RESEARCH ARTICLES

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Visual and tactile interhemispheric transfer compared with the method of Poffenberger

Abstract In a simple manual reaction time task, reaction times are longer if the responding hand and visual field of the stimulus are contralateral than when the hand and field are ipsilateral. This small crossed vs. uncrossed difference (CUD) has often been attributed to the interhemispheric transmission time incurred when the hemisphere receiving the sensory input is not the one initiating the motor response. We assessed the generality of the visual CUD by comparing it to the CUD for tactile stimuli. Visual and tactile CUDs did not differ significantly in magnitude, and in both modalities the CUD showed a strong asymmetry, with a positive CUD occurring only for the left hand. This outcome indicates that the properties of the visual CUD are not determined by neural pathways, or hemispheric asymmetries, that are specific to the visual system.

Keywords Poffenberger · Somatosensory · Asymmetry · Lateralized · Handedness

Introduction

In a simple manual reaction time task, when the responding hand is contralateral to the hemifield of a visual stimulus, reaction times (RTs) are longer than when the responding hand is ipsilateral with the hemifield of the stimulus. This crossed vs. uncrossed difference (CUD) was first described by Poffenberger in 1912, and is

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generally found to be in the range of 2–6 ms, averaging about 3 ms (for reviews see Bashore 1981; Marzi et al. 1991). The CUD has often been attributed to the interhemispheric transfer time (IHTT) when the hemisphere which receives a sensory input is not the one initiating a motor response, and more specifically to the time required for information to cross the corpus callosum (e.g. Berlucchi et al. 1971, 1995; Marzi et al. 1991; Milner and Lines 1982; Poffenberger 1912; see Berlucchi et al. 1995 for an overview). The fact that the CUD jumps into the range of 12–50 ms in acallosal subjects (Aglioti et al. 1993; Clarke and Zaidel 1989; Distefano et al. 1992; Jeeves 1969; Milner et al. 1985) and 30–90 ms in subjects in whom the corpus callosum has been sectioned (Aglioti et al. 1993; Clarke and Zaidel 1989; Distefano et al. 1992; Marzi et al. 1999; Sergent and Myers 1984; Tassinari et al. 1994) lends credence to this interpretation. However, there has been a good deal of uncertainty regarding the nature of the transferred information. Most investigations that have addressed this issue have concluded it is likely to be motor in nature (Berlucchi et al. 1971; Forster and Corballis 1998; Milner and Lines 1982), since the CUD is largely unaffected by sensory factors such as luminance and visual eccentricity. On the other hand, Volpe et al. (1982) found no crossed visual control of finger responses in patients in whom the posterior 3 cm of the callosum (splenium) was sectioned, and Tassinari et al. (1994) failed to find evidence of an increased CUD in partial callosotomy patients with an intact splenium. Since the information transferred across the splenium is primarily visual, Tassinari et al. (1994) have proposed that simple, speeded manual responses can be mediated by the transfer of either sensory or motor neural signals. Bisiacchi et al. (1994) have made a similar proposal, arguing for a "horse-race" model in which crossed responses can be initiated by either sensory or motor signals.

Explanations of the CUD based upon interhemispheric delays are further complicated by the frequent appearance of reports showing that the CUD has a response-hand dependent asymmetry. Specifically, when the right hand is responding, the CUD is typically smaller than when the

left hand is responding (Bisiacchi et al. 1994; see Braun 1992 and Marzi et al. 1991 for meta-analyses). In his meta-analysis, Marzi et al. (1991) found a mean cross-study CUD of 2 ms when responses were made with the right hand, and 5.8 ms when responses were made with the left hand. Attempts to measure the CUD using evoked potentials have also provided indications of this asymmetry (Brown et al. 1994; Rugg et al. 1984; Saron and Davidson 1989; see Brown et al. 1994 for a review). Explanations of this asymmetry based on a right hemisphere advantage for light detection and/or left hemisphere advantage for manual responses are possible (see "Discussion"), but Bisiacchi et al. (1994) failed to find evidence of such specializations in a simple RT task. Marzi et al. (1991) have proposed this asymmetry may reflect a basic asymmetry in callosal transmission rates, and Saron et al. (2002) have suggested that such a callosal asymmetry could derive from asymmetries in occipital cortex, which would result in an asymmetric number of callosal projections.

A potential problem for callosal relay models of the CUD is that 3 ms is near the lower limit of possible transmission rates for the largest fibers in the corpus callosum (Aboitiz et al. 1992; Ringo et al. 1994), with only 5–15% of callosal fibers falling in this size range (Aboitiz et al. 1992; Tomasch 1954). It is therefore not surprising that electrophysiological investigations of callosal transfer rates yield longer estimates of interhemispheric transmission times than simple RT measures (Brown et al. 1994; Meyer et al. 1995; Rugg et al. 1984; Saron and Davidson 1989), although this difference is more pronounced in posterior than central cortical regions (e.g., Rugg et al. 1984). Moreover, electrophysiological measures of the CUD have been found to be uncorrelated with simple RT measures (Saron and Davidson 1989). Choice RT paradigms have also yielded longer CUDs than simple RT measures (Bashore 1981; Filbey and Gazzaniga 1969; although see Brysbaert 1994). Considerations such as these have led some investigators to suggest that the CUD for simple RTs may not really be a measure of the callosal IHTT, and alternative accounts of the CUD have been proposed (Braun et al. 1996; Kinsbourne 1974; Saron et al. 2002; Swanson et al. 1978). However, more recent studies utilizing transcranial magnetic stimulation have produced estimates of callosal transfer rates that are commensurate with the RT based estimates. These studies demonstrate that interhemispheric facilitation and inhibition of motor responses can appear with latencies as short as 4 ms (Ferbert et al. 1992; Hanajima et al. 2001; Daskalakis et al. 2002).

