



Disentangling the relationship between hemispheric asymmetry and cognitive performance

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ABSTRACT

It is widely believed that advantages of hemispheric asymmetries originated in better cognitive processing, hence it is often implied that the relationship between hemispheric asymmetry and cognitive performance is linearly positive: the higher the degree of lateralization in a specific cognitive domain, the better the performance in a corresponding task. Yet, the empirical evidence for this notion is mixed and the statistical methods to analyze this relationship have been criticized. The present study therefore investigated the relationship between hemispheric asymmetries and cognitive performance in two behavioral tasks (a left-lateralized word-matching task and a right-lateralized face-decision task) in 230 participants (140 women, 90 men) by using two different approaches. Both methods correspondingly revealed that a relationship between hemispheric asymmetries and cognitive performance does exist. Contrary to a positive (linear) relationship however, the data could be best described by an inverted U-shaped curve. Although the optimal degree of lateralization seemed to be task-specific, a slight or moderate degree of hemispheric asymmetry achieved best cognitive performance in all tasks. Moreover, performances deteriorated towards extreme ends of lateralization (i.e., participants with either extreme left or right hemispheric biases). Taken together, the present study provides evidence against the notion that higher lateralization is related to enhanced cognitive performance.

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1. Introduction

For more than 100 years now, hemispheric asymmetries are known to be a basic principle of human brain organization. Particularly in the last decade, however, hemispheric asymmetries have also been reported in many other species, comprising vertebrates such as mammals, birds, reptiles, amphibians and fish (for review see Rogers & Andrew, 2002; Vallortigara & Rogers, 2005) and invertebrates such as insects (Letzkus et al., 2006) and octopuses (Byrne, Kuba, Meisel, Griebel, & Mather, 2006). Since lateralization is such a wide-spread phenomenon it likely contains a selection advantage over a symmetric brain. For example, it has been suggested that a lateralized brain prevents conflicts between the two hemispheres (Vallortigara, 2000), eliminates functional incompatibility between processing familiar events and producing novel behavior (Vallortigara, Rogers, & Bisazza, 1999) or leads to a 'de-duplication' of functions and increasing neural capacity (Levy, 1969, 1974, 1977). Moreover, lateralization is supposed to enhance parallel processing.

While one hemisphere is occupied with a certain task, the other hemisphere can simultaneously perform an additional process (Rogers, 2006). Taken together, most of those theories suggest that hemispheric asymmetries emerged because its development led to enhanced cognitive processing. Taking interindividual differences in the degree of lateralization into account, it is widely believed that a positive relationship between the degree of lateralization and cognitive performance exists (Güntürkün et al., 2000). That is, the higher the degree of lateralization in a specific cognitive domain, or in other words, the more a cognitive domain is lateralized to a particular hemisphere relative to the other hemisphere, the better is the cognitive performance in a corresponding task.

However, empirical evidence for this notion is rather patchy with some studies showing the exact opposite. For example, more lateralized participants were outperformed by less lateralized participants on a single task (Ladavas & Umiltà, 1983) and also when performing two tasks simultaneously (Hirnstein, Hausmann, & Güntürkün, 2008). Furthermore, mathematically gifted participants exhibit a more symmetrical activation of brain regions than those of average math ability (O'Boyle et al., 2005). On the other hand, a recent study (Chiarello, Welcome, Halderman, & Leonard, 2009) found positive correlations between visual field asymmetries and reading performance, but only in young adults

