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Research Report

REPRESENTATION OF VISUOTACTILE SPACE IN THE SPLIT BRAIN

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Abstract—Recent neurophysiological research in the monkey has revealed bimodal neuronal cells with both tactile receptive fields on the hand and visual receptive fields that follow the hands as they move, suggesting the existence of a bimodal map of visuotactile space. Using a cross-modal congruency task, we examined the representation of visuotactile space in normal people and in a split-brain patient (J.W.) as the right arm assumed different postures. The results showed that the congruency effects from distracting lights followed the hand around in space in normal people, but failed to do so in the split-brain patient when the hand crossed the midline. This suggests that cross-cortical connections are required to remap visual space to the current hand position when the hand crosses the midline.

There has long been considerable interest (Harris, Blakemore, & Donaghy, 1980; Morrell, 1972; Russell, 1948) in how the brain achieves a common representation of space across different sensory modalities, such as vision and touch. Contemporary neuroscience has revealed bimodal cells that represent visual and tactile stimuli in approximate spatial register; such cells have been found in several areas of the cat and monkey brain, including the putamen, superior colliculus, ventral premotor cortex, and parietal area 7b (e.g., Graziano & Gross, 1993, 1996; Graziano, Yap, & Gross, 1994; Groh & Sparks, 1996; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Stein, Magalhães-Castro, & Kruger, 1975; Wallace, Meredith, & Stein, 1992). For instance, if such a cell is responsive to tactile stimuli on one hand, it will also respond to visual stimuli presented near the hand, and the visual receptive field (RF) of this bimodal cell follows the hand around in space as different postures are adopted (e.g., Graziano & Gross, 1993, 1996).

Studies in both normal people (Driver & Spence, 1998; Spence, Pavani, & Driver, 1998) and patients (di Pellegrino, Lådavas, & Farnè, 1997; Lådavas, di Pellegrino, Farnè, & Zeloni, 1998; Mattingley, Driver, Beschin, & Robertson, 1997) have provided evidence for similar neural representations of space in humans. For example, di Pellegrino et al. reported a patient with right fronto-temporal brain damage who failed to perceive tactile stimulation on his left hand whenever there was either simultaneous tactile stimulation to his right hand or visual stimulation near his right hand. That is, the visual and tactile events near the right hand extinguished the perception of the otherwise above-threshold stimulation to the left hand. Visual stimulation near the right hand still extinguished tactile stimuli presented to

the left hand when the patient crossed his hands, again suggesting that the visual RFs of bimodal cells are remapped when posture changes. The authors suggested that visual stimuli near the hand activate somatosensory representations of the hand through bimodal cells, like those found in the monkey brain. However, it is not clear at present whether in humans maintaining the registration of visuotactile space as posture changes relies on bimodal cells in cortical structures (such as ventral premotor cortex and parietal area 7b), subcortical structures (such as the putamen and superior colliculus), or both.

We addressed this issue by administering a cross-modal congruency task (Spence, Pavani, & Driver, 1998) to a patient who had his left and right cortices surgically disconnected (split-brain patient J.W.). For split-brain patients, the left hemisphere controls the right hand and receives direct visual projections from the right field. Similarly, the right hemisphere controls the left hand and receives direct visual projections from the left field. Therefore, in most situations, visual and tactile stimuli from the same spatial location map onto the same hemisphere (i.e., right hand and right field map onto the left hemisphere; left hand and left field map onto the right hemisphere). But what happens when a hand is crossed into the other field? For instance, if the right hand of a split-brain patient is placed in the left field, will visual events in the left field map onto the tactile RFs of the right hand, as they apparently do for the intact human brain (di Pellegrino et al., 1997; Driver & Spence, 1998)? If this normal remapping does not occur, then bimodal cells in cortical structures (e.g., ventral premotor cortex, parietal area 7b, or both)—which are disconnected in the split brain—would appear to be crucial for remapping the visual RF onto the tactile RF of the hand when it crosses the midline. Conversely, if this normal remapping does occur in the split brain, then bimodal cells in subcortical structures (e.g., putamen or superior colliculus)—which are shared between the disconnected hemispheres—would be implicated.

