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Interhemispheric relations in hierarchical perception: A second look

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Abstract—This study reevaluates the role of interhemispheric interactions in the consistency effect (global interference with local decisions) in hierarchical perception. In an earlier study, Robertson *et al.* [22] (*Neuropsychology*, Vol. 7, pp. 325–342, 1993) tested three split-brain patients on a hierarchical perception task in which stimuli, consisting of large (global) letters made up of smaller (local) letters, were unilaterally or bilaterally presented for identification. They found that, in general, the consistency effect did not occur in split-brain patients and argued that the effect is interhemispheric and normally mediated by the corpus callosum. We repeated the experiment with new stimuli in two of the same split-brain patients. We found that both patients demonstrated evidence for global interference, implying that the neocortical commissures are not necessary for eliciting the consistency effect in hierarchical perception. Copyright © 1996 Elsevier Science Ltd.

Key Words: interhemispheric interactions; split-brain; global interference; hierarchical perception.

Introduction

Navon [15] believed that the order of processing of hierarchically organized stimuli progressed in a top-down fashion with subjects processing the global picture (or 'gestalt') before the local elements (an example of which is provided in Fig. 1). This global advantage has been attributed to the fact that processing of the gestalt is both faster and more automatic than the processing of the elements that make up the gestalt [9, 10, 14]. One effect often attributed to global advantage is global interference. This results when responses to the local level of a stimulus are inhibited by inconsistency with the global level of the same stimulus. However, when the same subject is directed to respond to the global level, no comparable dependence on consistency with the local level occurs.

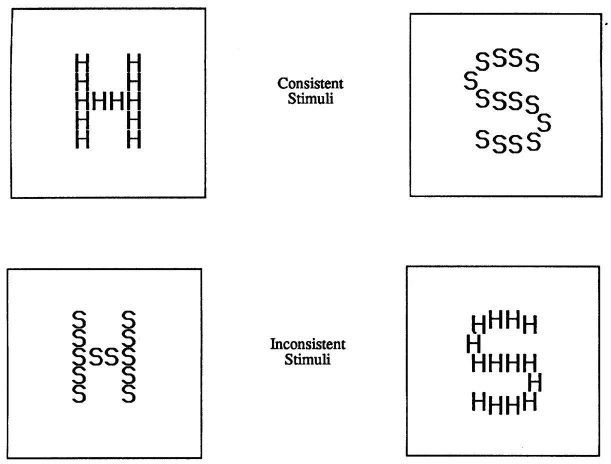

Fig. 1. The Global–Local array.

Support for the independence of global advantage and global interference comes from a number of different sources [9, 10, 11, 16]. Navon and Norman [16], for instance, have demonstrated that the magnitude of global interference could change without affecting the global advantage. This finding gave rise to the two-stage theory of global precedence, with level advantage being established in the first stage and interference in the second. Studies in patients with lesions to the superior temporal gyrus (STG) and adjacent inferior parietal lobe (IPL) confirm this independence [11]. Indeed, based on the data from these patient populations, it was hypothesized that the STG has a direct role in determining the relative speed of global and local processing, while the IPL plays a role in the allocation of attention to them. Further, it has been hypothesized that global interference, unlike global precedence, depends on interhemispheric inter-

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actions [6, 22]. This hypothesis is based on a number of findings including the fact that, while damage to the left STG impairs local processing and damage to the right STG impairs global processing, damage to either diminishes global interference. These studies provide evidence that global advantage and global interference are not only behaviorally distinguishable, but also may involve different neural mechanisms [11, 19]. However, other studies with normal subjects show a strong correlation between the two measures [16].

The assumption of differential hemispheric processing of the two levels of a hierarchically-organized stimulus fits well one of the earliest theories of the duality of the two cerebral hemispheres. It was hypothesized that the left hemisphere is specialized for processing detail [4] or higher spatial frequencies [23]. The right hemisphere, on the other hand, was said to be specialized for processing gestalts [4] or lower spatial frequencies [23]. Hence, we may predict that local features of hierarchical patterns are processed better in the left hemisphere and global forms are processed better in the right hemisphere. Evidence for this is particularly dramatic in brain-damaged populations. Earlier studies of patients with cortical damage to the temporal–parietal junction as well as of callosotomized patients demonstrated relative specialization of the two levels, with the right hemisphere being specialized for global processing and the left hemisphere for local processing [7, 8, 11, 18, 21, 22].

