

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Research report

The evolutionary origins of functional cerebral asymmetries in humans: Does lateralization enhance parallel processing?

Marco Hirnstein^{a,*}, Markus Hausmann^a, Onur Güntürkün^b

^a Department of Psychology, University of Durham, United Kingdom

^b Biopsychology, Institute of Cognitive Neuroscience, Ruhr-University Bochum, Germany

Received 26 June 2007; received in revised form 14 September 2007; accepted 19 September 2007

Available online 25 September 2007

Abstract

Functional cerebral asymmetries (FCAs) are a fundamental principle of brain organization in many species. However, little is known about *why* they have evolved. Since FCAs are such a widespread phenomenon they seem to constitute an evolutionary selective advantage. According to a prominent hypothesis, an asymmetric brain should be associated with advantages in parallel processing, i.e. doing two tasks simultaneously. The strong version of this hypothesis implies that lateralized, instantaneous and complementary tasks are performed more efficiently with a highly lateralized brain. Using a visual half-field procedure, we wanted to test this strong version of the parallel-processing hypothesis in humans. Thirty-two participants (17 women, 15 men) were investigated. First, we assessed the degree of lateralization in a face/non-face and a word/non-word discrimination task favouring the right and left hemisphere, respectively. Based on a median split, subjects were divided into a rather symmetric and a rather asymmetric group. Then, all participants completed both tasks simultaneously. The results revealed that the rather symmetrically organized participants outperformed asymmetric participants in accuracy *and* response times. Hence, the strong version of the parallel-processing hypothesis has to be revised.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Functional cerebral asymmetries; Evolution; Parallel processing; Dual task; Humans

1. Introduction

Hemispheric asymmetries are a widespread phenomenon among various species: They are present in most vertebrates, including fish, amphibians, reptiles [8,54], birds [22] and mammals (for review [28,29,47,52]), and they can be found on various levels, such as neuroanatomy, neurochemistry, and behaviour. Recently, lateralization has also been shown in invertebrates, e.g. fruit flies [41], honeybees [35] or octopuses [9]. Although a very large number of studies have described various asymmetries in dozens of species, there is still little known about why lateralization has evolved. Hemispheric asymmetries are not a static phenomenon, underlie dynamic changes and are rather relative than absolute [42,50]. However, given they are so ubiquitous, an evolutionary advantage for lateralization should exist.

It has been suggested that functional cerebral asymmetries (FCAs) might have arisen to avoid processing delays deriving from slow interhemispheric transfer [43], or to prevent interhemispheric conflicts [1,14,53] or functional incompatibility [55–57]. Another long standing hypothesis to explain FCAs is by saving neural capacity due to a reduction of redundant processes. While a specific neural circuit in one hemisphere is processing a specific task, the homologous area in the opposite hemisphere can perform different or complementary processes, allowing a more efficient use of cortical capacity [36]. Concomitantly, an asymmetric brain enhances parallel processing [17,19]. Although the parallel-processing hypothesis was originally adopted to account for human lateralization, most of the empirical support comes from animal studies. This hypothesis has a weak and a strong version. The weak version posits that participants allocate lateralized resources over time to use them sometimes in parallel, sometimes in succession. The strong version implies that task performance is optimized by always simultaneously using asymmetrical neural mechanisms. Up to now, all animal studies used a design that is similar to the weak version of the parallel-processing hypothesis.

* Corresponding author at: Department of Psychology, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, United Kingdom. Tel.: +44 191 3343268; fax: +44 191 3343241.

E-mail address: m.a.hirnstein@durham.ac.uk (M. Hirnstein).

Rogers et al. [46, see also 15,18,45,48] tested chicks in a parallel task paradigm. They had to discriminate grain from small pebbles, and simultaneously, detect a predator overhead (silhouette of a hawk that was moved over the cage). Previous studies with chicks or pigeons revealed a left hemispheric superiority for the grain-pebble discrimination task [23,49] and a right hemispheric superiority for the detection of predators [20,48]. To test the parallel-processing hypothesis, Rogers et al. [46] compared the performance of lateralized and non-lateralized chicks. The results revealed that in contrast to non-lateralized chicks, lateralized ones showed better grain-pebble discrimination and additionally were less disturbed by the predator [18]. However, the lower performance of the non-lateralized chicks was not simply due to an overall reduced performance, since both groups did not differ when only a single task (the grain-pebble discrimination without a predator) was accomplished. In support of the hypothesis, the results suggest that FCAs are adaptive for parallel processing. However, an asymmetrical cerebral organization does not seem to reveal any advantage, if parallel processing is kept to a minimum (as in the single task condition).

