ILLUSORY CONJUNCTIONS OF COLOR AND MOTION WITH SHAPE FOLLOWING BILATERAL PARIETAL LESIONS

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**Abstract**—The primate visual system responds to shapes, colors, and various other features more strongly in some brain areas than others. However, it remains unclear how these features are bound together so that an object with all its attributes is perceived. A patient (R.M.) with bilateral parietal-occipital lesions has been shown previously to miscombine the shape and color of items, making errors known as illusory conjunctions (ICs). In this study, we examined the effects of a third feature (motion) on this patient’s IC rates. R.M. was presented with two letters that moved in different ways. He often reported seeing the shape of one of the letters with the other letter’s motion. His performance on the same task with three features shows that correctly combining two features did not necessarily lead to correctly binding the third. These data support modularity of feature representations in the human brain and provide supporting evidence that spatial representations associated with the parietal lobe are necessary for normal feature integration.

An object has various properties, such as color, shape, and size. How does the visual system integrate these features when confronted with them in a cluttered scene? Treisman and Gelade’s (1980) feature integration theory (FIT) proposes that features are initially represented independently in different feature maps and then are bound together through spatial attention. If attention is not adequately focused on an object’s location, then features of that object may remain unbound or be miscombined with those of another object, producing feature conjunction errors known as illusory conjunctions (ICs).

ICs occur when viewers are shown a briefly presented display and attention is divided across the display (Treisman & Schmidt, 1982). For example, if a red X and a green S are presented between two task-relevant digits, a person may report seeing a red S. According to FIT, this occurs because spatial attention to the objects’ locations is compromised, affecting binding of the objects’ proper features (in this case, shape and color).

Although there have been different interpretations of IC rates in normal observers (e.g., Navon & Ehrlich, 1995), neuropsychological studies have found that impaired spatial attention and impaired spatial representation can increase the rate of ICs (Arguin, Cavanagh, & Joanette, 1994; Cohen & Rafał, 1991; Friedman-Hill, Robertson, & Treisman, 1995; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). Friedman-Hill et al. (1995) reported that a patient (R.M.) with intact primary vision but severe spatial deficits following bilateral parietal damage made errors combining shape and size and combining shape and color even when only two items were presented simultaneously for up to 10 s. They argued that intact ventral pathways that represent basic visual features of objects such as shape and color (Ungerleider & Mishkin, 1982) are not sufficient to account for normal binding abilities. Rather, the dorsal pathways’ representations of spatial information interact with the ventral pathways’ representations to produce the rapid perception of integrated objects. They proposed that R.M. had an impaired representation of space, and that this deficit caused his increased binding errors.

In the present experiment, we examined the effect of adding motion on R.M.’s feature integration of color and shape. There is evidence that motion of an object is a primary feature. First, in neurologically intact adults, motion of an item, like other features, causes it to “pop out” in visual search, whereas conjunctions of motion and color produce reaction time patterns indicative of serial search (e.g., Nakayama & Silverman, 1986; but see McLeod, Driver, & Crisp, 1988). Second, in a positron emission tomography study, Corbetta, Shulman, Miezin, and Petersen (1995) showed that searching for the conjunction of motion and color activates superior parietal and temporal lobes, but searching for targets defined by motion or color alone does not activate the parietal lobe although activation of the temporal lobe remains. Third, McLeod, Heywood, Driver, and Zihl (1989) showed that bilateral damage to the MT human homologue (occipital-temporal lobe; e.g., Zeki et al., 1991) impairs the ability to selectively attend to moving items but not to colored ones. Perhaps, then, motion perception may be normal while the ability to conjoint motion with other features may not be. Finally, it should be noted that R.M. spontaneously complained of seeing objects move (e.g., a house moving down the street) when he knew they were not moving. In other words, he may have experienced what might be considered real-world ICs of shape and motion. This perception of stationary objects as moving contrasts with the experience of a patient with bilateral ventral lesions, who lost the ability to perceive motion (e.g., she saw running water as a static icicle; Zihl, Von Cramon, & Mai, 1993).