The results have been less clear in normal subjects, with some studies supporting complementary specialization of both global and local processing [22, 24], others supporting specialization of local processing alone [13], and yet others supporting neither [3, 25]. A recent study done in our laboratory did not support hemispheric specialization of the two processes but did provide limited support for the dependence of global interference on interhemispheric interactions in normal subjects [5].

An account introduced by Robertson *et al.* [11, 17, 19, 22] attempts to explain both "dissociative" and "integrative" aspects of the processing of hierarchical patterns by positing that separate (or dissociated) modules process the two levels independently (i.e. global processing in the right hemisphere and local processing in the left hemisphere), while an integrative mechanism (mediated by the corpus callosum) allows for the perception of the two levels as a single stimulus unit and promotes interactions between the two levels, including global interference (i.e. the interference of inconsistent global distractors with local targets). The account is incomplete, however, in that it does not describe a detailed mechanism for the consistency effect; nor does it motivate the asymmetry of interference (global consistency with local decisions but not vice versa) given that both hemispheres appear capable of processing both global and local information, albeit unequally. Specifically, based on their studies of patients with left- and right-superior temporal gyrus lesions, Robertson and Lamb [19] predicted that commissurotomized patients will show a global advantage in the disconnected right hemisphere, a local advantage in the disconnected left hemisphere, and neither a consistency effect, nor a level $\times$ consistency interaction (i.e. no greater global interference than local interference). This prediction was borne out in the recent paper by Robertson *et al.* [22]. In two patients with complete cerebral commissurotomy (NG and LB), they found a left hemisphere advantage for both global and local decisions, although as expected, the global advantage was larger in the right hemisphere. Further, neither NG nor LB, the two patients with high accuracies in Robertson *et al.*'s [22] study, showed an overall consistency effect and neither showed any level $\times$ consistency interaction.

The present study further explores both the relative specialization of global and local processing and the role of interhemispheric communication in global interference by examining, again, performance patterns in two split-brain patients using the same paradigm which Carusi *et al.* [5] used with normal subjects. This allows a direct comparison between the two populations. The paradigm is also very similar to that used by Robertson *et al.* [22] with both normal and split-brain patients. It was predicted that the split-brain patients will show neither a consistency effect nor an interaction between level (Global/Local) and consistency.

While unilateral trials allow for an analysis of hemispheric specialization of the two levels, bilateral trials allow for an analysis of metacontrol processes (Levy and Trevarthan, 1976). We analyze metacontrol by asking which hemisphere regulates processing when both hemispheres have access to the same target information. Based on the study by Robertson *et al.* [22], it was predicted that performance on bilateral trials will mimic that of unilateral right visual field trials when the patient has to respond to the local level of a stimulus and mimic unilateral left visual field responses when he has to respond to the global level of the stimulus.

Method

Subjects

Two right-handed split-brain patients, LB and NG, were tested. Both had complete commissurotomy for the treatment of pharmacologically intractable epilepsy. Complete case histories of the two patients have been presented elsewhere [2, 26]. Completeness of neocommissurotomy was verified by MRI [1].

Materials and apparatus

The letters 'H' and 'S' were used to create both the global and the local levels of the stimuli. These labels ('Global' and 'Local') are used to refer to the characteristics of the contrived stimuli, not necessarily the perception of the subject. The two levels of these stimuli could just as easily be referred to as 'gestalt' and 'element'. We will, however, continue the convention used in previous studies for the purposes of clarity.

