Neuropsychologia 47 (2009) 933–937

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Note

Spatial attention and interhemispheric visuomotor integration in the absence of the corpus callosum

Eric Mooshagian[a,*], Marco Iacoboni[b,c], Eran Zaidel[a,b]

[a] Department of Psychology, University of California, Los Angeles, Los Angeles, CA 90095, United States
[b] Brain Research Institute, University of California, Los Angeles, Los Angeles, CA 90095, United States
[c] Ahmanson Lovelace Brain Mapping Center, Department of Psychiatry and Biobehavioral Sciences, Neuropsychiatric Institute, David Geffen School of Medicine at UCLA, University of California, Los Angeles, Los Angeles, CA 90095, United States

ARTICLE INFO

Article history:
Received 27 April 2008
Received in revised form
24 November 2008
Accepted 3 December 2008
Available online 13 December 2008

Keywords:
Reaction time
Poffenberger paradigm
Interhemispheric transfer
Task context
Split brain
CUD
Laterality

ABSTRACT

In the lateralized simple reaction time (SRT) task with unimanual responses (Poffenberger paradigm), 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) has typically been interpreted to reflect callosal transfer time. Indeed, acallosal subjects and split-brain subjects have longer CUDs than control subjects. However, a few recent studies have demonstrated that, contrary to classical findings, the CUD is also affected by non-anatomical factors. Here we show that the CUD is also affected by non-anatomical factors in patients with agenesis of the corpus callosum and complete commissurotomy where interhemispheric transfer must be subcallosal. We tested acallosal subject M.M. and split brain patient A.A. on a lateralized SRT task with their arms alternately uncrossed (natural arms position) or crossed (unnatural arms position) across blocks of trials. The results revealed a significant effect of arms crossing on the size and direction of the CUD as previously found in normal subjects [Mooshagian, E., Iacoboni, M., & Zaidel, E. (2008). The role of task history in simple reaction time to lateralized light flashes. *Neuropsychologia*, *46*(2), 659–664]. This suggests that non-anatomical factors that modulate interhemispheric visuomotor integration may occur in absence of the corpus callosum. Anterior commissure and interhemispheric cortico-subcortical pathways are likely implicated in these effects.

1. Introduction

Poffenberger (1912) demonstrated that reaction times to lateralized light flashes are faster with ipsilateral response hand–visual hemifield (uncrossed) combinations than with contralateral response hand–visual hemifield (crossed) combinations. These results have traditionally been ascribed to the anatomical pathways between the cerebral hemisphere receiving the stimulus and the hemisphere controlling the response. In the uncrossed condition, the same hemisphere receives the stimulus and controls the motor response. In the crossed condition, on the other hand, interhemispheric transfer, presumably via the corpus callosum, is required between the hemisphere that receives the stimulus and the hemisphere that controls the response hand. The reaction time difference between the crossed and uncrossed conditions (crossed uncrossed difference, or CUD) divided by two has long been used as a behavioral estimate of interhemispheric transfer time. The CUD in normal subjects is typically ~3–4 ms (Marzi, Bisiacchi, & Nicoletti, 1991). The anatomical interpretation of the CUD, as a measure of interhemispheric transfer time via callosal fibers, is supported by longer CUDs in commissurotomy patients (~30–60 ms) compared to normal subjects (Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993; Clarke & Zaidel, 1989; di Stefano, Sauerwein, & Lassonde, 1992; Forster & Corballis, 1998; Iacoboni & Zaidel, 1995), and intermediate CUDs in the case of callosal agenesis (~15 ms) (Aglioti et al., 1993; di Stefano et al., 1992; Forster & Corballis, 1998; Milner, Jeeves, Silver, Lines, & Wilson, 1985). In both cases, the absence of the corpus callosum results in much longer RTs to lateralized light stimuli in the crossed condition than in the uncrossed condition (For a review, see Zaidel and Iacoboni, Eds., 2003).

