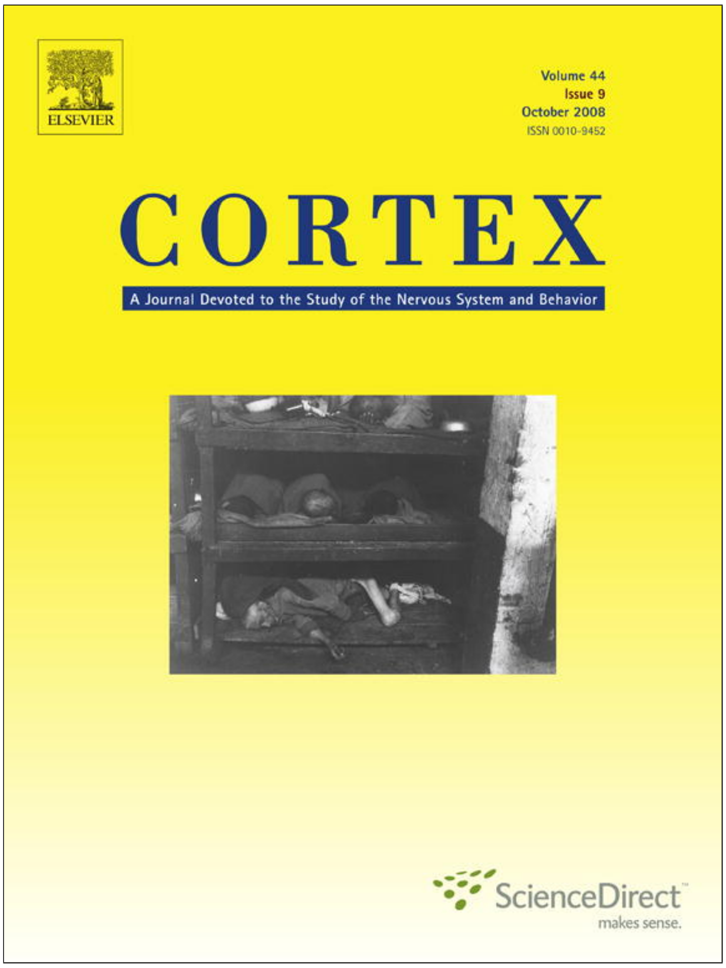
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Research report

# Cognitive representation of orientation: A case study

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ABSTRACT

Although object orientation in the human brain has been discussed extensively in the literature, the nature of the underlying cognitive representation(s) remains uncertain. We investigated orientation perception in BC, a patient with bilateral occipital and parietal damage from a herpes encephalitis infection. Our results show that in addition to general inaccuracy in discriminating and reproducing line orientations, her errors take the form of left–right mirror reflections across a vertical coordinate axis. We propose that in BC, the cognitive impairment is in failing to represent the direction of tilt for line orientations. Our results suggest that there exists a level of representation in the human brain at which line orientations are represented compositionally, such that the *direction* of a line orientation's tilt from a vertical mental reference meridian is coded independently of the *magnitude* of its angular displacement. Reflection errors across a vertical axis were observed both in visual and tactile line orientation tasks, demonstrating that these errors arise at a supra-modal level of representation not restricted to vision, or, alternatively, that visual-like representations are being constructed from the tactile input.

## 1. Introduction

Among the important functions of the visual system is that of computing the orientation of visual stimuli. Information about orientation is necessary for appreciating how visual features, surfaces, and objects are arranged relative to one another and to the perceiver. Accordingly, processing of orientation plays a crucial role in a variety of perceptual functions, including recognizing and interacting with objects. Orientation perception has been studied extensively, especially from developmental and neuropsychological perspectives, and a number of intriguing phenomena have been reported, such as dissociations between knowledge of an object's identity and its orientation, selective impairments in mirror-image discrimination after brain damage, and developmental anisotropies in the perception of oblique

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orientations (e.g., Best, 1917/Ferber and Karnath, 2003; Rudel and Teuber, 1963; Corballis and Beale, 1976; Bornstein, 1982; Rudel, 1982; Riddoch and Humphreys, 1988; Turnbull et al., 1995; Gold et al., 1995; Turnbull and McCarthy, 1996; Turnbull et al., 1997; Karnath et al., 2000; Warrington and Davidoff, 2000; Goodale, 2000; Cooper and Humphreys, 2000; Davidoff and Warrington, 2001; Riddoch et al., 2004). However, issues concerning how orientation is represented have not been fully discussed. In this article we report the case of a young woman, BC, who suffered brain damage in early childhood. We show that BC is severely impaired in distinguishing oblique lines from their mirror reflections, and argue that her performance has implications for understanding orientation representation in the human brain.

Developmental research has shown that normal infants and young children have especial difficulty with mirror-reflected obliques (for reviews see, e.g., Bornstein, 1982; Rudel, 1982). Four-month-old babies can discriminate between an oblique line (tilted 45° right of vertical) and a vertical line, but not between two mirror-reflected obliques, one tilted 45° left and the other 45° right of vertical (Bornstein et al., 1978). In other words, the babies can discriminate between lines differing in orientation by 45° when the stimuli are oblique versus vertical, but not between mirror-reflected obliques differing by 90°. The difficulty with the mirror-reflected obliques was not due to the mere obliqueness of the stimuli; babies were able to discriminate between two oblique lines differing by only 50°, when the lines were not mirror images.

Rudel and Teuber (1963) reported that difficulty distinguishing mirror-reflected obliques extended well into childhood. In one experiment children 3–8 years of age were given the following instructions:

> I am going to show you two cards; one of them is ''right'' and one is ''wrong'' that is ''correct'' or ''incorrect.'' At first you can only guess which is right, but after you've guessed I will tell you whether you guessed correctly – that is, whether you were right or wrong. After that, you must always pick the card which is ''right'' and never the card which is ''wrong.'' (Rudel and Teuber, 1963, p. 893)

A series of learning trials was then presented. On each trial the same two stimulus cards were presented, the child chose one of the cards as ''right,'' and the experimenter provided feedback. The task ended when either the child reached a criterion of 9 correct choices on 10 consecutive trials, or 50 trials had been administered.

When the stimuli on the cards were a vertical line and a horizontal line, almost all of the children succeeded in learning the discrimination, and even the youngest children (3-year-olds) required an average of only 14 trials to reach criterion. However, when the two stimuli were mirror-image obliques (i.e., a line tilted 45° left of vertical and a line tilted 45° right of vertical) none of the children in a 3-year-old group (0/12) and only one child in a 4-year-old group (1/12) learned the discrimination within 50 trials. In older age groups, children performed increasingly better, but even at oldest age tested (8 years), nearly one third (5/17) of the children failed to reach criterion in 50 trials.[1] Even for human adults, comparing mirror-image obliques takes substantially more time than comparing horizontal and vertical lines (Olson and Hildyard, 1977).

Difficulty discriminating oblique lines from their reflections across the vertical axis has also been reported in brain-damaged patients. Riddoch and Humphreys' (1988) patient LM performed virtually without error when matching horizontal and vertical lines to sample, but was almost at chance at matching oblique lines to sample when the distractors were mirror-reflected oblique lines. LM also made mirror-reflection errors when copying oblique lines. Patient MH (Riddoch et al., 2004) was impaired at detecting and localizing visual targets defined by orientation, and had particular difficulty distinguishing an oblique line from its mirror reflection. AH, studied by McCloskey et al. (1995), McCloskey and Rapp (2000a, 2000b) and McCloskey (2004), also confused oblique lines with their mirror reflections.

The difficulty with mirror-reflected oblique lines may be one manifestation of a more general difficulty in distinguishing visual stimuli that are left–right enantiomorphs (i.e., lateral mirror images). Discriminating between lateral mirror images is difficult and sometimes even impossible for human children and a variety of animal species (for reviews, see Corballis and Beale, 1976; Bornstein, 1982). For example, Bornstein et al. (1978) found that 3–4-month-old infants discriminated between right profiles of two different faces but not between the left and right profile of the same face. Further, a number of studies have described impairments in discriminating between lateral mirror images of objects (e.g., Riddoch and Humphreys, 1988; Turnbull and McCarthy, 1996; Warrington and Davidoff, 2000; Davidoff and Warrington, 2001; McCloskey, 2004). Even normal human adults often confuse lateral mirror images in memory tasks, at least when left–right orientation is considered unimportant. Interestingly, Rollenhagen and Olson (2000) found that neuronal responses recorded from inferotemporal cortex in the macaque monkey were more similar between members of a left–right mirror-image pair than between members of an up–down pair. Results such as these have been taken to

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[1] The children's difficulty with mirror-image obliques probably did not result from an inability to *perceive* the difference between the left- and right-tilting lines. Rudel and Teuber's (1963) discrimination procedure required children to remember from trial to trial which of the two mirror-image oblique lines was ''right'' and which was ''wrong.'' Other studies, however, tested children with a simultaneous match-to-sample procedure, in which participants decide which of two choice stimuli matches a standard stimulus that remains in view while the decision is made. In these studies 5–6-year-old children showed virtually perfect performance, and even 4-year-old children made very few errors (e.g., Bryant, 1973; Over and Over, 1967). Also, Dilks et al. (2004) asked 3–7-year-old children to reproduce the orientation of a target line by rotating a response line about its center. When the target remained in view throughout the trial, 5–7-year-old children made no mirror reflection errors, and even 3–4-year-olds made few such errors. Hence, children's difficulty in discrimination tasks apparently stems not from difficulty in perceiving the difference between mirror-image obliques, but rather from difficulty in retaining from trial to trial accurate mental representations of the ''right'' and ''wrong'' orientations.

suggest that at some level(s) of processing, the perceptual system in humans and other animals treats left–right enantiomorphs as equivalent.