The stimuli were created using a Macintosh version of the

Canvas software. As can be seen in Fig. 1, 'Consistent' stimuli contained the same letter at both levels, whereas 'Inconsistent' stimuli contained a different letter at each level. The global letter was an 'H' in half the trials and an 'S' in the other half. In addition, half the local stimuli consisted of the letter 'H' and the other half consisted of the letter 'S'. Unlike the stimuli in Robertson *et al.*'s [21] experiment, the current study used a rounded 'S' so as to make the stimuli appear more similar to what would be encountered in a natural setting. In every case, each global stimulus which measured $3.6^\circ \times 2.3^\circ$ comprised 12 ($0.64^\circ \times 0.42^\circ$) local stimuli. Stimuli were presented with the innermost edge 1° from fixation and with the center 2.15° from fixation.

Procedure

Each patient was seated 57.3 cm from the display monitor with his/her chin resting in a chin rest, which had been centered relative to the monitor. The task was divided into four blocks, two in which the patient had to identify the global letter and two in which the patient had to identify the local letters. Each trial began with a fixation cross which appeared in the center of the screen. The patient was instructed at the beginning of each block to fixate on this cross and not to move his/her eyes during the trial. This was followed 200 msec later by the stimulus which appeared for 105 msec. The patient was given a maximum of 5 sec to respond to each trial. This response then triggered a 600 msec delay before the onset of the next trial.

Each of the four possible stimuli (Global 'H'/Local 'H', Global 'H'/Local 'S', Global 'S'/Local 'S', and Global 'S'/Local 'H') appeared 16 times in each of three visual field (VF) locations: left (LVF), right (RVF) and bilateral (BVF). In bilateral presentations, an identical copy of the stimulus appeared simultaneously in each VF. In total, there were 192 trials per block. Practice blocks were performed prior to each of the four test blocks. Stimuli were pseudorandomly presented, with the constraint that no more than three of the same type of trial occurred in succession. This meant that stimuli neither occurred in the same visual field nor were of the same consistency (consistent vs inconsistent) nor led to the same response ('H' vs 'S') for more than three trials in a row.

The patient responded with the left hand (Lh) for one global block and one local block, and with the right hand (Rh) for the other two blocks. The patient responded using the 'H', 'B', 'F' and 'V' keys of the Macintosh keyboard which was placed on the table directly in front of him. The 'H' and 'F' keys were labeled 'H', while the 'B' and 'V' keys were labeled 'S'. The labels remained on the keys throughout the experiment. The 'F' and 'V' keys were used for left-hand responses, and the 'H' and 'B' keys were used for right-hand responses.

Both patients participated in two testing sessions several months apart. The results reported reflect performance collapsed across sessions, as preliminary analyses revealed a similar performance across the two sessions.

Results

Although the experiment was run such that all conditions were completely counterbalanced, the following analyses were performed on unilateral trials using only ipsilateral conditions (i.e. where hand responses were to the ipsilateral visual field). This deletion was made so that significant interactions would represent pure hemispheric effects.

For bilateral trials, on the other hand, the results from both hands were included in the analyses. This was done after preliminary ANOVAs on the bilateral trials demonstrated the absence of both a main effect of Hand and of an interacion between Hand, Level and Consistency.

Error rates were relatively low for both LB and NG (7% and 13%, respectively) and neither patient demonstrated any evidence for a speed-accuracy tradeoff.

Latency analyses for LB

First, a three-way ANOVA was performed with trials as a random variable and with Level (global or local), Visual Field × Ipsilateral Hand combinations (LVF-Lh, RVF-Rh, BVF-Lh + Rh) and Consistency (consistent, inconsistent) as between-trial variables. All three variables showed significant main effects. There was a Level effect [$F = 130.58$, d.f. = 1, $P < 0.0001$] which resulted from a 123 msec advantage for global over local responses (638 and 761 msec, respectively). There was a Visual Field effect [$F = 10.23$, d.f. = 2, $P < 0.0001$] resulting from statistically equivalent latencies in the bilateral and right visual fields (686 and 683, respectively) which were more than 50 msec faster than the average latency for the left visual field (740 msec). There was also a Consistency effect [$F = 6.58$, d.f. = 1, $P < 0.01$] resulting from a 35 msec advantage for consistent (687 msec) over inconsistent (712 msec) stimuli.

We also found the critical Level × Consistency interaction [$F = 10.83$, d.f. = 1, $P < 0.001$], with local but not global responses showing a consistency effect. No other interactions were significant.