Almost all investigations of the CUD have employed visual lateralized targets. We were curious to what extent the properties of the CUD might depend on the use of visual stimuli. If the CUD is normally mediated by the transfer of strictly motor signals across the corpus callosum, one would not expect its properties to be tied to a particular sensory modality. However, to the extent that the CUD is mediated by the interhemispheric transfer of sensory signals, its characteristics could be modality dependent. For example, if the CUD asymmetry is related to asymmetries in visual cortex, the asymmetry might not be present in a non-visual modality. Moreover, in addition to the primary geniculostriate visual pathway there are several secondary visual pathways (see Cowey and Stoerig 1991 for an overview) that could potentially contribute to the visual CUD's brevity. Lines et al. (1992) suggested on the basis of evoked potential data that a pathway to extrastriate cortex might contribute to simple visual RTs. Somatosensory stimuli provide an alternative modality for studying the CUD. Like the visual pathways, the projection pathways for somatosensory input are also primarily crossed (Martin and Jessell 1991). A few investigations have addressed the CUD for simple RTs to somatosensory stimuli (Kaluzny et al. 1994; Moscovitch and Smith 1979; Muram and Carmon 1972; Peters 1982; Schieppati et al. 1984). However, no study has been specifically designed to compare visual and tactile CUDs. We know of only one investigation (Moscovitch and Smith 1979) in which both visual and tactile CUDs were measured, but the effects of sensory modality on the CUD were not this study's primary concern, and differences between the modalities were not statistically evaluated. In addition, previous studies of the tactile CUD delivered somatosensory stimulation to the responding limb, leaving open the possibility that local sensorimotor interactions, such as sensory feedback from the subject's motor responses or noncortical reflex arcs, could have influenced the crossed vs. uncrossed difference. In order to directly evaluate whether there are aspects of the visual CUD that are specific to vision, the current study measures and compares CUDs in the visual and somatosensory domains. To minimize any possible local sensorimotor interactions, we also delivered our tactile stimuli to a site that was always spatially removed from the responding hand.

Methods

Visual stimuli were presented with a Hewlett Packard 1310A X-Y monitor. This monitor is essentially a large screen (48 cm diagonal) oscilloscope and the unit we employed was customized with a P15 phosphor that had a luminance decay time to 1% of <12 µs. The monitor was driven by fast digital to analog converters controlled by a PC. With this arrangement, we were able to achieve a display refresh rate of 1,000 Hz, and avoid the potential RT artifacts associated with the increased brightness that has been reported (Ratinckx et al. 2001) on the right side of conventional raster-scan displays.

Eight subjects ranging in age from 20 to 57 years participated in this study, which was approved by the Dartmouth Committee for the Protection of Human Subjects. All subjects gave their informed consent prior to being included, and they were specifically informed that they could withdraw at any time without penalty. Six of the eight were right handed, based on a shortened version of the Edinburgh Handedness Inventory (Oldfield 1971). Each subject performed a sequence of 16 separate experimental blocks, distributed across four testing sessions, in which the sensory modality (visual vs. tactile) and the response hand (left vs. right) were counterbalanced. Each block contained 96 trials, with a random sequence of 48 target presentations ipsilateral to the responding hand and 48 presentations contralateral to the responding hand. Subjects sat at a table in a darkened room 57 cm from the

screen of the 1310A monitor, which displayed a stationary central fixation point. They viewed the display binocularly. A soft-click response button was positioned on the table at their midline. Subjects rested the index finger of their responding hand on the button. On each trial, the fixation point turned to a 1/2 degree X for 100 ms as a warning that the trial was starting. After a variable delay, ranging from 500 to 1,500 ms, a visual or tactile target stimulus was presented. Each block contained a random sequence of 48 left and right side targets. Subjects were instructed to respond as quickly as possible to the target by pressing the button.

In the visual blocks, the target was an outline square (10 arcmin a side) presented on the horizontal meridian 5° to the left or right of the fixation point for 20 ms. The lines that formed the target had a luminance of 5.5 cd/m^2, and were presented against a nominally black background. The visual display was refreshed at 1,000 Hz.