The cross-modal congruency task (Spence, Pavani, & Driver, 1998) involves making speeded tactile discriminations (deciding whether a touch is “above,” at the index finger, or “below,” at the thumb; see Fig. 1g) while a distracting visual stimulus is presented at the same elevation as the target or a different elevation. The typical finding is that people can discriminate the elevation of tactile targets more rapidly when the elevation of the visual distractor is congruent with the tactile target (either both up or both down) than when it is incongruent (tactile event on top and visual event on the bottom or vice versa). In the intact human brain, this cross-modal congruency effect depends on the irrelevant light appearing close to the stimulated hand, no matter whether the hand is placed in an uncrossed or crossed posture (Spence, Pavani, & Driver, 1998). That is, the visual RFs appear to follow the hands around in space as different postures are adopted. In the present study, we investigated whether similar results would occur for the disconnected human brain, assessing cross-modal congruency effects in J.W. and in 2 age-matched control participants under several different postures.

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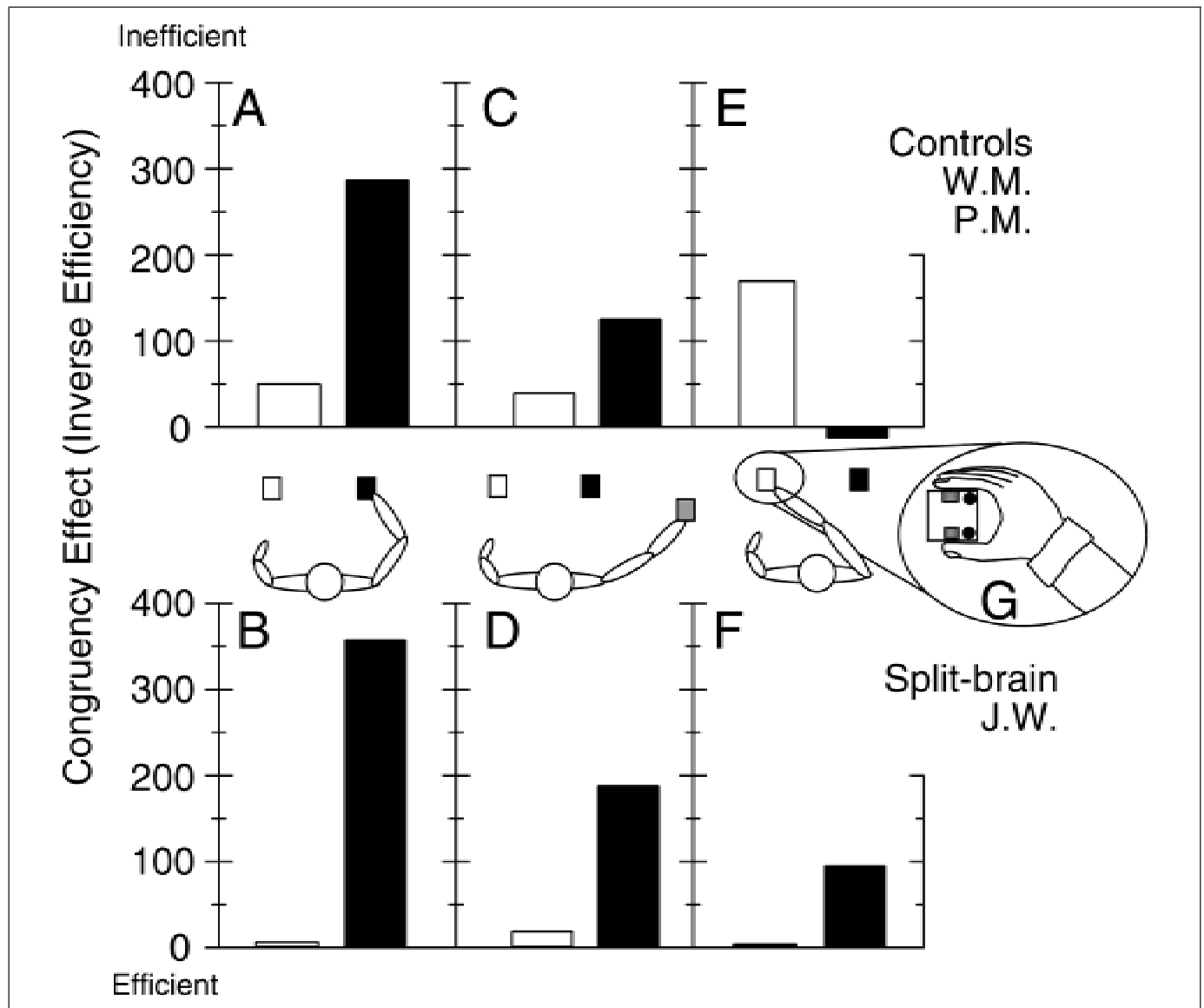