A second three-way ANOVA was performed with the same three independent variables but using a natural log transformation of the reaction time data as the dependent variable. This was done in order to equate variance across cells and to normalize the reaction time distribution, if necessary. The significant effects revealed from this analysis were identical to those listed above. Specifically, there were main effects of Level [$F = 158.21$, d.f. = 1, $P < 0.0001$], of Visual Field [$F = 13.04$, d.f. = 2, $P < 0.0001$] and of Consistency [$F = 10.00$, d.f. = 1, $P < 0.002$].

There was also a two-way interaction between Level and Consistency [$F = 13.16$, d.f. = 1, $P < 0.0003$] (Fig. 2). No other interactions reached significance.

Latency analyses for NG

A three-way ANOVA was performed with Trial as a random variable and with Level (global or local), Visual Field × Ipsilateral Hand (LVF-Lh, RVF-Rh, BVF-Lh + Rh) and Consistency (consistent, inconsistent) as between-trial variables. All three main effects were significant. There was a Level effect [$F = 20.74$, d.f. = 1, $P < 0.0001$] which resulted from a 62-msec advantage of global over local responses (688 and 750 msec, respectively). A Visual Field effect [$F = 42.27$, d.f. = 2, $P < 0.0001$] resulted from latencies in the right visual field (643 msec) being significantly faster than in bilateral presentations (713 msec) which were, in turn, significantly faster than in the left visual field (840 msec). A Consistency effect [$F = 3.89$, d.f. = 1, $P < 0.049$] resulted from an advantage of consistent (702 msec) over inconsistent (737 msec) stimuli.

We also found a significant interaction between Level and Visual Field [$F = 3.82$ d.f. = 1, $P < 0.02$] with only the left visual field demonstrating a difference between global and local responses, such that global responses were faster (Fig. 4). No other interactions were significant (Fig. 3).

A second three-way ANOVA was performed using the same three independent variables but using a natural log transformation of the reaction time data as the dependent variable. The significant effects revealed from this analysis were identical to those listed above. Specifically, there were main effects of Level [$F = 18.18$, d.f. = 1, $P < 0.0001$], Visual Field [$F = 45.20$, d.f. = 2, $P < 0.0001$] and Consistency [$F = 6.00$, d.f. = 1, $P < 0.02$].

There were also two-way interactions between Level and Visual Field [$F = 3.24$, d.f. = 2, $P < 0.04$]. No other interactions reached significance (Fig. 3).

Discussion

Two general findings of hierarchical perception experiments were replicated in the present study. Global precedence (i.e. the main effect of level) was maintained in both the split-brain patients, as was a main effect of consistency. However, global interference in the face of generally smaller or negligible local interference (i.e. a level × consistency interaction) was demonstrated only in LB. Furthermore, the effects of visual field were found for both patients, although for slightly different reasons. LB demonstrated evidence of a horse-race model of metacontrol where the faster of the two hemispheres (in this case, the RVF/Left Hemisphere) dominated the responses to bilateral trials [28]. NG, on the other hand, demonstrated evidence of some averaging between the two hemispheres, with responses to bilateral trials being significantly slower than RVF trials and significantly faster than LVF trials.

It may be argued that the hierarchical paradigm used here may not be ecologically optimal for testing true top-down influences in perception. For example, the local elements are not inherent parts of the global form (Kimchi, personal communication), the stimuli are linguistic, and they are presented briefly. However, results with normal individuals do not show an overall RVF advantage, although the task does show a significant global interference and a significant interaction between the level and consistency in this population. In any case, the focus of this paper is to qualify previous conclusions on interhemispheric effects in this particular paradigm, rather than to determine its generalizability or validity.