Corballis and Beale (1976) suggest that the problem with left–right mirror images is a problem of labeling and remembering the mirror images as distinct, rather than an inability to perceive the differences. In this context, it is typically suggested that generalizing across left–right mirror images is adaptive because the left–right orientation of an object is generally irrelevant to the object's identity (e.g., Corballis and Beale, 1976; Bornstein et al., 1978; Walsh, 1996). According to this argument, an apple is an apple and a predator is a predator regardless of left–right orientation, and for this reason, the mechanisms of pattern recognition have evolved to recognize and label patterns independently of the specific left–right orientation of the physical sensory input. Corballis and Beale (1976) suggest that in addition to *reduction coding*, storing descriptions of shapes that are independent of their left–right orientation, the brain may also use another mechanism to achieve mirror-image equivalence, *duplication coding*, storing information about shapes in alternate forms, one the lateral mirror image of the other. Different versions of duplication coding have also been suggested (e.g., Noble, 1968; Deregowski et al., 2000). Reduction or duplication coding could contribute to difficulties in mirror-image discrimination; however, given that humans are not incapable of distinguishing left–right mirror images – and given that making the distinction is often important, as in determining which way a predator is facing – we must assume that the brain implements some form(s) of representation that differentiates mirror images.

Another relevant hypothesis is that the representation of an oblique line is more complex than that of a horizontal or a vertical. For example, Rudel and Teuber (1963), Olson and Hildyard (1977) and Rudel (1982) discuss the complexity of obliques with respect to linguistic expressions and point out that there are no separate linguistic items for the two opposite obliques as there are for horizontal and vertical. Olson and Hildyard (1977) suggest that analogous to the linguistic representation, the mental representation of an oblique line may be more complex than that of a horizontal or a vertical. In fact, a large body of literature shows that normal human subjects and many animal species are better at detecting, discriminating and remembering stimuli that are horizontally and vertically oriented than those that are oblique (for reviews, see Appelle, 1972; Rudel, 1982). This orientation anisotropy, *the oblique effect*, has been observed in various experimental settings and in different sensory modalities (e.g., Mansfield, 1974; Orban et al., 1984; Heeley and Buchanan-Smith, 1990; Saarinen and Levi, 1995; Gentaz and Hatwell, 1995; Heeley et al., 1997; Gentaz et al., 2001; Luyat et al., 2001), and it has been suggested to have an innate basis (Leehey et al., 1975; but see also Annis and Frost, 1973). In the visual modality, the oblique effect is believed to arise at a level higher in the visual system than the retina (Maffei and Campbell, 1970; Mansfield, 1974; Furmanski and Engel, 2000), and one of the proposed accounts is that it is due to the predominance of cortical neurons with receptive fields optimally sensitive to horizontal and vertical stimuli (Mansfield, 1974). Whether the preference for vertical and horizontal orientations is due to a single underlying cause in all the different tasks and settings tested, however, is unclear.

In sum, empirical evidence shows that animals, human children and neuropsychological patients often confuse left–right mirror images of visual stimuli, including oblique lines. Although this finding is robust and well-documented, the nature of the underlying representations remains uncertain, aside from suggestions that the difficulty with mirror-image obliques is related to their more complex mental representations and to the broader problem with lateral mirror images. In this paper, we attempt to investigate the nature of the cognitive representation for object orientation that underlies these empirical phenomena. We present a study of a brain-damaged individual, BC, who is remarkably impaired at perceiving, discriminating and matching oblique line stimuli. With oblique lines, BC makes left–right reflection errors in which the orientation of an oblique line is mirror reflected across a vertical coordinate axis. Through this case study, we propose that the representation of the orientation of oblique lines has compositional structure. According to our account, the neural processes computing the orientation of single lines operate by representing the magnitude and direction of a line orientation's tilt independently of each other in the human brain.

## 2. Case report

BC is a left-handed woman, 15–16 years old at the time of the present investigation. Medical reports show that she was a healthy, normally developing child, when at the age of 3 years she was taken to the hospital for headache, vomiting, fever, and seizures. She was treated for a presumed herpes encephalitis infection for 21 days, during 4 of which she was comatose. At the time of discharge, she was unable to walk and was noted to have suffered complete loss of vision. She recovered the ability to walk within a few weeks, and after 6 months also gradually began to regain her vision.

BC underwent a structural MRI at age 5. According to the radiologist's report, the test revealed cortical damage in both right and left occipital regions, intruding into secondary and tertiary occipital and parietal regions in the left hemisphere. Both gray and white matter were affected.

An ophthalmologic evaluation at age 7 found a dense right hemianopia and a partial left hemianopia, oculomotor apraxia and color agnosia. Visual acuity was 20/30–20/40 with approximately 10° of visual field. Neuro-ophthalmological evaluation at age 14 confirmed the earlier finding of right hemianopia, but found that the left visual field extended 15°–20° from fixation. Visual acuity was 20/25 with correction for myopia and astigmatism. No other visual defects were identified, and oculomotor functions were found to be normal. A follow-up examination at age 15 found that BC's vision had remained stable.

Physical and occupational therapy evaluations at ages 8 and 9 reported that BC had spatial orientation problems such as difficulty replicating postures and walking without a guide, and that she was easily distracted and overwhelmed in a crowded classroom. In a neuropsychological evaluation at age 10, BC's performance in verbal subtests on standardized tests of intellectual ability ranged from significantly below average (for verbal reasoning skills) to high average (in serial digit recall). The test results included a WISC-III Verbal IQ of 85, with particularly low scores in arithmetic and comprehension. The profile was reportedly similar to previous psychological testing two years earlier. Despite problems in complex verbal reasoning, BC was observed to present well in spontaneous conversation and vocabulary.

In the present testing at Johns Hopkins University, BC was studied for 9 months. A profound visuo-spatial impairment was evident in both everyday behavior and neuropsychological testing. BC was often not fully able to avoid objects while walking, despite being always guided, and she was unwilling even to try walking alone along a straight corridor with no obstacles. After a 2-h testing session, she still seemed confused about the spatial properties of the room, such as the location of the door through which she had entered or where she had hung her coat. Although her visual acuity and visual fields were sufficient to support reading, she had learned to read in Braille, presumably because of her impairment in processing visual–spatial information. Informal assessment suggested, however, that BC's Braille reading skills were well below grade level, possibly because her spatial deficit extended to processing of tactile stimuli [see Experiment 3 (Section 6)]. She was able to write some letters and digits accurately, but made orientation errors on others. For example, when asked to write the numbers 1–10, she wrote 1–5 and 7–10 accurately but failed to produce 6, stating "I don't like 6." When urged to attempt the digit, she drew it left–right reversed, and even when given a model to copy she was unable to succeed.

Despite these difficulties, BC did not present as intellectually impaired. She engaged in conversation fluently and with a sense of humor, picking up quickly on social cues and expressing emotion adequately. She was also an enthusiastic writer with a vivid imagination, her stories portraying a physically disabled young woman in the throes of interpersonal conflicts and romantic relationships. For writing, she used computer software designed for the visually disabled.

## 3. Neuropsychological assessment

### 3.1. Visual object recognition

In tasks requiring recognition and naming of pictures and objects, BC's performance suggested a visual apperceptive agnosia (see, e.g., Farah, 1990). Her efforts to name pictures gave the impression of a piecemeal perceptual process, in which she recognized individual details of objects but made numerous mistakes in identifying the whole. For example, on the Boston Naming Test (Goodglass and Kaplan, 1983) she scored within the 5–6-year-old range (24/60), with errors including "bicycle" for wheelchair and "chair or desk" for bed. BC also showed impairment on object recognition tasks from the Birmingham Object Recognition Battery (BORB; Riddoch and Humphreys, 1993; see Table 1). In the Foreshortened View Test objects are shown from a perspective that foreshortens the main axis, and thereby distorts the overall shape of the object and the relations among its parts. On this task BC scored more than 2.5 standard deviations below the normal mean. She also scored more than one standard deviation below the normal mean on the Minimal Feature View task, which requires recognition of objects from an unusual view in which the main identifying feature is obscured.

**Table 1 – BC's performance on the Birmingham object recognition battery (Riddoch and Humphreys, 1993)**

| Test | Score |
|---|---|
| *Object recognition* | |
| Foreshortened view | 15/25[b] |
| Minimal feature view | 20/25[a] |
| *Perception* | |
| Line length match A (same/different) | 19/30[b] |
| Large difference | 5/5 |
| Intermediate difference | 3/5 |
| Small difference | 0/5 |
| Identical | 11/15 |
| Line length match B (same/different) | 23/30[b] |
| Large difference | 5/5 |
| Intermediate difference | 3/5 |
| Small difference | 2/5 |
| Identical | 13/15 |
| Circle size match A (same/different) | 24/30[a] |
| Large difference | 5/5 |
| Intermediate difference | 4/5 |
| Small difference | 3/5 |
| Identical | 12/15 |
| Circle size match B (same/different) | 25/30 |
| Large difference | 5/5 |
| Intermediate difference | 4/5 |
| Small difference | 4/5 |
| Identical | 12/15 |

a Score 1 SD or more below published control data.
b Score 2 SD or more below published control data.

### 3.2. Visual–spatial perception

BC showed impaired performance on a broad range of visual–spatial perception tasks. On BORB tasks (Riddoch and Humphreys, 1993) in which she made same–different judgments concerning line length or circle size, she was intact at detecting large length and size differences, but her error rate increased as the differences became smaller (see Table 1). In addition she occasionally indicated that identical stimuli were different. As indicated in the table, BC scored more than two standard deviations below the mean for normal control participants (Riddoch and Humphreys, 1993) on 3 of the 6 tasks administered to her, and more than one standard deviation below the control mean on 2 of the remaining 3 tasks. These results must be interpreted with some caution, because Riddoch and Humphrey's normal control participants were older adults (age 50–80). However, it seems unlikely that normal 15-year-olds would perform more poorly than older adults, and hence BC's performance strongly suggests substantial visual–spatial impairment.