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with strong and consistent hand preferences and less so in mixed handers. The probably most extensive study dealing with the relationship between hemispheric asymmetry and cognitive performance was conducted by Boles, Barth, and Merrill (2008) who reanalyzed data from nearly 800 participants on various dichotic-listening and visual half-field (VHF) tasks by correlating the mean of left and right hemispheric performances with a *laterality index* which was also derived from left (LH) and right hemispheric (RH) performances. For the majority of these tasks, the analyses revealed significant linear relationships between both measures. However, whether correlations were positive or negative was dependent on the cognitive process. For example, while auditory processing produced only positive correlations, only negative correlations were found for visual lexical processing. Similar positive and negative correlations were reported in other studies (Birkett, 1977; Bryden & Sprott, 1981; Springer & Searleman, 1978), further suggesting that the relationship between the degree of lateralization and cognitive performance is task-dependent. According to Boles et al. (2008), the crucial factor that determines whether the relationship is positive or negative is the age, in which a particular cognitive function becomes lateralized. The relationship between hemispheric asymmetries and cognitive performance is said to be positive, when the cognitive function lateralizes early (≤ 5 years of age) or relatively late (>14 years of age) during ontogenesis, whereas negative relationships should emerge, if lateralization in cognitive functions is established between the age of 5 and 11 years.

There are studies that investigated the relationship between the strength of handedness (as an indicator of hemispheric asymmetry) and performance on different manual tasks (e.g. Annett & Manning, 1990a, 1990b). Obviously, manual asymmetries and performance on manual tasks cannot be compared directly to hemispheric asymmetries in cognitive functions and performance on cognitive tasks because different systems are involved. Even when only cognitive functions are examined, some cognitive functions may favor a more asymmetrical brain organization while others may favor if both hemispheres contribute rather symmetrically. Yet, another problem with these studies lies in the statistical approach that was used and this problem also affects studies that investigated cognitive performance. According to Leask and Crow (2006, 2003) the problem is that the two correlated variables, degree of lateralization and performance, are statistically dependent. The degree of lateralization in those studies is typically derived from accuracy and reaction times of the left (LH) and right hemisphere (RH) by simply calculating the difference between LH and RH performances or by calculating a lateralization index which additionally takes the overall performance into account. This lateralization measure is then correlated with either the LH or RH performance or a mean/sum from LH and RH performances. But the LH and RH are often correlated themselves. It is thus possible that correlations between the lateralization and cognitive performance measures are confounded by the correlation between LH and RH in the first place. As Leask and Crow (2006) conclude: “[...] presentations of such data, in which one variable is the function of the other, are vulnerable to misinterpretation.” (p. 222). To avoid this problem, one could determine the degree of lateralization with a certain task and measure cognitive performance in a different but related task (Leask & Crow, 2001). However, in previous studies (e.g. Boles et al., 2008) such independent but related tasks were not always available. Alternatively, Leask and Crow (1997, 2006) intended to solve the problem of dependent lateralization/cognitive performance measures by using a different methodological approach. The authors had a large dataset of more than 10,000 school children (10–11 years of age) and plotted the degree of lateralization (measured as hand dominance in a box-marking or match-picking task) against the mean performance in those tasks (and also against an independent verbal and nonverbal task). In

addition, empirical data were used to generate reference plots, in which any correlation between LH and RH performance was removed. These plots served as reference lines for the empirical plots and revealed an inverted U-shape relationship between the degree of manual asymmetry and the mean performance. That is, participants with a particular (and rather weak) degree of manual asymmetry performed best while performance deteriorated towards extremely left- or right-handed participants. As outlined above however, manual asymmetries as in Leask and Crow (2006) are not equivalent to lateralization in cognitive processes. The present study therefore wanted to investigate how cognitive performance in a specific function is related to the lateralization of this function.

Taken together, research on the relationship between hemispheric asymmetries and cognitive performance is inconclusive. One reason might be that different studies used different statistical approaches each having their own advantages and disadvantages. The ‘traditional’ approach of calculating correlations (Annett & Manning, 1990a, 1990b; Boles et al., 2008) has the inherent limitation that the relationship between hemispheric asymmetries and cognitive performance might be confounded by the correlation of left and right performances. The ‘alternative’ approach (Leask & Crow, 2006) however has the inherent limitation that it is purely descriptive and that the observed relationship between lateralization and performance is mathematically modeled. The present study therefore sought to combine both approaches to overcome these potential limitations. The major aims of the present study were threefold: (1) to investigate whether a significant relationship between hemispheric asymmetries and cognitive performance exists, (2) to clarify whether this relationship is indeed positively linear, as it is commonly believed, and (3) to compare the outcomes of the traditional with the alternative approach.

