

# Is interhemispheric communication disturbed when the two hemispheres perform on separate tasks?

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## Abstract

The coordination of sensorimotor tasks involving both visual half-fields requires exchange of information between the brain hemispheres. So far, this interhemispheric information transfer has never been investigated under conditions where the two hemispheres receive different visual inputs and each hemisphere performs on a different task. The present study asked whether such conditions affect the transfer of information between the hemispheres, and if so, at which processing stage. We addressed these issues by pairing a face comparison task with a visual discrimination task (I-task) designed to interfere with the interhemispheric information transfer required for face comparison. One version of the I-task (experiment 1) required discrimination of the faces of John Lennon and Yoko Ono; the other version (experiment 2) required discrimination between the names 'JOHN' and 'YOKO'. Thus, the two I-task versions overlapped at early visual processing stages where visual feature analysis is carried out, but differed at later processing stages where words or faces are represented as objects. We found that both I-task versions disrupted the interhemispheric information transfer for the face comparison task. This indicates that when both hemispheres are occupied by separate tasks, interhemispheric communication is less efficient. In addition, our results suggest that the hemispheres exchange sensory information already at a rather early visual processing stage. Hence, visual feature analysis in one hemisphere is probably informed about feature analysis in the other hemisphere and may also be modulated by it.

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## 1. Introduction

When fixating a point, visual stimuli on the right are projected to the left brain hemisphere and vice versa (Mason & Kandel, 1991). This division of input is also found in the fovea (Chiang, Walsh, & Lavidor, 2004; Lavidor & Walsh, 2004) and only visual stimuli along the vertical meridian are transmitted bilaterally as recent studies showed (Chiang et al., 2004; Lavidor & Walsh, 2004; Reinhard & Trauzettel-Klosinski, 2003). This architecture of our visual system makes it necessary for the two hemispheres to exchange input from both visual half-fields in order to coordinate sensorimotor behavior.

Two paradigms have been used in prior research to investigate interhemispheric information exchange. One paradigm

presents the same task and the same stimuli to both hemispheres to measure the so-called redundancy gain (e.g., Corballis, 1998; Iacoboni & Zaidel, 2003; Miniussi, Girelli, & Marzi, 1998; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001). In the other paradigm, one hemisphere receives the visual input and the other controls the motor response (Poffenberger, 1912), so that the two sides are sequentially active, not simultaneously. However, in everyday life, neither do the two hemispheres receive identical visual input, nor does one hemisphere remain inactive; therefore, none of these paradigms reflects natural conditions.

Consequently, a somewhat more natural paradigm for studying interhemispheric communication would provide dissimilar visual information in the two visual half-fields and require distinct information processing in the two hemispheres. Such dual task paradigms in which each hemisphere performs on a separate task have been used earlier to study hemispheric asymmetries, the effects of split-brain surgery, and the anatomical locus of the psychological refractory period (Franz, Eliassen, Ivry, &

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Gazzaniga, 1996; Holtzman & Gazzaniga, 1985; Ivry, Franz, Kingstone, & Johnston, 1998; Kee, Bathurst, & Hellige, 1984; Pashler et al., 1994). It was found that in neurologically intact participants task execution in one hemisphere can interfere with task performance in the opposite hemisphere (Franz et al., 1996; Holtzman & Gazzaniga, 1985; Ivry et al., 1998; Kee et al., 1984; Pashler et al., 1994). This raises the question as to whether task execution in the two hemispheres interferes with the *inter-hemispheric information transfer*, a possibility that has actually been considered before in the homolog activation hypothesis (Witelson, 1974). According to this hypothesis, bilaterally presented similar stimuli activate homologous areas in the two hemispheres, thereby causing a disruption of communication between these areas.

So far, only two studies have addressed this issue (Hicks, Frank, & Kinsbourne, 1982; Parlow & Dewey, 1991). In both these studies, a sequential tapping task was trained in one hemisphere but tested in the opposite hemisphere, so that an interhemispheric information transfer was required. To find out whether this transfer could be disrupted by the introduction of a second task, the other hemisphere was either busied with another motor task (dual task condition) or not (single task condition). Unfortunately, these two studies did not involve a non-transfer control condition in which the *same* hemisphere was trained and tested. Therefore, the studies did not distinguish whether the second task interfered with task performance in the other hemisphere (i.e. a general performance reduction for the dual task condition relative to the single task condition) or with the *inter-hemispheric information transfer* (i.e. additional dual task costs arising specifically in the transfer condition, but not in the non-transfer condition). As a result of this shortcoming, the question as to whether parallel task execution in the two hemispheres interferes with interhemispheric communication remains unresolved.

To investigate this issue, we designed the following dual task experiment. For one task, participants compared pictures of two unknown faces appearing consecutively on the screen (delayed matching to sample task, DMTS-task). The two faces were presented to the same hemisphere in one condition (non-transfer) and to different hemispheres in the other condition (transfer condition; Fig. 1). Crucially, in the transfer condition, participants could only compare the faces if their hemispheres exchanged information.

We then introduced a second task (interference task, I-task) to investigate whether the interhemispheric information transfer of the DMTS task could be disrupted by engagement of the other hemisphere. This task never required any information transfer between the hemispheres; it was introduced only to disturb the interhemispheric information transfer required in the DMTS-task.

The I-task involved discrimination between the faces of John Lennon and Yoko Ono. Photographs of these two faces were presented repeatedly in pseudorandom order, as in a rapid serial visual presentation (see Fig. 1, Section 2.1 and Appendix A). Each time one of the faces appeared, participants were supposed to indicate per button press whose face it was (John or Yoko). As can be seen in Fig. 1 and Appendix A, I-task stimuli were

presented both during sample and match phase of the DMTS-task.

In the dual task condition, both tasks (DMTS- and I-task) had to be performed simultaneously: While one hemisphere was shown a face for the DMTS-task, the other hemisphere was presented with stimuli of the I-task. Thus, the hemispheres received different visual inputs and performed on separate tasks. In the single task condition, only the DMTS task was presented.

We hypothesized that if the I-task interfered with the inter-hemispheric information transfer, the transfer condition should be more affected by the I-task than the non-transfer condition. Hence, in addition to unspecific dual task costs (Franz et al., 1996; Holtzman & Gazzaniga, 1985; Ivry et al., 1998; Kee et al., 1984; Pashler et al., 1994), and interhemispheric information transfer costs (Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Aboitiz, Lopez, & Montiel, 2003; Ringo, Doty, Demeter, & Simard, 1994; Schüz & Preissl, 1996), we expected that the DMTS-task performance should be further reduced when dual task and transfer were combined.

## 2. Experiment 1

### 2.1. Methods

#### 2.1.1. Participants

The experimental group consisted of 11 females and 11 males with normal or corrected-to-normal vision. Participants received either payment of € 15 or course credits for participation. All participants gave written consent prior to participation. The procedures were approved by the local ethics committee and were in accordance with the Helsinki convention on human experimentation. Participants had a mean age of 26.1 years (S.D. = 5.0), and were right-handed as measured by the Edinburgh handedness inventory (Oldfield, 1971;  $M = 79.1$ ; S.D. = 22.15).