BC also evidenced impairment on the Developmental Test of Visual Perception (DTVP-2; Hammill et al., 1993), a standardized test assessing a variety of visuo-spatial abilities. Age-equivalent scores for the four administered subtests were remarkably low for a 15-year-old: <3;11 for the Figure-Ground task (finding target figures embedded in complex displays), 4;3 for Visual Closure (matching target figures with fragmented test figures), 4;9 for Form Constancy (matching target shapes with figures that have a different size, position and/or shading, and that may be hidden in distracting backgrounds), and 6:0 for Position in Space (finding target figures among rotated and reflecting distractors). BC's percentiles relative to the oldest age group in the DTVP-2 norms (10 years through 10 years 11 months) were <1, <1, 9, and 5, respectively.

In the DAS Block Construction test (Elliot, 1990), which involves copying spatial patterns using colored blocks, BC scored at the first percentile, representing an age equivalent of 4;1. Her visuo-spatial short-term memory performance on the Corsi Block Tapping Test (Milner, 1971) was also extremely limited: she was able to point to one block correctly after the experimenter, but consistently erred in sequences of two or more blocks. In contrast, her digit span was 7, arguing against the possibility of a general problem with memory or attention (for a similar case, see Hanley et al., 1991). BC was also tested on her ability to reach for objects placed to her left or right on a table in front of her; in this task she always reached to the correct side.

### 3.3. *Drawing*

Drawing caused particular difficulty for BC. The qualitative impression of her performance was that of a young child. Her drawing of a person was unsophisticated in the extreme, and when she was asked to draw a house, she gave up after failing to produce a square (see Fig. 1). In the Beery–Buktenica Developmental Test of Visual-Motor Integration (VMI; Beery and Buktenica, 1997), her age equivalent was less than 5 years. She was able to copy single lines and circles but unable to reproduce a triangle (Fig. 2A) or a square. Although her copy of a cross was reasonably good Fig. 2B, arrowheads at the ends of the lines caused a complete breakdown in her ability to reproduce the global shape of the model (Fig. 2C).

Further exploration of BC's drawing revealed that her difficulties were not limited to tasks with visual stimuli. Results were similar whether BC was asked to copy a visual stimulus shape, draw a shape presented tactually, or draw a shape from dictation. Although she could draw individual lines and (usually) right angles, her performance broke down in all conditions with more complex shapes (see Fig. 3 for examples). She was able to draw a right angle in 9/11 trials (although 3/9 were mirror-reversed), but all attempts to reproduce the shape of a triangle, square or diamond ended in failure. Drawing a square, for example, was consistently impossible for her, in spite of her ability to reproduce all the necessary individual elements: vertical and horizontal lines, right angles, and even three sides of a square. A highly similar pattern was observed when she was asked to connect dots with straight lines to form geometric shapes: she was able to reproduce only the most elementary shapes (see Fig. 4). Although BC was severely impaired in all of the drawing tasks, she showed no signs of neglect in any of these tasks (or in any other task).

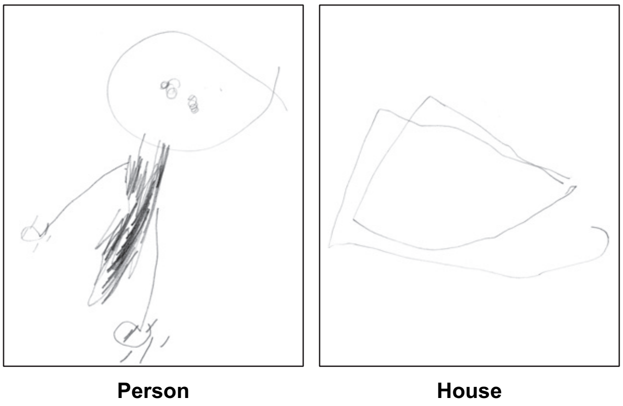

**Fig. 1 – BC's spontaneous drawings of a person and a house.**

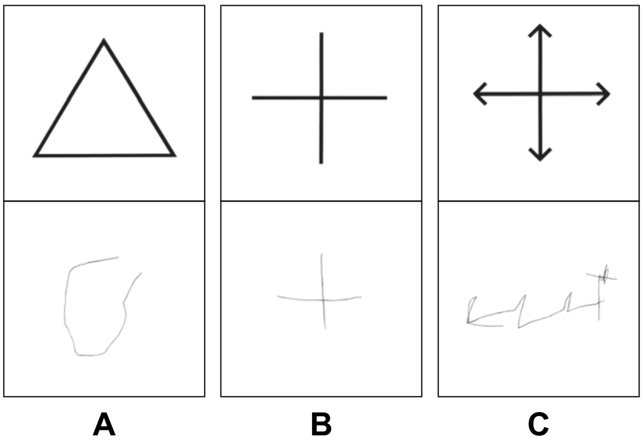

**Fig. 2 – Examples of BC's direct copies from the VMI (Beery and Buktenica, 1997). In each example the target figure is at the top, and BC's copy is at the bottom.**

Oblique lines are often more difficult to plan and produce than horizontal or vertical lines, and processing of diagonals may be more easily disrupted after neural insult (e.g., Smith and Gilchrist, 2005; Olson, 1970). However, BC's problems with drawing were not specifically related to oblique lines. As Figs. 3 and 4 show, she often failed to produce the required horizontal or vertical lines and incorrectly drew oblique lines instead.

### 3.4. *Interpretation*

BC's poor performance in these tasks is unlikely to have resulted solely from her restricted visual field. In the first place her performance in drawing tasks was no better with auditory or tactile stimuli than with visual stimuli (see Figs. 3 and 4). Further, her difficulties in object recognition and drawing were clearly determined not by the visual angle subtended by the stimuli or responses, but rather by stimulus and response complexity. Compare, for example, Fig. 2B and C.

Nor is it likely that a visuo-motor deficit can explain the results. Some tasks showing impairment (e.g., object naming) did not include a visuo-motor component, and even for tasks with such a component a visuo-motor deficit does not offer a plausible explanation. For example, BC was able to produce all of the individual movements needed to draw a square (as

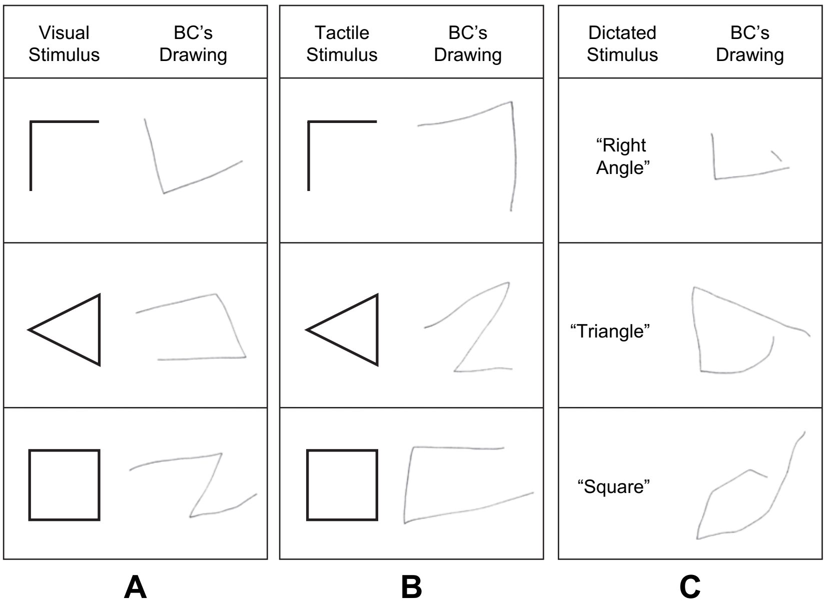

**Fig. 3 – Examples of BC's attempts to draw simple geometric shapes from a visual model (A), a tactile model (B), or dictation (C). She was asked to close her eyes when feeling the tactile model with her hand, and to open them when drawing.**

evidenced by her ability to draw right angles), yet never came close to producing an entire square correctly. Similarly, when given three dots and asked to connect them into a triangle, she could draw lines from one dot to another, but never succeeded in drawing the full set of lines needed to form the triangle.

BC's performance in visual–spatial tasks suggests that she suffers from a profound cognitive impairment that could be descriptively referred to as a severe limitation in the resources available for spatial representation and processing. In tasks with very simple stimuli her performance was often reasonably good (albeit not fully normal), as in drawing a line or right angle. However, even a slight increase in stimulus complexity often caused a complete breakdown in performance, as when she was asked to draw a triangle or square. These observations suggest that BC may be virtually unable to create or process spatial representations that include more than a very few elements (e.g., lines) or spatial relations among elements (e.g., intersections at particular angles). BC might, then, be described as simultanagnosic in the sense of being impaired in combining the various elements of a complex stimulus into a coherent percept, although not in the sense of being unable to perceive more than one object at a time.

