The Role of Task History in Simple Reaction Time to Lateralized Light Flashes

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Abstract

In lateralized simple reaction time (SRT) tasks with unimanual responses, reaction times (RTs) are faster with ipsilateral (uncrossed) than with contralateral (crossed) response hand- target hemifield combinations. The difference between crossed and uncrossed responses (CUD) is typically interpreted to reflect callosal transfer time. Indeed, split brain patients have much longer CUDs than control subjects. However, while many studies have supported the hypothesis that the CUD reflects callosal transmission time, a few studies have suggested that the CUD may be affected by non-anatomical factors. We investigated the nature of these inconsistent results in two experiments. In the first, we asked half of our subjects to cross their arms while performing the task. The CUD was not affected by arms crossing, supporting the anatomical model of the CUD. In the second experiment, however, all subjects were asked to cross their arms in half of the trials. In this experiment, arms crossing significantly affected the CUD, thus showing that spatial attention modulates the CUD. These latter results cannot be readily explained by a simple callosal relay interpretation of the CUD. Rather, the CUD seems to reflect a mix of anatomical and non-anatomical factors produced by task history. Thus, the seemingly inconsistent results of previous studies can be reconciled by taking into account differences in task history across studies.

Keywords

Reaction time; Poffenberger paradigm; Interhemispheric transfer; Spatial attention; Task context

Introduction

In lateralized simple reaction time (SRT) tasks, ipsilateral, or uncrossed, responses (i.e., the left hand responding to a left visual field (LVF) stimulus or the right hand responding to a right visual field (RVF) stimulus) are faster than contralateral, or crossed, responses (i.e., left hand –RVF, or right hand – LVF) (Clarke & Zaidel, 1989; di Stefano *et al.*, 1992; Marzi *et al.*, 1991; Poffenberger, 1912). This pattern of responses is typically explained in terms of an anatomical model in which in the uncrossed condition, the same hemisphere that receives the

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stimulus controls the manual response, while in the crossed condition, the hemifield of the stimulus and the responding hand are controlled by opposite hemispheres, thus requiring transfer of information between the hemispheres and consequently a longer reaction time (RT). The crossed – uncrossed difference (CUD), where the two uncrossed conditions are subtracted from the two crossed conditions and then divided by two, is taken as a measure of interhemispheric transmission time through the corpus callosum and is typically ~3–4 msec in normal subjects (Marzi et al., 1991). Evidence in support of the anatomical hypothesis, that the CUD measures interhemispheric transfer time via callosal fibers, comes from commissurotomy (Aglioti *et al.*, 1993; Clarke & Zaidel, 1989; di Stefano et al., 1992; Forster & Corballis, 1998; Iacoboni & Zaidel, 1995), and callosal agenesis (Aglioti et al., 1993; di Stefano et al., 1992; Forster & Corballis, 1998; Milner *et al.*, 1985) patients in whom absence of the corpus callosum results in much longer RT to lateralized light stimuli in the crossed condition than in the uncrossed condition (For a review, see Zaidel and Iacoboni, Eds., 2003).

Anzola and colleagues (1977) performed a seminal study that provided robust evidence in favor of the anatomical, callosal relay, interpretation of the CUD. They had subjects respond with uncrossed arms (that is, left arm on the left side and right arm on the right side) and with crossed arms (that is, left arm on the right side and right arm on the left side) in the standard Poffenberger paradigm as well as in a choice reaction time task to lateralized stimuli. Their results yielded no effect of arms crossing in the Poffenberger paradigm but a reliable effect of arms crossing in the choice task, lending support to the callosal relay interpretation of the CUD in the Poffenberger paradigm (Anzola *et al.*, 1977). Findings from several other studies seem compatible with the anatomical model (Berlucchi *et al.*, 1977; Clarke & Zaidel, 1989; Iacoboni & Zaidel, 1995; Marzi, 1999).