#### 2.1.2. Stimuli

Stimuli were presented 57 cm away from participants' eyes, so that 1 cm on the screen corresponded to a visual angle of 1°. A white 2 cm × 2 cm fixation cross was displayed in the screen center. Pictures of John Lennon and Yoko Ono were downloaded from the internet. The background of the stimuli was black as was the screen behind. For the DMTS-task, 210 male and 210 female faces of unknown individuals were used (144 for training and 276 for data acquisition), so that in every trial completely new faces were presented. All faces were shown without hair, in black and white and sized 6.8 cm × 7.8 cm. To make transfer and non-transfer conditions equally difficult, all photographs were vertically symmetrized. The faces were taken with permission from the Faces Database of the Max Planck Institute for Biological Cybernetics in Tübingen (Germany), the Psychological Image Collection at Stirling, the Yale Face Database, the CVL Face Database and the Database of Faces (AT&T Laboratories Cambridge). The center of all stimuli was 7.5 cm eccentric to the fixation cross and the inner border had a distance of 4 cm to the fixation cross.

#### 2.1.3. Devices

Stimuli were presented on a 17 in. computer monitor with a refresh rate of 75 Hz. Stimulus presentations and recording of keyboard responses were controlled by a 1 GHz PC. All keys except for the response buttons were hidden below a plastic frame. Eyelink version 1.1 was used on a 200 MHz PC for gaze monitoring. Self-written software running on another 1 GHz PC aborted trials instantaneously if gaze deviated from the fixation cross by more than 2° for more than 12 ms. A LINXCEL KVM PCS 104 monitor switch connected to the latter PC was used to switch from trial presentation to Eyelink calibration and back when fixation was lost. All PCs were connected by BNC cable and the two fast PCs by a selfbuilt cable connecting their parallel ports and the gameport of the PC used for trial presentation.

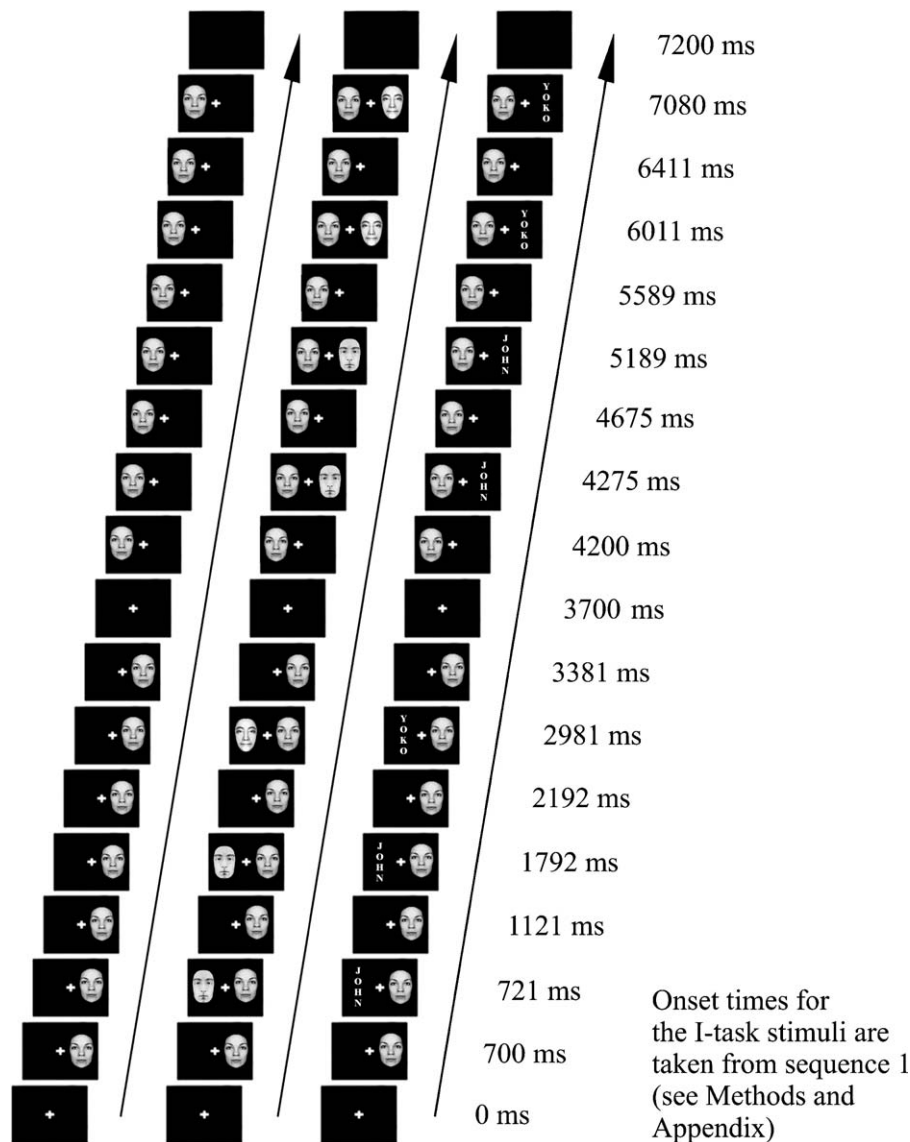


Fig. 1. Trial structure in experiments 1 and 2. The left sequence (single task condition) shows DMTS-task trials without I-task in the transfer condition, in which the two faces appeared on different sides, so that an interhemispheric information transfer was required for comparison. In the non-transfer condition (not shown) faces appeared on the same side. The central sequence (dual task condition) shows DMTS-task transfer trials with the I-task version used in the first experiment (involving the faces of John Lennon and Yoko Ono), while the right sequence (dual task condition) shows DMTS-task transfer trials with the I-task version used in the second experiment (with the names of John Lennon and Yoko Ono). Note that the I-task did *never* require any interhemispheric transfer and that several I-task stimuli appeared both during sample and match phase of the DMTS-task. For lack of space are only those transfer trials shown, in which first the left and then the right hemisphere is stimulated. However, in the experiments both transfer directions occurred equally often. See Sections 1 and 2.1 for further details.

#### 2.1.4. Instruction

Instructions were read out aloud while participants could join reading. Participants were instructed to fixate the cross in the center of the computer screen, and to react as quickly and as accurately as possible by pressing the appropriate keyboard buttons. They were also instructed to prioritize the response for the DMTS-task in case of response conflict between both tasks. To relax their eyes, participants were encouraged to blink or close their eyes between trials.