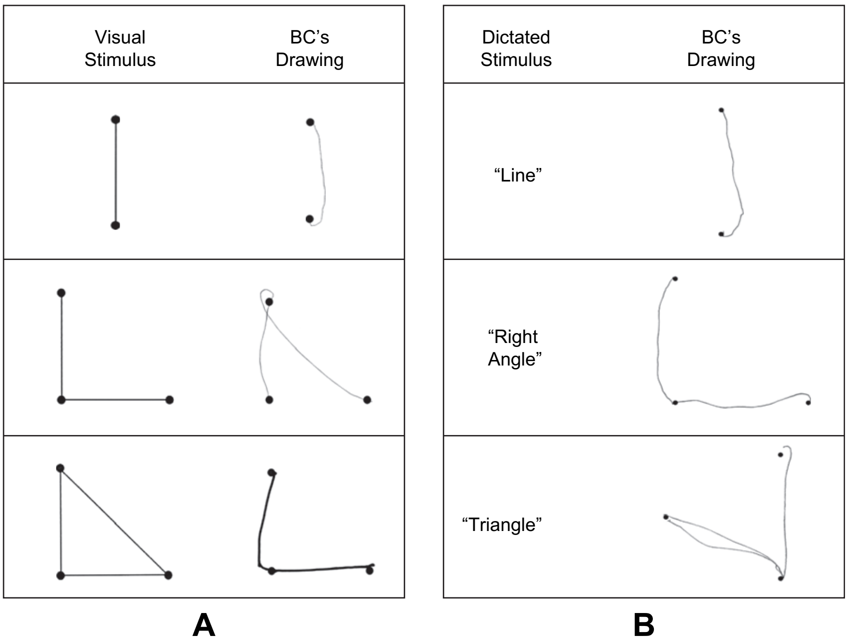

**Fig. 4 – Examples of BC's attempts to connect dots to draw geometric shapes. A. Copying a visual model. B. Drawing from dictation.**

Given her profound impairment in spatial tasks with any degree of complexity, the experiments in this study were designed to probe BC's performance with very simple stimuli. A potentially interesting pattern emerged from a line orientation discrimination task (Experiment 1), which led to the study's specific focus on orientation perception.

The experiments in this study were approved by the Johns Hopkins University Homewood Institutional Review Board, and they were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. BC gave her assent and her parents their permission for the testing.

## 4. Experiment 1: same–different judgments of arrow orientation

### 4.1. *Introduction*

In this experiment, pairs of arrows were presented visually, and BC judged for each pair whether the orientations of the two arrows were the same or different.

### 4.2. *Stimuli and procedure*

Each stimulus consisted of two arrows printed in black on white paper. Each arrow was composed of a 35-mm straight line with a pointed arrowhead at one end. At the viewing distance of 50 cm each arrow subtended a visual angle of 4°. Each arrow was enclosed within a circle, and the two circles were arranged vertically on the page, with a 90-mm center-to-center distance. BC's task on each trial was to say whether or not the arrows were pointing in the same direction. One hundred and twenty-four stimulus pairs were presented (40 Same pairs and 84 Different pairs). In the Different pairs the arrows differed in orientation by 30°–180°.

### 4.3. *Results and discussion*

BC responded correctly to all 40 of the Same pairs. However, she also responded 'same' to 18 of the 84 Different pairs (21%), despite the fact that the smallest orientation difference between the arrows in a pair was 30°. For pairs with orientation differences of 90°–180° she was 92% correct (50/54); however, for pairs with differences of 30°–60°, she detected the difference only 60% of the time (18/30), $\chi^2(1) = 13.3$, $p < .001$. Thus, BC was impaired in detecting orientation differences that would be obvious to a normal observer.

BC appeared to have particular difficulty with Different pairs in which the two arrows were left–right reflections of one another (e.g., one arrow tilted 30° clockwise and the other tilted 30° counterclockwise from vertical). As shown in Table 2, her accuracy was 83% for non-reflected Different pairs (i.e., pairs in which the arrows were not left–right or up–down reflections), and 86% for up–down reflections; however, she was only 64% correct on the left–right reflection pairs, $\chi^2(1) = 3.94$, $p < .05$, for the comparison between left–right reflection pairs and the other two Different types combined. This result suggests that in addition to difficulty apprehending small angular differences, BC may also exhibit a tendency specifically to confuse left–right reflections. However, this conclusion must be drawn tentatively, because the stimulus set in Experiment 1 was not designed to support systematic comparisons among non-reflected, left–right reflected, and up–down reflected Different pairs. As is apparent from Table 2, the absolute orientation difference was not carefully controlled across the three stimulus types. BC's orientation processing was therefore examined more systematically in the following experiments.

## 5. Experiment 2: reproduction of line orientation

### 5.1. *Introduction*

This experiment used a procedure developed by Dilks et al. (2004): a target and response line were shown on a computer monitor, and BC turned a dial to match the orientation of the response line to that of the target.

### 5.2. *Stimuli and procedure*

BC sat in front of a computer screen (distance 50 cm) divided into upper and lower halves by a horizontal line (see Fig. 5). A target line (length 6 cm, width .3 cm, visual angle 6.8°) was displayed on the upper half of the screen, and a response line (length 4.5 cm, width .3 cm, visual angle 5.1°) on the

**Table 2 – BC's accuracy for Different Pairs in Experiment 1**

| Orientation difference (deg) | Trial type | | | | | |
|---|---|---|---|---|---|---|
| | Rotated | | Up–down reflected | | Left–right reflected | |
| | Correct/total | % Correct | Correct/total | % Correct | Correct/total | % Correct |
| 30 | 2/6 | 33 | 0/2 | 0 | 0/2 | 0 |
| 45 | 9/12 | 75 | | | | |
| 60 | | | 3/4 | 75 | 2/4 | 50 |
| 90 | 16/16 | 100 | 10/10 | 100 | 7/10 | 70 |
| 120 | | | 4/4 | 100 | 4/4 | 100 |
| 150 | | | 2/2 | 100 | 1/2 | 50 |
| 180 | 6/6 | 100 | | | | |
| Total | 33/40 | 83 | 19/22 | 86 | 14/22 | 64 |

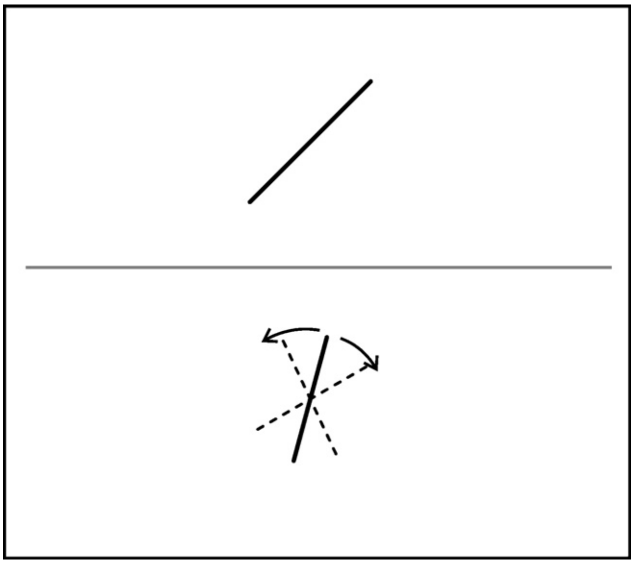

**Fig. 5 – Experiment 2: BC sat in front of a computer screen showing a target line (top) and a response line (bottom). The response line rotated about its center when BC turned a dial on the table in front of her.**

lower half; the midpoints of the two lines were aligned vertically with a midpoint-to-midpoint distance of 10.3 cm (11.6°). BC was instructed to make the orientation of the response line look exactly like that of the target by turning a dial on the table. The response line rotated clockwise and counter-clockwise about its midpoint when the dial was turned in the corresponding direction. Both lines remained in view until BC verbally indicated she had completed her response. Instructions made clear that the task was non-speeded, and that BC could look back and forth between target and response lines as often as she wished. Because of her restricted visual field, the target and response lines were pointed out to her at the beginning of each trial.

In describing line orientations we designate vertical as 0°, and treat tilts clockwise and counterclockwise from vertical as positive and negative, respectively. For example, a line tilted 45° counter-clockwise from vertical has an orientation of −45°, and a horizontal line may be described equivalently as having a −90° or +90° orientation.

In Experiment 2a, BC was tested with 12 target orientations: −90° through +75°, in 15° increments. These orientations are shown along the x-axis in Fig. 7. Three trials per target orientation were presented in random order. On each trial, the initial orientation of the response line was 45° or 90° from the target. Three practice trials preceded the 36 test trials. Experiment 2b was identical except that the target and response lines were displayed inside circles on the computer screen.

Following Dilks et al. (2004) we calculated the absolute error on each trial as the smaller of the two rotations that would bring the response line into alignment with the target line. Consider, for example, a trial with a target line of −15° and a response line of −25°. The response line could be aligned with the target by a 10° clockwise rotation, or a 170° counter-clockwise rotation. For this trial the absolute error was scored as 10°. Because the smaller of the two rotations needed to align a response line with a target line cannot exceed 90°, the maximum possible error on each trial in the task was 90°.

### 5.3. *Results and discussion*

BC's mean absolute error was 31° in Experiment 2a (range 1°–88°) and 27° (range 3°–82°) in Experiment 2b. For purposes of illustration, Fig. 6 shows BC's responses for each of the target orientations in Experiment 2a. Because her performance was virtually identical in Experiment 2a and b, results were collapsed across experiments for the analyses reported below.

BC's absolute errors appear remarkably large, and results from control participants confirm this impression. Dilks et al. (2004) tested 12 normal adults with the procedure used in Experiment 2a, and the mean absolute error ranged from 1.1° to 2.8° across subjects, with a grand mean of 1.6°. BC's performance was worse even than that of 5–7-year-old children: for 10 normally-developing 5–7-year-olds, Dilks et al. (2004) found a mean absolute error of 4.8°, with a range across subjects of 3.0°–7.0°.

The results shown in Fig. 6 suggest that BC's abnormally high absolute error scores may have resulted in part from a tendency to mirror-reflect the orientation of oblique target lines. For example, the figure shows that BC's responses to −45° targets in Experiment 2a all fell close to the mirror-reflection orientation of 45°.