In humans, processing two concurrent events has been extensively investigated, e.g. by using tachistoscopic paradigms as we did here. However, nobody so far to our knowledge has addressed how the degree of asymmetry affects performance on parallel processing. The seminal experiments by Banich and co-workers [3,4,6,7], for instance, revealed that when different stimuli are presented to both visual fields, the performance was enhanced in demanding tasks, when processing is distributed among both hemispheres, whereas in simple tasks the performance is enhanced when processing is restricted to a single hemisphere. Similarly to the experiments we conducted here, Nettleton and Bradshaw [39] presented faces and names to both visual fields simultaneously. They found that both hemispheres are capable of processing either stimuli but with varying levels of efficiency. However, none of these studies reported whether high degrees of lateralization were associated with better performance.

On the other hand in *single* task conditions the relationship between FCAs and performance has been investigated. Surprisingly, a negative correlation has been reported between an asymmetry index derived from both visual fields and the reaction time of a centrally presented stimulus [34], indicating that slower responses correspond to larger differences between visual fields. According to the authors, this finding is due to a better cooperation between both hemispheres in a less lateralized brain, presumably mediated by interhemispheric cross-talk. In support of this notion there is evidence for a link between the size of the corpus callosum, which is likely to mediate the interhemispheric cross-talk, and cognitive performance. For example, a larger corpus callosum (and hence an enhanced cooperation between the hemispheres) is associated with higher intellectual abilities [11,21,30,38,51] and shorter interhemispheric transfer time [33].

Taken together, the existing animal studies support the parallel-processing hypothesis. Our aim was to seek for similar evidence in humans. Based on the animal literature, we expected more lateralized participants to outperform less lateralized ones in parallel processing. According to the weak and the strong ver-

sion of the parallel-processing hypothesis, there are two different ways to approach the question. One is to test differently lateralized subjects in a dual task that avoids the need for instantaneous parallel processing. This is the design employed up to now in animal research using, e.g. birds with their laterally placed eyes. Here, chicks are faced with two separate task demands that require asymmetrical and complementary resources but are rather free to allocate their visual attention over time. The other alternative is to require participants to instantaneously respond to two different tasks given to the left or the right hemisphere. Here, the participants have no degrees of freedom but have to simultaneously respond to both tasks at a time point determined by the experimenter. This is the approach taken by the present experiment.

2. Methods

2.1. Participants

Thirty-two neurologically healthy subjects (17 women, 15 men) participated in this study. The mean age for women was 25.12 years (S.D. = 5.77, range: 19–39 years) and 24.87 years (S.D. = 7.00, range: 18–47 years) for men. All participants were right handed, as determined by the Edinburgh Handedness Inventory [40]. The laterality-index (LQ), provided by this test is calculated by $LQ = [(R - L)/(R + L)] \times 100$, resulting in values between -100 and +100. Positive values indicate a preference for the right hand, while negative values indicate left handedness. Women had a mean LQ of 89.74 (18.87, range: 43–100), while the mean LQ for men was 86.24 (15.86, range: 50–100).

2.2. Lateralization measures

To test the hypothesis that stronger FCAs are associated with better parallel processing of the two hemispheres, we used a face- and a lexical-discrimination task which are known to reveal robust right- and left-hemispheric superiorities, respectively [25,27]. In the first step of our experiment, both visual half-field (VHF) tasks were applied separately, i.e. participants had to discriminate either faces from non-faces or words from non-words. This procedure allowed us to quantify the advantage of the left (LVF) and right visual half-field (RVF) for both tasks.

Participants were asked to place their head on a chin rest, at a distance of approximately 57 cm from a monitor, so that 1 cm represents 1° visual angle. To ensure that lateralized stimuli were presented more than 2° visual angle to the left or right of a central fixation cross, we instructed our participants to keep their head and body still and to fixate that cross during the whole experiment. All stimuli were presented in a frame of 3.9 cm width and 5.1 cm height. As in (our) previous studies, all stimuli were presented tachistoscopically for 185 ms.

In the face-discrimination task, participants had to indicate as quickly and correctly as possible whether the presented stimuli was a “normal” face or an altered “non-face”. The faces were taken from a US college album from the 1950s, showing male, clean shaven, short haired students without glasses in their early 20s [27]. All face stimuli were framed with an ovoid overlay to cover distractors like clothes or background. In some photographs typical facial characteristics have been altered resulting in a non-face, e.g. the position of an eye and a mouth was swapped or everything was deleted except for the nose, etc. All faces had the same orientation and an unemotional, neutral expression. A trial started with a 2 s presentation of a central fixation cross. Then the stimulus was displayed in the LVF or RVF (in a pseudo-randomized order), while an empty frame appeared simultaneously in the contralateral VHF. Subsequently, a question mark instructed our participants to indicate by pressing a “Yes” or “No” button, whether the stimulus was a normal face. Seventy trials were employed by this procedure, the first 10 practice trials were excluded from the analysis. After 40 trials the responding hand was changed in a balanced order.