In contrast to these results in simple reaction time tasks, which require only stimulus detection, choice reaction time tasks, which require the subject to discriminate the stimulus and choose the correct response, based on some stimulus attribute (e.g., location, color, etc.), have long been known to be sensitive to non-anatomical factors. For example, spatial stimulus–response compatibility effects occur in choice reaction time tasks. Here too, there is an advantage of ipsilateral (compatible) compared to con-

---

[*] Corresponding author at: Brain Stimulation Unit, National Institute of Neurological Disorders and Stroke, National Institutes of Health, MSC 1440, 10 Center Drive, Bethesda, MD, 20892-1440, USA. Tel.: +1 301 402 2584; fax; 1 301 480 2909.
E-mail address: mooshage@ninds.nih.gov (E. Mooshagian).

0028-3932/$ – see front matter. Published by Elsevier Ltd.
doi:10.1016/j.neuropsychologia.2008.12.005

tralateral (incompatible) response hand × target visual field motor responses to lateralized sensory stimuli in these tasks, but this advantage is not tied to the anatomy and seems rather due to attentional mechanisms that control stimulus–response associations (Wallace, 1971, 1972). Anzola, Bertoloni, Buchtel, and Rizzolatti (1977) and Berlucchi, Crea, di Stefano, and Tassinari (1977) performed the definitive studies of the effect of attention (spatial compatibility) on the CUD in SRT. For example, Anzola et al. 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 on the CUD in the Poffenberger paradigm, lending support to the anatomical (callosal relay) interpretation of the CUD in simple reaction time, but the expected effect of arms crossing in the choice task supporting an attentional effect on the CUD in choice reaction time tasks (Anzola et al., 1977).

In a recent study, Mooshagian, Iacoboni, and Zaidel (2008), reconsidered the effects of arms position on the CUD in simple reaction time. Unlike Anzola et al., they varied arms position within-subjects. They demonstrated that the manipulation of task history by alternating between natural and unnatural arms positions during the testing session modulated the size of the CUD. These results suggest that the CUD is not a pure measure of IHTT and, in part, reflects the influence of spatial attention. Other recent behavioral studies also cast doubt on the CUD as a pure measure of interhemispheric transfer time via callosal relay (Braun, Larocque, & Achim, 2004; Hommel, 1996; Weber et al., 2005).

In the present experiment, we tested the hypothesis that the corpus callosum mediates these spatial attention effects. Split-brain patients are the ideal subjects to test this hypothesis. We tested patient A.A., who underwent complete cerebral commissurotomy, and an acallosal subject, M.M., on the lateralized (Poffenberger) simple reaction time paradigm with the arms alternating between the natural and unnatural positions.

2. Materials and methods

2.1. Subjects

A.A. is a right-handed man who underwent complete cerebral commissurotomy for treatment of intractable epilepsy at age 14. The corpus callosum, anterior commissure and hippocampal commissure were severed in a single operation. He is right-handed. Magnetic Resonance (MR) images have shown the completeness of the surgical procedure (Bogen, Schultz, & Vogel, 1988). A.A. was 50 years old at the time of testing.

M.M. is a right-handed man with agenesis of the corpus callosum with some sparing of the anterior most fibers (Fig. 1). He was 29 years old at the time of testing.

Both subjects gave informed consent in accordance with the guidelines of the UCLA institutional review board.

2.2. Procedure

2.2.1. A.A.

A.A. was tested using a Macintosh IIsi computer with the software package MacProbe (Hunt, 1994). He was seated 57 cm from the monitor with his chin in a chin rest and eyes aligned with a fixation cross in the middle of the screen. Index fingers were placed on response switches mounted on wood panels with the hands positioned comfortably with thumbs up and palms toward the body. The response switches were placed approximately 20 cm on either side of the midline, approximately 30–36 cm from the body, and approximately 36 cm from the screen. He responded to lateralized light stimuli with unimanual index finger presses on response microswitches. For all trials, the task was to make a response to stimulus presentation regardless of stimulus location. A fixation cross was displayed during the entire experiment. On each trial the stimulus appeared after a random interval (250–1000 ms) following a warning tone. Stimuli were presented for 45 ms and were white squares against a black background. Stimuli subtended 2.0° of visual angle and were 4.0° (=4 cm) from the fixation cross to the center of the stimulus. Subject's eyes were visually monitored throughout the experiment to verify fixation, as in our previous studies (Clarke & Zaidel, 1989; Iacoboni, Rayman, & Zaidel, 1997; Iacoboni & Zaidel, 1995, 1996, 2000; Mooshagian et al., 2008; Weems & Zaidel, 2004).