The scatterplot in Fig. 7 presents BC's error pattern more fully and succinctly. The figure plots each response from Experiment 2a and b, with the target orientation on the x-axis and BC's response orientation on the y-axis. For each target orientation, a correct response would fall on the diagonal with positive slope (solid line in Fig. 7), and a mirror reflection response on the negative-sloping diagonal (dashed line). The scatterplot shows that BC's responses fell in the vicinity of either the target or its mirror-reflected orientation. Across the 60 trials with oblique target orientations, BC's response was closer to the target orientation than to the mirror-reflected orientation in 33 instances (55%); these are the points in the upper right and lower left quadrants of the scatterplot. However, on 27 of the 60 oblique-target trials (45%) her response was closer to the target's mirror reflection than to the correct orientation; these responses appear in the upper left and lower right quadrants.

Although the scatterplot in Fig. 7 suggests a systematic tendency to mirror-reflect the target orientation, more formal evidence is required. In presenting this evidence it will be useful to characterize the orientation of a line in terms of a tilt magnitude and a tilt direction. For example, a line with an orientation of −30° has a tilt magnitude of 30° and a tilt direction of negative (counter-clockwise). Given the magnitude/direction distinction, the mirror reflection of a line is the line with the same tilt magnitude but the opposite tilt direction.

In the scatterplot (Fig. 7) trials for which BC's response line had the same tilt direction as the target line are

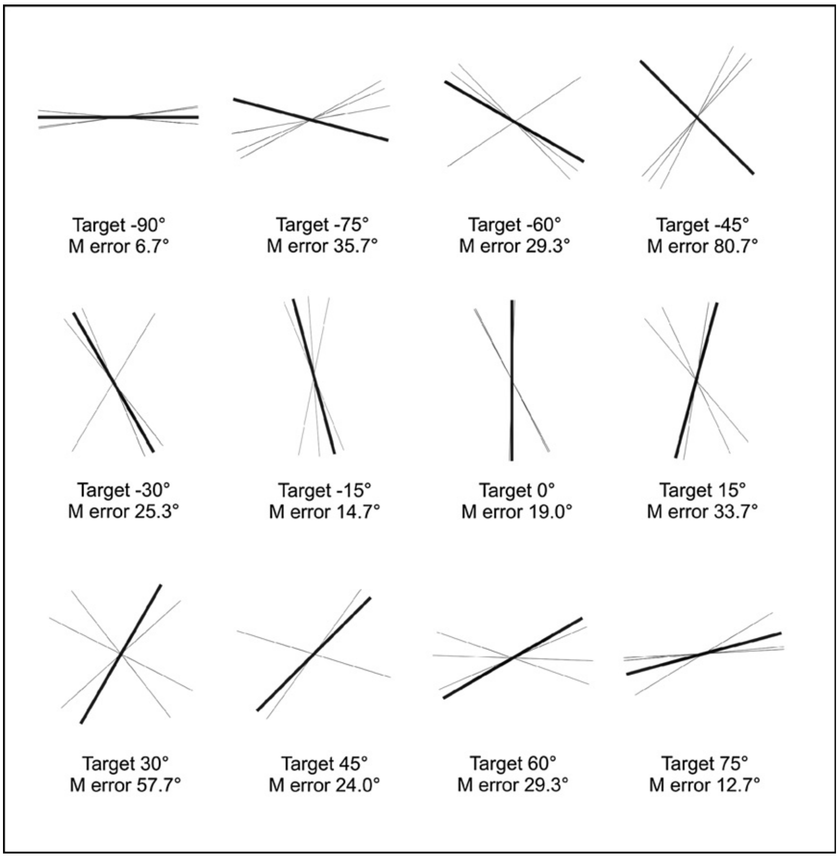

**Fig. 6 – BC's responses in individual trials in Experiment 2. BC's responses were very inaccurate, errors ranging up to the possible maximum. The response pattern suggests she frequently mirror-reflected the target when producing her response. The thick lines depict the target orientation and the thin lines show individual responses. Depicted results are from Experiment 2a, and mean absolute errors are averaged across all three trials per target orientation.**

depicted in the lower-left and upper-right quadrants. Trials for which the response line had a tilt direction opposite to that of the target appear in the upper-left and lower-right quadrants. The scatterplot shows that BC's responses to oblique targets were frequently tilted in the wrong direction. However, this result does not by itself demonstrate that BC often mirror-reflected the target orientation in producing her responses. Even in the absence of a systematic tendency toward mirror-reflection, BC could have produced some wrong-direction responses. Perhaps, for example, on some trials BC responded randomly, without regard to the orientation of the target line. Random responses to oblique targets would be tilted in the wrong direction about half of the time by chance. Another possibility is that on some trials BC encoded an oblique target line only as 'tilted,' without representing the orientation more specifically (see, e.g., Bryant, 1969, for a similar suggestion concerning young children's difficulty in tasks requiring discrimination of oblique lines). A 'tilted' target encoding would dictate a tilted response, but would not specify the tilt direction (or magnitude). As a consequence, the resulting responses would be tilted in the wrong direction about half of the time.

To say that BC mirror-reflected a target is to say that she responded systematically to the target's tilt magnitude while nevertheless tilting her response line in the wrong direction. Accordingly, in true mirror-reflection responses, we would expect the tilt magnitude of the response line to be correlated with the tilt magnitude of the target line. For example, mirror-reflection responses to targets with a tilt magnitude of 60° should have a larger tilt magnitude than mirror-reflection responses to targets with a tilt magnitude of 30°.

Therefore, if BC's wrong-direction responses are true mirror reflections, we expect these responses to show a correlation between target and response tilt magnitude. In contrast, the alternative interpretations for the wrong-direction responses – random responding or encoding of oblique target lines only as 'tilted' – predict that target and response tilt magnitude should be uncorrelated. According to these interpretations, information about the target's tilt magnitude does not contribute to wrong-direction responses.

The scatterplot in Fig. 7 suggests that target and response tilt magnitude are indeed correlated across BC's wrong-direction responses: within each of the wrong-direction quadrants the response tilt magnitude appears to vary systematically with the target tilt magnitude. Consistent with this impression, the correlation between target and response tilt magnitude across the 27 wrong-direction responses is .63, and this correlation is significant beyond

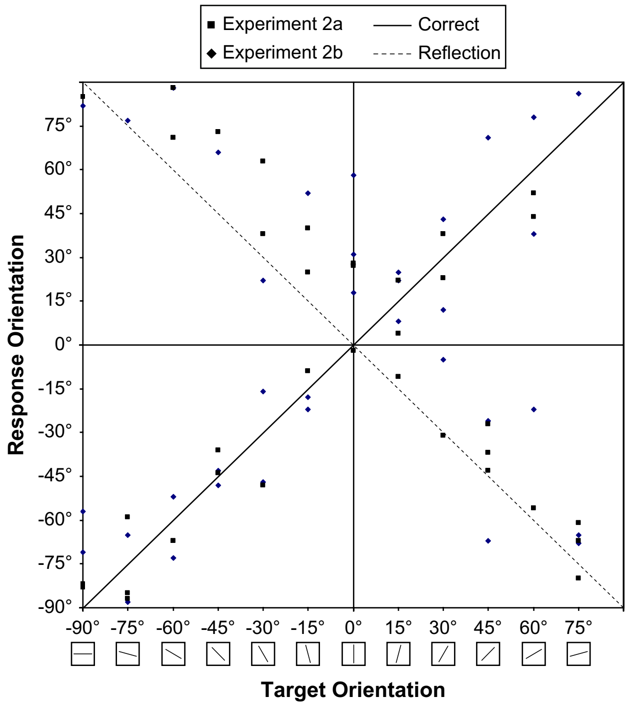

**Fig. 7 – Experiment 2: a scatterplot of BC's responses (y-axis) in individual trials according to target orientation (x-axis). Responses fall along two opposite diagonals, one that depicts correct target orientations (solid line) and one that depicts the targets' mirror reflection (dashed line).**

the .01 level.[2] The relationship between target and response tilt magnitude is also evident in the mean tilt magnitude of the responses to each target tilt magnitude: for target tilt magnitudes of 15°, 30°, 45°, 60°, and 75° the mean response tilt magnitudes were 32°, 32°, 48°, 65°, and 70°, respectively. These results demonstrate that BC showed a strong and systematic tendency to mirror-reflect the target orientation in producing her responses.

BC's high absolute error scores (mean = 31°) clearly resulted in part from her frequent mirror-reflection of targets. However, in addition to these tilt-direction errors she also evidenced substantial imprecision in reproducing tilt magnitude, in both correct- and wrong-direction responses. This imprecision is evident in the scatterplot: BC's responses usually did not fall exactly on either the correct or mirror-reflection diagonal. Her mean tilt magnitude error was 20.3° for horizontal and vertical target lines, 10.9° for correct-direction responses to oblique target lines, and 15.7° for wrong-direction responses to oblique targets. (For wrong-direction responses error was assessed relative to the orientation of the target's mirror reflection.)

In contrast to BC the normal adults tested in the Dilks et al. (2004) study showed no tendency to mirror-reflect the target, and were far more accurate in matching the target's tilt magnitude (mean absolute error = 1.6°). The same was true of the 5–7-year-old children tested by Dilks et al.: these children made no mirror reflection errors, and were much more accurate than BC in reproducing tilt magnitude (mean absolute error = 4.8°). Hence, the results of Experiment 2 suggest two forms of impairment: a strong tendency to mirror-reflect the target, and greater-than-normal imprecision in reproducing tilt magnitude.

However, one might wonder whether BC's restricted visual field – rather than impairments in processing orientation information – might be responsible for her poor performance on the task. BC's visual field is wide enough that she could readily see the entire target line or the entire response line at once; however, she could not see the entire target-plus-response-line display simultaneously, and so had to look back and forth between the target and response lines. Although she was free to look back and forth as often as she desired (and typically did so many times on each trial) her inability to see both lines at once may have increased the difficulty of the task.