Hemispheric specialization of global and local processing

The current results give no indication that global processing is specialized to the right hemisphere or that local processing is specialized to the left hemisphere (Fig. 4). Had processing been specialized, we would have found

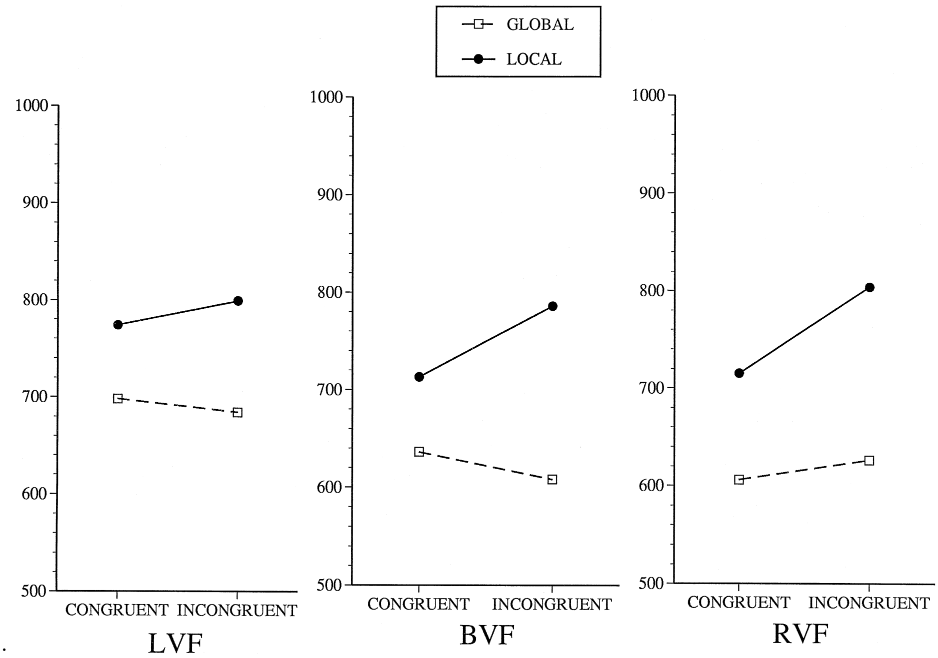


Fig. 2. The Visual Field × Level × Consistency interaction for LB.

an interaction between level and visual field. In the case of NG, the interaction was significant [$F = 3.82$, d.f. $= 2$, $P > 0.02$], with global trials being responded to faster than local trials in the LVF. However, this interaction did not reach significance in LB [$F = 1.50$, d.f. $= 2$, $P > 0.22$] (Fig. 4). Furthermore, there was no evidence in accuracy measures for a level × visual field interaction for either patient. Thus, in general, each disconnected hemisphere appears to be equally capable of processing both global and local patterns.

It has also been argued that one might expect left hemisphere specialization of both global and local forms, given the linguistic nature of the stimuli. However, the results from neither the present study nor previous studies, which used virtually identical stimuli, support an overall left hemispheric specialization for the task. Furthermore, there are several examples in the literature of other tasks calling for the comparison of single letters where no specialization has been observed.

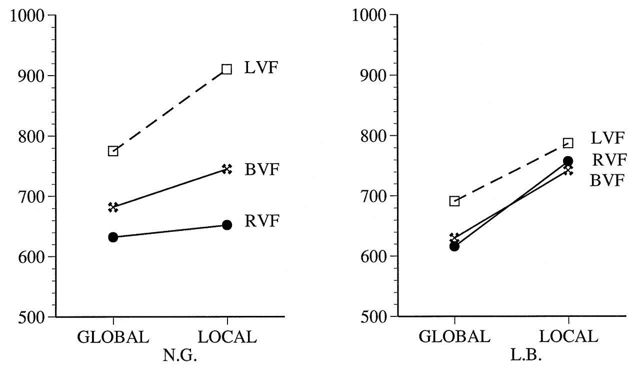


Fig. 4. The Level × Visual Field interaction for NG and LB.

The role of interhemispheric interactions in global interference

The current results do not support a necessary role for the corpus callosum in global interference. The clearest result is with LB who showed both a global advantage and global interference in all three visual fields, including the bilateral presentations. In the bilateral condition, LB also had a significant level × consistency interaction, with significant global interference but with no local interference. Indeed, LB demonstrates global interference that is comparable to that seen in the neurologically intact subjects, and he shows no consistency effect during processing of the global level. In normal individuals, there is often a smaller effect of consistency in the global level than in the local level rather than complete absence of consistency for global decisions [5].