Some more recent studies, however, have provided evidence not entirely compatible with the hypothesis that the CUD reflects callosal relay. For instance, Hommel (1996) used a modified version of the Poffenberger paradigm. The response hand could vary every 8 trials (high-frequency blocks) or 80 trials (low-frequency blocks). The results revealed a reaction time advantage for uncrossed trials, compared to crossed trials, that was larger for the high-frequency compared to the low-frequency condition. By itself, this result does not rule out an anatomical basis for the larger CUD in the high-frequency condition. For example, the high- and low-frequency conditions may be associated with transfer through different callosal channels. However, an additional experiment demonstrated the same effect with responses from either the index or middle finger of the same hand. The within-hemisphere control of the responses rules out an anatomical (callosal) interpretation of the result (Hommel, 1996). Braun et al. (2004) suggested that the result with alternating fingers may be attributable to a reprogramming of the response code. Indeed, again using a modified SRT task, they demonstrated that the CUD is largest immediately after a shift in response preparation from one hand to the other and decreased as the interval since the last change in response hand increased (Braun *et al.*, 2004). Weber et al. (2005) recently examined the role of spatial attention in measures of the CUD during SRT by varying the proportions of crossed and uncrossed trials. They reasoned that subjects are more likely to attend to the hemifield where the stimulus is likely to occur. Using this paradigm, Weber and colleagues demonstrated that the size of the CUD varied from −2.5 msec with predominantly crossed trials to 6.5 msec with predominantly uncrossed trials. Equal proportions of crossed and uncrossed trials resulted in a CUD of 4.4 msec, in line with the meta-analytic estimate of the CUD (Marzi et al., 1991). Thus, allocation of attention for action preferentially to one hemifield or the other, or more precisely, the probability of a crossed versus an uncrossed trial, was enough to change the size and direction of the CUD. The simple anatomical model of the CUD as interhemispheric transfer time has also been challenged with electrophysiological evidence revealing bilateral activity even for simple uncrossed responses (Saron *et al.*, 2003a; Saron *et al.*, 2003b).

How can one reconcile these findings? We believe that an often-neglected source of variance across studies is task history. Anzola and colleagues manipulated arms crossing between subjects, whereas the more recent studies showing experimental modulation of the CUD (Braun et al., 2004; Hommel, 1996; Weber et al., 2005) all used within-subjects manipulations, thus affecting changes in 'task history' more than the design adopted by Anzola and colleagues. In principle, then, the inconsistency between studies supporting the purely callosal relay interpretation of the CUD and studies supporting a more complex nature of the CUD may be explained by differences in task history. Experimental designs that do not vary spatial attention may be more likely to yield results compatible with a pure callosal relay interpretation of the CUD, whereas designs that do vary spatial attention are more likely to yield results compatible with the view that the CUD reflects both callosal relay and attentional factors.

To test this hypothesis, we first replicated the between-subjects experimental design of Anzola and colleagues (1977) (Experiment 1) followed by a second experiment in which arms crossing was varied within subjects. If our working hypothesis is correct, the first experiment should yield results consistent with the anatomical model, similar to Anzola et al, whereas the second experiment should yield results consistent with spatial attentional effects, more in line with the results of Hommel, Braun et al, and Weber et al. Unlike Hommel, Braun and Weber who used modified SRT paradigms and manipulated spatial attention by changing stimulus-response assignments, we used a classic SRT (Poffenberger) task and manipulated spatial attention with arms crossing.

Experiment 1

Materials and methods

We performed this experiment to replicate Anzola et al. (1977). 28 subjects participated in the experiment (19 female, 9 male). All subjects were strongly right-handed as determined by a modified version of the Edinburgh handedness Inventory (Oldfield, 1971). Subjects were undergraduate students at the University of California, Los Angeles. Each subject was paid a small fee or received course credit for their participation in the study.

Subjects were tested using a Macintosh IIsi computer with an RGB monitor. Subjects were seated 57 cm from the monitor with their chins in a chin rest and their eyes aligned with a fixation cross in the middle of the screen. Index fingers were placed on response switches mounted vertically on wood panels with the hands positioned comfortably with thumbs up and palms toward the body. The response switches were placed ~6.5 in. on either side of the midline, approximately 12–14 inches from the body, and approximately 14 inches from the screen. The experiment was run using the software package MacProbe (Hunt, 1994). Subjects responded to lateralized light stimuli with unimanual index finger presses on response micro switches. For all trials, the subject's task was to make a response to stimulus presentation regardless of stimulus location. A fixation cross was displayed during the entire experiment. For each trial, the stimulus appeared after a random interval (500–2500 ms) following a warning tone. Stimuli were presented for 45 msec and were white squares against a black background. Stimuli subtended 2.0 degrees of visual angle and were 4.0 degrees (= 4 cm) from the fixation cross to the center of the stimulus. Subjects' eyes were visually monitored throughout the experiment to verify fixation. There is a great deal of evidence to show that participants rarely move their eyes in tasks of covert attention (Corbetta *et al.*, 2002; Corbetta *et al.*, 1993). The subjects participated in one practice block of 10 trials in the same arms position – response-hand - visual-field condition as their first test block. There were 16 test blocks consisting of 40 trials each. In half of the blocks stimuli were presented in the left visual field (LVF) and in the other half, stimuli were presented in the right visual field (RVF). Blocked visual field presentation was used instead of the more prevalent random visual field presentation in order to replicate the method of Anzola (Anzola et al., 1977) as well as to minimize shifts of spatial attention