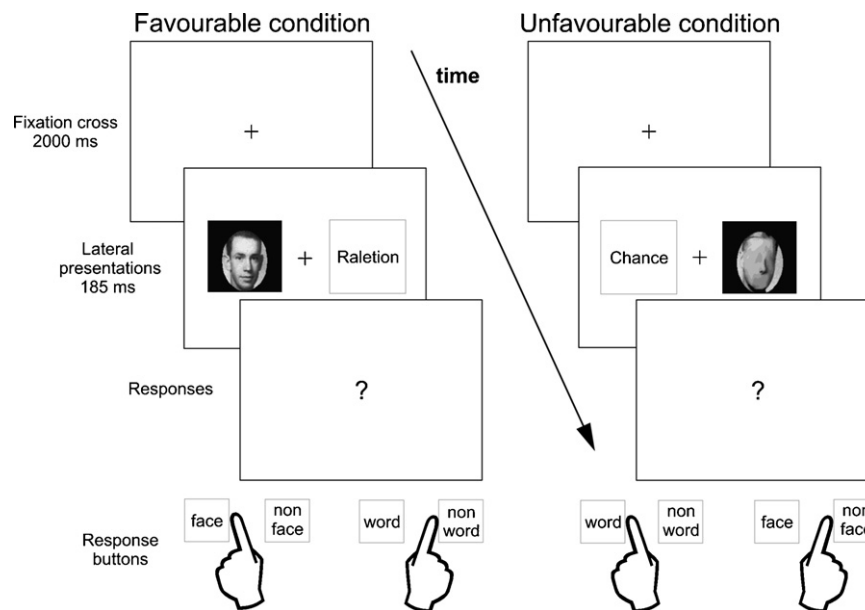


Fig. 1. Experimental setup of the parallel task. In the “favourable” condition a face or a non-face was always presented in the superior LVF and a word or a non-word in the superior RVF, whereas in the “unfavourable” condition a face or a non-face was presented in the inferior RVF and a word or a non-word in the inferior LVF.

In the lexical-discrimination task, participants had to indicate as quickly and correctly as possible whether a true German word or a non-word was presented. Only abstract nouns of at least four up to a maximum of eight letters were used to maximize the left-hemispheric advantage [5]. The experimental procedure was identical to the face-discrimination task. In previous studies (e.g. [24–27]) both tasks revealed the expected functional asymmetries, i.e. a LVF advantage for face discrimination and a RVF advantage for lexical decision. Although the purely behavioural tasks used in the present study are indirect measures of hemispheric activation, a recent functional imaging study has shown that lateralization patterns are highly related to the underlying neuronal activation patterns if the half-field technique fulfils the appropriate standards [31]. For both tasks, frequency and medial reaction time for correct responses were measured for each VHF. To determine the absolute individual degree of asymmetry, we calculated an asymmetry index (AI) for the frequency of correct responses and the reaction times as $AI = |[right - left \text{ visual field performance}] / [right + left \text{ visual field performance}]|$.

2.3. The parallel task

For the parallel task, we used the same stimuli as in the face and word discrimination task. A trial started with presentation of the fixation cross (duration 2 s). Then, a face/non-face was tachistoscopically presented within LVF or RVF while in the contralateral VHF a word/non-word was presented simultaneously. The exposure time for all stimuli was again 185 ms. Thus, by using the VHF paradigm two different conditions are possible: a “favourable” condition in which the face/non-face appeared in the superior LVF and a word/non-word in the superior RVF and an “unfavourable” condition, where the face/non-face was presented in the inferior RVF and the word/non-word in the inferior LVF (Fig. 1). This procedure allowed investigating whether a potential advantage of an asymmetric brain also persists, if the stimuli are presented to the subdominant hemispheres. The frequency of words and faces vs. non-words and non-faces was counterbalanced and our participants completed 48 trials in the favourable and 48 trials in the unfavourable condition. Prior to every condition, 10 practice trials were completed. After presentation of the stimuli, participants had to make *two* responses as quickly and correctly as possible. Participants responded with the *left* hand to stimuli in the LVF and with the *right* hand to stimuli in the RVF, respectively. That is, in the favourable condition, they responded with the *right* hand to words/non-words in the RVF and with the *left* hand to faces/non-faces in the LVF. Likewise in the favourable condition, they responded with the *right* hand to faces/non-faces in the RVF and with

the *left* hand to words/non-words in the LVF. A trial was considered only as correct, if *both* responses were correct. For both conditions, we measured the frequency of correct responses, and the medial reaction time of the second button press.