A.A. participated in eight testing sessions on separate days. Each session started with one practice block of 10 trials in the same arms position – response-hand – visual-field condition as the first test block. Each session was composed of 16 blocks 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). Visual field of stimulus presentation was blocked. In half the blocks the hands were placed in a natural arms position, while in the other half hands were placed in an unnatural arms 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 arms position, were counterbalanced across all sessions. Each testing session began with the hands in the natural arms position. Both hands remained on their response switches throughout the experiment.

2.2.2. M.M.

The procedures were the same as for A.A. except for the following. M.M. was tested using a PC computer with the software package E-Prime (Psychological Software Tools, Pittsburgh, PA). Stimuli were presented for 50 ms and were black squares against a white background. Stimuli subtended 1.0° of visual angle and were 5.0° (=5 cm) from the fixation cross to the center of the stimulus. M.M participated in eight testing sessions across 5 days of testing. Each session began with one practice

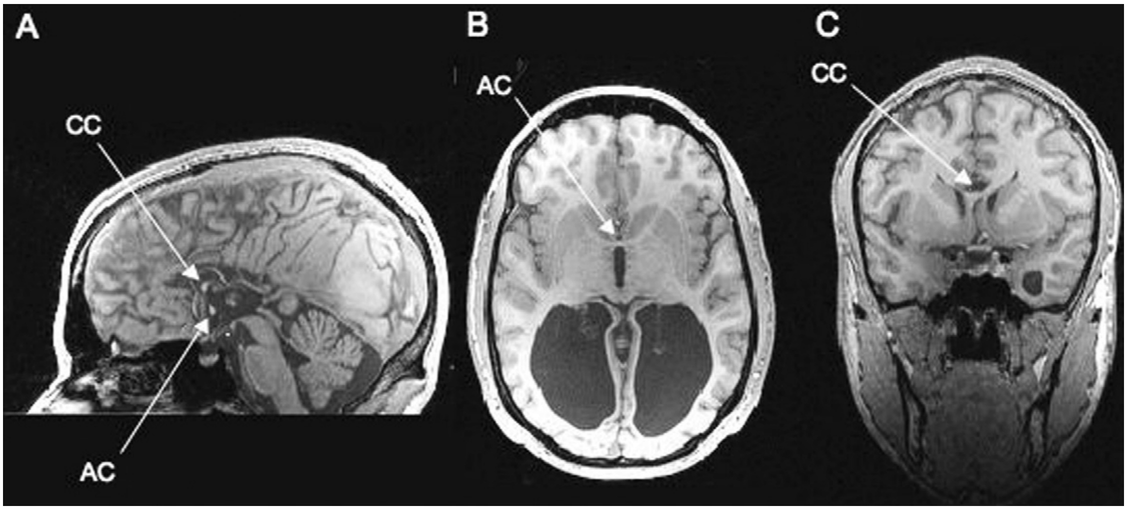

Fig. 1. The acallosal brain of M.M. in three planes. (A) The midsaggital view reveals agenesis of the corpus callosum except for a small portion superior to the anterior commissure. (B) The horizontal plane shows an intact anterior commissure and a marked colpocephaly. (C) The coronal plane shows the small portion of developed corpus callosum. *Note*: AC, anterior commissure; CC, corpus callosum. (Images courtesy of Mike Tyszka, Ralph Adolphs, and Lynn Paul at the Caltech Brain Imaging Center, Pasadena, CA.)

Table 1
Mean RT (ms) for the four hand-hemifield combinations, in natural (arms uncrossed) and unnatural (arms crossed) arm positions for A.A. and M.M.

Subject	Response hand	Natural		Unnatural	
		LVF	RVF	LVF	RVF
A.A.	Lh	394.25	423.01	418.21	407.03
	Rh	455.71	385.61	459.73	403.47
M.M.	Lh	215.34	231.93	218.90	228.79
	Rh	233.69	216.57	230.52	221.34

Abbreviations: LVF, left visual field; RVF, right visual field; Lh, left hand; Rh, right hand.

block of 10 trials in the same arms position – response-hand – visual-field condition as the first test block. Each session was composed of 32 blocks of 26 trials. Stimuli were presented randomly to the LVF and RVF. Response hand was counterbalanced ABBABAAB, etc. throughout the session. Arms Position switched every two blocks.