due to reorienting of attention across the midline, required with random visual field presentations. Visual field and response hand switched after every block. Half of the subjects performed the task in the natural position (arms uncrossed) and half performed the task in the unnatural position (arms crossed). Both hands remained on their respective response switches even though only one hand was used to respond in any given block.

Subjects participated in a total of 640 trials. Data were submitted to repeated measures ANOVA with Arms Position (natural, unnatural) as a between-subjects variable, and Response Condition (crossed, uncrossed) as a within-subjects variable. The dependent variable was median response latency.

Results

There was no effect of Arms Position. There was a main effect of Response Condition, $F(1, 26) = 7.285$, $p = .0121$, with uncrossed trials significantly faster ($M = 243.679$) than crossed trials ($M = 247.389$) (Figure 1). The CUD was 2.286 msec in the natural arms position and decreased to 1.425 msec in the unnatural arms position. Critically, however, there was no interaction of Arms Position x Response Condition, indicating no effect of arms position on the CUD, or equivalently, no effect of spatial attention on the CUD.

Discussion

We replicated the classic result of Anzola et al. (1977), namely, that arms position did not significantly change the CUD. Moreover, the CUDs observed in this experiment are also in line with previously published meta-data (Marzi et al, 1991).

At first sight, the results of Experiment 1 are in contrast with the data of Hommel (1996), of Braun et al. (2004) and of Weber et al (2005). However, a way of reconciling the results of Experiment 1 and of Anzola and colleagues with the more recent, conflicting studies is to posit that the task histories of the more recent studies involved changes in response codes (Hommel, Braun et al) and in spatial attention (Weber et al) that modulated the CUD. In contrast, the design of Experiment 1 and Anzola et al. involved no such changes. To test this hypothesis, we conducted a new experiment in which Arms Position was varied within subjects while they performed the task. Switching from the natural to unnatural arms position and vice versa likely requires some dynamic changes in both spatial attention and response codes. The prediction is that it is not arms position itself that matters, but rather whether arms position changes during the task.

The question may occur why the overall RTs in the unnatural arms position were faster than in the natural arms position. One possibility is that the unnatural arms position resulted in more attention to the task in general compared to the natural arms position. The increased attention to the task in turn resulted in faster responses.

Experiment 2

We conducted a second experiment identical to Experiment 1 except that arms position was varied within-subjects. We predict that this change in spatial attention during the task will result in a shift in the CUD. More specifically, there will be a reduced CUD when the arms are in the unnatural compared to the natural position.

Materials and methods

16 subjects participated in the experiment (8 female, 8 male). All subjects were strongly right-handed as determined by a modified version of the Edinburgh handedness Inventory (Oldfield, 1971). Subjects were undergraduate students at the University of California, Los Angeles.

Subjects were each was paid a small fee or received course credit for their participation in the study.

The apparatus and procedure were the same as in Experiment 1 except for the following. Each subject participated in 4 separate sessions for a total of 2560 trials. During the first session, subjects participated in one practice block consisting of 10 trials in the same arms position – response-hand – visual-field condition as their first test block. Each session included 16 test blocks of 40 trials each. Importantly, arms position was varied *within-subjects* so that in half the trials the hands were placed in a natural position, while in the other half hands were placed in an unnatural position, so that they were closer in space to the stimulus in the opposite visual field. Response hand switched after every block while arms position was switched after every four blocks. Order of visual field presentation, arms position, and top hand in the unnatural condition, were counterbalanced across all subjects. As in the first experiment, both hands remained on their response switches throughout the experiment.

Data were submitted to repeated measures ANOVA with Arms Position (natural, unnatural), and Response Condition (crossed, uncrossed) as within-subjects variables. To evaluate whether starting arms position influenced the results, Starting Arms Position (natural, unnatural) was included as a between-subjects variable. The dependent variable was median response latency.