In the tactile blocks, the target was a small tap delivered to the subject's left or right dorsal mid-calf by a tactile stimulator which consisted of 2.25" 8-Ω speaker with the paper cone removed. We chose stimulation locations that were distant from the hands to eliminate potential confounds due to sensorimotor interactions, such as the compatibility effects reported by Broadbent and Gregory (1965). The taps were produced by applying a 20 ms AC-coupled pulse to each speaker. The backs of the speakers were covered with a sound absorbing foam jacket, and held snugly but comfortably against the subject's leg by a Velcro strap. Despite the foam jackets, they produced a barely audible click when the pulse was administered. To mask this click, subjects wore headphones that delivered continuous pink noise. For uniformity, the pink noise was also delivered during the visual trials.

Since there was bound to be some variability in the absolute strength of the stimuli when we strapped the tactile stimulators to the legs of our subjects, we adjusted the left and right tactile stimuli to subjective equality prior to each tactile block. At the start of these blocks, repetitive pulses were delivered alternatively to the left and right stimulators with a 1-s ISI. The pulse voltage to the stimulator that was judged weaker was increased until the subject reported that the magnitude of the taps felt identical.

Responses were recorded on an IBM PC with a resolution of 1 ms. Responses shorter than 100 ms were considered anticipations and responses over 500 ms were considered misses. Trials excluded as anticipations or misses were rerun at the end of each block so that a full set of 384 responses could be collected from each subject in each of the four experimental conditions (right hand response, visual target [RHV]; left hand response, visual target [LHV]; right hand response, tactile target [RHT]; left hand response, tactile target [LHT]). Because a small number of very early (0 latency) responses were not correctly flagged at runtime as errors, 21 of the total set of 12,288 responses had to be discarded from the data during analysis.

Results

Visual and tactile CUDs

RTs for each condition were averaged within and then across the subjects. Seven out of eight subjects, including both of our left-handed subjects, showed a positive CUD with visual targets, while all eight subjects had a positive CUD when presented with tactile targets. The results for the individual subjects are shown in Fig. 1A, B, while group results are shown in Fig. 2. For visual targets the mean uncrossed RT was 267.42 ms and the mean crossed RT was 270.85 ms, yielding a CUD of 3.43 ms. For tactile targets the mean uncrossed RT was 249.01 ms and the mean crossed RT was 254.55 ms, yielding a mean CUD of 5.54 ms. A repeated-measures (2×2) analysis of variance indicated that the main effect of crossed vs. uncrossed targets was significant ($F_{(1,7)}$=63.3, p<.001). In addition,

the response times to tactile targets were significantly faster than to visual targets ($F_{(1,7)}$=15.5, p<.01). The CUD did not, however, interact with sensory modality ($F_{(1,7)}$=1.04, NS).

CUD asymmetry

To investigate asymmetries in the CUD, we split the data according to whether subjects were responding with their left or right hand. Mean crossed and uncrossed response times for the left and right hands are plotted in Fig. 3.

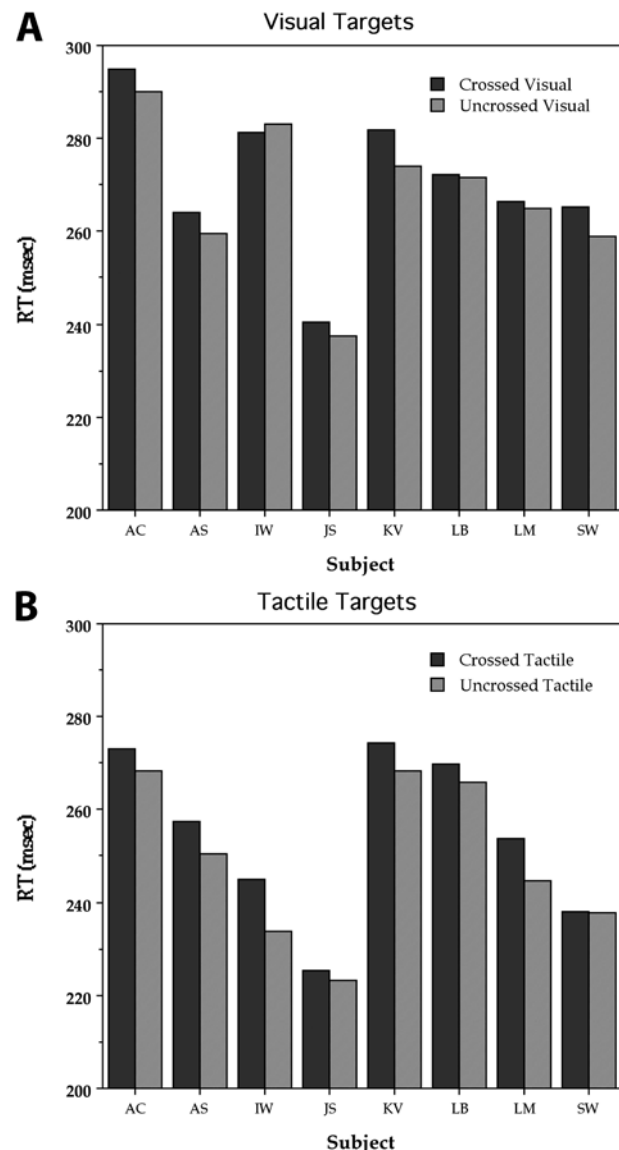Every subject showed a positive CUD for both visual and tactile targets when responding with their left hand. In