Results from Dilks et al. (2004) indicate, however, that BC's poor performance cannot be attributed solely to her restricted visual field. The Dilks et al. study included not only a No-Delay condition in which target and response lines were displayed simultaneously (as in the present experiment), but also a Delay condition in which the target line was removed before the response line was presented for adjustment. In the Delay condition participants first inspected the target line for as long as they wished; the target line then disappeared from the screen, and after a 5-sec delay the response line was displayed. We would expect the Delay task to be more difficult than the task faced by BC in the present experiment, because the Dilks et al. participants could not look back at the target once it was removed. Hence, if BC's poor performance reflected only her inability to see both lines at once, the participants in the Dilks et al. Delay condition should have performed even more poorly.

Looking first at mirror-reflection errors, Dilks et al.'s adult participants made none in the Delay condition, and even the 5–7-year-old children made very few. Clearly, then, BC's tendency to mirror-reflect the target cannot be attributed to her inability to see both target and response lines at once. With respect to matching the tilt magnitude of the target, the adults in the Dilks et al. Delay condition were far more accurate than BC (mean absolute error = 3.8°, range = 2.0°–5.2°), and the 5–7-year-old children were comparable to BC even though they were about 10 years younger than she (mean absolute error = 15.9°, range 8.1°–21.1°). Given especially that BC could look back and forth between the target and response lines whereas the participants in the Dilks et al. Delay condition could not, these data strongly suggest that BC's imprecision in reproducing the target's tilt magnitude is greater than would be expected solely from her inability to see both target and response lines at once. We conclude that BC's frequent mirror reflection errors, and probably also her tilt magnitude imprecision, stem from impairments in processing orientation information, and cannot be attributed solely to her restricted visual field.

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[2] It might appear that since we are considering only the points in the upper left and lower right quadrants of the scatterplot, we are guaranteed to find a non-zero correlation. However, by computing the correlation over tilt magnitude values (which range from 0° to 90°) rather than full orientation values (which range from −90° to 90°) we in effect collapse the upper left and lower right quadrants of the scatterplot into a single square region. For example, 30° and −30° targets both enter the analysis as target tilt magnitudes of 30°. Given that the correlation was computed over a square 'space,' the computed value could in principle have ranged from −1.0 to +1.0.

## 6. Experiment 3: tactile reproduction of line orientation

### 6.1. Introduction

The aim of this experiment was to investigate whether BC's tendency to mirror-reflect oblique lines extends to the tactile modality. While seated at a table blindfolded, BC felt the orientation of a fixed wooden target stick, and then rotated a response stick to match the target orientation.

### 6.2. Stimuli and procedure

The experiment was conducted in two parts (Experiment 3a and b). In both parts the response apparatus consisted of a wooden stick (11.5 cm long, 1 cm wide, 2 mm thick) mounted to a flat surface with a bolt through its center, such that it could rotate about the center. BC was instructed to turn the response stick so that its orientation exactly matched the target. She was given unlimited time to respond.

In Experiment 3a the target was a wooden stick (36 mm long, 2 mm wide, and 2 mm thick) fixed to a flat surface. The target was placed on the table directly in front of BC, and the response apparatus was positioned to the left of the target. BC felt the target stick with her right hand and adjusted the response stick with her left hand. The target orientations ranged from −90° through +75° in 15° increments and were tested in 1–3 trials each, with a total of 18 trials.

In Experiment 3b the target stick was the same size as the response stick. The target was positioned on the table immediately in front of BC, and the response apparatus was directly above the target (i.e., on the table farther away from BC). She used her (dominant) left hand both to feel the stimulus and to rotate the response. She was encouraged to go back and forth between the target and response sticks whenever necessary. Twenty-four trials were presented, with the same target orientations as in Experiment 3a.

### 6.3. Results and discussion

BC's performance was very similar to that observed with visual stimuli. Her absolute error scores ranged from 0° to 89° (max = 90°) with an average of 29.0°. As in Experiment 2, BC's responses showed both imprecision and a tendency toward mirror reflections (see Figs. 8 and 9). With respect to mirror reflection, responses with a tilt direction opposite to that of the target (i.e., responses falling closer to the target's mirror reflection than to the target orientation) occurred in both Experiment 3a and b. These wrong-direction responses, which appear in the upper left and lower-right quadrants of the scatterplot in Fig. 9, were observed on 41% of the oblique trials (12/29) overall (comparable to 45% in Experiment 2). Among the wrong-direction responses to oblique targets, the correlation between target and response tilt magnitude was positive (.27), suggesting that BC was responding to the tilt magnitude of the target line even when she tilted her response line in the wrong direction. This correlation did not, however, reach significance, perhaps due to the small number of data points (12, *vs.* 27 in Experiment 2), and to the presence of a single outlier (target 30°, response −82°) in which BC's wrong-direction response was quite discrepant in tilt magnitude from the target. (With this outlier excluded the correlation rises to .47.) Nevertheless, the data strongly suggest that BC frequently mirror-reflected the target line in making her responses.

In addition to mirror reflections BC showed substantial imprecision in reproducing the target's tilt magnitude. For response with the correct tilt direction, the mean absolute distance from target orientation was 13.3°, and for wrong-direction responses the mean distance from the reflection of the target location was 18.2°.

In sum, BC's performance in the tactile line orientation reproduction task was very similar to that in the visual version. In both versions she exhibited imprecision, and a tendency to mirror-reflect oblique lines. These results suggest that her impairments in representing line orientation affect processing of orientation information from both visual and tactile modalities.

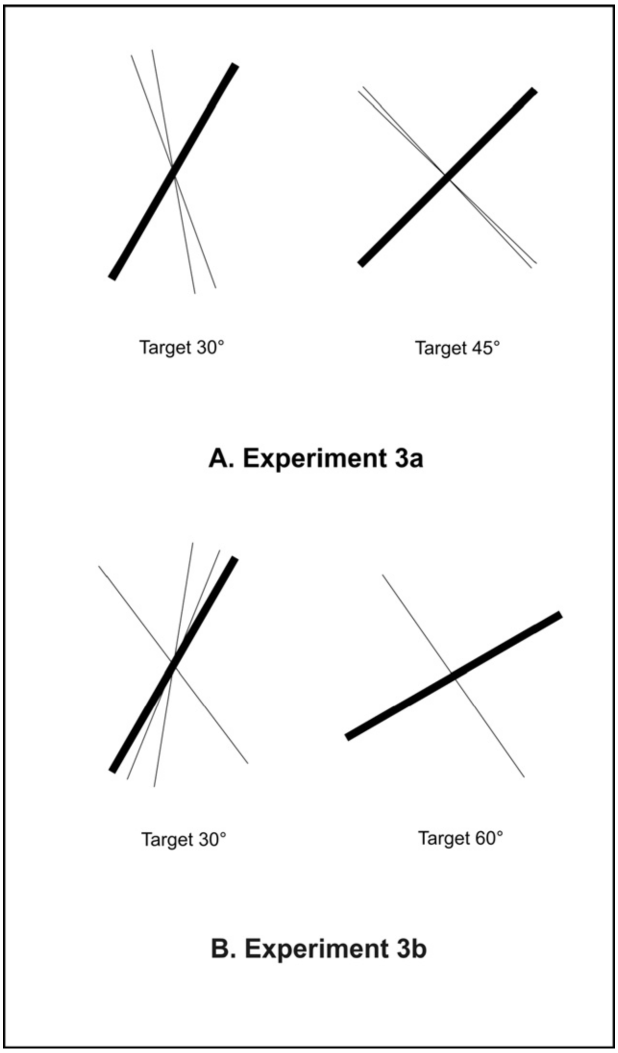

**Fig. 8 – Examples of BC's reflection errors in tactile reproduction of line orientation, Experiments 3a (horizontal alignment, small stimuli) and b (vertical alignment, larger stimuli). Thick lines show the target orientation, and thin lines responses in individual trials.**

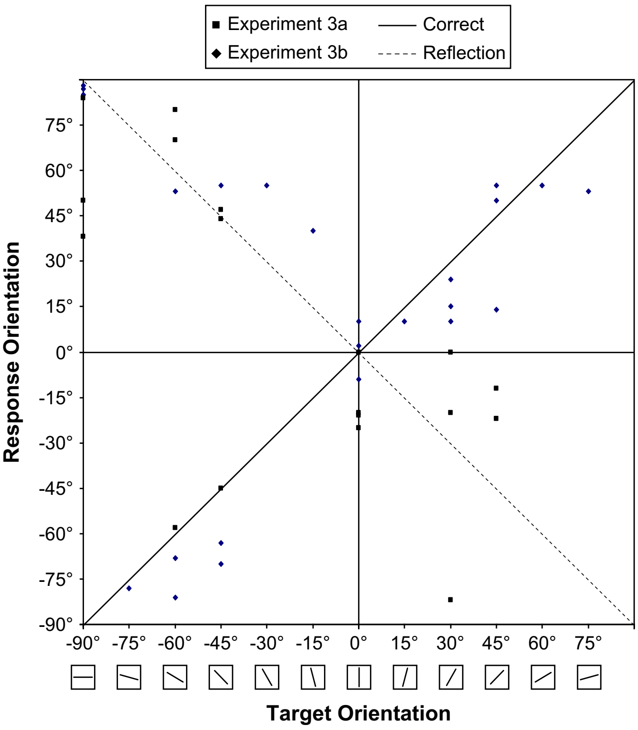

**Fig. 9 – Experiment 3: a scatterplot depicting BC's responses (y-axis) in individual trials according to target orientation (x-axis). Responses fall along two opposite diagonals, one that depicts correct target orientations (solid line) and one that depicts the targets' mirror reflection (dashed line).**

## 7. Experiment 4: visual orientation reproduction for lines with differentiated ends

### 7.1. Introduction

Experiments 1–3 demonstrated that BC made frequent mirror-reflection errors in tasks requiring her to process the orientation of a line. However, one question that has not yet been addressed systematically concerns the specific form of the reflections: Do BC's mirror-reflection errors result from left–right reflection of target lines (i.e., reflection across a vertical axis), from up–down reflection (i.e., reflection across a horizontal axis), or from a mixture of both error types? Experiment 1 suggested that BC was more likely to confuse a line with its left–right reflection than with its up–down reflection; however, this experiment was not designed to support systematic comparisons between left–right and up–down reflections. Nor can Experiments 2 and 3 resolve the issue. Because the stimulus lines in these experiments were identical at both ends, left–right and up–down reflections could not be distinguished. For example, a −45° response to a 45° target line (see, e.g., Fig. 8A) could have occurred via either left–right or up–down reflection of the target.

