarct in March 1992. Neuropsychological evaluation in the fall of 1992 revealed symptoms of Balint’s syndrome (Holmes, 1918; Holmes & Horrax, 1919; Balint, 1909, 1995) including: optic ataxia (a deficit in visually guided reaching), spatial disorientation, and dorsal simultanagnosia (a difficulty in perceiving more than one object at a time).

At the time of testing (April 1997 to July 1998), he displayed symptoms of moderate optic ataxia, spatial disorientation, and difficulties in perceiving more than a few objects at once, but no clinical signs of any other deficits in sensory function nor any apparent cognitive decline. He could raise his left or right hand on command and was capable of pointing to the left and right sides of his own body. An ophthalmological examination revealed intact visual fields, as well as normal acuity, color vision, and contrast sensitivity. An audiogram performed in October 1997 revealed that his hearing was within the range of normal young adults for tones between 500 and 2000 Hz, with a 15-dB SPL threshold in both ears for 1 kHz, the stimulus frequency used in this study.

Three-dimensional MRI reconstruction of RM’s brain in 1994 revealed nearly symmetrical lesions concentrated primarily in Brodmann’s areas 7 and 39 (Figure 11). Damaged tissue volume was estimated at 31.9 and 36.5 cm³ for the right and left parieto-occipital lesions, respectively. Primary visual, somatosensory and motor cortex, the supramarginal gyri, and the entire temporal lobes were intact on both sides (see Robertson et al., 1997 for details).

Control Subjects
Controls consisted of five age-matched males (AM1–AM5) between the ages of 56 and 64 (mean age: 59.8) and three younger controls (Y1–Y3) between the ages of 25 and 28 (mean age: 26.3). RM and all age-matched controls were naive to these psychophysical paradigms. All participants had normal or corrected to normal vision. All subjects, with one exception, had normal hearing for the stimuli used in this study. AM5 was excluded from the auditory tasks based on his asymmetric and higher thresholds (35 dB higher for the right ear and 63 dB higher for the left ear relative to the other control subjects, see Auditory Threshold Measurements below).

Stimuli and Apparatus
All experiments were conducted in a double-walled sound booth (IAC) lined with sound attenuating foam (Soneex). A personal computer and a Tucker–Davis Technologies digital signal processing system controlled stimulus generation, delivery and data acquisition. All acoustic stimuli were delivered through one of 15 different 3.5-in. speakers (Pyle, dual cone DD2) placed at 4° intervals in azimuth and 0° in elevation (see Recanzone, Makhamra, & Guard, 1998). Stimulus intensity was matched between all speakers of the array, and all stimuli were presented at 30 to 40 ± 2 dB above the detection threshold for each speaker as defined psychophysically for each of the subjects (see below).

The visual stimuli were green LEDs (0.125° diameter, 1° above each speaker, 200 msec in duration) and a red fixation LED (0.125° diameter, +12° in elevation, and
0° in azimuth, illuminated throughout each trial). Acoustic stimuli consisted of 1 kHz tone pips (200 msec in duration; 6 msec rise/fall), which was chosen because it was in the frequency range in which all subjects in this report had normal hearing. This stimulus is relatively well localized, produces minimal harmonic distortions across speakers in this apparatus, and the entire psychometric function can be defined within the range of speaker locations tested (see Recanzone et al., 1998).

### Psychophysical Paradigms

All psychophysical tasks were approved by the UC Davis Human Subjects Review Committee. Each subject provided informed consent prior to participation in the study. Age-matched control subjects and RM were paid for their participation; the younger control subjects were members of the laboratory. During testing, the subjects sat facing the speaker array. The room was darkened such that the subjects could see the LED stimuli, but not the speakers. The fixation stimulus and a head restraint oriented the subjects to 0° along the horizontal axis. Stimulus modality for each paradigm was blocked by session and counter-balanced. RM was tested using both the auditory and visual stimuli on the same day, except for the control experiments for Experiment 3 (Figure 5). While we were unable to directly monitor eye position throughout the experiments, we believe that all subjects maintained fixation throughout the trials based on subject reports and video camera monitoring. In a separate study conducted during the same period, RM’s eye movements were monitored with a camera focused on his eyes and revealed stable fixation on 97% of the trials (unpublished observation, Schendel and Robertson).