Fig. 1A, B Average response times of individual subjects when sensory stimuli are crossed and uncrossed. For visual stimuli **(A)**, seven out of eight subjects took longer to respond when the target was contralateral or crossed in relation to the responding hand. For tactile stimuli **(B)**, all eight subjects took longer to respond when the target was contralateral to the responding hand
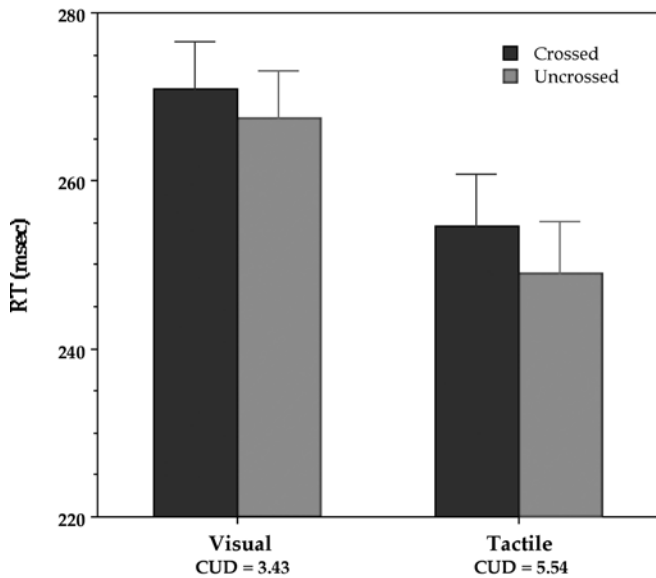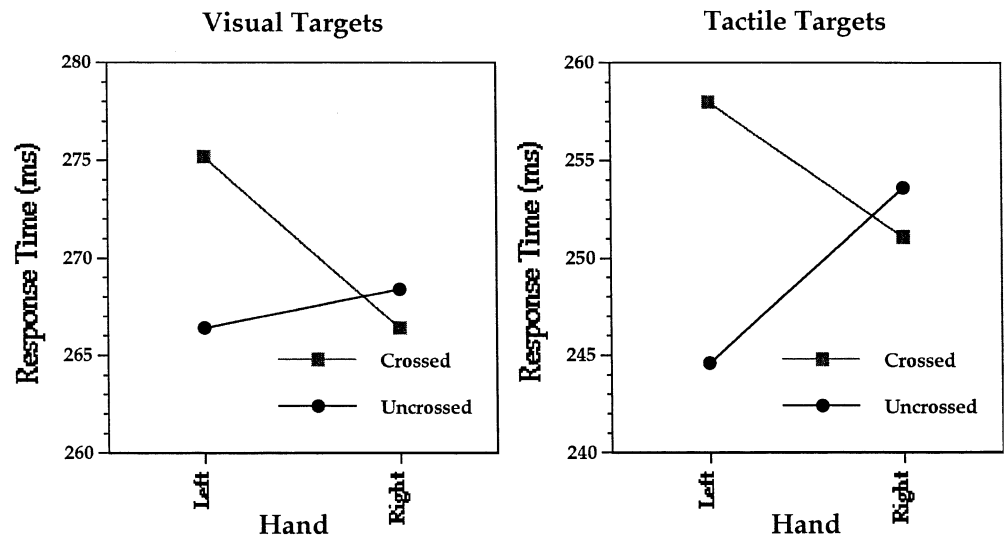
Fig. 2 Average reaction times were significantly longer for both visual and tactile targets when the target stimulus was crossed (contralateral) in relation to the hand that was making the response. Although reaction times to tactile stimuli were somewhat faster than those made to visual targets, this effect was nonsignificant. *Error bars* are standard errors

contrast, when responding with their right hand, most subjects failed to show a positive CUD. The group mean CUD for left-handed responses was 8.81 ms with visual targets and 13.47 ms with tactile targets, while the corresponding values for right-handed responses were −1.94 and −2.41. We performed a three-way repeated-measures ANOVA on the group data, with hand, crossed-uncrossed, and modality as factors. As expected, there is a significant hand × crossed-uncrossed interaction ($F_{(1,7)}$=15.851, p=.0053). However, there was no significant three-way interaction between hand, crossed-uncrossed, and modality ($F_{(1,7)}$=.523, p=.49), indicating that the CUD asymmetry did not differ in the visual and tactile modalities. The main effect of hand is non-significant. In

However, an additional analysis indicates there is an effect of side of stimulation ($F_{(1,7)}$=.15.849, p=.0053), with faster responses for left field visual stimuli (5 ms) and left body-side tactile stimuli (7 ms).