Thus, while A.A. responded to blocked visual field stimuli, M.M. responded to stimuli presented randomly to the left and right visual field. These differences in visual field presentation across the two subjects tested have been demonstrated not to influence the CUD (Marzi et al., 1991).

2.3. Data analysis

Data were submitted to single-subject analysis of variance (ANOVA) in which session was treated as the random variable. Previous studies with single session data of individual subjects have treated trial as the random variable (Iacoboni & Zaidel, 1995, 1999; Lambert & Naikar, 2000). Since we were able to collect many more data on our two patients compared to previous studies, we used session, rather than trials, as the random variable. Arms Position (natural, unnatural), and Response Condition (crossed, uncrossed) were the independent variables. Median latency of the response was the dependent measure. For A.A. latencies less than 150 ms were discarded as anticipatory errors and latencies longer than 800 ms were discarded as attentional errors. For M.M. latencies less than 150 ms were discarded as anticipatory errors and latencies longer than 600 ms were discarded as attentional errors.

3. Results

Reaction time data for A.A. and M.M. for response hand, visual field and arms position are presented in Table 1.

3.1. A.A.

There was no main effect of Arms Position. There was a main effect of Response Condition, *F*(1, 7) = 26.818 with uncrossed trials (*M* = 393.89) faster than crossed trials (*M* = 434.75). There was a significant two-way interaction of Arms Position by Response Condition, *F*(1, 7) = 15.74, *p* = .005. We conducted separate analyses of the Natural and Unnatural trials. There was a main effect of Response Condition in the natural arms position, *F*(1, 7) = 31.791, *p* = .001, with uncrossed trials (*M* = 383.73) faster than crossed trials (*M* = 441.93). There was also a main effect of Response Condition in the unnatural arms position, *F*(1, 7) = 9.847, *p* = .016, with uncrossed responses (*M* = 404.06) faster than crossed responses (*M* = 427.58) (Fig. 2). Uncrossed trials remained faster than crossed trials even in the unnatural arms position. However, in the unnatural arms position, uncrossed trials became slower compared to uncrossed trials in the natural arms position, *F*(1, 7) = 32.597, *p* = .001. The CUD was 29.10 ms in the natural arm position, and it changed to 11.76 ms in the unnatural arms position.

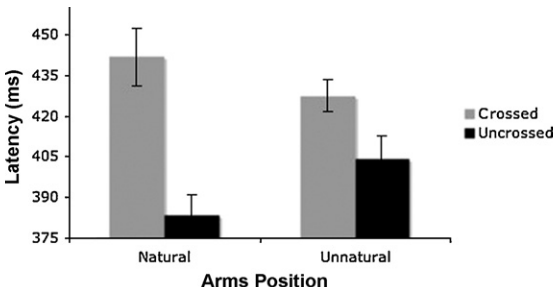

Fig. 2. Means of median reaction times of the anatomically uncrossed (left hand – LVF; right hand – RVF) and crossed hand-visual field (left hand – RVF; right hand – LVF) combinations in the natural (arms uncrossed) and unnatural (arms crossed) arms positions for subject A.A. Error bars indicate standard error of the mean.

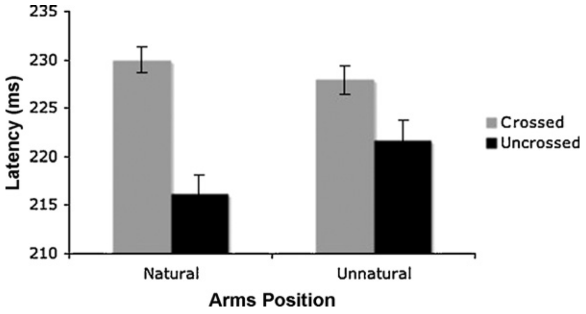

Fig. 3. Means of median reaction times of the anatomically uncrossed (left hand – LVF; right hand – RVF) and crossed hand-visual field (left hand – RVF; right hand – LVF) combinations in the natural (arms uncrossed) and unnatural (arms crossed) arms positions for subject M.M. Error bars indicate standard error of the mean.