3. Results

3.1. Single tasks

The effect size is given as the proportion of variance accounted for (η^2) throughout. To investigate whether the face- and lexical-discrimination task revealed a LVF and RVF advantage, respectively, a mixed $2 \times 2 \times 2$ ANOVA with VHF (LVF, RVF) and hand (left, right) as repeated measures and sex as between-participants factor for the frequency of correct responses and medial reaction times was computed. In the *face-discrimination task*, a significant main effect VHF for both frequency of correct responses ($F(1,30) = 7.6$, $p = .01$, $\eta^2 = 20.3$) and reaction time ($F(1,30) = 8.2$, $p = .008$, $\eta^2 = 21.4$) was found. As expected, participants responded more accurate to the LVF ($76.6\% \pm \text{S.E.} = 1.9$) than to the RVF ($71.4\% \pm \text{S.E.} = 1.7$) and faster in the left (951 ± 30.2 ms) than in the RVF (985 ± 30.9 ms), indicating a robust LVF advantage, corresponding to a right-hemispheric superiority. All other main effects and interactions were not significant (all $F \leq 1.3$, $p \geq .26$, $\eta^2 \leq 4.1$). The *lexical-discrimination task* also yielded a significant VHF advantage for the frequency of correct responses ($F(1,30) = 20.7$, $p < .001$, $\eta^2 = 40.9$) and the reaction times ($F(1,30) = 8.6$, $p = .006$, $\eta^2 = 22.2$). Participants were more accurate in the RVF ($82.8\% \pm 2.2$) than in the LVF ($71.2\% \pm 3.4$) and made faster responses in the RVF (1160 ± 49.2 ms) right than in the LVF ($1280 \text{ ms} \pm 67.1$), indicating the predicted robust left-hemispheric advantage. Again, no further main effects or interactions were found (all $F \leq 2.6$, $p \geq .12$, $\eta^2 \leq 7.9$).

The results revealed that the lexical- and the face-discrimination task were strongly lateralized to the left or right cerebral hemisphere, respectively. Furthermore, no significant sex differences were found (all $F \leq 2.6$, $p \geq .12$, $\eta^2 \leq 7.9$).

3.2. Parallel task

It is important to bear in mind that participants were asked for two responses—each with a hit rate of 50%. Thus, overall chance level was at 25%. All groups in subsequent analyses differed highly significant from chance level (all $t(15) \geq 7.9$, $p < .001$), indicating that participants were capable of the task.

To obtain an overall degree of lateralization, we calculated a mean asymmetry index (AI_M), derived from the asymmetry indices of the face and the lexical decision task. Since both reaction time and accuracy consistently revealed FCAs, one AI_M was computed for accuracy and one AI_M was computed for reaction times.

We started our analysis with the AI_M based on accuracy. Participants with high AI_M scores had strong asymmetries in both tasks, while participants with low AI_M scores were rather symmetrically organized. We then performed a median split, resulting in a more lateralized and a less lateralized group. The frequency of correct responses and the reaction times in the parallel task were compared using a mixed $2 \times 2 \times 2$ ANOVA with condition (favourable vs. unfavourable) as within- and group (more vs. less lateralized) and sex as between-participants factors. Participants responded faster ($F(1,30) = 6.6$, $p = .016$, $\eta^2 = 19.1$) and more accurate ($F(1,30) = 22.8$, $p < .001$, $\eta^2 = 44.9$) in the favourable than unfavourable condition as indicated by significant main effects of condition (Table 1). Unexpectedly, a main effect group emerged, revealing that less lateralized participants responded significantly faster (1713 ± 90.3 ms) than more lateralized ones (2004 ± 90.3 ms, $F(1,30) = 4.9$, $p = .035$, $\eta^2 = 14.9$). There was no significant difference ($F(1,30) = .3$, $p = .56$, $\eta^2 = 1.2$) between less lateralized ($42.7\% \pm 2.0$) and more lateralized participants ($40.8\% \pm 2.0$) in accuracy.

We then repeated the whole procedure with AI_M based on reaction times, i.e. a median split was performed for AI_M based on reaction times, resulting in a less and a more lateralized group and a mixed 2×2 ANOVA with condition (favourable vs. unfavourable) and group (more vs. less lateralized) for

the frequency of correct responses and reaction times in the parallel task was computed. Similarly, participants responded faster ($F(1,30) = 6.6$, $p = .016$, $\eta^2 = 19.1$) and more accurate ($F(1,30) = 21.9$, $p < .001$, $\eta^2 = 43.4$) in the favourable than in the unfavourable condition. Surprisingly, less lateralized participants ($44.9\% \pm 1.8$) responded more accurate than more lateralized ones ($38.7\% \pm 1.8$) as indicated by a main effect group ($F(1,30) = 7$, $p = .013$, $\eta^2 = 20.1$), but they did not significantly respond faster ($F(1,30) = 1.6$, $p = .217$, $\eta^2 = 5.4$). In neither analysis significant interactions between group and condition emerged (all $F \leq 1.9$, all $p \geq .183$, $\eta^2 \leq 6.3$). Also no sex effects were found (all $F \leq 2.3$, all $p \geq .144$, $\eta^2 \leq 7.5$). Thus, when the groups were split according to accuracy, the difference between less and more lateralized participants emerged for reaction times, whereas, when the median split was based on reaction times, a difference was observed in accuracy. Although we do not see a plausible explanation on a methodological level, it should be noted that no trade-off between accuracy and reaction times exists (neither analysis revealed better performance of more lateralized participants), and thus cannot explain the main finding of the present study, namely a superiority in parallel processing for less lateralized individuals.