### Auditory Threshold Measurements

Thresholds for the auditory stimuli in each ear were determined twice on interleaved sessions using a staircase method, with stimuli initially presented below threshold and increasing in intensity by 0.5 dB steps until the subject indicated the presence of the tone by a button response. Stimulus intensity then decreased until no response was made, and then increased again. Threshold was defined as the average intensity of the last 20 reversals of the stimulus intensity. All subjects with the exception of AM3 and AM4 were tested monaurally through headphones. The thresholds for RM.
determined in this manner were consistent with the results from the audiogram performed earlier (see above). Free-field thresholds were also measured in all subjects for speaker locations at $-16^\circ$, $-8^\circ$, $0^\circ$, $8^\circ$, and $16^\circ$. For all subjects tested (except AM5), the threshold for 1 kHz stimuli was equivalent between the two ears (within $5\text{ dB}$) and between locations.

**Experiment 1**

Subjects pressed a button to initiate a trial and released the button when they perceived the stimulus to change location (Figure 1A). A series of three to eight stimuli (S1) were presented every 1100 msec from $0^\circ$, followed by an identical test stimulus (S2) presented from one of nine possible locations, one of which was identical to the S1 location (catch trials). The S2 (including catch trials) was presented as the fourth through ninth stimulus with equal probability on any given trial. Subjects could not infer the result of a particular trial, as hits and false-positives were identical to the subjects, as were misses and catch trials. For the auditory task, the control subjects performed two (AM4) or three (all others) sessions (10 trials/location/session). For the visual task, the control subjects performed one (AM5) or two (all others) sessions (10 trials/location/session). Patient RM completed two sessions (10 trials/location/session) for both the auditory and the visual stimulus.

**Data Analysis**

The hit rate was calculated for each S2 location as the number of trials in which the subject made a response within 150–1100 msec from the S2 stimulus onset divided by the total number of S2 stimuli presented at that location. Responses with reaction times less than 150 msec from the onset of any stimulus were not included in these calculations (exclusion range 0–0.15% of trials/session; mean 0.1% of trials/session across subjects). The use of the hit rate instead of a performance function that takes into account the percent of false-positives is justified in these experiments due to the low false-positive rates (1–2% per session across subjects, maximum $<5$%; see Recanzone, Jenkins, Hradek, & Merzenich, 1991).

A 95% confidence range was calculated for each location tested based on the performance of the age-matched controls. Tests of dispersion and $F$-ratios were used to compare the shape of the psychometric functions of RM and the control subjects. A weighted mean location ($M$) of response was calculated by multiplying the number of hits at each location by the eccentricity ($\circ$) of that location and dividing the sum of these values over the total number of hits. The expected mean-squared [$E(M^2)$] was similarly calculated, and the variance in the mean response location was computed as the square root of [$E(M^2)-(M^2)$]. For all experiments, we incorporated the Bonferroni correction when conducting multiple $t$ tests.

**Experiments 2 and 3**

The first stimulus (S1) was presented from $0^\circ$ followed 800 msec later by a second stimulus (S2) from one of seven possible locations (Figure 2A). Subjects were required to indicate the location of the second stimulus relative to that of the first by a verbal response: “Left,” “Same,” or “Right,” recorded by the experimenter via an intercom system. Each response type was equally likely. Each control completed three auditory and two visual sessions (10 trials/location/session). Patient RM completed three sessions for each modality. In Experiment 3, the S1 location was presented at $-12^\circ$, $0^\circ$, and $+12^\circ$ on randomly interleaved trials. In this case, the S2 stimuli were presented within a range of $\pm 12^\circ$ at $4^\circ$ intervals from the S1 location for that particular trial.