Results

There was a main effect of Response Condition, $F(1, 15) = 15.901$, $p = .0012$, with uncrossed trials (M = 244.483) faster than crossed trials (M = 247.945). There was a significant 2-way interaction of Arms Position by Response Condition, $F(1, 15) = 16.186$, $p = .0011$. There was no main effect or interaction with Starting Arms Position. We conducted separate analyses of the Natural and Unnatural trials. The analysis of the Natural arms position revealed a main effect of Response Condition, $F(1, 15) = 32.941$, $p = .0001$. By contrast, the analysis of the Unnatural arms position, revealed a non significant effect of Response Condition, $F(1, 15) = .760$, $p = .3970$ (Figure 2). The CUD was 2.985 msec in the natural arms position, and it changed to .48 msec in the unnatural arms position. The difference between CUDS in the natural and unnatural arms positions for each subject are presented in Figure 3. Fourteen of the 16 subjects demonstrated a decrease or reversal of the CUD in the unnatural compared to the natural arms position (Figure 3).

Discussion

The significant decrease in the CUD from the natural to the unnatural arms position in this experiment indicates that changing the relative left-right position of the left and right arms during the task is sufficient to modulate the CUD. Thus the CUD cannot be completely explained by conduction relay through callosal connections. Importantly, this pattern was also observed at the subject level. Fourteen of 16 subjects exhibited a decreased CUD in the unnatural arms position. These individual data suggest that the effect is quite robust and largely automatic, not influenced by individual cognitive strategies.

It is noteworthy that spatial attention helped significantly increase the speed of the crossed condition in the unnatural relative to the natural arms position but did not slow down the speed of the uncrossed condition in the unnatural relative to the natural arms position. Further experiments need to explore the reason for this asymmetry in the effect of spatial attention.

General Discussion

The major aim of the present study was to determine whether the standard Poffenberger paradigm always provides a pure anatomically determined measure of interhemispheric

transfer time in the CUD or whether the CUD can be affected by shifts of spatial attention during the task. Crossing of the arms is perhaps the simplest manipulation for testing the anatomical nature of the CUD. However, heretofore, effects of attention have not been clearly demonstrated in the standard Poffenberger paradigm using the arms crossing approach (Anzola et al., 1977; Berlucchi et al., 1977). Given that attentional effects in modified SRT tasks have been demonstrated (Braun et al., 2004; Hommel, 1996; Weber et al., 2005), why didn't crossing the arms show a similar effect of spatial attention in SRT either in the Anzola experiment or in our replication?

In Experiment 2 of the present study, we introduced shifts in spatial attention *throughout* the task by having subjects switch between the natural and unnatural arms positions, thereby effectively manipulating the 'history' of the experiment. The results demonstrated an effect of crossing the arms on the size and direction of the CUD that cannot be explained by the anatomical model. This is in contrast to Anzola et al. (1977) and to Experiment 1 of the present study in which crossing the arms had no effect on the size or direction of the CUD. However, in both the Anzola experiment and Experiment 1 of the present paper, arms crossing was varied *between*-subjects, such that the location of the responding hand (and response key) in relation to the location of the stimuli did not vary throughout the course of the experiment. Thus, for subjects in the natural arms position, the left hand was always on the left side of the body and to the left of the right hand, etc., and vice versa for subjects in the unnatural arms position. This was not so in Experiment 2, in which arms crossing was manipulated *within*-subjects.

Task history has been shown to influence performance in other tasks. In the Simon task (Simon, 1969), subjects are asked to respond to some stimulus feature other than location, such as color, so that stimulus position is irrelevant for the task. Subjects, however, respond faster when the position of the stimulus (left or right) corresponds with the location of the response (left or right), thus revealing an implicit form of spatial attention. Why is there a spatial attention effect in choice reaction time, particularly in the Simon effect, but not in SRT? Choice reaction time tasks require discrimination of the stimuli and thus assign (covert) attention to the target in preparation for foveating (see Rubichi et al. 1997) and processing, i.e., acting on, it. Once the stimuli are discriminated, they assimilate distinguishing attributes, even when such attributes are not explicitly required for the task. Stimulus attributes automatically activate corresponding response attributes and stimulus-response compatibility effects are then due to an overlap between those stimulus and response attributes. A prominent example of such attributes is the spatial features of the stimulus. When stimuli and responses are both spatially separated there occurs an automatic mapping between the spatial code of the stimuli and the spatial code of the responses. That mapping mediates the spatial stimulus-response compatibility effect. However, in the case of SRT, the stimuli do not need to be discriminated and thus do not assimilate spatial attributes. The exception to this occurs when the spatial relation between the response effectors changes frequently. This introduces a spatial attribute to the task and it is assimilated by the stimuli, thus engaging a spatial attention effect. These conclusions are in keeping with the imaging results that demonstrate an overlap in the functional anatomy of the SRT (CUD) and spatial stimulus-response compatibility tasks (Iacoboni et al. 1996; Iacoboni et al. 1997; Iacoboni et al. 1998; Marzi et al. 1999; Iacoboni and Zaidel 2004).