We wanted to determine empirically (a) whether or not R.M.—whose inferior temporal areas are anatomically and, as far as we can determine, functionally intact—would make motion-color ICs, motion-shape ICs, or both under unlimited viewing conditions; (b) whether or not introducing motion would draw spatial attention and decrease color-shape ICs; and (c) whether R.M.’s patterns of results would implicate a problem with spatial representation or spatial attention. A patient with spatial representation deficits may represent the spatial locations of separate features erroneously or with abnormal variability, so focusing attention to the relevant location of one feature (which may be wrong) should result in an elevated IC rate. In a patient such as R.M., the proper binding of two features need not produce correct binding of a third if the deficit is in spatial representation. However, if spatial attention is affected directly, then once attention is directed to a location of one feature (e.g., shape), all other features at that location should be bound to that feature (in this case, shape).

**METHOD**

**Case Report**

R.M. was 54 years old when he suffered his first stroke from a likely embolic infarct in July 1991. In March 1992, he suffered a second, similar stroke that resulted in nearly symmetric bilateral
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Parietal-occipital damage, shown in Figure 1. The data presented here were obtained during testing that occurred almost 4 years after his second stroke. (See Robertson et al., 1997, for a more detailed description of his deficits, abilities, and mental status over this time period.)

In 1992, R.M. presented with Balint’s syndrome, sometimes known as dorsal simultagnosia (Balint, 1909; Farah, 1990), resulting in the inability to perceive more than one object at a time. Formal ophthalmological examination showed normal visual acuity, visual fields, color vision, and contrast sensitivity. Other tests revealed that R.M.’s perception of kinetic depth, structure from motion, and stereopsis in random-dot stereograms was normal, as was his sensitivity for dim lights. His symptoms included severe spatial localization deficits, optic ataxia, and an optic apraxia. These gradually improved, although not completely, by the time the data presented here were collected. At this time, he was able to see several objects at a time, and his reaching and eye movement abilities had improved, although they were still abnormally slow and inaccurate. He was living relatively independently, performing routine daily activities with only limited assistance. He was alert, motivated, and engaged throughout the testing sessions.

Stimuli

The stimuli were three uppercase letters (X, T, O), subtending approximately 1˚ of visual angle. They were presented with a notebook computer with an active color-matrix screen. Each letter could be printed in red, green, or yellow (in the color conditions) or white (in the monochrome conditions), and the background was black. Colors were not isoluminant. The letters could have one of three possible motion directions: static (no motion), horizontal, or vertical. Horizontal and vertical motion consisted of oscillation, moving 1˚ in one direction before reversing, at approximately 2˚/s. The initial direction of motion (up vs. down for vertical; right vs. left for horizontal) was randomized. In one task, the letters were replaced with filled circles. All stimuli were presented centrally on the screen. Each display was presented until R.M. responded, but for a maximum of 10 or 30 s, depending on the task. Eye movements were neither restricted nor formally monitored. The experimenter remained in the room throughout testing.

In the crucial conditions, two items were presented simultaneously. The items in these displays were positioned approximately 1˚ to 2.5˚ apart, depending on the motion directions and position of the items in the cycle.

Fig. 1. Three-dimensional reconstruction of R.M.'s magnetic resonance imaging (MRI). The lesions are nearly symmetrical. The dark areas in the lateral views (a) show damage to the parietal cortex, whereas the temporal lobes appear normal. The occipital view (b) demonstrates that the primary visual cortex is spared. One coronal MRI is shown in (c); the three-dimensional images were constructed from 3-mm slices of MRI images. Reprinted with permission from Friedman-Hill, Robertson, and Treisman (1995). Copyright 1995, American Association for the Advancement of Science.
Design, Procedure, and Tasks

All testing was done at the patient’s home during daylight hours. The room lights were off, and there was natural light from several windows, but no other attempt was made to control for lighting conditions. R.M. was seated approximately 50 cm from the computer monitor. He was presented with five double-item tasks. Figure 2 shows display schematics for four of these tasks and notes some examples of a correct conjunction, IC, and intrusion. Single-item versions of these same four displays (with tasks identical to those for the two-item displays) were included for purposes of comparison.

• **Conjunction of color with shape (two letters, two colors).** On each trial, two of the three possible letters were shown simultaneously. Both remained stationary. The letters shown in a trial were never identical nor the same color. (This was the case for all the tasks.) The task was to report first one letter (either one) and then its color. R.M. was never required to report on the shape or color of the other letter. The letters remained on the screen for up to 10 s.