#### 2.1.5. Procedure

The experiment took ~2.5 h. After adjustment of the Eyelink cameras and calibration of the Eyelink system, one experimental session was done with the I-task and one without (in counterbalanced order). Sessions were preceded by 96 training trials and consisted of 184 trials of the DMTS task, half of them same-trials, half of them different-trials in randomized order. Each half involved an equal portion of male and female faces. Between and within experimental sessions, participants were given breaks where the headset of the eyelink with the

cameras was removed. In each experiment, one half of the participants pressed “p” for “same”/“w” for “different”, and “.” for “John”/“x” for “Yoko” while the other half used the reversed pairings. The “p” and “.” button presses were made with the right hand, the “w” and “x” button presses with the left hand. There were four trial types: (1) first face left/second face right (transfer), (2) first face right/second face left (transfer), (3) both faces right (non-transfer), (4) both faces left (non-transfer). These trial types occurred equally often and were presented in random order. Prior to each trial, participants fixated a white calibration point and then pressed the ENTER button (the drift correction of the Eyelink system). A trial began with the appearance of the fixation cross, which was continuously visible during the whole trial. After 700 ms, the first face for the DMTS-task appeared for 3000 ms, followed by a delay of 500 ms. Then the second face for the DMTS-task appeared and lasted until the correct response was made, but maximally for 3000 ms. Thereafter, the screen went black for 400 ms to ensure a minimum relaxation time (300 ms if no response was made). Afterwards, participants could decide by themselves when to start the next trial.

Participants' gaze was controlled by the Eyelink system to ensure that every stimulus on the screen was projected exclusively to the contralateral brain hemisphere. Trials were aborted if the participants' gaze deviated from the fixation cross by more than  $2^\circ$  for more than 12 ms, allowing for brief blinks and microsaccades. When a trial was aborted, the calibration point appeared on the screen center and participants had to fixate this point and press the ENTER button to start the next trial. Aborted trials were dropped from the analyses and were not repeated. The faces of those trials were not used again.

In the experimental session with the I-task, the I-task stimuli were presented on the opposite screen side of the DTMS-task stimuli so that they were projected to the opposite hemisphere. They were shown for 400 ms in pseudorandomized order. After every I-task stimulus presentation, a response interval in the range of 300–900 ms (pseudorandomized) was given before onset of the next I-task stimulus. Response intervals were varied so that participants could not develop a routine and switch their attention regularly between the tasks. To pseudorandomize response intervals and order of I-task stimuli, 16 sequences were constructed (see Appendix A). One sequence was used for maximally 12 trials, so that participants would not be able to learn the sequences. Since trials were randomized, participants could not foresee which sequence would be used next. The sequences were gained with normally distributed random numbers ( $M = 600$  ms; S.D. = 164 ms for response intervals/ $M = 1000$ ; S.D. = 300 for stimuli). John Lennon was assigned to all random numbers above the median and Yoko Ono to all below the median so that both would appear equally often. Then stimuli were ordered by the product of two different normally distributed random numbers (both distributions had a mean of 1000; S.D. = 300) and assigned to the sequences. The timing of the DTMS-task stimuli was the same irrespective of the I-task sequence used.

### 2.1.6. Data analysis

Only trials in which participants properly maintained fixation were analyzed to avoid potentially flawed results due to foveal stimulation of the presented stimuli. Fixation varied considerably across participants, on average 75.59 trials per participant (20.65%) had to be removed (S.D. = 32.42). Accuracy was analyzed with the sensitivity measure  $P_r$  as recommended by Snodgrass and Corwin (1988). Extreme hit and false alarm rates (of 1.0 and 0.0, respectively) were corrected as suggested by Macmillan and Creelman (1991). Means of reaction times for correct trials were analyzed after outlier correction. Outliers were defined as values higher than the mean of all reaction times for correct trials from a given participant plus three times the standard deviation of their distribution. On average, this resulted in a loss of 2.21% of trials (maximally 3.52%). Thus, on average remained per participant 292 trials for the accuracy analysis and 286 trials for the reaction time analysis. Data were analyzed in  $2 \times 2$  ANOVAs with the two repeated measures factors interhemispheric transfer (with/without) and I-task (with/without). Although transfer direction and hemispheric superiority were not the main focus of the study, they were analyzed in another ANOVA involving the two repeated measures factors interhemispheric transfer (with/without) and hemisphere (left/right).

## 2.2. Results

### 2.2.1. DTMS-task

The factor transfer was significant: performance on the DTMS-task was significantly reduced. When an interhemispheric transfer was required, reaction times increased ( $M = 756.205$  ms; S.E.M. = 25.935 ms without transfer versus  $M = 787.657$  ms; S.E.M. = 30.275 ms with transfer) ( $F(1,21) = 11.662$ ;  $p < 0.01$ ) and accuracy decreased ( $M = 0.783 P_r$ ; S.E.M. = 0.025  $P_r$  without transfer versus  $M = 0.655 P_r$ ; S.E.M. = 0.028  $P_r$  with transfer) ( $F(1,21) = 67.076$ ;  $p < 0.01$ ), indicating that the interhemispheric transfer caused a loss of both speed and accuracy.

The factor I-task was significant, too: performance on the DTMS-task was significantly reduced when DTMS-task and I-task were carried out simultaneously, reaction

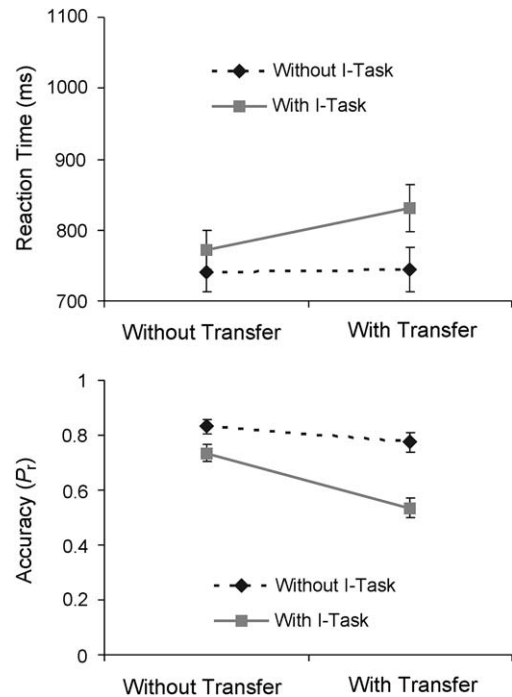


Fig. 2. Influence of the I-task on the interhemispheric information transfer in experiment 1. Error bars indicate standard error of mean.

times increased ( $M = 742.153$  ms; S.E.M. = 29.154 ms without I-task versus  $M = 801.709$  ms; S.E.M. = 30.220 ms with I-task) ( $F(1,21) = 8.196$ ;  $p < 0.01$ ) and accuracy decreased ( $M = 0.803 P_r$ ; S.E.M. = 0.030  $P_r$  without I-task versus  $M = 0.635 P_r$ ; S.E.M. = 0.029  $P_r$  with I-task) ( $F(1,21) = 30.074$ ;  $p < 0.01$ ). Thus, performance in the dual task condition was significantly lower than performance in the single-task condition.