3.3. Correlation between degree of asymmetry and parallel task performance

Bivariate correlations with AI_M (based on accuracy and reaction times) and the frequency of correct responses and reaction times in the parallel task were calculated. We found a significant positive correlation between AI_M based on accuracy and the reaction times in the favourable condition ($r = .37$, $p = .037$), indicating slower responses in that participants who were more lateralized. No further correlations between AI_M and performance in the parallel task were significant (all $r \leq .28$, all $p \geq .128$) (Table 2).

3.4. Is the advantage of a less lateralized brain in parallel processing a result of single processing?

The previous analyses cannot clearly answer the question whether the superior performance of the less lateralized participants is only restricted to the parallel task, or whether less

Table 1
Mean frequencies of correct responses and reaction times (\pm S.E.) across strongly and weakly lateralized participants for favourable and unfavourable conditions

Lateralization (AI_M)	Mediansplit (accuracy)		Mediansplit (reaction times)	
	Reaction time (ms)	Correct responses (%)	Reaction time (ms)	Correct responses (%)
Strong				
Favourable condition	1945.4 \pm 95.4	45.1 \pm 2.1	1847.1 \pm 102.6	41.1 \pm 1.8
Unfavourable condition	2063.6 \pm 99.7	36.6 \pm 2.3	2011.9 \pm 103.3	36.2 \pm 2.3
Overall	2004.5 \pm 90.2	40.8 \pm 2.0	1929.5 \pm 96.1	38.7 \pm 1.8
Weak				
Favourable condition	1629.8 \pm 95.4	45.7 \pm 2.1	1728.1 \pm 102.6	49.6 \pm 1.8
Unfavourable condition	1795.7 \pm 99.7	39.6 \pm 2.3	1847.4 \pm 103.3	40.1 \pm 2.3
Overall	1712.8 \pm 90.2	42.7 \pm 2.0	1787.7 \pm 96.1	44.9 \pm 1.8

Results for AI_M based on accuracy are on the left hand, results for AI_M based on reaction time on the right hand. Note: Chance level is at 25%.

Table 2

Pearson product moment correlation coefficients and associated probability (two-tail) between mean asymmetry index (AI_M) based on either accuracy (left hand) or reaction times in the single tasks (right hand) and frequency of correct responses and reaction times in the parallel task

Performance parallel task		AI_M (based on accuracy)	AI_M (based on reaction time)
Correct responses	Favourable condition	-.275	-.202
	Unfavourable condition	-.027	-.012
Reaction time	Favourable condition	.370*	.220
	Unfavourable condition	.267	.237

* $p < .05$.

lateralized participants were also better in the single tasks and just maintain their superiority in the parallel task. However, the classification in less or more lateralized participants is based on a mean asymmetry index (AI_M) which itself has been obtained from the performances in the LVF or RVF in the single tasks. Thus, FCAs and performance are interrelated, making it difficult to disentangle both measures. We try to address this issue by restricting any further analysis to reaction times in single tasks, when AI_M was based on accuracy and by restricting our analyses to accuracy in single tasks, when AI_M was based on reaction times. Nevertheless, reaction time and accuracy in the single tasks were not independent of each other, so any result should be interpreted carefully.

We repeated the 2×2 ANOVA we computed for the *single tasks* (with hand and VHF as between-participants factors), but now with group (less vs. more lateralized) as between-participants factor, resulting in a $2 \times 2 \times 2$ mixed ANOVA. When the median split was based on accuracy, less lateralized participants responded faster in the face and lexical decision task, as expressed by main effects of group for faces ($F(1,30) = 8.5$, $p = .007$, $\eta^2 = 22.1$) and words ($F(1,30) = 11.8$, $p = .002$, $\eta^2 = 28.2$). Accordingly, when the analysis was based on reaction times, less lateralized participants responded more accurate in the face ($F(1,30) = .4$, $p = .523$, $\eta^2 = 1.4$) but significantly more accurate in the lexical decision task ($F(1,30) = 10.2$, $p = .003$, $\eta^2 = 25.4$).

4. Discussion

According to the hypothesis of parallel processing it has been claimed that one reason why FCAs have evolved is because they allow two different or complementary processes simultaneously. This has been supported by studies on chicks, fish, and marmosets [15,18,45,46,48]. In the present study, we aimed to test this hypothesis in humans. In accordance with animal studies, we hypothesized that participants with strong FCAs would outperform less lateralized participants in a parallel-task paradigm. However, we found the exact opposite: Less lateralized participants responded faster and more accurate than more lateralized participants. We also found evidence for a better performance of less lateralized participants in the single tasks, making it difficult to disentangle whether the superiority of the less lateralized participants is attributable to a better parallel or “single”-processing.

But wherever the advantage of the less lateralized participants stem from, our data – at first glance – are not in alignment with the strong version of the parallel-processing theory.