Two of our eight subjects were left-handed. When we limited our analysis to our six right-handed subjects, the pattern of the differences was in all respects unchanged. With tactile stimuli, the mean CUD was 13.47 ms for left-hand responses and −2.41 ms for right-hand responses. With visual stimuli, the mean CUD was 8.81 for left-handed responses and −1.84 ms for right-handed responses. Right-handed subjects continued to show significant hand × crossed-uncrossed interactions ($F_{(1,5)}$=7.311, p=.0426) and no significant three-way interaction between hand, crossed-uncrossed responses, and sensory modality ($F_{(1,5)}$=.029, p=.87). Both of our left-handers followed the pattern of our right-handed subjects in the tactile modality, showing a large left hand CUD in the tactile modality with a reversed CUD for the right hand. In the visual modality only one left-handed subject (AC) showed this pattern of results, while the other (KV) showed a positive CUD for both hands, with a greater CUD in the right hand. These results tend to support the observation that the CUD asymmetry, although typically present, is less likely to be found in sinistral than dextral subjects (Marzi et al. 1991).

Correlations

We also looked for correlations between the subject mean RTs distributions (visual left and right hand crossed and uncrossed, tactile left and right hand crossed and uncrossed), and between the subject mean CUD distributions. The RT distributions were generally very strongly correlated, both within and across the visual and tactile modalities. Thus, subjects who were relatively fast in one condition tended to be fast in other conditions, irrespective of response hand, side of the stimulus, or sensory modality. In contrast, when we considered the CUD

Fig. 3 The difference between crossed and uncrossed reaction times (CUD) was greatest when subjects were responding with their left hand. There was no difference between crossed and uncrossed responses when subjects were responding with their right hand

distributions, we found only weak evidence of correlations between the left and right hand CUDs within each modality (visual: left vs. right hand, $r=-.44$, NS; tactile: left vs. right hand, $r=-.67$, $p<.06$), and no evidence of CUD correlations between the modalities (left hand: visual vs. tactile, $r=.01$, NS; right hand: visual vs. tactile, $r=.18$, NS). Although positive CUD correlations between the modalities would have supported the hypothesis that visual and tactile CUDs are mediated by a common transfer mechanism, it is difficult to draw any inferences from the absence of such correlations. Because the CUD is a small value based upon the difference between much larger RT measures, the statistical jitter in the subject mean RTs could easily mask correlations between the CUD distributions. Therefore, while the CUD can be discerned in subject group means, the inherent noise in this measure can make it difficult to compare the CUDs across individual subjects and across conditions within single subjects (Iacoboni and Zaidel 2000; St John et al. 1987; Kaluzny et al. 1994). We note, however, that Corballis (2002) has also reported that the visual CUD obtained with one hand is negatively correlated with the CUD obtained with the other hand. He attributes this to a difference in hemispheric processing speeds which is stable within each subject, but collectively do not favor either hemisphere across subjects. If, in fact, there is a reciprocal relationship between left and right hand CUDs, our data suggest that, whatever the underlying cause, it is not modality specific.

Discussion

The results of this investigation suggest the CUDs for tactile and visual stimuli are similar, with respect to both magnitude and the hand dependent asymmetry. In both modalities, the CUD is robust when the left hand responds (so that the sensory to motor pathway in the crossed condition is from the left to right hemisphere), but small or absent when the right hand responds (so that the sensory to motor pathway in the crossed condition is from the right to left hemisphere). Although we did not find a clear relationship between visual and somatosensory CUDs within individual subjects, these group similarities suggest that the CUD has a common basis across the sensory modalities. The visual CUDs are, therefore, not unique to visual afferent pathways, and the asymmetry in the visual CUD does not appear to depend on any hemispheric differences that are specific to occipital cortex. Our data therefore fail to support Saron et al.'s (Saron and Davidson 1989; Saron et al. 2002) proposal that the asymmetry is due to an asymmetric number of occipital callosal projections.

Previous psychophysical investigations of the tactile CUD show little consistency with each other. With tactile stimulation delivered to the hand and a finger response, Muram and Carmon (1972) report a CUD of about 10 ms for both left and right hand responses. Peters (1982) failed to find any significant CUD with either hand. Schieppati et al. (1984), utilizing only the right hand, reports a CUD of

15 ms. Kaluzny et al. (1994), using weak electrical stimulation of the hand and a finger response, report a mean CUD of 7 ms with the left hand vs. 2 ms with the right. This is the expected pattern of asymmetry, though these investigators stress that they observed large inter-subject differences. Moscovich and Smith (1979) measured both tactile CUDs with finger stimulation and visual CUDs with tachistoscopically presented black dots.[1] In their study separate groups of left and right-handed subjects responded with a keypress. For the right-handed subjects, Moscovich and Smith (1979) report respective tactile and visual CUDs of 17.4 and 11.8 ms when the right hand is responding, and 11.4 ms and 6.7 ms when the left hand is responding. For the left-handed subjects, the tactile and visual CUDs are respectively 12.7 and 13.4 ms when the right hand is responding, and 4.9 ms and 7.9 ms when the left hand is responding. While the tactile CUDs are larger than the visual CUDs with the right-handers, this difference is not statistically evaluated and is not present with the left-handers. In addition, there is a clear trend in this data towards larger CUDs when the right hand is responding, which is at odds with the prevalent asymmetry found in the literature. However, Moscovich and Smith report that within each modality the effect of response hand is non-significant. In our data, the tactile CUDs are also slightly larger than the visual CUDs, but this difference is not significant. The effect of response hand is significant, however, in the direction predicted by Marzi et al. (1991) in their meta-analysis. In both modalities, we found a positive CUD only for left handed responses.