Fig. 1. Mean cross-modal congruency effects for the control group (a, c, and e) and split-brain patient J.W. (b, d, and f) as a function of the posture adopted and the position of the visual distractor. On each trial, the participant held a sponge cube in the right hand and was asked to judge the elevation (top vs. bottom) of a tactile stimulus; a visual distractor might be presented on either the left or the right sponge immediately in front of the participant (shown here as white and black squares, respectively), and could appear in either of two locations (top vs. bottom). Results are shown separately for when participants held the right sponge (a, b), a sponge even further to the right (c, d), or the left sponge (e, f). Inset g shows a right hand holding a sponge cube with vibrotactile stimulators (shaded rectangles) and visual distractor lights (black circles). In the graphs, the white bars represent performance when distractors were presented on the white cube, and the black bars represent performance when the distractors were presented on the black cube. The congruency effects represent a difference score: performance on incongruent-distractor trials (i.e., trials on which the target and distractor appeared at different elevations) – performance on congruent-distractor trials (i.e., trials on which the target and distractor came from the same elevation), measured in terms of inverse efficiency (average response time divided by the proportion correct for each condition; Townsend & Ashby, 1978, 1983), which combines speed and accuracy to allow comparisons among conditions uncontaminated by possible speed-accuracy trade-offs (cf. Aktar & Enns, 1989; Christie & Klein, 1995; Kennett, Eimer, Spence, & Driver, in press; Murphy & Klein, 1998).

METHOD

J.W. is a 45-year-old male who had intractable epilepsy since 1972. His corpus callosum was sectioned in 1979, with the anterior commissure left intact (see Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981, for a detailed description of J.W.'s neurological status).

J.W. and 2 age-matched, neurologically normal control participants held a sponge cube between the thumb and index finger of their right hand while adopting one of the three postures shown in Figure 1. While fixating a central fixation point (with an experimenter moni-

Visuotactile Space in the Split Brain

toring), participants were presented with a random sequence of 128 suprathreshold tactile stimuli presented unpredictably to the forefinger (up) or thumb (down) of the right hand in each posture. Participants made speeded discrimination responses regarding the elevation (up vs. down) of these tactile stimuli using their right foot (toe = up, heel = down), so tactile targets and pedal responses were confined to the same left hemisphere. On each trial, a distracting visual stimulus was also presented, at one of four possible locations (top or bottom of either of two cubes placed to the left or right of the participant). The locations of the tactile target and visual distractor were completely independent, and the visual and tactile stimuli on a given trial could be at either the same or different elevations. Participants were instructed to ignore the lights as much as possible.

RESULTS

The results were very clear. When control participants and J.W. held the right cube in their right hand, cross-modal congruency effects were larger for lights on the right (near the hand) than for lights on the left (which were far from the hand; see Figs. 1a and 1b). This result is consistent with the proposal that visual stimulation near a hand activates its somatosensory representation, hence causing interference when tactile and visual stimuli occur at different elevations (di Pellegrino et al., 1997). Cross-modal congruency effects from the light on the right were reduced when either control participants or J.W. (Figs. 1c and 1d, respectively) moved their right hand further to the right (but still within the same hemispace), presumably because the tactile target and visual distractors no longer occupied the same spatial location. Thus, both groups showed evidence of sensory remapping as the right hand moved within the right hemifield. When the right hand crossed over to left hemispace, control participants showed larger cross-modal congruency effects from lights on the left than from lights on the right (Fig. 1e). This change of posture led to very different results for J.W. (Fig. 1f): The lights on the right still elicited larger congruency effects than the lights on the left, even though the lights on the right were no longer near the relevant tactile targets on the right hand, which now lay in left hemispace. This clear failure to remap across the midline strongly supports the role of cross-cortical connections in maintaining an up-to-date bimodal representation of visuotactile space.

