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Taking the high road on subcortical transfer

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Abstract

Kingstone and Gazzaniga (1995) presented conceptually ambiguous word pairs, such as HOT–DOG, to a split-brain patient. Each hemisphere received only one of the words. With one hand, the patient drew the word pairs literally (e.g., a dog panting in the heat) but never drew the emergent object (e.g., a frankfurter in a bun). This finding suggested that each hemisphere has a remarkable capacity to switch control of the same response hand. The present study tested this idea directly. The results indicated that each hemisphere could draw words with either the contralateral or the ipsilateral hand. This capacity of disconnected hemispheres to switch control of the response hand can create the illusion of subcortical transfer of higher-order information and must be taken into account in studies with split-brain patients.

1. Introduction

Patients who suffer from intractable epilepsy sometimes undergo surgical section of the cerebral commissures. Disconnection of the two hemispheres not only provides control over the patient's epilepsy, it also provides a unique opportunity to examine each cerebral hemisphere in isolation as well as allowing for determining what information, if any, is passed subcortically between the hemispheres.

In the prototypical split-brain study, visual information is presented to either one or both visual fields. In this fashion, left visual field (LVF) information is processed by the right hemisphere (RH), and right visual field (RVF) information is processed by the left hemisphere (LH). Typically, when manual responses are required, left-hand responses are more accurate for LVF (RH) stimuli, and right-hand responses are more accurate for RVF (LH) stimuli, indicating that control of a response hand is preferentially lateralized to the contralateral (opposite) hemisphere.

Over the years, there have been numerous studies demonstrating that only crude perceptual information can be transferred subcortically between the disconnected hemispheres. In recent years, however, there have been reports suggesting that higher-order perceptual information can be transferred subcortically between the hemispheres (see Seymour, Reuter-Lorenz, & Gazzaniga, 1994 for an excellent review). Recently, Kingstone and Gazzaniga (1995, Experiment 1) reported an intriguing new finding that appeared to demonstrate unequivocally that subcortical transfer of higher-order information does occur between the disconnected hemispheres. Two words were presented briefly, one to each field, e.g., the word "TEN" appeared in the RVF (LH) and "CLOCK" in the LVF (RH). When asked to draw what was presented, a split-brain patient drew with one hand a picture of a clock set to 10 o'clock. This, and many findings like it, suggested that the word information that was divided between the disconnected hemispheres was transferred subcortically, combined, and then drawn.

In Experiment 2, this subcortical explanation of the "integration phenomenon" was tested with conceptually ambiguous word pairs, such as HOT–DOG. These word

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pairs could be depicted literally (e.g., a dog panting in the heat) or they could be integrated to form an emergent object (e.g., a frankfurter in a bun). The subcortical transfer explanation predicted that emergent illustrations would occur. Kingstone and Gazzaniga, however, found that although literal combinations of the words were frequently drawn, emergent illustrations were never drawn. These authors concluded that a subcortical transfer explanation of higher-order information was not supported. In its place, they speculated that the integration phenomenon is a remarkable demonstration of each hemisphere rapidly switching control of the same response arm and hand. Such an account, if correct, would require that each hemisphere be capable of drawing its word item both with the contralateral hand (as is normally understood) and with the ipsilateral hand (as has been speculated). The aim of the present study was to put this proposal to a direct test.

2. Method

Commissurotomy patient JW participated in the study. JW is a 46-year-old right-handed male who suffered from intractable epilepsy for seven years before his corpus callosum was sectioned surgically in 1979. Both his hemispheres comprehend English, although speech is lateralized to his LH (see Gazzzaniga, Nass, Reeves, & Roberts, 1984 for a detailed description of JW).

JW was positioned 57 cm from the computer screen and fixated a central dot. On each trial he was instructed by the experimenter to focus on a central fixation point. The experimenter initiated each trial, resulting in one or two words (mean frequency of 265 per million) being presented for 150 ms (see Table 1A). JW then drew a picture of what he saw. The experimenter removed the drawing from the drawing pad and instructed JW to prepare for the next trial. When central fixation was achieved, a new trial was initiated. When two words were presented they might be divided between visual fields (bilateral presentation) or occupy the same visual field (unilateral presentation). Words were capitalized (subtending $1^\circ \times 0.6^\circ$) and lateralized 4°; when two words were presented to the same field they were positioned symmetrically about the horizontal meridian with the center-to-center separation between words measuring 4°. One- or two-word presentations were determined randomly. For one-word, and two-word unilateral presentations, the visual field was selected at random.

Most people, including split-brain participants, look at the picture they are drawing. When visual feedback of a drawing is permitted, both hemispheres of a split-brain subject can observe what is being drawn. To assess whether this visual feedback has any effect on what word information was drawn, we controlled whether or not the split-brain subject could observe what was being drawn. In one condition, visual feedback of the drawing was excluded by positioning a paper screen ($10''$ high $\times$ $3'$ long) $6''$ away from the subject, and $4''$ above the table top. The screen blocked JW's view of his drawings, but it did not interfere with his drawing movements nor did it block his view of the display screen.