Our mean visual and tactile CUDs of 8.81 and 13.47 ms for left-handed responses are commensurate with the attribution of the CUD to the time required for signals to transfer across the corpus callosum. On the other hand, for right-handed responses our measured visual and tactile CUDs are actually negative (-1.94 and -2.41 ms), though not significantly different from zero. This outcome was also reported by Bisiacchi et al. (1994) in their study of visual CUD asymmetries, and our visual data forms a good match with Bisiacchi's. In the Marzi et al. (1991) review of 16 studies, the mean CUD for right handed responses was found to have a mean value of $+2$ ms, but is negative in three of the studies reviewed and less than 2 ms in ten of those studies. Marzi et al. (1991) have proposed that the CUD asymmetry may be due to more rapid transfer from the right to left than left to right callosal IHTT. Although the negative CUD values may only reflect the inherent variability in CUD estimates, the extremely small CUDs frequently found when the flow of information is from the right to left hemisphere seem to pose a problem for any callosal interpretation of the CUD, since transmission times of less than 2 ms are beyond the

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[1] The purpose of this study was to compare the CUD in subjects with a normal vs. inverted writing posture. Testing was conducted with the visual, tactile and auditory modalities. Only the visual and tactile outcomes for subjects with a normal writing posture are considered here. The CUDs cited are computed from the RTs given in Moscovitch and Smith, Table 1.

capabilities of even the largest callosal fibers (Aboitiz et al. 1992).

This consideration gives credence to arguments that the CUD may not be a straightforward index of the callosal IHTT. Several alternative accounts of the CUD have been proposed. Saron et al. (2002) reports electrophysiological data that suggest that even when a response is ipsilateral to the field of a visual stimulus, there are interhemispheric interactions before a response is initiated. They argue that comparisons between the crossed and uncrossed conditions in simple RT experiments may therefore be contrasting different types of interhemispheric interactions rather than measuring the speed of interhemispheric transmission alone. Marzi et al. (1999), however, has failed to obtain PET data to support this idea (see below). Braun (1992) has proposed that IHTTs are determined by the interplay of slow callosal and fast noncallosal channels. Kinsbourne (1974) and Swanson et al. (1978) have proposed an account of the CUD based on attentional biasing, and Braun et al. (1996) have proposed a "balance of cost" model in which the CUD reflects hemispheric processing loads. Another possibility is that even when the primary flow of sensory information is being routed to the right hemisphere, a pathway exists which can alert the left cerebral hemisphere that there has been a sensory event. Once alerted, the left hemisphere could initiate a pre-set motor response without specific knowledge as to the nature of the sensory event. However, the present data argues against a pathway into the extrastriate visual cortex, as Lines et al. (1992) have suggested.

In addition, a right hemisphere advantage for stimulus processing could also contribute to CUD asymmetries. Marzi et al. (1991) have specifically acknowledged that the CUD asymmetry could reflect a right hemisphere advantage for light detection or a left hemisphere advantage for initiating manual responses. They point out that if both of these advantages are present, they could effectively cancel each other so that neither would be revealed by a comparison of the uncrossed conditions in a Poffenberger paradigm. Bisiacchi et al. (1994) attempted to evaluate this possibility by measuring manual (key-press) RTs with a bi-hemispheric (foveal) stimulus, and RTs for a bi-hemispheric motor response (a head-nod) with visually lateralized stimuli. No indication of a detection or motor advantage was found for either hemisphere. They conclude that the probable source of CUD asymmetries is in fact an asymmetry in interhemispheric transfer rates. Nevertheless, because in our data responses are faster or uncrossed stimuli presented to the left (by 2 ms for visual stimuli and 10 ms for tactile stimuli), we cannot rule out the possibility that a faster right hemisphere response contributed to CUD asymmetry. If this is the case, our data indicates this advantage is not specifically visual in nature.

Any noncallosal account of the CUD must take into account the elevated CUDs found in acallosal and callosotomized subjects. However, generalizations about the normal CUD based on such patients must be viewed with caution. In a recent PET investigation, Marzi et al. (1999) found that in a simple motor task, the areas of activation in a callosotomy patient were very different from those observed in normal observers. In a spatial cueing task, Reuter-Lorenz and Fendrich (1990) found that spatial pre-cues in the wrong hemisphere produce extremely large RT costs in callosotomy patients, relative to the costs produced in normal observers. This suggests the interhemispheric transfer of attention is very slow in these patients, so any biasing of attention by the sensory input (such as Kinsbourne 1974 has proposed) might contribute to the longer CUD. Alternatively, a general reciprocal competition between the hemispheres in these patients could produce the same result, with the sensory input activating one hemisphere at the expense of the other. This could be the case irrespective of the role of attention and/or hemispheric activations in the CUD of normal subjects. However, the simple loss of the callosal transfer pathway in callosotomy and acallosal patients remains the parsimonious way of accounting for their elevated CUDs.