3.2. M.M.

There was no main effect of Arms Position. There was a main effect of Response Condition, *F*(1, 7) = 58.324, *p* = .0001, with uncrossed trials (*M* = 218.91) faster than crossed trials (*M* = 228.97). There was a significant two-way interaction of Arms Position by Response Condition, *F*(1, 7) = 13.404, *p* = .008 (Fig. 3). We conducted separate analyses of the Natural and Unnatural trials. The CUD was significant in both the natural and the unnatural arms positions. The analysis of the natural arms position revealed a main effect of Response Condition, *F*(1, 7) = 93.335, *p* = .0001, with uncrossed responses (*M* = 216.19) faster than crossed responses (*M* = 230). The analysis of the unnatural arms position, revealed a significant effect of Response Condition, *F*(1, 7) = 11.300, *p* = .012, with uncrossed responses (*M* = 221.63) faster than crossed responses (*M* = 227.94). Uncrossed trials remained faster than crossed trials even in the unnatural arms position. However, in the unnatural arms position, uncrossed trials became slower compared to uncrossed trials in the natural arms position, *F*(1, 7) = 8.208, *p* = .024. The CUD was 6.91 ms in the natural arms position, and it changed to 3.16 ms in the unnatural arms position.

4. Discussion

The aim of the present study was to determine whether the corpus callosum is necessary to mediate the effect of spatial attention on the CUD observed in lateralized simple reaction time in the normal brain (Braun et al., 2004; Hommel, 1996; Mooshagian et al., 2008; Weber et al., 2005). As in Mooshagian et al. (2008), we manipulated the 'history' of the experiment by having A.A. and M.M. alternate between the natural and unnatural arms position throughout the experiment. Thus, on half of the trials, the left arm was on the left side of the body and the right arm was on the right side of the body (natural arms position), while on the other half of trials, the arms were crossed, such that the right hand was to the left of the left hand and the left hand was to the right of the right hand (unnatural arms position). The results demonstrated an effect of arms crossing on the size and direction of the CUD in both subjects, indicating a non-anatomical component of the CUD measured in the split and in the acallosal brain. These results are consistent with the results from normal subjects using the same lateralized simple reaction time paradigm that also demonstrated an effect of arms crossing on the CUD (Mooshagian et al., 2008).

Task history has been shown to influence performance in other tasks. In the Simon task, 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 nonetheless respond faster when the position of the stimulus (left or right) corresponds with the location of the response (left or right) (Simon, 1969), thus revealing an implicit form of spatial attention (Hommel & Prinz, 1997; Proctor & Reeve, 1990). Several recent studies have demonstrated a reduction or reversal in the Simon Effect when subjects first perform an incompatible SRC task, thus revealing that task history modifies the Simon effect as well (Tagliabue, Zorzi, & Umilta, 2002; Tagliabue, Zorzi, Umilta, & Bassignani, 2000).

That the history of the task, in the form of alternating arms position throughout a simple reaction time task, influences the CUD similarly in normal subjects, an acallosal subject, and a split-brain subject, suggests that the corpus callosum is not necessary for mediating these effects in lateralized simple reaction time. In the absence of the corpus callosum, extracallosal pathways must mediate responses in the crossed condition, which require interhemispheric transfer. The behavioral data reported here do not speak directly to the exact pathway through which interhemispheric transfer occurs in these patients, but several possibilities arise. One possibility is that interhemispheric transfer occurs via the anterior commissure which has been shown to interconnect extensive cortical areas (Di Virgilio, Clarke, Pizzolato, & Schaffner, 1999) and has been implicated in the interhemispheric transfer for simple information (e.g., Clarke & Zaidel, 1989). The anterior commissure remains intact and is a possible pathway of interhemispheric transfer in M.M. While a trace of the anterior corpus callosum remains intact in this patient, the functional significance of these fibers is not clear. A.A., on the other hand, underwent complete commissurotomy, including the anterior commissure. This rules out the anterior commissure as the point of interhemispheric transfer, at least in this commissurotomy patient. Thus, a more likely possibility is that interhemispheric transfer, in this subject, occurs through cortico-subcortical interactions with transfer occurring via the superior colliculus. The alternative of transfer via the thalamus is excluded by the fact that the massa intermedia was sectioned in A.A. (e.g., Clarke & Zaidel, 1989).