This raises a number of questions: First, why did our results differ fundamentally from previous animal studies? Second, which neural mechanisms might account for the superiority in parallel (and possibly single) processing of the less lateralized participants? Third, which implications can be derived from our data for the evolution of FCAs?

4.1. Animal studies

At a first glance, our results seem to be fundamentally different to previous animal studies. While the species tested up to now were more efficient in dual tasks when being highly lateralized [15,18,45,46,48], we obtained the reverse data pattern. However, as outlined in the introduction, our differing results were obtained with a different experimental design. In contrast to chicks, for example, who were allowed to “choose” which eye or which hemisphere to use at a certain time, the stimulus presentation to each hemisphere of the participants in the present study was experimentally constrained in terms of side and time point. Thus, our data pattern probably does not reflect a species but, at least more likely, a design difference. A second point of divergence are the less lateralized individuals. While they represent the lower half of the normal fluctuation in case of our human participants, they are, for the avian studies, constituted by dark-incubated chicks [46]. These animals lack an asymmetrical pre-hatch light input and substantially differ in terms of asymmetrical behaviour and anatomy from light-reared chicks [45]. Thus, the difference between lateralized and non-lateralized individuals is probably smaller in our participants.

It is important to note at this point that we obtained highly significant differences between the more and the less lateralized participants. So, we did not find the expected pattern. But we discovered an equally fascinating effect into the reverse direction. We therefore have to discuss why participants with lower asymmetry scores obtain superior results in our parallel-processing paradigm. This is what we will discuss in the next section.

4.2. The role of the corpus callosum

In the following we will argue that that interhemispheric transfer via the corpus callosum plays a key role in understanding why an increase of asymmetry reduces performance in our dual task paradigm. First of all, several neuropsychological models suggest that interhemispheric cross-talk is an essential mechanism in establishing FCAs. The most widespread view in explaining FCAs by callosal mechanisms is reciprocal inhibition in which a stimulus-specific activation of one hemisphere inhibits the other one during task processing [12,13]. Second, transecting the corpus callosum affects parallel processing. Split-brain patients and neurologically healthy participants had to search for a target item in stimulus arrays that were presented unilaterally either in the LVF or RVF or in both VHF (bilaterally). In the control group, the search rate between the bilateral and unilateral condition did not differ, whereas split-brain

patients responded about twice as fast for the bilateral condition than for the unilateral arrays [2,37]. The authors conclude that after resection of the corpus callosum, split-brain patients are capable of directing attention to both VHF simultaneously. Similarly, it has been shown that callosotomized monkeys show less interference between the two hemispheres than neurologically intact monkeys when two concurrent stimuli are presented to each visual field [44]. Given that interhemispheric transfer is essential for FCAs and parallel processing, why should this lead to a better performance of less lateralized participants?

The re-analysis of the data suggests that the superiority of the less lateralized participants in the parallel condition might have resulted from a superiority in the single condition. One should bear in mind, however, that even in the single condition both hemispheres are involved. Hemispheric asymmetries always represent only relative differences between hemispheres. Therefore, the single condition might also involve parallel-processing albeit reduced to a minimum. In either case a model has to explain both the superiority of the less lateralized participants in the parallel and in the single task condition.

We propose that less lateralized participants benefit from a better cooperation between hemispheres. Although the right hemisphere is superior in processing faces and the left hemisphere in processing words, the contralateral, non-specialized hemisphere contains at least some capabilities for processing faces or words. This can be seen, for instance, from our data in the single condition or from neuroimaging studies which typically reveal bilateral activations, though with stronger activations in the specialized hemisphere [10,32,39]. Via interhemispheric transfer the non-specialized hemisphere might assist the superior one proportional to its own capabilities. However, the more capabilities the non-specialized hemisphere has, the less is the function lateralized, resulting in an enhanced performance of the less lateralized group. But an enhanced cooperation between the hemispheres would not only be beneficial for the parallel condition, which might account for the superiority of the less lateralized participants in the single condition. This nicely fits the data of Ladavas and Umiltà [34], who also found that less lateralized participants responded faster than more lateralized ones in a single task paradigm. Although we can only speculate about the underlying neural mechanisms of our results, interhemispheric transfer might play a crucial role.

5. Conclusions

What implications can we derive from our data about the evolution of FCAs and the parallel-processing hypothesis? Prima facie our data suggest that parallel (and single) processing in humans is enhanced with a rather symmetric brain. This is true at least for the strong version of the parallel-processing hypothesis as used here as a starting point. This strong version posits that lateralized, instantaneous and complementary tasks are performed more efficiently with a highly lateralized brain. Our data show that this conception is certainly wrong and that even the reverse applies.