In the current study, we did not attempt to equate the sensory intensity of our visual and tactile stimuli; both were simply set to levels that could be comfortably detected. Therefore, we cannot say for certain that our CUDs are not specific to the stimulus intensities that we employed. While the stimuli in both modalities could have been run at more than one intensity level to ascertain their generality, the sheer number of trials that would have been required made this impractical. Although simple RTs can vary with stimulus intensity, several investigations (Clarke and Zaidel 1989; Forster and Corballis 1998; Milner and Lines 1982) have found that stimulus intensity does *not* affect the visual CUD. Thus, the existing evidence suggests that our observed CUDs were not stimulus-intensity specific.

The present finding that the visual and tactile CUDs are not significantly different with respect to either their magnitude or asymmetry is compatible with both callosal and noncallosal accounts of the CUD. If the callosal IHTT does play a role in the CUD, the present investigation fits with Berlucci et al.'s (1995) proposal that the CUD is the IHTT for motor signals rather than for sensory informa-tion, since one would expect the CUD to be independent of sensory modality. However, the possibility that the present data simply reflects the presence of similar transfer channels for visual and tactile information cannot be ruled out. Moreover, the fact that in both our investigation and that of Moscovitch and Smith (1979) the tactile CUD is larger than the visual CUD leaves open the possibility that a significantly longer CUD could be demonstrated if sufficient data were gathered. The present study provides no indication, however, that mechanisms underlying the visual and tactile CUDs differ in any fundamental way, or that the properties of the visual CUD are determined by neural pathways that are unique to the visual system.

References

Aboitiz F, Scheibel AB, Fisher RS, Zaidel E (1992) Fiber composition of the human corpus callosum. Brain Res 598:143–153

Aglioti S, Berlucchi G, Pallini R, Rossi GF, Tassinari G (1993) Hemispheric control of unilateral and bilateral responses to lateralized light stimuli after callosotomy and in callosal agenesis. Exp Brain Res 95:151–165

Bashore TR (1981) Vocal and manual reaction time estimates of inter-hemispheric transmission time. Psychol Bull 89:352–368

Berlucchi G, Heron W, Hyman R, Rizzolat G, Umilta C (1971) Simple reaction times of ipsilateral and contralateral hand to lateralized visual stimuli. Brain 94:419–430

Berlucchi G, Aglioti S, Marzi CA, Tassinari G (1995) Corpus callosum and simple visuomotor integration. Neuropsychologia 33:923–936

Bisiacchi P, Marzi CA, Nicoletti R, Carena G, Mucignat C, Tomaiuolo F (1994) Left-right asymmetry of callosal transfer in normal human subjects. Behav Brain Res 64:173–178

Braun CMJ (1992) Estimation of interhemispheric dynamics from simple unimanual reaction times to extrafoveal stimuli. Neuropsychol Rev 3:321–364

Braun CMJ, Villeneuve L, Achim A (1996) Balance of cost in interhemispheric relay: evidence from omission errors in the Poffenberger paradigm. Neuropsychology 10:565–572

Broadbent DE, Gregory M (1965) On the interaction of S-R compatibility with other variables affecting reaction time. Br J Psychol 56:61–67

Brown WS, Larson EB, Jeeves MA (1994) Directional asymmetries in interhemispheric transmission time—evidence from visual-evoked potentials. Neuropsychologia 32:439–448

Brysbaert M (1994) Behavioral estimates of interhemispheric transmission time and the signal-detection method—a reappraisal. Percept Psychophys 56:479–490

Clarke JM, Zaidel E (1989) Simple reaction-times to lateralized light-flashes—varieties of interhemispheric communication routes. Brain 112:849–870

Corballis MC (2002) Hemispheric interactions in simple reaction time. Neuuropsychologia 40:423–434

Cowey A, Stoerig P (1991) The neurobiology of blindsight. Trends Neurosci 14:140–145

Daskalakis ZJ, Christensen BK, Fitzgerald PB, Roshan L, Chen R (2002) The mechanisms of interhemispheric inhibition in the human motor cortex. J Physiol 543:317–326

Distefano M, Sauerwein H, Lassonde M (1992) Influence of anatomical factors and spatial compatibility on the stimulus-response relationship in the absence of the corpus-callosum. Neuropsychologia 30:177–185

Ferbert A, Priori A, Rothwell JC, Day BL, Colebatch JG, Marsden CD (1992) Interhemispheric inhibition of the human motor cortex. J Physiol 453:525–546

Filbey R, Gazzaniga M (1969) Splitting the normal brain with reaction time. Psychon Sci 17:335–336

Forster B, Corballis MC (1998) Interhemispheric transmission times in the presence and absence of the forebrain commissures: effects of luminance and equiluminance. Neuropsychologia 36:925–934

Hanajima R, Ugawa Y, Machii K, Mochizuki H, Terao Y, Enomoto H, Furubayashi T, Shiio Y, Uesugi H, Kanazawa I (2001) Interhemispheric facilitation of the hand motor area in humans. J Physiol 531:849–859

Iacoboni M, Zaidel E (2000) Crossed-uncrossed difference in simple reaction times to lateralized flashes: between and within subject variability. Neuropsychologia 38:535–541