It is noteworthy that while the absolute differences in the CUDs between the natural and unnatural arms positions are larger in A.A. (∼17 ms) and M.M. (∼4 ms) than the difference previously reported in normal subjects (∼2.5 ms; Mooshagian et al., 2008), the relative differences in the natural and unnatural CUDs are similar for A.A. (.42) and M.M. (.37), but smaller than in normal subjects (.72). This makes sense. Indeed, non-anatomical effects on the CUD are larger, in relative terms, in the normal brain compared to the split and acallosal brains because the anatomical component of the CUD must be longer in the split and acallosal brain compared to the healthy brain.

It is noteworthy that the effect in both subjects seems to be driven by a slowing of the uncrossed response condition in the unnatural arms position without a comparable speeding of the crossed response condition in the unnatural arms position, particularly in M.M. This makes sense given the stimulus detection nature of the SRT. The anatomical CUD comprises the fastest reactions possible to stimulus detection. An influence of spatial attention predicts faster uncrossed responses and slower crossed responses in the unnatural, compared to the natural, arms position. While it is possible for reactions to anatomically uncrossed conditions in the unnatural arms position to slow down, the speeding up of reactions to anatomically crossed conditions in the unnatural arms position is limited by the lower bound on physical reaction time.

Previous studies have suggested a transient effect of non-anatomical factors on the CUD, whereby they are more likely to influence the CUD immediately after a change in response condition (Braun et al., 2004; Hommel, 1996). To test whether this phenomenon affected our results, we reanalyzed the data for M.M. (we were unable to do so for A.A.). We divided each block into quartiles and considered the interaction of quartile with the Response Condition × Arms Position interaction. Also, as the arms position varied every other block, we considered the interaction of "early" versus "late" blocks with the Response Condition × Arms Position interaction. Neither analysis revealed an interaction of quartile, or recentness of change in response code, with the CUD. These additional analyses suggest that the influence of non-anatomical factors on the CUD reported here is not due only to trials immediately after a change in stimulus–response assignment. We have proposed a model attributing the effects of spatial attention on the CUD to changes in stimulus–response assignment. Such changes are introduced in our SRT task by arms crossing (Mooshagian et al., 2008).

The CUD has long been taken to reflect callosal interhemispheric transfer time. The present results do not deny this assertion and, in fact, are consistent with it, as evidenced by the longer CUDs in acallosal and split brains, due to longer, less efficient transfer in crossed conditions via subcortical pathways. Rather, our data suggest that the corpus callosum is not necessary for shifts in spatial attention to modulate the CUD in the standard Poffenberger paradigm.

Acknowledgements

We thank A.A. and M.M. for their participation in the experiments, Aakash Kishore for assistance with data analysis, and three anonymous reviewers for comments on a previous draft of the manuscript. This work was supported by a grant from the National Institutes of Health (NIH NS-20187).

References

Aglioti, S., Berlucchi, G., Pallini, R., Rossi, G. F., & Tassinari, G. (1993). Hemispheric control of unilateral and bilateral responses to lateralized light stimuli after callosotomy and in callosal agenesis. *Experimental Brain Research*, *95*(1), 151–165.

Anzola, G. P., Bertoloni, G., Buchtel, H. A., & Rizzolatti, G. (1977). Spatial compatibility and anatomical factors in simple and choice reaction time. *Neuropsychologia*, *15*(2), 295–302.

Berlucchi, G., Crea, F., di Stefano, M., & Tassinari, G. (1977). Influence of spatial stimulus–response compatibility on reaction time of ipsilateral and contralateral hand to lateralized light stimuli. *Journal of Experimental Psychology: Human Perception & Performance*, *3*(3), 505–517.

Bogen, J. E., Schultz, D. H., & Vogel, P. J. (1988). Completeness of callosotomy shown by magnetic resonance imaging in the long term. *Archives of Neurology*, *45*(11), 1203–1205.

Braun, C. M., Larocque, C., & Achim, A. (2004). Experimental disentangling of spatial-compatibility and interhemispheric-relay effects in simple reaction time (poffenberger paradigm). *Experimental Brain Research*, *157*(4), 442–456.