Moreover, several studies revealed interindividual differences in the degree of lateralization. Although more recent studies suggest that sex differences in lateralization are, if any, relatively small (Boles, 2005; Sommer, Aleman, Bouma, & Kahn, 2004), this study was also interested in whether interindividual (sex) differences in the relationship between hemispheric asymmetries and cognitive performance exist. In terms of gender, two previous studies (Boles, 2005; Leask & Crow, 2001) failed to find a substantial difference between men and women.

2. Methods

2.1. Participants

Overall, 140 women and 90 men were included in the present study. The data was partly taken from previous studies (Hausmann, Becker, Gather, & Güntürkün, 2002; Hausmann & Güntürkün, 1999, 2000; Hausmann, Güntürkün, & Corballis, 2003). All participants were right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). The laterality-quotient (LQ), provided by this test is calculated by $[(R - L)/(R + L)] \times 100$, 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 91.18 (SD = 15.7, range: 18–100), while the LQ for men was 89.18 (SD = 17.47, range: 9–100). Although the majority of participants were university students, also older adults were included (women: $M = 36.96$, SD = 16.27, range 19–80; men: $M = 36.18$, SD = 16.72, range 19–70). The large age-range suggests a rather representative sample compared to the frequently tested student populations.

2.2. Visual half-field tasks

Two VHF-tasks were used in the present study, the word-matching task and the face-decision task. In both tasks, partici-

pants were asked to place their head on a chin rest in front of a computer screen and keep their head and body still during the whole experiment. All stimuli were presented within a frame of 4° visual angle width and 3.8° visual angle height. The distance between a central fixation cross and the inner edge of the frame was 2.2°, which ensured lateralized presentation of the stimuli. In both tasks, participants completed 70 trials (10 practice trials and 30 experimental trials with the left and right hand each, starting hand was balanced across participants) and reaction times and frequency of correct responses in percent were recorded.

2.2.1. Word-matching task

A pool of 120 German nouns, consisting of at least four to a maximum of eight letters, were selected for their high degree of abstraction (e.g. “theory” or “form”) to maximize the left-hemispheric advantage (Baschek, Bredenkamp, Oehrlé, & Wippich, 1977). After presentation of a fixation cross for 2 s, one of these nouns was presented for 185 ms at the center of the screen. Then the fixation cross appeared again for 2 s, followed by a word, which was presented for 185 ms to either the left (LVF) or right visual half-field (RVF) while an empty frame appeared on the contralateral side. Stimuli presentation was pseudorandomized and participants were asked to indicate via button press whether the laterally presented word matched the previously presented word or not.

2.2.2. Face-decision task

Participants were presented either normal or ‘distorted’ non-faces in one VHF while an empty frame was shown on the contralateral side (stimulus time 185 ms). Photographs for the faces were taken from a US college album of the 1950s. The students on these pictures were all male, clean shaven, short-haired and without glasses. To avoid further nonfacial characteristics, all photographs were framed with an ovoid overlay which covered the background and the clothes. The distorted faces were generated by translocating some facial characteristics, like swapping the mouth and one eye or deleting the eyes. Participants were asked to indicate via button press whether a picture showed a normal or a ‘distorted’ face as quickly and as accurately as possible.

Several previous studies revealed and replicated a consistent RVF/left hemisphere (LH) advantage for the word-matching and a consistent LVF/right hemisphere (RH) advantage for the face-decision task (Hausmann & Güntürkün, 1999, 2000; Hausmann et al., 2002, 2003). In fact, a recent magnetic resonance imaging study found activations during the word-matching task particularly in the left inferior frontal gyrus, which is typically associated with verbal processing (Weis et al., 2008). Further support for a LVF/RH advantage for face-processing in VHF-tasks comes from another imaging study (Yovel, Tambini, & Brandman, 2008) and yet another imaging study demonstrated that VHF experiments can accurately measure hemispheric asymmetries and correlate with the hemodynamic response (Hunter & Brysbaert, 2008).