**Data Analysis**

Data were plotted as the percentage of Left, Same, and Right responses made at each of the S2 locations [(number of responses / total number of stimuli) $\times 100$]. To normalize across locations, all Left responses were assigned a value of $-1$, all Same responses a value of $0$, and all Right responses a value of $+1$. The mean response value was then calculated for each location, with values closer to $-1$ indicating a tendency to respond Left and values closer to $+1$ indicating a tendency to respond Right.

**Experiment 4**

Subjects were instructed to depress a button to initiate each trial and release the button when they perceived the stimulus to be directly ahead and aligned with their body midline (Figure 6A). Stimuli were randomly presented every 3 sec from one of seven different locations (three to the left, one at the midline, and three to the right) with an equal probability (143). Each control completed one session for both auditory and visual stimuli (20 trials/location/session). RM completed two sessions with the auditory stimuli and three sessions with the visual stimuli. RM also completed four sessions (20 trials/location total) using a more leftward range of target locations for both the auditory and visual stimuli.

**Data Analysis**

Data were pooled across sessions and analyzed as the response rate for each stimulus location as [(number of responses/total number of stimuli presented at that location) $\times 100$]. Locations with high response rates indicate that the stimuli were perceived as being in

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alignment with the body midline more often than locations with low response rates. A separate chi-square test for independence was used to compare the results from RM with each control subject. Data were fitted by a gaussian function using commercial software (Sigma Plot).

**Experiment 5**

Prior to the beginning of each session, subjects were instructed to attend to either the auditory or the visual stimuli for all the trials, and to release a button when they detected a change in location of the attended stimulus. Each trial began with an auditory and a visual S1 simultaneously presented at 0° (S1). The S2 stimulus varied by the location of the attended and unattended stimulus resulting in three different categories (inset of Figure 8). On Both-Move trials, both the auditory and visual stimuli were presented at the same peripheral location. On Attended-Moves trials, the attended stimulus was presented at a location other than 0° while the unattended stimulus was presented from 0°. On Unattended-Moves trials, the attended stimulus was presented from 0° and the unattended stimulus was presented from a different location. Trial types were randomly interleaved, and there was an equal probability that the attended stimulus would or would not change location. Control subjects (AM1–AM3, Y1–Y3) completed three sessions resulting in the attended stimulus changing to each location on 15 trials. Patient RM completed four sessions in each modality resulting in the attended stimulus changing to each location on 20 trials. Each subject also completed a session in which only one stimulus modality was presented (Baseline trials) from each location other than 0° for 15 trials.

**Data Analysis**

Hit rates for each condition were calculated for each attended S2 location using the same methods described above for Experiment 2. False-positive and anticipatory responses were not included in these calculations (exclusion range 0–0.013%; mean across subjects .002%). A separate chi-square analysis was performed at each S2 location to compare the hit rate between Baseline and Both-Move trials, and Baseline and Attended-Moves trials.

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**Notes**

1. Partial results from this study were presented in poster format at the Annual Society for Neuroscience Meeting (Phan, Schendel, Recanzone, & Robertson, 1997).

2. An alternative interpretation is that RM was unable to judge whether stimuli were aligned vertically. For most experiments, we used a visual fixation point located 12° up and along the midline, so that all experimental stimuli were in nonfoveal vision. If this were the case, or if the main deficit of RM was an inability to perceive more than one visual stimulus at a time (dorsal simultanagnosia), his performance should have improved on the auditory fixation and no fixation trials, a result that was never observed.

3. Although occasional changes in eye position were likely, such eye movements should not affect any of these results or our interpretations for several reasons. First, RM is capable of making sustained fixations and does so in other psychophysical tasks (Robertson et al., 1997 and unpublished observations). Second, the effects of eye position on auditory localization abides is on the order of only 3° with shifts of eye position as great as 22.5° (Lewald, 1998). Finally, comparisons between sessions in which RM used a visual, auditory, or no fixation stimulus revealed nearly identical results. Fixation of an invisible auditory stimulus (or no stimulus) would be expected to result in more eye movements than fixation of a visual stimulus. These three factors indicate that small eye movements made by these subjects would have had a negligible effect on the results.

**REFERENCES**


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