• **Conjunction of motion with shape (two letters, two motions).** Two letters were shown simultaneously in white against a black background. Each letter moved either horizontally or vertically or was stationary. The task was to report first one letter and then its motion. The letters remained on the screen up to 10 s.

• **Conjunction of motion with color (two colors, two motions).** Two colored circles (in red, green, or yellow), each with one of the three motions, were shown. The task was to report only one color and its motion. The circles remained on the screen until a response was made or for 30 s. The time was increased as this task proved to be more difficult than the others.

• **Conjunction of color and motion with shape (two letters, two colors, two motions).** Two colored letters, with two types of motion, were shown simultaneously. The task was to report first one letter and then its color and its motion. The letters remained on the screen until a response was made or for 30 s.

• **Single-letter condition (one letter, one motion, one color).** Single-letter or -circle versions of the preceding tasks were presented to determine baseline performance.

• **Localization task (two letters).** Two letters were presented simultaneously for 10 s. R.M. was asked to report one letter and its location (right or left). The purpose of this task was to determine R.M.’s explicit awareness of the locations of the letters shown in the other tasks. The distance between the letters was 1.5˚ (average distance in previous tasks) or 5˚. We tested the 5˚ distance to determine whether R.M.’s performance would improve with larger separation.

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1. We attempted another experiment in which letters, colors, and motion were all present, but the instructions changed. In one case, R.M. was to report only one letter and its color. In another case, he was to report one letter and its motion, and in another, he was to report one color and its motion. However, R.M. could not easily omit naming the letter or the color under these conditions. For instance, he said, “Red X, moving up and down” even if instructed not to report the letter. He could not ignore the irrelevant dimension.

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Fig. 2. Schematics of four different displays. An (r) indicates that the item appeared in red, and a (g) indicates that the item appeared in green. If no color is indicated, the item appeared in white. The arrows indicate the direction of motion, and the absence of an arrow indicates that the item remained stationary. An example of a display requiring a conjunction of color with shape is shown in (a). The task was to name a letter and its color. An example of a correct conjunction is “X is red.” An example of a color intrusion is “X is yellow.” An example of a color illusory conjunction is “X is green.” An example of a display requiring a conjunction of motion with shape is shown in (b). The task was to name a letter and its motion. An example of a display requiring a conjunction of motion with color is shown in (c). The task was to name a color and its motion. An example of a display requiring a conjunction of color and motion with shape is shown in (d). The task was to name a letter, its color, and its motion.
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Letters, colors, and motions were counterbalanced; trials were blocked by task type, and trial order was randomized. Several different tasks were given each day, and the same task was given on more than one day. Order of the tasks was different across days. Because R.M.’s stamina varied, the number of tasks and trials varied from day to day. R.M. responded verbally, and the experimenter, who could not see what was presented, typed his responses on the keyboard.

Data Analysis

To correct for guessing, we subtracted intrusions (reporting a feature that is not present) from absolute ICs and then divided by the total number of trials to obtain an IC rate (Treisman & Schmidt, 1982). Also, we subtracted intrusions from correct conjunctions and then divided by the total number of trials to obtain a correct-conjunction rate. This calculation of the IC rate may overestimate the “true” IC rate (i.e., percept of miscombined features rather than percept of unbound features). However, models applied to R.M.’s earlier data using conservative guessing algorithms (Ashby, Prinzmetal, Ivry, & Maddox, 1996) showed that ICs between color and shape occurred regularly (Robertson et al., 1997). On some occasions, the features may have remained unbound and separate, but few intrusions occurred, suggesting that features of the display were registered accurately but not properly bound together. In addition, the rate of correct conjunctions is relevant to the issue of how R.M.’s binding errors may be related to problems with spatial representation or spatial attention. The data particularly crucial to this issue are the probabilities of an unbound third feature being reported given that two are correctly bound. Whether conjunction errors are due to true ICs or separate registration of features that are not properly bound is not critical in addressing this issue.