Jeeves MA (1969) A comparison of interhemispheric transmission times in acallosals and normals. Psychon Sci 16:245–246

Kaluzny P, Palmeri A, Wiesendanger M (1994) The problem of bimanual coupling: a reaction time study of simple unimanual and bimanual finger responses. Electroencephalogr Clin Neuropsychol 93:450–458

Kinsbourne M (1974) Lateral interactions in the brain. In: Kinsbourne M, Smith WL (eds) Hemispheric disconnection and cerebral function. Charles C. Thomas, Springfield, IL, pp 239–59

Lines CR, Rugg MD, Milner AD (1992) The effect of stimulus intensity on evoked potential estimates of interhemispheric transmission time. Exp Brain Res 57:89–98

Martin JH, Jessell TM (1991) Anatomy of the somatic sensory system. In: Kandel ER, Schwartz JH, Jessell TM (eds) Principles of neural science. Elsevier Science, New York

Marzi CA, Bisiacchi P, Nicoletti R (1991) Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. Neuropsychologia 29:1163–1177

Marzi CA, Perani D, Tassinari G, Colleluori A, Maravita A, Miniussi C, Paulesu E, Scifo P, Fazio F (1999) Pathways of interhemispheric transfer in normals and in a split-brain subject—a positron emission tomography study. Exp Brain Res 126:451–458

Meyer BU, Roricht S, Einsiedel HGv, Kruggel F, Weindl A (1995) Inhibitory and excitatory interhemispheric transfers between motor cortical areas in normal humans and patients with abnormalities of the corpus-callosum. Brain 118:429–440

Milner AD, Lines CR (1982) Inter-hemispheric pathways in simple reaction times to lateralized light flash. Neuropsychologia 20:171–179

Milner AD, Jeeves MA, Silver PH, Lines CR, Wilson J (1985) Reaction times to lateralized visual stimuli in callosal agenesis: stimulus and response factors. Neuropsychologia 23:323–331

Moscovitch M, Smith L (1979) Differences in neural organization between individuals with inverted and non-inverted hand-writing postures. Science 205:710–713

Muram D, Carmon A (1972) Behavioral properties of somatosensory-motor interhemispheric transfer. J Exp Psychol 94:225–230

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9:97–113

Peters M (1982) Reaction times to tactile stimuli presented ipsi- and contralaterally to the responding hand. Q J Exp Psychol 35A:397–410

Poffenberger AT (1912) Reaction time to retinal stimulation with special reference to the time lost in conduction through nerve centers. Arch Psychol 23:1–73

Ratinckx E, Brysbaert M, Vermeulen E (2001) CRT screens may give rise to biased estimates of interhemispheric transmission time in the Poffenberger paradigm. Exp Brain Res 136:413–416

Reuter-Lorenz PA, Fendrich R (1990) Orienting attention across the vertical meridian: evidence from callosotomy patients. J Cogn Neurosci 2:212–237

Ringo JL, Doty RW, Demeter S, Simard PY (1994) Time is of the essence: a conjecture that hemispheric specialization arises from interhemispheric conduction delay. Cereb Cortex 4:331–343

Rugg MD, Lines CR, Milner AD (1984) Visual evoked potentials to lateralized visual stimuli and the measurement of interhemispheric transmission time. Neuropsychologia 22:215–225

Saron CD, Davidson RJ (1989) Visual evoked-potential measures of interhemispheric transfer time in humans. Behav Neurosci 103:1115–1138

Saron CD, Vaughan H, Foxe J, Simpson V (2002) Electrophysiological indices of intra- and interhemispheric integration. In: Zaidel E, Iacoboni M, Pascual-Leon A (eds) The parallel brain: the cognitive neuroscience of the corpus callosum. MIT Press, Cambridge, MA

Schieppati M, Musazzi M, Nardone A, Seveso G (1984) Interhemispheric transfer of voluntary motor commands in man. Electroencephalogr Clin Neuropsychol 57:441–447

Sergent J, Myers JJ (1984) Manual, blowing, and verbal simple reactions to lateralized flashes of light in commissurotomized patients. Percept Psychophys 37:571–578

St John R, Shields C, Krahn P, Timney B (1987) The reliability of estimates of interhemispheric transmission times derived from unimanual and verbal response latencies. Hum Neurobiol 6:195–202

Swanson J, Ledlow A, Kinsbourne M (1978) Lateral asymmetries revealed by simple reaction time. In: Kinsbourne M (ed) Asymmetrical function of the brain. Cambridge University Press, Cambridge, MA, pp 274–291

Tassinari G, Aglioti S, Pallini R, Berlucchi G, Rossi GF (1994) Interhemispheric integration of simple visuomotor responses in patients with partial callosal defects. Behav Brain Res 64:141–149

Tomasch J (1954) Size, distribution, and number of fibers in the human corpus callosum. Anat Rec 119:119–135

Volpe B, Sidtis J, Holtzman J, Wilson D, Gazzaniga M (1982) Cortical mechanisms involved in praxis: observations following partial and complete section of the corpus callosum in man. Neurology 32:645–650