Most importantly, however, the interaction of the two factors transfer and I-task was also significant in both measures, reaction times ( $F(1,21) = 25.257$ ;  $p < 0.01$ ) and accuracy ( $F(1,21) = 14.440$ ;  $p < 0.01$ ) as can be seen in Fig. 2 ( $M = 740.308$  ms; S.E.M. = 28.243 ms without I-task and without transfer versus  $M = 743.997$  ms; S.E.M. = 30.719 ms without I-task and with transfer versus  $M = 772.102$  ms; S.E.M. = 27.876 ms with I-task and without transfer versus  $M = 831.317$  ms; S.E.M. = 33.516 ms with I-task and with transfer/ $M = 0.831 P_r$ ; S.E.M. = 0.027  $P_r$  without I-task and without transfer versus  $M = 0.774 P_r$ ; S.E.M. = 0.035  $P_r$  without I-task and with transfer versus  $M = 0.735 P_r$ ; S.E.M. = 0.030  $P_r$  with I-task and without transfer versus  $M = 0.536 P_r$ ; S.E.M. = 0.035  $P_r$  with I-task and with transfer). Thus, the I-task indeed interfered with the interhemispheric transfer required for the DTMS-task.

### 2.2.2. Reanalysis potential effects of task difficulty

As can be seen in Fig. 2, accuracy in the conditions without I-task was close to maximum. Thus, it is conceivable that a ceiling effect could have prevented transfer costs from manifesting in the single-task conditions, while allowing them to arise in the dual task conditions where performance was lower. To rule out that the interaction in the accuracy data was merely due to a ceiling effect, we did a post hoc test only for the condi-



tions without I-task. As transfer costs were also significant here ( $t(1,21)=3.488$ ;  $p<0.05$ ), a ceiling effect can not account for the interaction in the accuracy data.

We also examined the possibility that the interaction between I-task and transfer did not result from the disturbance of transfer as hypothesized above, but merely from the higher difficulty of the transfer condition relative to the non-transfer condition. After all, the transfer condition required comparison of two spatially separate stimuli, which may make this condition more susceptible to dual task interference than the non-transfer condition requiring comparison of two stimuli in identical positions. We reasoned that this differential task difficulty could make it harder for subjects to combine the I-task with the DTMS task in the transfer condition relative to the non-transfer condition. This idea was tested with two approaches: one focusing on performance differences *within subjects* and one aimed at performance differences *across subjects*.

*Across subjects.* If the interaction of I-task and transfer resulted from the enhanced difficulty of the transfer condition, then the interaction effect should correlate negatively with performance, i.e., with the ability to combine transfer and I-task. In other words, the interaction effect should be stronger for individuals who were less able to combine the I-task with the transfer condition relative to individuals who were better able to do so. To test this, the interaction effect was quantified as the difference in transfer costs between the dual-task condition (i.e., with I-task) and the single-task condition (i.e., without I-task), in correspondence with the  $2 \times 2$  ANOVA interaction term comparing the two differences. This interaction effect was then correlated, first, with I-task performance in the relevant condition combining transfer and I-task, and secondly, with DTMS task performance in that same condition. As for the first, we found that I-task performance did not correlate significantly with the interaction effect in the reaction times ( $r=-0.175$ , n.s.), but did so with the interaction effect in accuracy ( $r=0.498$ ,  $p=0.018$ ). Note, however, that this correlation went into the opposite direction than would have been expected under the assumption that the interaction effect resulted from the relatively high difficulty of the transfer condition. Secondly, DTMS-task performance in the condition combining transfer and I-task did not correlate significantly with the interaction effect, neither in reaction times ( $r=0.416$ , n.s.), nor in accuracy ( $r=0.369$ , n.s.). Moreover, this correlation was positive where it should have been negative under the assumption that the interaction effect resulted from the difficulty of combining the two tasks.

*Within subjects.* If the interaction effect resulted from the difficulty of the condition combining transfer and I-task, one would expect the interaction to be particularly strong on trials where I-task performance was relatively poor. Conversely, the interaction effect should be smaller for trials on which subjects were relatively well able to combine the two tasks. To test this possibility, we sorted DTMS trials of each subject according to the number of correct I-task responses (median-split). We then re-analysed DTMS task performance a) for trials with high I-task performance and b) for trials with low I-task performance. Results replicated the significant interaction effect of I-task  $\times$  transfer for both types of I-task trials (see Fig. 3),

those with above median performance (RT:  $F(1,21)=17.890$ ;  $p<0.05$ ; accuracy:  $F(1,21)=10.165$ ;  $p<0.05$ ), and those with below median performance (RT:  $F(1,21)=9.384$ ;  $p<0.05$ ; accuracy:  $F(1,21)=9.014$ ;  $p<0.05$ ).

In summary, both the *within subjects* and the *across subjects* approach strongly discourage the notion that the relevant interaction has anything to do with the difficulty of the task.

### 2.2.3. Hemispheric asymmetries

There were no significant differences between left and right hemisphere performance in reaction times ( $F(1,21)=2.063$ ; n.s.). However, the right hemisphere showed higher accuracy than the left hemisphere ( $F(1,21)=4.498$ ;  $p<0.05$ ).

Analyses performed to elucidate the possible role of transfer direction revealed that there were no significant differences between right–left and left–right transfer, neither in reaction times ( $F(1,21)=0.612$ ; n.s.), nor in accuracy ( $F(1,21)=0.350$ ; n.s.). This suggests that the interhemispheric transfer of facial information tends to be symmetric.

### 2.2.4. I-task

We also analyzed the I-task performance to determine how it was affected by the transfer manipulation of the DMST-task. The I-task performance (measured as the number of correct button presses for the I-task summed over DMST-task trials) did not differ between transfer and non-transfer condition of the DMST-task ( $t(1,21)=1.729$ ; n.s.).

## 2.3. Discussion

The aim of this study was to investigate whether the interhemispheric information transfer is impaired when the two hemispheres perform separate tasks. To investigate this issue we combined a delayed-matching-to-sample-task (DMST-task) with an interference task (I-task). In the transfer condition, the DMST-task required the interhemispheric transfer of face-specific information. The I-task never required any interhemispheric transfer, but was introduced solely to interfere with the interhemispheric transfer of the DMST-task. Thus, in addition to a general performance reduction caused by the introduction of the secondary task (main effect I-task), and to a performance reduction due to interhemispheric transfer (main effect transfer), we expected the I-task to specifically interfere with the interhemispheric transfer of DMST-task information, resulting in a significant interaction of the factors I-task and transfer.

As demonstrated by higher reaction times and lower accuracy scores in the transfer condition compared to the non-transfer condition, we indeed found the necessity to exchange visual information across hemispheres to be associated with significant costs, as expected (main effect transfer). This transfer of visual information must have relied on callosal fibers since subcortical commissures can not transfer information detailed enough to allow for face comparison (Sergent, 1990). Therefore, the transfer costs probably result from limitations imposed by callosal transmission, such as a relatively low fiber number (Aboitiz et al., 1992; Schüz & Preissl, 1996; Tomasch, 1954) and, on average, relatively slow conduction times (Aboitiz et al., 2003;