Table 1A
Three- and four-letter words used in the present study

GUN	PAN	POT	CUP	BEE
DOG	JET	PIG	HAT	TUB
LION	HOOK	BOOK	SHOE	BALL
BULL	WORM	FISH	HILL	GATE
DUCK	LOCK	COMB	BIKE	ROOF
LAMP	DISH	STAR	DOOR	BOOT
SHED	PIPE	MOON	DESK	ROCK
BABY	BOAT	SLED	PONY	FORK

Within each of the two feedback conditions, the split-brain patient either knew, or did not know, in advance which hand he would be asked to use for drawing. Feedback and drawing-hand knowledge were crossed to produce 6 blocks of 40 trials. In each block of 40 trials, the 40 possible words were presented twice, once in each hemisphere, in random order. The test order was as follows: no visual feedback with left-hand drawing only; no visual feedback with right-hand drawing only; visual feedback with right-hand drawing only; visual feedback with left-hand drawing only; no visual feedback, drawing hand unknown; visual feedback, drawing hand unknown. In the conditions when drawing hand was unknown, the split-brain patient was informed which hand to use for drawing immediately after the stimuli had been presented. Rest breaks of 10 min separated each block. Each block lasted approximately 30 min.

3. Results and discussion

Drawings were assigned to one of two possible categories (i) the drawn word indicated contralateral control of the response hand (e.g., a LVF word projecting to the RH was drawn by the left hand), and (ii) the drawn word indicated ipsilateral control of the response hand (e.g., a LVF word projecting to the RH was drawn by the right hand). This scoring was performed independently by the two authors (with an interrater reliability of 100%). Initial analysis of the data categorized by presentation (uni/bilateral), field (LVF/RVF), visual feedback (yes/no), and drawing hand (blocked/mixed) turned out not to be significant (all chi squares <.50). These data were then collapsed across conditions yielding the data in Table 1B.

Table 1B represents the results of the 200 trials with the unilateral presentations of word or words. The percentages of words drawn by the contralateral (87.5%) and ipsilateral (62.5%) response hand were significantly

Table 1B
Number of times (and percentage) JW demonstrated contralateral and ipsilateral control of the drawing hand for one-word and two-word unilateral presentations

	Contralateral hand control	Ipsilateral hand control
Correct trials/total trials (%)	105/120 (87.5%)	50/80 (62.5%)

greater than zero (both $ps < .001$), although the percentage of words drawn by the contralateral hand was significantly greater, as would be expected, than the percentage of words drawn by the ipsilateral hand ($\chi^2 = 11.87$). Interestingly, though, this difference between hemispheric control of the contralateral and ipsilateral hands was only significant for right-hemisphere control (RH; contralateral 75% versus ipsilateral 35%: LH; contralateral 100% versus ipsilateral 90%). This means that the left hemisphere was able to control the ipsilateral hand nearly as well as the contralateral hand, replicating Kingstone and Gazzaniga's previous finding that hand control is preferentially lateralized to the dominant left hemisphere.

Forty trials included bilateral presentation of words, one-word presented simultaneously to each visual field. JW never drew both words as he did in the original Kingstone and Gazzaniga (1995) study, but the two words in this study were never meant to complete a single object (e.g., "TEN" and "CLOCK") and we never pressed JW to draw more objects than he was naturally inclined to draw. Even in the trials in which two words were presented simultaneously to one visual field, JW only drew both words in 8 out of the possible 80 trials. All 8 of those drawings were done by the left hemisphere (7 with the contralateral right hand and 1 by the ipsilateral left hand). Interestingly, though, in 3 of the 20 bilateral presentations in which the pen was placed in his left hand, the left hand drew the word presented to the left hemisphere (RVF) instead of the word simultaneously presented to the right hemisphere (LVF). The right hand always drew the word presented to the left hemisphere (RVF). So, in cases of competition between the hemispheres for control of a hand, the hemisphere contralateral to the hand dominated except in the few cases where the left hemisphere actually won control of the ipsilateral hand.

Together these findings provide a compelling demonstration that each hemisphere of a split-brain patient can exert control over the contralateral and ipsilateral response hand. In doing so, the present study highlights a suggestion originally advanced by split-brain investigators that has tended to be overlooked by researchers across the subsequent decades - the distinction between controls of distal versus proximal musculatures by disconnected hemispheres. Exclusive control of the opposite hand by a hemisphere appears to be limited to the distal muscles used typically for fine motor movements; a disconnected hemisphere is able to exert control of the proximal muscles for *both* arms and hands (Gazzaniga, Bogen, & Sperry, 1962) sufficient for rough drawings. In sum, the present investigation provides strong and direct empirical support for the proposal advanced by Kingstone and Gazzaniga (1995) that there exists a remarkable capacity of the left and right hemispheres to switch control of a response hand/arm. This capacity to switch control of the response hand can create the illusion of subcortical transfer of higher-order information and must be taken into account in studies with split-brain patients.

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