Experiment 4 was designed to investigate the direction of reflection. The procedure was the same as that in Experiment 2, except that one end of each target and response line was red. To rule out the possibility that BC's error pattern might reflect a particular alignment of the target and response lines on the screen, the experiment was conducted in two conditions, in which the target and the response displays were arranged vertically (Experiment 4a) and horizontally (Experiment 4b) on the computer screen.

### 7.2. Stimuli and procedure

The target and response lines used in Experiment 2 were modified such that one end of both lines had a red tip. The lines were placed inside circles. Twenty-four target orientations (−180° through 165 in 15° increments) were each tested in 4 trials in both Experiment 4a and b. One Experiment 4b trial was discarded due to experimenter error. Stimuli and procedure were otherwise identical to those in Experiment 2.

### 7.3. Results and discussion

As in the preceding experiments, BC's responses were very inaccurate. The mean absolute error was 27.0° in Experiment 4a (vertical target–response alignment) and 31.1° in Experiment 4b (horizontal alignment).

Once again the response pattern showed not only imprecision but also mirror reflection of oblique target orientations. We first classified BC's responses to oblique targets according to the location of the red tip in the response line relative to its location in the target line. As illustrated in Fig. 10, the classification was based on a division of the target and response displays into quadrants defined by horizontal and vertical axes

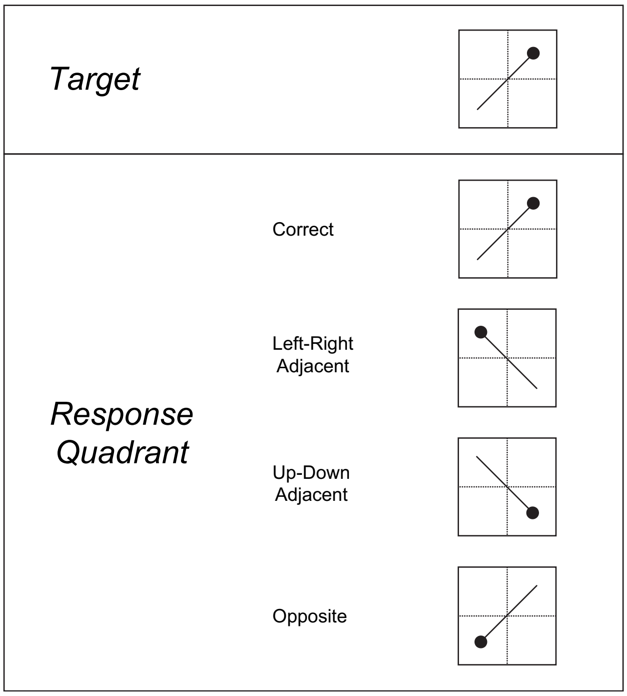

**Fig. 10 – Illustration of the four categories into which responses were sorted in Experiment 4: correct-quadrant, left–right adjacent quadrant, up–down adjacent quadrant, and opposite quadrant. The black dot at one end of each line indicates the location of the red tip.**

through the midpoint of the line. (Note that these quadrants should not be confused with quadrants in a scatterplot.) Responses were classified into one of four categories: correct quadrant, left–right adjacent quadrant, up–down adjacent quadrant, and opposite quadrant (see Fig. 10 for examples). Left–right adjacent responses are potential left–right reflections, and up–down adjacent responses are potential up–down reflections. Table 3 presents the distribution of responses across categories in Experiments 4a and b. The pattern was virtually identical in the two experiments ($\chi^2 < 1$). Collapsing across experiments, 65% of the responses fell into the correct quadrant, 26% into the left–right adjacent quadrant, 8% into the up–down adjacent quadrant, and 1% into the opposite quadrant. One point immediately apparent from these results is that BC was sensitive to the red tips on the target and response lines. Had she ignored the red tips, no difference in frequency should have been found between correct- and opposite-quadrant responses, or between left–right adjacent and up–down adjacent responses. (See Fig. 10 for illustrations of these orientations.) In fact, however, correct-quadrant responses were significantly more frequent than opposite-quadrant responses (101 *vs* 1, respectively, $p < .001$ by binomial test), and left–right adjacent responses were significantly more frequent than up–down adjacent responses (41 *vs* 13, respectively, $p < .001$).

The finding that many of BC's responses fell into the left–right adjacent quadrant suggests that she frequently made left–right reflection errors, and the scatterplot in Fig. 11 corroborates this conclusion. The scatterplot is somewhat more complex than those from Experiments 2 and 3: because one end of each line was marked, target and response orientations varied from −180° to 165°, and the maximum possible error was 180°. As in the previous scatterplots, correct responses lie along the major diagonal with positive slope (the solid diagonal in Fig. 11), and left–right reflections fall along the major negative-slope diagonal (dashed line in the figure). Up–down reflections lie along the minor negative-slope diagonals in the upper right and lower-left sections of the scatterplot (dotted lines in the figure). For example, the up–down reflection for a 45° target is 135°, which lies along the negative diagonal in the upper right section. The small squares in the scatterplot are systematically related to the four response categories: correct-quadrant responses are those within the squares lying along the correct-response diagonal (i.e., the major positive diagonal); left–right adjacent responses are within the squares that lie along the left–right reflection diagonal (the major negative diagonal); up–down adjacent responses are in the squares along the up–down reflection diagonals (the minor negative-slope diagonals), and opposite-quadrant responses are in the four remaining (and virtually empty) squares.

The pattern in the scatterplot shows that the vast majority of responses lie along either the correct-response diagonal, or along the left–right reflection diagonal. The latter result suggests that BC often left–right reflected the target in producing her response. To determine whether the apparent left–right reflections were true reflections (as opposed to, say, random responses that happened by chance to fall within the left–right adjacent quadrant), we assessed whether BC was responding to the target's tilt magnitude even when she tilted her response line in the wrong left–right direction. In particular we computed the correlation between target and response tilt magnitude across all responses with an incorrect left–right tilt direction: the 41 left–right adjacent responses, and the 1

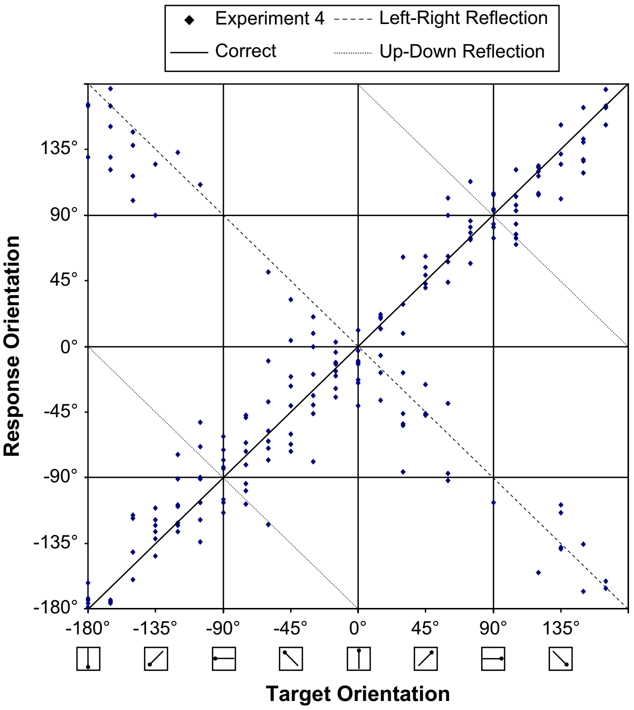

**Fig. 11 – Experiment 4: a scatterplot showing BC's responses (*x*-axis) in individual trials according to target orientations ( *y*-axis). Responses fall along four diagonals, one that depicts correct target orientations (solid line), two that depict left–right reflections (dotted line) and one that depicts up–down reflections (broken line). The majority of the reflection responses occurred in the left–right direction.**

**Table 3 – BC's responses for oblique targets in Experiment 4, classified according to their location among the four possible quadrants defined relative to the target orientation (correct quadrant, left–right adjacent, up–down adjacent, opposite quadrant)**

| Response location | Experimental condition | | | | | |
|---|---|---|---|---|---|---|
| | Vertical alignment (Exp. 4a) | | Horizontal alignment (Exp. 4b) | | Collapsed (Exp. 4a and b) | |
| | N | % | N | % | N | % |
| Correct quadrant | 52 | 65 | 52 | 66 | 104 | 65 |
| Left–right adjacent | 22 | 28 | 19 | 24 | 41 | 26 |
| Up–down adjacent | 6 | 7 | 7 | 9 | 13 | 8 |
| Opposite quadrant | 0 | 0 | 1 | 1 | 1 | 1 |

opposite-quadrant response.[3] The correlation was extremely high: .92 ($p < .001$). This finding rules out the possibility that the wrong-left–right-direction errors resulted from random responding or encoding of the target merely as 'tilted,' and strongly supports the conclusion that BC frequently made true left–right reflections in performing the task.