This, however, does not necessarily mean that the parallel-processing hypothesis of the evolution of asymmetries has to

be abandoned. It has, however, to be more precisely specified. It is possible that tasks that allow participants to more freely allocate resources over tasks, hemispheres and time might reveal an advantage of being asymmetric. If this would be the case, the evolutionary advantage of FCAs might come into play when individuals are allowed to sequence their complementary tasks according to their own mental strategy. They might then switch to the highly specialized and asymmetrically organized system when focussing on a certain problem.

Acknowledgements

We thank all participants for their help and cooperation and Jürgen Dukart for conducting parts of the experiments. Parts of this work were presented on the conference “Psychology and Brain 2007” in Dortmund, Germany.

References

- [1] Annett M. The right shift theory of a genetic balanced polymorphism for cerebral dominance and cognitive processing. *Curr Psychol Cogn* 1995;14(5):427–80.
- [2] Arguin M, Lassonde M, Quattrini A, Del Pesce M, Foschi N, Papo I. Divided visuo-spatial attention systems with total and anterior callosotomy. *Neuropsychologia* 2000;38(3):283–91.
- [3] Banich MT, Weissman DH. One of twenty questions for the twenty-first century: how do brain regions interact and integrate information? *Brain Cogn* 2000;42(1):29–32.
- [4] Banich MT, Belger A. Interhemispheric interaction: how do the hemispheres divide and conquer a task? *Cortex* 1990;26(1):77–94.
- [5] Baschek IL, Bredenkamp J, Oehrle B, Wippich W. Determination of imagery, concreteness and meaningfulness of 800 German nouns. *Z Exp Angew Psychol* 1977;24(3):353–96.
- [6] Belger A, Banich MT. Costs and benefits of integrating information between the cerebral hemispheres: a computational perspective. *Neuropsychology* 1998;12(3):380–98.
- [7] Belger A, Banich MT. Interhemispheric interaction affected by computational complexity. *Neuropsychologia* 1992;30(10):923–9.
- [8] Bisazza A, Rogers LJ, Vallortigara G. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci Biobehav Rev* 1998;22(3):411–26.
- [9] Byrne RA, Kuba MJ, Meisel DV, Griebel U, Mather JA. Does *Octopus vulgaris* have preferred arms? *J Comp Psychol* 2006;120(3):198–204.
- [10] Carreiras M, Mechelli A, Estevez A, Price CJ. Brain activation for lexical decision and reading aloud: two sides of the same coin? *J Cogn Neurosci* 2007;19(3):433–44.
- [11] Cherkassky VL, Kana RK, Keller TA, Just MA. Functional connectivity in a baseline resting-state network in autism. *Neuroreport* 2006;17(16):1687–90.
- [12] Chiarello C, Maxfield L. Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. *Brain Cogn* 1996;30(1):81–108.
- [13] Cook ND. Callosal inhibition: the key to the brain code. *Behav Sci* 1984;29(2):98–110.
- [14] Corballis MC. *The lopsided ape: evolution of the generative mind*. New York: Oxford University Press; 1991. p. 206–14.
- [15] Dadda M, Bisazza A. Does brain asymmetry allow efficient performance of simultaneous tasks? *Anim Behav* 2006;72(3):523–9.
- [17] Deacon T. *The symbolic species*. Harmondsworth, UK: The Penguin Press; 1997. p. 309.
- [18] Dharmaretnam M, Rogers LJ. Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behav. Brain Res* 2005;162(1):62–70.
- [19] Dunaif-Hattis J. *Doubling the brain*. New York: Peter Lang; 1984.