RESULTS AND DISCUSSION

R.M. performed all tasks well above chance levels, ranging between 35% and 99% accuracy. Chance performance is 7.2% to 22.1%, depending on the task. See Tables 1 and 2 for performance data for the two-item and one-item displays, respectively. For single-item displays, R.M.’s mean accuracy to identify a shape and its color, a

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Table 1. R.M.’s responses on all tasks with two-item displays

<table>
<thead>
<tr>
<th>Task</th>
<th>Total N</th>
<th>No. of correct conjunctions</th>
<th>No. of color ICs</th>
<th>No. of motion ICs</th>
<th>No. of shape intrusions</th>
<th>No. of color intrusions</th>
<th>No. of motion intrusions</th>
<th>Percentage of color ICs</th>
<th>Percentage of motion ICs</th>
<th>Total percentage correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Color with shape</td>
<td>281</td>
<td>250</td>
<td>27</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
<td>8.2</td>
<td></td>
<td>87.5</td>
</tr>
<tr>
<td>Motion with shape</td>
<td>576</td>
<td>451</td>
<td>106</td>
<td>8</td>
<td>20</td>
<td></td>
<td></td>
<td>14.9</td>
<td></td>
<td>74.8</td>
</tr>
<tr>
<td>Motion with color</td>
<td>216</td>
<td>114</td>
<td>75</td>
<td>0</td>
<td>27</td>
<td></td>
<td></td>
<td>22.2</td>
<td></td>
<td>40.3</td>
</tr>
<tr>
<td>Color and motion with shape</td>
<td>864</td>
<td>534</td>
<td>231</td>
<td>8</td>
<td>68</td>
<td>6.1</td>
<td>18.9</td>
<td>53.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. IC = illusory conjunction.

Table 2. R.M.’s responses on all tasks with single-item displays

<table>
<thead>
<tr>
<th>Task</th>
<th>Total N</th>
<th>No. of colors correct</th>
<th>No. of motions correct</th>
<th>No. of color intrusions</th>
<th>No. of motion intrusions</th>
<th>Percentage of color intrusions</th>
<th>Percentage of motion intrusions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single letter:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape and color</td>
<td>144</td>
<td>142</td>
<td>—</td>
<td>2</td>
<td>—</td>
<td>1.4</td>
<td>—</td>
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<tr>
<td>Single letter:</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Shape and motion</td>
<td>576</td>
<td>—</td>
<td>489</td>
<td>—</td>
<td>87</td>
<td>—</td>
<td>15.1</td>
</tr>
<tr>
<td>Single circle:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Color and motion</td>
<td>144</td>
<td>—</td>
<td>110</td>
<td>—</td>
<td>34</td>
<td>—</td>
<td>23.6</td>
</tr>
<tr>
<td>Single letter:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape, color, and motion</td>
<td>351</td>
<td>350</td>
<td>303</td>
<td>1</td>
<td>48</td>
<td>0</td>
<td>13.7</td>
</tr>
</tbody>
</table>

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shape and its motion, or a shape and its color and motion ranged between 76.4% and 99%. Intrusion rates for the color-shape displays were 1.38% (2/144) in the single-item condition and 1.42% (4/281) in the double-item condition. For the double-item motion-shape display, the intrusion rate was 3.5%. R.M. made a fairly large number of motion intrusions in the single-circle (23.6%), single-letter-with-motion (15.1%), single-letter-with-motion-and-color (13.7%), and double-circle (12.5%) cases. As motion is a translation over space, this result is not necessarily surprising. Even with the relatively large number of motion intrusions in the double-letter task in which shape, color, and motion were reported (68 out of 864 trials), R.M. did have a significant number of motion-shape binding errors that could not be accounted for by these intrusions or by his baseline performance in the single-item conditions. Performance in reporting the shape and color of a single letter was almost perfect, with no shape intrusions and only two color intrusions.

Before we report IC rates, it is important to note an assumption we made for calculating performance levels. Shape was assumed to be the primary, or anchor, feature to which the other features were bound. We adopted this assumption because R.M.’s instructions were to name the shape he saw first. This approach also seemed reasonable because R.M. made only one shape intrusion in 1,721 double-letter trials. Traditional clinical assessments of patients with Balint’s syndrome have assumed they perceive at least one object correctly because they are able to name the object, which can be done solely on the basis of shape. What they appear not to be able to do is perceive more than one shape at a time. Thus, shape seems to capture attention. They can see two colors at the same time if they occur in the same object (Humphreys & Riddoch, 1993). We also performed analyses assuming that color was the anchor because there were few color intrusions. Results were similar to those when shape was assumed as the anchor, and conclusions would be the same.