The fact that NG demonstrated a consistency effect at both the local and global levels in bilateral presentations and only at the local level in RVF presentations is also not in line with a callosally-mediated, interhemispheric account of global interference.

While there was no evidence for consistent lateralization of the two levels, similar to Carusi *et al.*'s [5] results with normal subjects, where the experimental parameters were nearly identical to those used in the current study (except that the former study used the same eccentricity of 2.7° as the Robertson study, as against 1° here), there is some evidence to suggest that the consistency effect may still be interhemispheric in the normal brain. Carusi *et al.* performed a multiple stepwise linear regression with global interference as the dependent variable, and with various level, precedence, and visual field combinations of latencies as independent variables. The program selected latencies to LVF-local decisions minus latencies to RVF-global decisions as the highest multiple

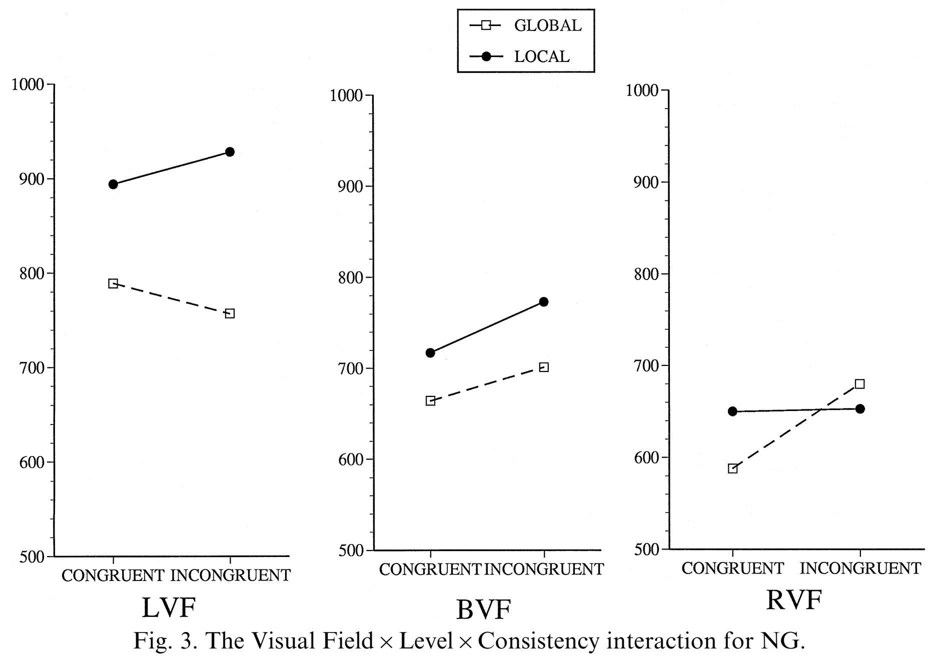


Fig. 3. The Visual Field × Level × Consistency interaction for NG.

partial correlation coefficient (r) of 0.5679, accounting for 32% of the variance.

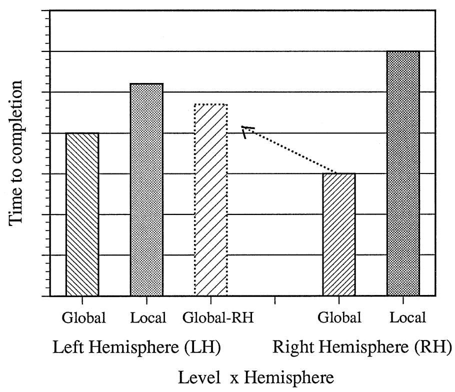
At issue, then, is the disparity between our results and those reported by Robertson *et al.* [22] for the same task and patient population. There were a few methodological differences between the two studies. First, the stimulus presentation differed in the two experiments. In the earlier study, white block letters were presented on a gray screen, whereas in the current study, black curved letters were presented on a white background. These differences would lead to shorter stimulus persistence on the screen in the latter case. Also, the eccentricities varied in the two studies, with the present study using a smaller eccentricity (1°) than Robertson *et al.*'s study (2.7°). Still, there is no obvious reason why this difference would lead to such disparate results given that earlier studies show no change in either effect with changes in eccentricity much larger than those involved here [16].