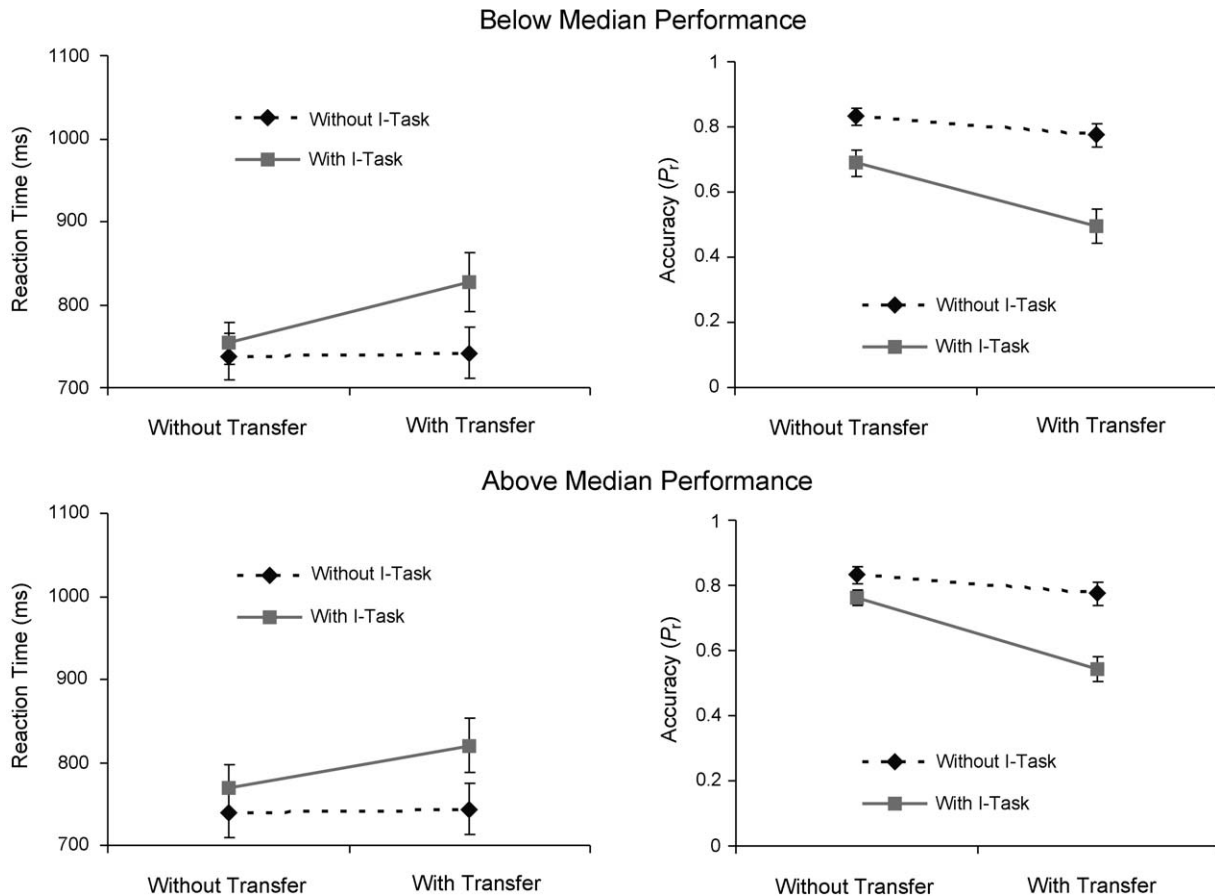


Fig. 3. Influence of the I-task on the interhemispheric information transfer in high vs. low performance I-task trials in experiment 1.

Ringo et al., 1994). This means that the interhemispheric information transfer reflects a bottleneck that slows down reactions and reduces accuracy of responses. Hence, our results support the idea that time-critical neuronal processing is better handled within one hemisphere than across the hemispheres (Ringo et al., 1994).

The second expected effect, the interference between I-task and DMTS-task, was also observed: Introduction of the I-task significantly reduced DMTS-task performance, whether or not transfer was required (main effect I-task). Thus, even if participants could have been switching between tasks, this potential strategy could obviously not have prevented dual task costs. This corresponds with previous studies showing that task execution in one hemisphere can interfere with task performance in the other hemisphere (Franz et al., 1996; Holtzman & Gazzaniga, 1985; Ivry et al., 1998; Kee et al., 1984; Pashler et al., 1994).

Finally, and most importantly, the I-task was also effective in interfering specifically with the interhemispheric information transfer required for the DMTS-task, as shown by the interaction of the two factors transfer and I-task. Thus, task execution in one hemisphere interferes not only generally with task performance in the opposite hemisphere, but also with the communication between the hemispheres. Like any interaction, this reflects a superadditive effect going beyond the effects of the factors transfer and I-task alone. When both hemispheres carried out face processing tasks, the interhemispheric transfer of facial infor-

mation was associated with a further loss of time and accuracy. This finding is consistent with assumptions made in the homolog activation hypothesis (Witelson, 1974).

However, this significant disturbance of the transfer raises an important question: By which means can a task performed by one hemisphere interfere with the interhemispheric information transfer required for another task? Two tasks interfere with each other when they share at least one processing stage (Pashler & Johnston, 1998). Hence, a transfer disturbance can be expected to occur when the I-task recruits the same processing stage that is required for transfer by the DMTS-task. Accordingly, no transfer disturbance should arise if the I-task involves different resources.

To specify the processing stage that was responsible for the transfer-relevant interference observed in our design, two alternative possibilities must be distinguished: (1) The transfer of stimulus information could commence already at an early visual processing stage at which the two hemispheres process elementary visual features. In this case, any I-task stimulus should produce transfer interference as long as it contains basic visual information like contrast, edges, and lines that are present in letters as well as in faces or other objects. (2) Alternatively, the transfer of stimulus information could occur only relatively late, at higher levels in the visual hierarchy at which raw visual information is combined to represent meaningful objects like faces and words. In that case, only I-task stimuli belonging to the same object class should result in transfer interference.

Two lines of evidence point to the second alternative. First, at early processing stages, callosal connections may not transfer stimulus information from the entire two visual half-fields. Early visual areas with small receptive fields exchange merely stimulus information along the vertical meridian, whereas later visual areas with large receptive fields communicate stimulus information from the whole visual field (Aboitiz & Montiel, 2003). Thus, the exchange of visual stimulus information is probably very limited at early processing stages. Second, in tasks requiring any stimulus analysis interhemispheric cooperation was found exclusively for familiar stimuli such as famous faces, words, or frequently used Japanese signs, but not for unfamiliar stimuli such as unknown faces, non-words or uncommon Japanese signs (Mohr, Pulvermüller, & Zaidel, 1994; Mohr, Landgrebe, & Schweinberger, 2002; Schweinberger, Baird, Blumler, Kaufmann, & Mohr, 2003; Yoshizaki, 2001). These lines of evidence suggest that interhemispheric communication seems to rely mostly on late processing stages at which visual stimuli are recognized and categorized as familiar.

To find out whether the interference of the interhemispheric exchange observed in experiment 1 occurred at an early or a late visual processing stage, we repeated the experiment with a different version of the I-task. By using stimuli from a different object class, this version was designed to involve partially different visual processing stages. Instead of discriminating between the faces of John Lennon and Yoko Ono as required in experiment 1 (Fig. 1), we now had subjects discriminate between the written names 'JOHN' and 'YOKO' (Fig. 1). Thus, the new I-task required word processing instead of face processing in this second experiment. Otherwise, the two versions of the I-task were identical. Since the faces and names refer to the same individuals, the evoked semantic associations should also be similar in both I-task versions.