Clarke, J. M., & Zaidel, E. (1989). Simple reaction times to lateralized light flashes. Varieties of interhemispheric communication routes. *Brain*, *112*(Part 4), 849–870.

di Stefano, M., Sauerwein, H. C., & Lassonde, M. (1992). Influence of anatomical factors and spatial compatability on the stimulus–response relationship in the absence of the corpus callosum. *Neuropsychologia*, *30*(2), 177–185.

Di Virgilio, G., Clarke, S., Pizzolato, G., & Schaffner, T. (1999). Cortical regions contributing to the anterior commissure in man. *Experimental Brain Research*, *124*(1), 1–7.

Forster, B., & Corballis, M. C. (1998). Interhemispheric transmission times in the presence and absence of the forebrain commissures: Effects of luminance and equiluminance. *Neuropsychologia*, *36*(9), 925–934.

Hommel, B. (1996). S-r compatibility effects without response uncertainty. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *49A*(3), 546–571.

Hommel, B., & Prinz, W. (1997). *Theoretical issues in stimulus–response compatibility*. Amsterdam: Elsevier.

Hunt, S. M. J. (1994). Macprobe: A macintosh-based experimenter's workstation for the cognitive sciences. *Behavior Research Methods, Instruments, and Computers*, *26*(3), 345–351.

Iacoboni, M., Rayman, J., & Zaidel, E. (1997). Does the previous trial affect lateralized lexical decision? *Neuropsychologia*, *35*(1), 81–88.

Iacoboni, M., & Zaidel, E. (1995). Channels of the corpus callosum. Evidence from simple reaction times to lateralized flashes in the normal and the split brain. *Brain*, *118*(Part 3), 779–788.

Iacoboni, M., & Zaidel, E. (1996). Hemispheric independence in word recognition: Evidence from unilateral and bilateral presentations. *Brain and Language*, *53*(1), 121–140.

Iacoboni, M., & Zaidel, E. (1999). The crossed–uncrossed difference in simple reaction times to lateralized auditory stimuli is not a measure of interhemispheric transmission time: Evidence from the split brain. *Experimental Brain Research*, *128*(3), 421–424.

Iacoboni, M., & Zaidel, E. (2000). Crossed–uncrossed difference in simple reaction times to lateralized flashes: Between- and within-subjects variability. *Neuropsychologia*, *38*(5), 535–541.

Lambert, A., & Naikar, N. (2000). Selective attention and interhemispheric response competition in the split-brain. *Brain and Cognition*, *44*(3), 511–546.

Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, *29*(12), 1163–1177.

Milner, A. D., Jeeves, M. A., Silver, P. H., Lines, C. R., & Wilson, J. (1985). Reaction times to lateralized visual stimuli in callosal agenesis: Stimulus and response factors. *Neuropsychologia*, *23*(3), 323–331.

Mooshagian, E., Iacoboni, M., & Zaidel, E. (2008). The role of task history in simple reaction time to lateralized light flashes. *Neuropsychologia*, *46*(2), 659–664.

Proctor, R. W., & Reeve, T. G. (1990). *Stimulus–response compatibility: An integrated perspective*. Amsterdam: Elsevier.

Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology*, *81*(1), 174–176.

Tagliabue, M., Zorzi, M., & Umilta, C. (2002). Cross-modal re-mapping influences the simon effect. *Memory and Cognition*, *30*(1), 18–23.

Tagliabue, M., Zorzi, M., Umilta, C., & Bassignani, F. (2000). The role of long-term-memory and short-term-memory links in the simon effect. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 648–670.

Wallace, R. J. (1971). S-r compatibility and the idea of a response code. *Journal of Experimental Psychology*, *88*(3), 354–360.

Wallace, R. J. (1972). Spatial s-r compatibility effects involving kinesthetic cues. *Journal of Experimental Psychology*, *93*(1), 163–168.

Weber, B., Treyer, V., Oberholzer, N., Jaermann, T., Boesiger, P., Brugger, P., et al. (2005). Attention and interhemispheric transfer: A behavioral and FMRI study. *Journal of Cognitive Neuroscience*, *17*(1), 113–123.

Weems, S. A., & Zaidel, E. (2004). The relationship between reading ability and lateralized lexical decision. *Brain and Cognition*, *55*(3), 507–515.

Zaidel, E., & Iacoboni, M. (Eds.). (2003). *The parallel brain: The cognitive neuroscience of the corpus callosum*. Cambridge, MA: MIT Press.