DISCUSSION

Several previous studies have compared uncrossed and crossed postures in the split brain to address questions concerning the spatial coding responsible for particular effects (e.g., Aglioti, Tassinari, & Berlucchi, 1996), especially stimulus-response spatial-compatibility effects, such as the Simon effect (see Simon, 1990, for a review). However, note that stimulus-response compatibility cannot explain our cross-modal congruency effects, because we always ensured that not only the required discrimination (up vs. down) but also the required response (toe vs. heel) was orthogonal to the direction in which target and distractor position were varied (i.e., same vs. different eccentricity). Moreover, J.W.'s failure to remap visuotactile space cannot have been caused by his left hemisphere "not seeing" the lights on the left (which project initially to the right hemisphere), because numerous studies have shown that J.W.'s left hemisphere not only is aware of spatial information on the left side of extrapersonal visual space, but can direct spatial attention there as well (Gazzaniga, 1987;

Holtzman, 1984; Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995), presumably because of interconnections between cortical and subcortical visual areas (rather than via cortico-cortico connections; see Bittar, Ptito, Faubert, Dumoulin, & Ptito, 1999; Hazrati & Parent, 1991). Moreover, neurophysiological findings in the monkey have shown that midbrain structures, such as the superior colliculus and putamen, do remap visuotactile space following changes in posture such as moving the eyes (Groh & Sparks, 1996) or hands (Graziano & Gross, 1993).

Several researchers have reported that elevation-discrimination responses for tactile targets presented to the left or right hand can be facilitated by the prior presentation of a spatially nonpredictive visual cue from the same side (e.g., Chong & Mattingley, 2000; Kennett, Eimer, Spence, & Driver, in press; Spence, Nicholls, Gillespie, & Driver, 1998). These cross-modal exogenous cuing effects typically last for 100 to 300 ms after the presentation of the visual cue. There are, however, several reasons why the present findings should probably be thought of in terms of cross-modal congruency effects rather than in terms of cross-modal cuing effects per se. First, cross-modal cuing effects tend to facilitate responses to all targets presented at the same azimuth as the cue (i.e., no matter what their elevation; see Chong & Mattingley, 2000; Spence & Driver, 1997; Spence, Nicholls, Gillespie, & Driver, 1998). Therefore, any cross-modal cuing effects in this study would be expected to facilitate responses to both congruent and incongruent tactile targets occurring on the same side as the visual distractor. Second, the slowest responses are typically reported on trials on which the visual distractor appears on the same side as the tactile target but at an incongruent elevation (e.g., Spence, Pavani, & Driver, 1998); this pattern of results is also more consistent with an explanation based on cross-modal congruency than with an explanation based on cross-modal cuing. Finally, cross-modal cuing effects are typically much smaller in magnitude than the interference effects reported here (e.g., see Spence & Driver, 1997; Spence, Nicholls, Gillespie, & Driver, 1998). These considerations suggest that although the visual distractors in the present study probably elicited a cross-modal shift of tactile attention to the distractor location, the interference effects reported primarily reflect the effects of cross-modal congruency instead (i.e., response competition between the target and distractor on incongruent trials).

Our results provide direct support for the proposal, made by di Pellegrino et al. (1997), that visual stimulation near a hand activates its somatosensory representation. The results also show that the region of visual peripersonal space that must be stimulated to produce this somatosensory activation in normal people moves with the hand as different postures are adopted, just as reported for bimodal single cells in the monkey brain (Graziano et al., 1994; Graziano & Gross, 1993, 1996; Groh & Sparks, 1996). These results demonstrate for the first time that cross-cortical connections are required for the maintenance of an accurate representation of visuotactile space. It appears that without these cross-cortical connections, the RFs of bimodal neurons do not move in register with the hand when it crosses over the midline.

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