The rationale behind this procedure is that the two versions of the I-task were similar with regards to elementary visual processing stages since face perception and name reading both involve elementary visual feature analysis such as the detection of orientation, contours, boundaries etc. (Mason & Kandel, 1991; Kandel, 1991). However, the two versions of the I-task diverged at late processing stages as face recognition and name reading differ on later, object-specific processing stages (Burton, Bruce, & Johnston, 1990; Bruce & Young, 1986; Fiebach, Friederici, Müller, & von Cramon, 2002; Haxby, Hoffman, & Gobbini, 2000; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Neuner & Schweinberger, 2000; Proverbio, Vecchi, & Zani, 2004).

We hypothesized that, if the transfer of the DMTS-task stimulus occurs at an early processing stage where elementary visual feature analyses are performed, then the new I-task version should disturb the information transfer for the DMTS-task as did the first version used in experiment 1. On the other hand, if the transfer of the DMTS-task face occurs only at a stage at which faces are already analyzed and represented as coherent objects, then the new I-task version should not disturb the information transfer for the DMTS-task since unlike the first version, it does not involve any face processing.

### 3. Experiment 2

#### 3.1. Methods

##### 3.1.1. Participants

Participants in experiment 2 had a mean age of 30.0 years (S.D. = 7.9) and were right-handed as measured by the Edinburgh handedness inventory (Oldfield, 1971) ( $M = 78.4$ ; S.D. = 43.2). The two experimental groups were not different with respect to age ( $t(21) = 1.891$ , n.s.) or handedness ( $t(21) = 0.064$ , n.s.).

##### 3.1.2. Stimuli

The names 'JOHN' and 'YOKO' were presented in grey Times New Roman letters with font size 36, so that they had the same size as the faces of John Lennon and Yoko Ono used in experiment 1. They were written vertically to avoid possible artefacts due to left hemisphere superiority with horizontally written words (Windmann, Daum, & Güntürkün, 2002).

##### 3.1.3. Data analysis

Again fixation varied considerably across participants. On average 68.23 trials per participant (18.48%) were removed (S.D. = 42.53). From the remaining trials on average 2.22% of a participants' trials were removed for outlier correction (maximally 3.59%). Thus, on average remained per participant 300 trials for the accuracy analysis and 293 trials for the reaction time analysis. In all other respects, the methods were as described in experiment 1.

#### 3.2. Results

##### 3.2.1. DMTS-task

The factor transfer was significant again: performance on the DMTS-task was significantly reduced when an interhemispheric transfer was required, reaction times increased ( $M = 839.091$  ms; S.E.M. = 47.988 ms without transfer versus  $M = 872.266$  ms; S.E.M. = 53.831 ms with transfer) ( $F(1,21) = 10.447$ ;  $p < 0.01$ ) and accuracy decreased ( $M = 0.822 P_r$ ; S.E.M. = 0.020  $P_r$  without transfer versus  $M = 0.705 P_r$ ; S.E.M. = 0.023  $P_r$  with transfer) ( $F(1,21) = 30.259$ ;  $p < 0.01$ ), indicating that the interhemispheric transfer caused a loss of both time and accuracy.

The factor I-task was also significant again: performance on the DMTS-task was significantly reduced when DMTS-task and I-task were carried out simultaneously, reaction times increased ( $M = 795.881$  ms; S.E.M. = 44.314 ms without I-task versus  $M = 915.477$  ms; S.E.M. = 64.118 ms with I-task) ( $F(1,21) = 7.715$ ;  $p < 0.05$ ) and accuracy decreased ( $M = 0.812 P_r$ ; S.E.M. = 0.026  $P_r$  without I-task versus  $M = 0.715 P_r$ ; S.E.M. = 0.020  $P_r$  with I-task) ( $F(1,21) = 12.462$ ;  $p < 0.01$ ). Thus, performance in the dual task condition was significantly worse than performance in the single-task condition.

Crucially, the interaction of the two factors transfer and I-task was again significant in reaction times ( $F(1,21) = 9.820$ ;  $p < 0.01$ ) and accuracy ( $F(1,21) = 8.363$ ;  $p < 0.01$ ) as can be seen in Fig. 4 ( $M = 789.309$  ms; S.E.M. = 40.977 ms without I-task and without transfer versus  $M = 802.452$  ms; S.E.M. = 47.986 ms without I-task and with transfer versus  $M = 888.874$  ms; S.E.M. = 61.604 ms with I-task and without transfer versus  $M = 942.079$  ms; S.E.M. = 67.225 ms with I-task and with transfer/ $M = 0.848 P_r$ ; S.E.M. = 0.029  $P_r$  without I-task and without transfer versus  $M = 0.776 P_r$ ; S.E.M. = 0.029  $P_r$  without I-task and with transfer versus  $M = 0.796 P_r$ ; S.E.M. = 0.023  $P_r$  with I-

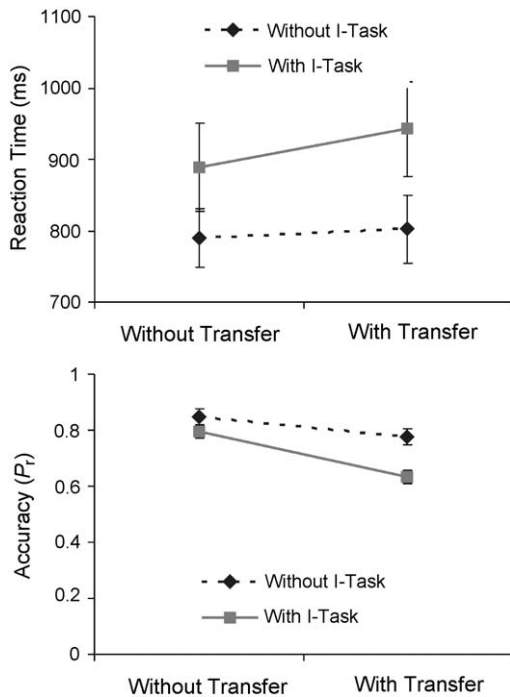


Fig. 4. Influence of the I-task on the interhemispheric information transfer in experiment 2. Error bars indicate standard error of mean.

task and without transfer versus  $M = 0.633 P_T$ ; S.E.M. =  $0.025 P_T$  with I-task and with transfer).

A post hoc analysis collapsed over the data from both experiments revealed that this interaction effect was not significantly different for the first and the second experiment, neither in reaction times ( $F(1,42) = 0.838$ ; n.s.), nor in accuracy ( $F(1,42) = 1.079$ ; n.s.).

### 3.2.2. Reanalysis: potential effects of task difficulty

As in experiment 1, transfer costs in the conditions without I-task were found to be significant in a pairwise analysis ( $t(1,21) = 2.834$ ;  $p < 0.05$ ), rendering a potential role of ceiling effects unlikely.

*Across subjects.* We performed the same correlation analyses as in experiment 1 and found the interaction effect neither to be correlated with I-task performance (RT:  $r = -.038$ , n.s.; accuracy:  $r = -.013$ , n.s.), nor with DTMS-task performance (RT:  $r = 0.157$ , n.s.; accuracy:  $r = 0.042$ , n.s.) in the relevant condition combining transfer and I-task.