The scatterplot in Fig. 11 also gives evidence of imprecision: BC's responses rarely fell exactly on either the correct or the left–right reflection diagonal. For correct-quadrant responses, her mean absolute error was 12.7°, and for left–right adjacent responses the mean distance from the target's left–right reflection was 18.1°.

Whereas the data from Experiment 4 give clear evidence of left–right mirror reflections, and imprecise matching of target tilt magnitude, no clear evidence of up–down reflections was observed. Only 13 of BC's responses to oblique targets (8%) fell into the up–down adjacent quadrant (compared to 41 left–right adjacent responses). Furthermore, all 13 of the up–down adjacent responses involved target orientations within 30° of horizontal, and 10 of the 13 involved targets only 15° from horizontal. Given the imprecision in BC's responses, most or all of these responses could have resulted simply from imprecise reproduction of the target's tilt magnitude (rather than being true up–down reflections). For example, on one trial BC responded to a target of 75° (15° above horizontal) by setting her response line to 94° (4° below horizontal). This response may have resulted merely from imprecision in reproducing the 75° tilt magnitude, instead of being a true reflection of the target across the horizontal axis.

Inspection of Fig. 11 reinforces these points. Note that responses on or near the up–down reflection diagonals (the negative minor diagonal) occur only for targets near the horizontal orientations (−90° and 90°). Note also that these responses fall reasonably close to the correct response, suggesting that they may result from simple imprecision. Note in contrast that left–right reflections occurred not only for orientations close to the vertical axis, but also for far-from-vertical orientations (e.g., 45°). These latter errors clearly cannot be interpreted as resulting from simple imprecision. Hence, the results provide clear evidence of frequent left–right reflection errors but no clear evidence of up–down reflections. Conceivably, BC occasionally made true up–down reflection errors, but such errors, if any, were far less frequent and less flagrant than the left–right reflections.

To summarize, the present results confirmed the finding from previous experiments that BC exhibits imprecision and reflection errors in processing line orientation. In addition, the results establish that BC's reflection errors are predominantly if not entirely left–right reflections. This result is consistent with the findings from Experiment 1, which suggested that BC was more likely to confuse left–right reflections than up–down reflections.

## 8. Discussion

We investigated orientation perception in BC, a young woman who suffered bilateral occipital and parietal cortical damage at an early age. Results from four experiments revealed that BC was severely impaired in discriminating and reproducing line orientations, and that in addition to general imprecision, her errors involved left–right mirror reflections. We presented evidence to show that BC's impaired performance could not be attributed to her restricted visual field. Further, we demonstrated that the mirror-reflection errors were true mirror reflections, and not random responses or responses resulting from encoding of oblique targets merely as 'tilted.'

Additional results indicated that a visuo-motor impairment could not account for BC's error pattern. The four orientation experiments encompassed three different forms of response: same–different judgments (Experiment 1), turning a dial to adjust the orientation of a response line (Experiments 2 and 4), and turning a wooden stick to match the orientation of a target stick (Experiment 3). Despite the widely differing visuo-motor requirements, BC's performance pattern was consistent across tasks: imprecision in processing target tilt magnitude, and a strong tendency to mirror-reflect the target (with left–right reflections predominating in tasks that allowed us to distinguish left–right and up–down reflections). Furthermore, whereas visuo-motor deficits could conceivably cause reflection errors given some forms of response (e.g., drawing), it is not at all clear how visuo-motor impairment would lead to systematic mirror reflections with the dial-turning procedure used in Experiments 2 and 4. Finally, the same–different procedure in Experiment 1 did not require any form of visuo-motor response, yet still revealed difficulty discriminating similar tilt magnitudes and confusion of left–right mirror reflections.

Our findings are consistent with a large body of empirical research showing that humans and other animals confuse mirror-reflected oblique orientations more easily than oblique orientations that are not mirror-reflections, even when the degree of rotation between the stimuli is the same (Bornstein et al., 1978; Bornstein, 1982; Appelle, 1972; Corballis and Beale, 1976; Rudel, 1982). The results also extend findings from brain-damaged individuals with selective impairments in lateral mirror-image discrimination tasks with object and line stimuli (Riddoch and Humphreys, 1988; McCloskey et al., 1995; Turnbull and McCarthy, 1996; Turnbull et al., 1997; McCloskey and Rapp, 2000a, 2000b; Davidoff and Warrington, 2001; McCloskey, 2004; Riddoch et al., 2004).

Previous research has suggested that occipito-parietal areas of the brain are important for orientation perception and mirror-image discrimination, and patients with orientation impairments often have suffered brain damage to these areas (e.g., Turnbull and McCarthy, 1996; Davidoff and Warrington, 2001; Priftis et al., 2003; Riddoch et al., 2004). Given that BC's lesions implicate occipital and parietal regions, our results are consistent with these findings. However, because BC's brain damage is extensive and probably diffuse, and because we lack precise lesion localization data, we cannot draw strong conclusions about the specific lesion loci implicated in her impaired performance on the orientation tasks.

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[3] This correlation in effect collapses the upper left and lower right quadrants of the scatterplot into a single square region. Including opposite-quadrant as well as left–right-adjacent responses ensures that the area is in fact square, and hence that the correlation could in principle range from −1.0 to 1.0.

BC's reflection errors may be interpreted by assuming that the underlying orientation representations are compositional. We suggest that at some level(s) of mental representation the orientation of a line is represented relative to a reference axis (e.g., vertical), with tilt direction and tilt magnitude specified separately. For example, a line orientation of 45° clockwise from vertical might be represented as [*tilt direction* +], [*tilt magnitude* 45°]. Given these assumptions, BC's pattern of left–right reflection errors may be interpreted by assuming that she sometimes failed to represent the direction of tilt from a vertical reference axis. For example, she may sometimes have represented a target line tilted 45° clockwise from vertical only as [*tilt magnitude* 45°], and hence may have been equally likely to orient her response clockwise or counterclockwise from the vertical. The imprecision in BC's reproduction of tilt magnitude may be explained by assuming that whereas she is able to encode tilt magnitude, she does so with less than normal precision.

Most if not all of BC's reflection errors occurred in the left–right direction (i.e., across a vertical axis), suggesting that she represented line orientation relative to a vertical reference meridian. A horizontal reference axis might also be used for representing orientation; however, our data do not directly speak to this possibility, given that BC usually or perhaps always used a vertical reference meridian.

Our hypothesis concerning representation of line orientation may be viewed as an elaboration on theoretical suggestions offered previously in the literature. McCloskey et al. (1995), McCloskey and Rapp (2000a, 2000b) and McCloskey (2004) have suggested that mental representations of spatial locations have compositional structure. According to their hypothesis, spatial locations are represented in a mental coordinate system defined by reference axes projected from an origin, with direction of displacement from the origin specified separately from displacement distance for each axis. In addition, as mentioned earlier, Rudel and Teuber (1963), Olson and Hildyard (1977) and Rudel (1982) have suggested that oblique line orientations have a more complex representational structure than cardinal orientations do. In this paper we have postulated a representational system consistent with this suggestion, in which the complexity of obliques and the stability and priority of a vertical meridian become explicit and understandable. Finally, some authors (e.g., Riddoch et al., 2004) have discussed encoding of stimulus 'handedness' (which corresponds to tilt direction at least in the case of simple line stimuli) in terms suggesting that handedness might be represented separately from other aspects of orientation (e.g., tilt magnitude). (See McCloskey et al., 2006, for further discussion of orientation representation.)

Separate representation of tilt direction and magnitude relative to a vertical reference meridian might make a number of symmetry-related effects understandable. While the perspective in this paper so far has been on mirror images as stimuli problematic for the visual system, there is a second side to this coin. The visual system is specially tuned to recognize the principal meridians (e.g., Heeley and Buchanan-Smith, 1990), and symmetry with respect to the vertical is easier to detect than other symmetries (Herbert and Humphrey, 1996). Humans detect mirror symmetries more easily than other types of symmetries: the percept seems to emerge effortlessly and automatically under a wide range of tasks and conditions (Wagemans, 1995), and mirror symmetry can be computed from structures that can take on various orientations with respect to a vertical axis of symmetry (Rainville and Kingdom, 2000). Even neuropsychological patients with visual neglect who are incapable of making explicit symmetry judgments may nevertheless exhibit normal symmetry perception in tasks requiring figure-ground segregation (Driver et al., 1992). Presumably, detection of bilateral symmetry with respect to a vertical axis might be inherently easy for an organism that operates a visual system maintaining a level of representation at which the left–right direction of angular orientation is coded separately from the orientation's tilt (and left–right direction is coded separately from distance in location representations). A process monitoring whether [*direction* +] and [*direction* −] components are simultaneously activated with the same tilt value (in the case of orientation representations) or distance value (for location representations) could function as means of symmetry detection.

Finally, an interesting aspect of our results is that BC's reflection errors with lines also occurred with tactile stimuli. This finding indicates that vision and touch are both valid modes of input for the mental spatial coordinate system we have postulated for compositional representation of line orientations. Vision and touch are sense modalities that are known to share processing resources at a cognitive and at a physical level; for example, brain-imaging studies have demonstrated that tactile discriminations of orientation recruit visual cortical areas of the brain (Sathian et al., 1997), and that disrupting the function of the visual areas of the cortex with transcranial magnetic stimulation (TMS) interferes with tactile discrimination of orientation (Zangaladze et al., 1999). One possibility is that the locus of BC's orientation deficit is visual, but the tactile orientation task is performed using visual (or visual-like) representations constructed from the tactile input in the visual areas of the brain. Alternatively, it is also possible that the locus of impairment in BC is not purely visual, but rather arises at a higher, supra-modal level of representation.

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