Figure 3 shows the IC rates in the four tasks with two-item displays. For the color-with-shape conjunction task, there was a significant color IC rate, t(4) = 4.4, p < .007 (one-tailed t test with session as the random variable); for the motion-with-shape conjunction task, there was a significant motion IC rate, t(3) = 7.6, p < .001. For these two tasks, R.M. made significantly more motion ICs (86 of 576 trials) than color ICs (23 of 281 trials), χ²(1) = 6.4, p = .01. The fact that there were motion ICs suggests that the process of binding an object’s motion to its shape is similar to the process of binding the object’s other features to its shape.

To determine whether the conjunction of color with shape is affected by introducing motion, we compared the IC rate in the color-with-shape trials with the IC rate in the color-and-motion-with-shape trials (shown in Fig. 3). Adding motion to the color-shape displays did not change the rate of color ICs (23 of 281 trials, or 8.2%, vs. 53 of 864 trials, or 6.1%), χ²(1) = 2.26, p = .13; nor did it change the rate of correct color-shape conjunctions (89% vs. 92%). Similarly, the addition of color did not change the shape-motion IC rate significantly (86 of 576 trials, or 15%, vs. 163 of 864 trials, or 19%), χ²(1) = 3.0, p = .09, nor the rate of correct shape-motion conjunctions (78% vs. 73%).

In the motion-color task, there was a high IC rate (48 of 216 trials, or 22.2%), although it was not significantly different from the motion IC rates in the other tasks, χ²(2) = 1.01, p = .32. Recall that two filled circles were used, meaning that the shapes were no longer distinct. This may have accounted for the increased difficulty in perceiving motion in this task. R.M. was asked to report the color and motion of one of the two circles. Because both items had the same shape, he was forced to choose either one color or one motion on which to base his second response. Given the low number of intrusion errors for color (0 of 216 trials in this task and 11 of 1,361 trials for double-item conditions overall), we can safely assume that color acted as the anchor in this task. If the circles in these trials competed for R.M.’s attention,
more conflict could have arisen in this case. Informal observation supported the increased difficulty reflected in the data. R.M. took longer and seemed to struggle before responding.

In sum, the overall results indicate that adding motion to the shape-color displays did not influence the color IC rate or the correct-conjunction rate for shape and color conjunctions. In addition, adding color to the shape-motion displays did not change the motion IC rate nor the correct-conjunction rate for shape and motion. The rate of correct binding and the rate of binding errors were about the same for these dual combinations across different tasks.

**IMPAIRMENT IN SPATIAL REPRESENTATION OR SPATIAL ATTENTION?**

Patterns of performance for multiple features have important implications for understanding the underlying mechanisms responsible for feature integration, as well as for understanding whether R.M. has primarily a spatial representation deficit (intact spatial attention with an impaired spatial map to guide it) or primarily a spatial attention deficit (intact spatial map with an impaired attentional system). As briefly described in the introduction, an explanation in terms of a simple spatial attention deficit would argue that if features are integrated through attention to their common location in space, a conjunction error occurs because attention is not adequately focused at that location. This implies that if one feature (e.g., color) is properly bound to a specified anchor feature (e.g., shape), attention is adequately focused at that shape’s location, and consequently, a second feature (or third or fourth) should also be properly bound to that anchor feature because all the features share the same location. Thus, if R.M.’s impairment is fundamentally an attentional one, we would expect that when he does manage to attend to an object’s spatial location and can correctly report two features of that object, he should be able to report other features at that location correctly as well.

Theoretically, the spatial attention explanation of IC rates is different from an explanation that emphasizes a spatial representation deficit as being the primary source of R.M.’s problems. An explanation based on a direct deficit in spatial representation predicts that correctly binding motion with shape need not increase the likelihood that color will be correctly bound with shape. If R.M.’s ICs result directly from an impairment in spatial representation, motion should either have no effect on combining color with shape or impair performance. On the one hand, motion could decrease performance because the introduction of motion adds variation in an object’s location over time, perhaps making it more difficult to integrate the other features. On the other hand, motion might have no effect if an object’s motion, like any other basic visual feature, is separately registered in feature maps, so that no single feature influences another’s likelihood of being correctly linked to the object’s shape. In either case, however, correctly binding one feature to another need not increase the rate of correctly binding other features because there is no reason to suppose that attending to a particular location will accurately provide all the feature information at that location on every trial. A “location” is likely represented inconsistently—or, in the extreme, not at all.4 Consistent with this notion, Table 3 shows that when letters were presented 1.5° apart, R.M. was at chance in reporting the location of one letter relative to another.