*Within subjects.* For trials with above median I-task performance, the interaction effect of I-task and transfer on DTMS performance was significant for both reaction times ( $F(1,21) = 7.539$ ;  $p < 0.05$ ) and the accuracy measure ( $F(1,21) = 9.959$ ;  $p < 0.05$ ). For trials with below median performance, a significant interaction was found only for reaction times ( $F(1,21) = 6.787$ ;  $p < 0.05$ ), not for the accuracy measure ( $F(1,19) = 0.491$ ; n.s., see Fig. 5).

In summary, although the evidence is weaker than in the case of experiment 1, it seems unlikely that the difficulty of the transfer condition alone can account for the interaction between I-task and transfer.

### 3.2.3. Hemispheric asymmetries

Left and right hemisphere performance did not differ significantly, neither in reaction times ( $F(1,21) = 0.238$ ; n.s.) nor in accuracy ( $F(1,21) = 1.537$ ; n.s.). There were also no significant differences between right–left and left–right transfer, neither in reaction times ( $F(1,21) = 1.649$ ; n.s.), nor in accuracy ( $F(1,21) = 0.368$ ; n.s.), as in the previous experiment.

### 3.2.4. I-task

Again we compared the I-task performance for the transfer and non-transfer condition of the DMTS-task. As in the first experiment, I-task performance did not differ between the two conditions ( $t(1,21) = 1.791$ ; n.s.).

### 3.3. Discussion

The aim of this study was to replicate and extend the results of experiment 1. Specifically, we investigated whether the interhemispheric transfer disturbance found in experiment 1 would be absent when the secondary task involved detection of names instead of faces. This would indicate that it occurred exclusively at a late processing stage at which objects are represented, as suggested by previous research (Aboitiz & Montiel, 2003; Mohr et al., 1994; Mohr et al., 2002; Schweinberger et al., 2003; Yoshizaki, 2001). By contrast, if the name discrimination I-task used in experiment 2 would also produce a significant interference effect, just like the face discrimination I-task of experiment 1, this would indicate that interhemispheric transfer begins already at the level of basic visual feature analysis.

We found that the factors transfer and I-task were again significant, as in experiment 1, reflecting the expected transfer costs and dual task costs, respectively. More importantly, we found that the name discrimination I-task did indeed interfere with the information transfer of the DMTS-task, as revealed by the significant interaction of I-task and transfer. This interaction effect was not significantly different from experiment 1 (with a difference that was actually far from significance as revealed by the low  $F$ -values in both reaction times and accuracy). Therefore, we conclude that the transfer was disturbed by both I-task versions, and hence presumably involved an early processing stage common to both tasks. This suggests that at least a significant portion of interhemispheric transfer occurred already at the level of the occipital cortices, corroborating previous evidence (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984; Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998) and indicating that the occipital cortices accomplish more than the midline integration around the vertical meridian since stimuli were presented with  $7.5^\circ$  eccentricity.

Furthermore, the finding of interhemispheric information transfer at an early visual processing stage suggests that also interhemispheric cooperation should be possible at this processing stage. The evidence gained so far, however, suggests that interhemispheric cooperation is restricted to later processing stages at which stimuli are recognized as familiar (Mohr et al., 1994; Mohr et al., 2002; Schweinberger et al., 2003; Yoshizaki, 2001). The solution to this apparent



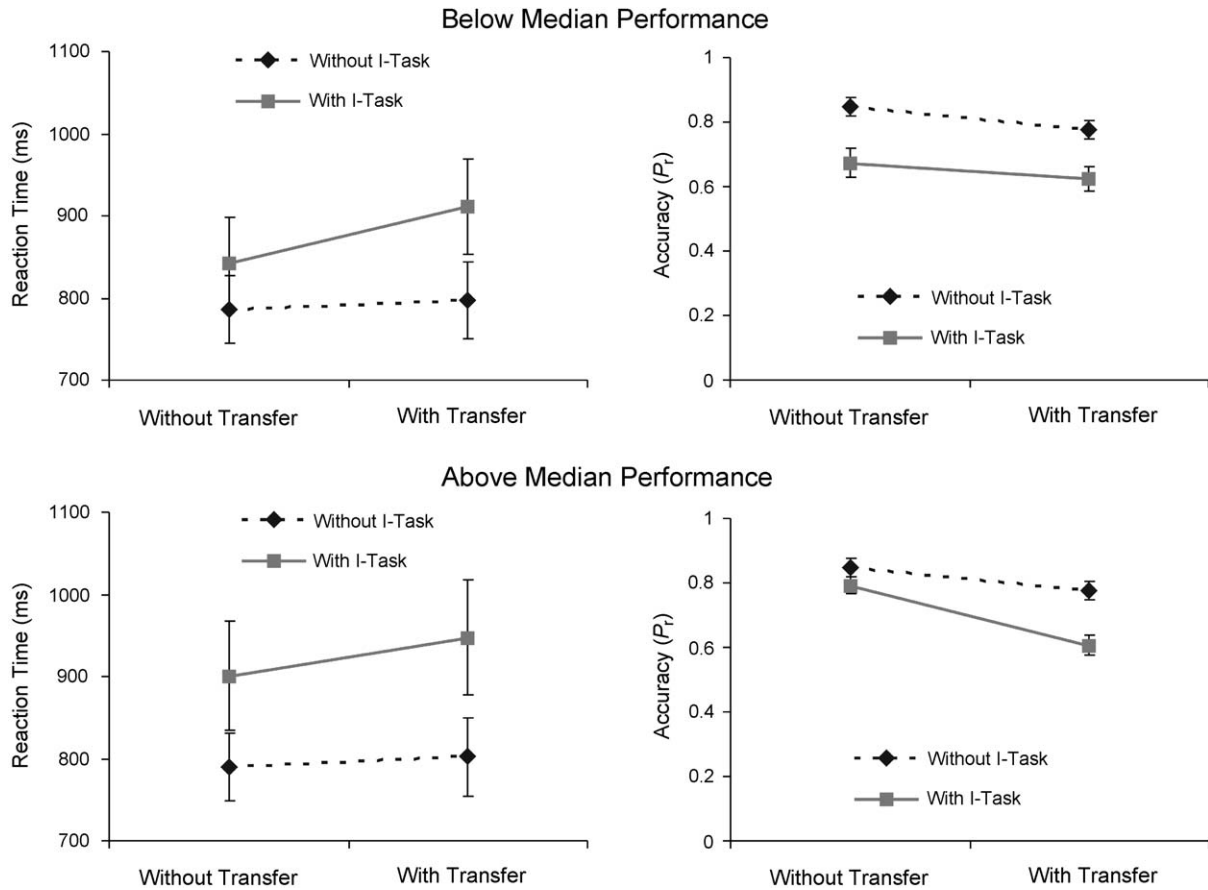


Fig. 5. Influence of the I-task on the interhemispheric information transfer in high vs. low performance I-task trials in experiment 2.

conflict could lie in the tasks used so far: lexical decision, face recognition and discrimination of facial expressions predominantly require more elaborative processing stages than elementary visual stimulus analysis. Thus, interhemispheric exchange of basic visual features cannot contribute much to performance on such tasks and may therefore remain undetected. Hence, it might be worthwhile to probe for interhemispheric cooperation in tasks tapping elementary visual stimulus analysis.