Another possible explanation for the disparity between the present data and that of Robertson and colleagues [22] is that, having received prior exposure to the stimuli, the patients may have changed their patterns of performance through some type of learning. The implication here is that both hemispheres learn over time to perform both global and local processing equally efficiently. In this way, the consistency effect begins to rely on intrahemispheric-, rather than interhemispheric, interference (Robertson, personal communication). In order to test this possibility, we partitioned each patient's first session data into three blocks. There was no evidence that hemispheric specialization decreased or that the consistency effect increased over blocks, and, therefore, no support for the learning hypothesis. Still, the possibility cannot be ruled out that the differences between the two experiments may reflect a longer-term, inter-session learning effect, rather than a shorter-term, intra-session effect.

It is possible, furthermore, that even these minor differences, in conjunction with one another, altered the cognitive window in which the consistency effect occurred. Thus, a passive control system might exist which is built into an interhemispheric network in which both specialized local and global decision mechanisms exist in each hemisphere, and which gives rise to an interhemispheric global interference effect. For example, suppose decisions at one level (e.g. global) interfere with decisions at another (e.g. local) if the faster one is completed within a certain time window of the slower. Suppose further that the timing difference between processing the two levels of a hierarchical stimulus within either hemisphere is outside that window. Then, there would be no intrahemispheric interference or consistency effect. Finally, suppose callosal relay of the processed global stimulus in the right hemisphere delays it just long enough to bring it within the time window to interfere with local processing in the left hemisphere. Then, global interference would reflect right hemisphere to left hemisphere transfer as suggested by the results of Carusi *et al.* ([5]; see [27]).

Figure 5 illustrates this model. The model assumes interhemispheric transfer of all decision codes to the other side. This is an unrealistically simple model. To test it, we need unbiased estimates of actual initial processing time of each code in each hemisphere and of callosal relay of a given code in a given direction. Such estimates are not yet available. However, the example represents an important class of models which account for interference effects by narrow 'windows of opportunity'.

One interesting observation regarding the two patterns of data in the same split-brain patients is that in Robertson *et al.*'s study hemispheric specialization is observed without any evidence of the consistency effect. In the present study, on the other hand, the consistency effect is observed without reliable hemispheric specialization. We might speculate, from these patterns, that there is a relationship between hemispheric specialization and callosal mediation of the consistency effect. Some support for such a relationship comes from the multiple regression performed by Carusi and colleagues [5] as well as from correlations performed by Robertson *et al.* [22]. We may speculate further that the consistency effect in a



The length of a bar designates the time course of a decision to completion. Callosal Relay delays arrival of a decision code to the other hemisphere and interference occurs only within a time window which is equal to the distance between two (y-axis) lines.

Fig. 5. A model for interhemispheric global interference.

given task is sensitive to the relative engagement of the left and right hemispheres in processing the local and global elements, respectively. When the two hemispheres show this pattern of specialization, the responsible modules are callosally interconnected and the consistency effect is callosally mediated. On the other hand, if there is no pattern of hemispheric specialization, processing of global and local levels may be assigned to the two hemispheres by attention, and the responsible modules may interact subcallosally, keeping the consistency effect interhemispheric, albeit, extracallosal. Alternatively, in the absence of hemispheric specialization, the consistency effect may simply become intrahemispheric. To date, however, we have not found any satisfactory explanation for why the split-brain patients show hemispheric specialization for the task on some occasions but not on others.

The two possible accounts of global interference discussed here, namely, interhemispheric interactions, either callosally-dependent or callosally-independent (i.e. extracallosal) vs intrahemispheric interaction cannot be completely disentangled by the present study. Further experiments are necessary for determining the range of parameters of the task for which callosal mediation of the consistency effect occurs.

However, the major conclusion of this study remains that the consistency effect need not depend on mechanisms mediated by the corpus callosum.

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