The question of whether correctly conjointing one feature with another affects the rate of correctly conjointing the third can be addressed most directly by the conditional analysis depicted in Figure 4. These data are from the task in which R.M. reported a letter shape, its color, and its motion while looking at the display. If R.M. accurately reported color of a shape on a particular trial, he was no more likely to report the motion of that shape correctly than he was to report motion of a shape correctly overall (67% vs. 65%). Similarly, when R.M. properly bound motion with shape, he was no more likely to properly bind color with shape (95% vs. 92%) than he was to bind color with shape correctly overall.

Figures 5 and 6 depict further subdivision of the conditional performance rates. R.M. made a correct motion-shape conjunction on 565 trials. Out of these, he made 534 correct color-shape conjunctions (94.5%) and 51 color-shape ICs (5.43%). R.M. made motion-shape ICs on 231 trials. Out of these, he made 204 correct color-shape conjunctions (88.3%) and 27 color-shape ICs (12%). The chi-square tests of significance indicate that motion performance (whether R.M. made a correct conjunction or an IC) is not predictive of correct color-shape conjunctions, χ²(1) = 1.11, p = .29 (see Fig. 5). There is a nonsignificant trend for motion performance influencing color ICs, χ²(1) = 3.1, p = .08. For the analogous comparisons of color-shape binding predicting motion-shape binding, see Figure 6. R.M. made a correct color-

3. A strong attention explanation of R.M.’s color-shape IC rate could predict that moving an object would help R.M. attend to the object’s location, thus improving his ability to conjoin its color and shape compared with the conditions with static letters. Direction of perceived motion does play a role in object identification in normal healthy subjects (Bernstein & Cooper, 1997), and there is evidence for an effect of spatial attention in such effects (Berlin, Cooper, & Robertson, 1998). However, motion did not influence R.M.’s perception: The proportion of color-shape IC errors was similar with and without motion (8.2% vs. 6.1%). In addition, R.M. was not more likely to report the moving letter when one moved and one was stationary (out of 576 trials, he named the moving letter 260 times, and his IC and intrusion rates were approximately the same as when both letters moved). This finding also questions the assumption that the motion used here attracted his attention. Casual observations by a clinical examiner indicated that motion attracts his attention, but the motion generated in clinical examination is typically long range and vigorous. Directing R.M.’s attention to motion seemed to take some time in the examination, and the motion was often accompanied by verbal direction, such as “Mr. M., please look over here.”

4. This prediction assumes that there are separate feature maps (Treisman & Gelade, 1980) and there is variability in spatial representations or variability in the mapping of feature locations onto locations on the master map. Such variability could be substantial in a patient such as R.M., who at one time could not report gross locations of letters that were more than 5° apart with better than chance accuracy (Robertson et al., 1997). This performance improved by the time of the present testing (see the location data in Table 3).

Table 3. **Localization performance (right-left discrimination) in two-item displays, as a function of degree of separation**

<table>
<thead>
<tr>
<th>Total N</th>
<th>Degree of separation</th>
<th>Percentage correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>72</td>
<td>1.5</td>
<td>54.15</td>
</tr>
<tr>
<td>36</td>
<td>5</td>
<td>82.3</td>
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shape conjunction on 795 trials. Of those trials, he made 473 correct motion-shape conjunctions (60%) and 140 (18%) motion-shape ICs. R.M. made 61 color-shape ICs. Of those trials, he made 26 correct motion-shape conjunctions (43%) and 29 motion-shape ICs (48%). (Note that because these numbers are corrected for intrusions, the percentages do not always add up to 100.) The analyses show that motion-shape accuracy was not significantly influenced by whether color was correct or not, \( \chi^2(1) = 2.5, p = .11 \). However, there was a significant difference between the motion IC rates as a function of color performance, \( \chi^2(1) = 12, p < .005 \). It should be noted that in this condition, there were relatively few color-shape errors (61 trials total, or 6.1%) from which to calculate these conditional rates, so the reliability of these estimates is questionable. Nevertheless, it is puzzling that color performance tended to influence motion performance even slightly (Fig. 6), but that motion performance did not influence color performance at all (Fig. 5). Whatever the reason for this asymmetry (low statistical power, weak asymmetrical link between features, or luminance information, e.g., Anstis, 1986), it is clear that on the majority of trials, conjoining two features accurately did not mandate the accurate report of a third.