#### 4. General discussion

The aim of the present study was two-fold. First, we set out to investigate whether interhemispheric information transfer is impaired when the two hemispheres receive differential visual input with a concomitant requirement for task processing in both hemispheres. Second, we wanted to narrow down the processing stage at which such an impairment of interhemispheric transfer might take place. As our experiments showed, the scheduling of two separate visual tasks in each brain hemisphere did indeed interfere with the interhemispheric information exchange. In addition, the fact that both experiments showed a transfer disturbance (i.e., regardless of whether the two hemispheres performed on stimuli of the same object-class or on stimuli of different object classes) suggests that this interhemispheric information

transfer occurred at least in part already at an early visual processing stage.

An interhemispheric transfer beginning already at an early processing stage could perhaps enable the organism to generate faster reactions to visual stimuli in sensorimotor tasks requiring the integration of information across the vertical meridian. Such an immediate information exchange should allow each hemisphere to respond to relevant stimulus attributes processed by the other hemisphere even before the object is coherently represented, identified and evaluated. However, early interhemispheric exchange may also have a downside in comparison with later interhemispheric exchange since it is most likely prone to more interference. Virtually all visual stimuli require feature analysis and will therefore be subject to the disturbing effects of information transfer from the other hemisphere occurring at this stage. By contrast, if interhemispheric transfer occurred at a late, object-specific representational stage, parallel visual processing in the two hemispheres could remain relatively undisturbed as long as the information does not reach the object-specific representational stage at which the transfer occurs.

Our finding that interhemispheric information exchange is impaired when the two hemispheres are engaged in the processing of different tasks implies that interhemispheric communication is even more restricted than previously gauged (Aboitiz et

al., 2003; Ringo et al., 1994). A restriction of interhemispheric communication was already deduced from anatomical studies revealing relatively low callosal fiber numbers (Aboitiz et al., 1992; Schüz & Preissl, 1996; Tomasch, 1954) with a majority of thin and unmyelinated axons (LaMantia & Rakic, 1990; Olivares, Montiel, & Aboitiz, 2001). These conditions bring about slow callosal conduction times (Ringo et al., 1994), so that interhemispheric exchange is less efficient than intrahemispheric communication (Aboitiz et al., 2003; Ringo et al., 1994). Our results demonstrate that the interhemispheric information transfer is additionally reduced by interference when the two hemispheres perform in parallel on separate tasks. Although the present study demonstrated interference only at the level of visual perception, it is likely that further transfer disturbance may arise at subsequent processing stages since two tasks can interfere also at later processing stages (Holtzman & Gazzaniga, 1985; Ivry et al., 1998; Pashler et al., 1994; Pashler & Johnston, 1998). In any case, the present results endorse the suggestion that task processing within hemispheres is probably more efficient than across hemispheres (Aboitiz et al., 2003; Ringo et al., 1994).

Finally, an important methodological characteristic of the present study is that interhemispheric communication was tested stimulating the two hemispheres with dissimilar visual inputs and separate tasks. Since under natural conditions sensory processes of the hemispheres differ while both hemispheres contribute to overall task performance, this procedure may be an advantage to paradigms previously employed to investigate the interhemispheric information exchange. These paradigms either stimulated the hemispheres with identical input as in the redundancy gain paradigm (e.g. Corballis, 1998; Iacoboni & Zaidel, 2003; Miniussi et al., 1998; Murray et al., 2001), or provided one hemisphere with a visual input and required the other to control a motor response as in the Poffenberger paradigm (Poffenberger, 1912). The latter in particular probably overestimates the extent of interhemispheric communication because it determines only the restrictions of interhemispheric communication imposed by anatomical constraints. In comparison, a dual task paradigm in which the two hemispheres perform on a different tasks might have a higher ecological validity. Our study is the first that has successfully employed such a paradigm to investigate the actual processing limits of interhemispheric information exchange during sensorimotor integration.

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### Appendix A

Stimulus onsets of the I-task stimuli in the 16 sequences. Timing of the DMTS-task stimuli was the same irrespective of the I-task sequence.

Sequence	Stimulus onsets of the I-task stimuli (in ms)
1	721 (JOHN), 1792 (JOHN), 2981 (YOKO), 4275 (JOHN), 5189 (JOHN), 6011 (YOKO), 7080 (YOKO)
2	916 (YOKO), 1886 (JOHN), 3147 (YOKO), 4319 (YOKO), 5316 (YOKO), 6105 (JOHN), 6809 (YOKO)
3	958 (JOHN), 1845 (YOKO), 2600 (YOKO), 3412 (JOHN), 4632 (YOKO), 5535 (YOKO), 6511 (YOKO)
4	1028 (JOHN), 1972 (JOHN), 3092 (YOKO), 4294 (YOKO), 5510 (YOKO), 6505 (YOKO)
5	803 (JOHN), 1986 (JOHN), 3232 (YOKO), 4529 (YOKO), 5595 (JOHN), 6446 (JOHN)
6	1196 (YOKO), 2041 (JOHN), 3027 (YOKO), 4313 (JOHN), 5415 (YOKO), 6140 (JOHN), 7188 (YOKO)
7	1105 (JOHN), 2012 (JOHN), 3101 (YOKO), 4217 (JOHN), 5040 (JOHN), 5996 (YOKO), 6861 (JOHN)
8	1150 (JOHN), 2160 (YOKO), 3155 (JOHN), 4456 (YOKO), 5482 (YOKO), 6320 (YOKO)
9	1031 (JOHN), 2164 (JOHN), 2994 (YOKO), 4188 (YOKO), 5066 (YOKO), 6112 (JOHN)
10	738 (YOKO), 1776 (JOHN), 2603 (JOHN), 3522 (JOHN), 4412 (JOHN), 5242 (YOKO), 6503 (YOKO)
11	1146 (YOKO), 2150 (JOHN), 3099 (YOKO), 4236 (JOHN), 5267 (JOHN), 6489 (YOKO)
12	1106 (JOHN), 2191 (JOHN), 3378 (YOKO), 4671 (JOHN), 5649 (YOKO), 6800 (JOHN)
13	788 (YOKO), 1488 (JOHN), 2292 (JOHN), 3397 (JOHN), 4498 (YOKO), 5207 (JOHN), 6316 (JOHN)
14	986 (JOHN), 1955 (JOHN), 2777 (YOKO), 3516 (JOHN), 4755 (JOHN), 5591 (YOKO), 6721 (JOHN)
15	1060 (YOKO), 2228 (JOHN), 3215 (YOKO), 4469 (YOKO), 5385 (YOKO), 6183 (JOHN), 7156 (YOKO)
16	1069 (JOHN), 2238 (JOHN), 3308 (YOKO), 4211 (YOKO), 4985 (YOKO), 5976 (JOHN), 6801 (YOKO)

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