In sum, we showed that the history of shifts in spatial attention during the task can affect the CUD in the standard Poffenberger paradigm. The CUD has typically been taken to reflect callosal functions. The current results should not be construed as evidence against the hypothesis that the CUD is a callosally mediated behavioral parameter. The corpus callosum has been associated with complex cognitive functions (e.g., Friederici *et al.*, 2007), and particularly with attention (Kinsbourne & Smith, 1974; Yazgan & Kinsbourne, 2003). We still believe that the corpus callosum plays a role in the CUD. However, rather than reflecting only

conduction relay through callosal axons, the CUD likely reflects the complex integrative cognitive functions of the corpus callosum, including attention and response selection.

The Anzola claim is important because it alleges that there exist tasks of sensorimotor integration that are insular to spatial attention. In other words, that sensorimotor integration can be "modular". It turns out this is not the case. The effect of attention is pervasive and ubiquitous.

Acknowledgements

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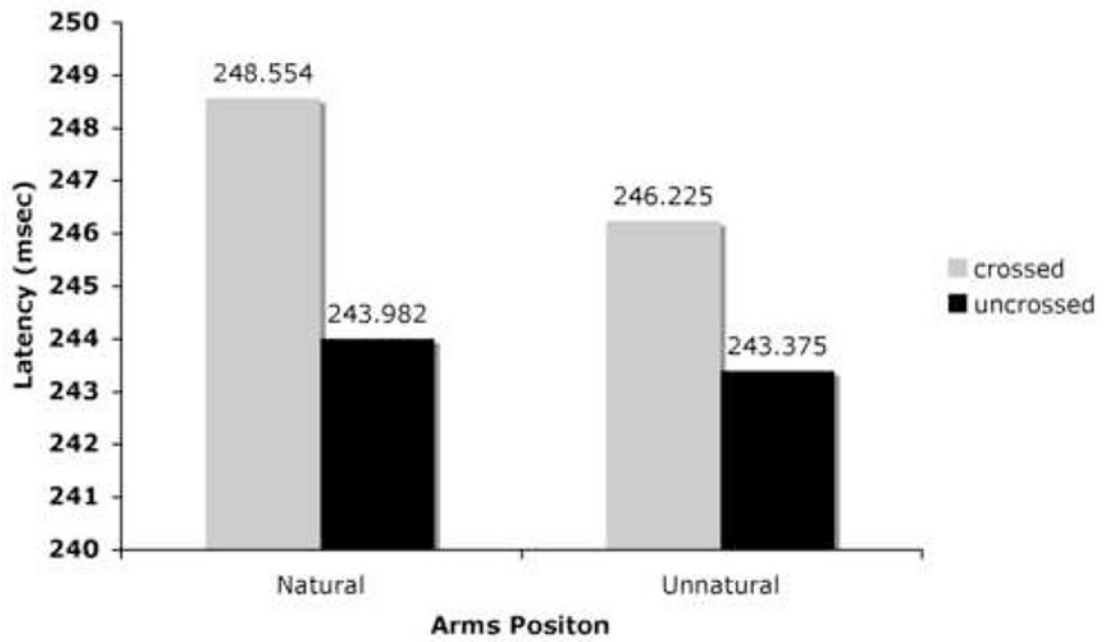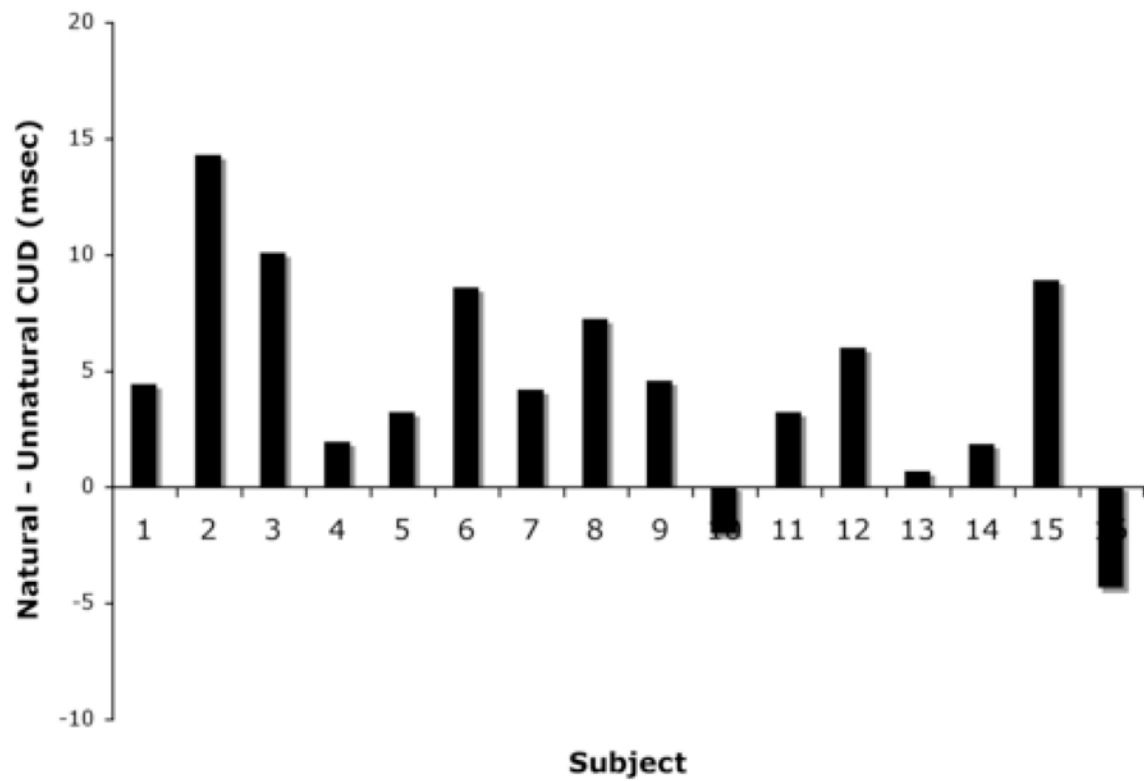
Figure 1.
Means of median reaction times of uncrossed and crossed hand-visual field combinations in the Natural and Unnatural Arms positions in Experiment 1.
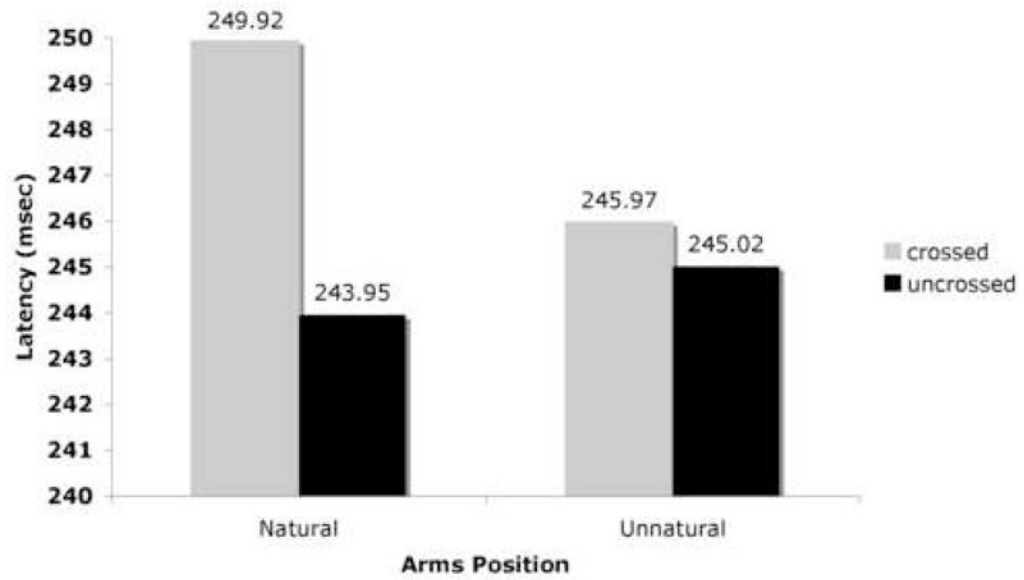
Figure 2.
Means of median reaction times of uncrossed and crossed hand-visual field combinations in the Natural and Unnatural Arms positions in Experiment 2.

Figure 3.
The differences in crossed-uncrossed conditions (CUD), between the natural and unnatural arms positions for each subject. The CUD was calculated by subtracting reaction time in the uncrossed conditions from reaction time in the crossed conditions and dividing by 2.