**GENERAL DISCUSSION**

R.M. produced significant miscombinations of motion with shape, color with shape, and color with motion. R.M.’s errors cannot be attributed to memory problems because he could take as long as he wanted to respond and did so while looking directly at the screen. He responded with confidence. His errors cannot be explained by distractibility because he made no fewer intrusion errors when a single item was presented than when two items were presented. It is also unlikely that the long display times affected results. In a previous study (Roberson et al., 1997), there was no significant difference in R.M.’s IC rates with presentation times of 500 ms, 3 s, or 10 s.
Consistent with other findings in the literature (Corbetta et al., 1995; Nakayama & Silverman, 1986), R.M.’s results suggest that an object’s motion is similar to the object’s other features such as color and size in its need to be bound to object shape. The addition of motion did not influence the rate of shape-color ICs or correct conjunctions, and the introduction of color did not affect the rate of motion ICs or correct conjunctions. This pattern of results is consistent with these features being separately registered early in processing, so that an independent signal is needed to bind them together properly. This signal seems to require intact parietal lobes.

The conditional analyses are relevant to neuropsychological theories of spatial attention. Parietal damage may cause direct impairment of attentional processes (Cohen & Rafal, 1991; Coslett & Saffran, 1991; Kinsbourne, 1987; Posner, Walker, Friedrich, & Rafal, 1984) or indirect impairment due to alterations in underlying spatial representations (Bisiach & Luzzatti, 1978; Robertson et al., 1997). Our conditional analyses examined errors when the conjunction of three features was required (e.g., color and motion with shape). Examining the data in this way suggested that the integration of features was not strictly dependent; that is, the rate of accurately binding three features was not affected by accurately binding two features. Presumably, if R.M.’s IC rates were caused by a lack of attention to an accurately represented location, then when he correctly reported two of the object’s features, the third feature should also have been reported correctly, and this should have happened whether there was a true IC or separate percepts of the features. However, a faulty representation of space quite naturally explains the results. If the representation of features in space is variable, then focused attention to a particular location should be variable. Therefore, the features at that location will not necessarily be represented as having the same spatial information at the same time. We do not mean to imply that all ICs result from a problem with spatial representation, however. There may be cases in which attention is directly damaged while spatial representations remain intact.

The data presented here support the conclusion that the spatial functions of the parietal lobes play an important role in the perception of bound visual features. For normal observers, Corbetta et al. (1995) reported neuroimaging data consistent with this conclusion, but they attributed the effects to interactions between areas involved in serial spatial attention and areas involved in feature representation. Visual search for conjunctions of color and motion activated areas in the parietal lobes that were not activated in visual search of either feature alone. The current data suggest a somewhat different account. The spatial information represented by the parietal lobes would be critical in explicitly directing spatial attention, but it is also critical for properly binding visual features. If R.M.’s difficulties were directly due to a deficit in moving attention to the location of an intact spatial map, then once his attention colocated two features, the third should have been evident as well. However, if his difficulties resulted from an altered spatial representation, then each feature’s location would be either random or unknown. Variable temporal coupling between feature signals might then account for the relative independence of correctly perceiving color with shape and correctly perceiving motion with shape. The data reported here are consistent with the proposal that accurate feature binding requires a “master map of locations” (Treisman & Gelade, 1980). They also suggest that interactions between parietal lobes and other areas of the cortex that register features (e.g., occipital-temporal lobe) are involved in proper feature binding.

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REFERENCES


Perhaps future research will find synchronous firing between neurons in parietal areas that are responsive to spatial information and neurons in occipital-temporal areas that are responsive to motion, color, and shape information. Electrophysiological evidence for synchrony between distributed neurons has been reported (Gray & McCormick, 1996), although it has not yet been linked directly to perception. Crick (1994) also has speculated that the biological mechanism that supports feature binding is this synchronization.

5. Data with normal subjects (Bernstein, Kaiser, & Johnson, 1996) show dependence (i.e., that when color or motion is bound to shape, then motion or color, respectively, is also). This would be expected given normal subjects’ presumably intact spatial representations.


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