- [20] Evans CS, Evans L, Marler P. On the meaning of alarm calls—functional reference in an avian vocal system. *Anim Behav* 1993;46(1):23–38.
- [21] Fine JG, Semrud-Clikeman M, Keith TZ, Stapleton LM, Hynd GW. Reading and the corpus callosum: an MRI family study of volume and area. *Neuropsychology* 2007;21(2):235–41.
- [22] Güntürkün O. Visual lateralization in birds: from neurotrophins to cognition? *Eur J Morphol* 1997;35(4):290–302.
- [23] Güntürkün O, Kesch S. Visual lateralization during feeding in pigeons. *Behav Neurosci* 1987;101(3):433–5.
- [24] Hausmann M, Güntürkün O, Corballis M. Age-related changes in hemispheric asymmetry depend on sex. *Laterality* 2003;8(3):277–90.
- [25] Hausmann M, Becker C, Gather U, Güntürkün O. Functional cerebral asymmetries during the menstrual cycle: a cross-sectional and longitudinal analysis. *Neuropsychologia* 2002;40(7):808–16.
- [26] Hausmann M, Güntürkün O. Steroid fluctuations modify functional cerebral asymmetries: the hypothesis of progesterone-mediated interhemispheric decoupling. *Neuropsychologia* 2000;38(10):1362–74.
- [27] Hausmann M, Güntürkün O. Sex differences in functional cerebral asymmetries in a repeated measures design. *Brain Cogn* 1999;41(3):263–75.
- [28] Hellige JB. *Hemispheric asymmetry: what's right and what's left*. Cambridge, MA: Harvard University Press; 1993. p. 136–67.
- [29] Hopkins WD. Comparative and familial analysis of handedness in great apes. *Psychol Bull* 2006;132(4):538–59.
- [30] Hulshoff Pol HE, Schnack HG, Posthuma D, Mandl RC, Baaré WF, van Oel C, et al. Genetic contributions to human brain morphology and intelligence. *J Neurosci* 2006;26(40):10235–42.
- [31] Hunter ZR, Brysbaert M. Visual half field procedures are a good measure of cerebral language dominance if used properly: evidence from fMRI. *Neuropsychologia*, in press.
- [32] Ishai A, Schmidt CF, Boesiger P. Face perception is mediated by a distributed cortical network. *Brain Res Bull* 2005;67(1–2):87–93.
- [33] Jäncke L, Steinmetz H. Interhemispheric transfer time and corpus callosum size. *Neuroreport* 1994;5(17):2385–8.
- [34] Ladavas E, Umiltà C. Do laterality measures relate to speed of response in central vision? *Brain Cogn* 1983;2(2):119–28.
- [35] Letzkus P, Ribl WA, Wood JT, Zhu H, Zhang SW, Srinivasan MV. Lateralization of olfaction in the honeybee *Apis mellifera*. *Curr Biol* 2006;16(14):1471–6.
- [36] Levy J. Possible basis for evolution of lateral specialization of human brain. *Nature* 1969;224(5219):614–5.
- [37] Luck SJ, Hillyard SA, Mangun GR, Gazzaniga MS. Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature* 1989;342(6249):543–5.
- [38] Nosarti C, Rubia K, Smith AB, Frearson S, Williams SC, Rifkin L, et al. Altered functional neuroanatomy of response inhibition in adolescent males who were born very preterm. *Dev Med Child Neurol* 2006;48(4):265–71.
- [39] Nettleton NC, Bradshaw JL. Name and face matching in one or two visual fields: a test of models of hemispheric specialization. *Brain Cogn* 1983;2(2):103–18.
- [40] Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 1971;9(1):97–113.
- [41] Pascual A, Huang KL, Neveu J, Preat T. Brain asymmetry and long-term memory. *Nature* 2004;427(6975):605–6.
- [42] Pratt H, Sinai A, Laufer I, Horev N. Time course of auditory cortex activation during speech processing. *J Basic Clin Physiol Pharmacol* 2002;13(2):135–49.
- [43] Ringo JL, Doty RW, Demeter S, Simard PY. Time is of the essence: a conjecture that hemispheric specialization arises from interhemispheric conduction delay. *Cereb Cortex* 1994;4(4):331–43.
- [44] Ringo JL, Doty RW, Demeter S. Bi-versus mono-hemispheric performance in split-brain and partially split-brain macaques. *Exp Brain Res* 1991;86(1):1–8.
- [45] Rogers LJ. Cognitive and social advantages of a lateralised brain. In: Malashichev YB, Deckel AW, editors. *Behavioral and morphological asymmetries in vertebrates*. Georgetown, TX: Landes Bioscience; 2006. p. 129–39.
- [46] Rogers LJ, Zucca P, Vallortigara G. Advantages of having a lateralized brain. *Proc Biol Sci* 2004;271(Suppl. 6):S420–2.
- [47] Rogers LJ, Andrew RJ. *Comparative vertebrate lateralization*. Cambridge, UK: Cambridge University Press; 2002.
- [48] Rogers LJ. Evolution of hemispheric specialization: advantages and disadvantages. *Brain Lang* 2000;73(2):236–53.
- [49] Rogers LJ. Light input and the reversal of functional lateralization in the chicken brain. *Behav Brain Res* 1990;38(3):211–21.
- [50] Sinai A, Pratt H. High-resolution time course of hemispheric dominance revealed by low-resolution electromagnetic tomography. *Clin Neurophysiol* 2003;114(7):1181–8.
- [51] Tramo MJ, Loftus WC, Stukel TA, Green RL, Weaver JB, Gazzaniga MS. Brain size, head size, and intelligence quotient in monozygotic twins. *Neurology* 1998;50(5):1246–52.
- [52] Vallortigara G, Rogers LJ. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav Brain Sci* 2005;28(4):575–89.
- [53] Vallortigara G. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain Lang* 2000;73(2):189–219.
- [54] Vallortigara G, Rogers LJ, Bisazza A. Possible evolutionary origins of cognitive brain lateralization. *Brain Res Rev* 1999;30(2):164–75.
- [55] Vallortigara G, Andrew RJ. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behav Processes* 1994;33(1–2):41–58.
- [56] Vallortigara G. Right hemisphere advantage for social recognition in the chick. *Neuropsychologia* 1992;30(9):761–8.
- [57] Vallortigara G, Andrew RJ. Lateralization of response by chicks to change in a model partner. *Anim Behav* 1991;41:187–94.