2.3. Data analysis

2.3.1. Traditional approach

According to Boles et al. (2008), the easiest and most common way to determine the degree of lateralization in accuracy and reaction times is a laterality index (LI) calculated as $[(RVF-LVF)/(RVF + LVF)] * 100$. In terms of clarity, this formula was used in a way, so that for both accuracy and reaction times, a negative index always indicates a LVF/RH and a positive index a RVF/LH advantage. The LI for each task (word-matching and face-decision) and each dependent variable (accuracy and reaction time) was then correlated with the mean LVF/RH and RVF/LH performance. Correlations were calculated for negative and positive LIs, indicating the

direction of the bias (hence termed directional LIs) and absolute LIs (i.e., the degree of lateralization irrespective of its direction). In addition to Boles et al. (2008) however, not only linear regressions but also a quadratic regressions were calculated, because both the data of Leask and Crow (2006) and the regression figures in the study of Boles et al. (2008) imply a U-shaped relationship between the degree of lateralization and overall cognitive performance when directional LIs were considered.

2.3.2. Alternative approach

The alternative approach was adopted from Leask and Crow (2006), for a more detailed description we thus refer to their paper. The basic idea is to compare the relationship between lateralization and cognitive performance in the real data with the relationship between lateralization and cognitive performance in reference models, which are generated from the real data but in which confounding intercorrelations between LVF and RVF were removed. The different steps of the alternative approach are described below and exemplified in Fig. 1.

First, the LI and the mean performance of RVF and LVF (for both accuracy and reaction times) were calculated and then plotted against each other. Instead of a simple linear regression line, however, LI and mean performance were smoothed by using locally weighted scatterplot smoothing (LOESS). LOESS is a modern smoothing method, which “[...] can be seen as a type of moving average, where the value of a ‘y’ for a given ‘x’ consists of the average of all the ‘local’ y-values, cubically weighted by their distance each side of x. This ‘smoothing kernel’ moves along the x-axis, calculating a mean value for y, with data further away contributing less and less” (Leask & Crow, 2006, p. 222). In contrast to simple linear regressions, LOESS does not make any presuppositions about the relationship between two variables and can therefore detect any linear and non-linear relationship between LI and mean performance.

Second, the reference models were generated. To this end, one side (say RVF) was displaced vertically with respect to the other side (LVF) by one row: the RVF performance of participant one was shifted to participant two and matched with his/her LVF performance, the RVF performance of participant two was matched with the LVF performance of participant three and so forth, generating a new variable (RVF₁). Then RVF₁ was displaced with respect to LVF by one row, creating RVF₂ and so forth. At the end, so many new RVF variables were generated, that the LVF performance of every participant matched the RVF of every participant. For example, 140 women completed the word-matching task. So, 139 displacements were made, resulting in 139 new RVF variables. To control for confounding intercorrelations between LVF and RVF, only those new RVF variables were retained that had close to zero correlations with the original LVF variable ($r < .05$). Just as in the case of the real data, an LI and a mean performance were calculated using the original LVF and each of the remaining, uncorrelated, new RVF variables. Then the LIs were plotted against the respective mean performances and smoothed using LOESS, serving as reference models for the real data.

Third, to reveal the relationship between lateralization and cognitive performance, one needs to examine the difference between the real data and the reference models. Fig. 2 therefore shows the difference between real data and reference models calculated as real data minus reference models. In other words, if there is no difference between real and modeled data (the dotted zero line in Fig. 2), no conclusion can be drawn about the relationship between lateralization and performance. However, if the real data exceed the reference models, performance is better than expected (i.e., better than expected on the basis of a model, in which intercorrelations between LVF and RVF were removed). If the reference models exceed the real data, performance is worse than expected.

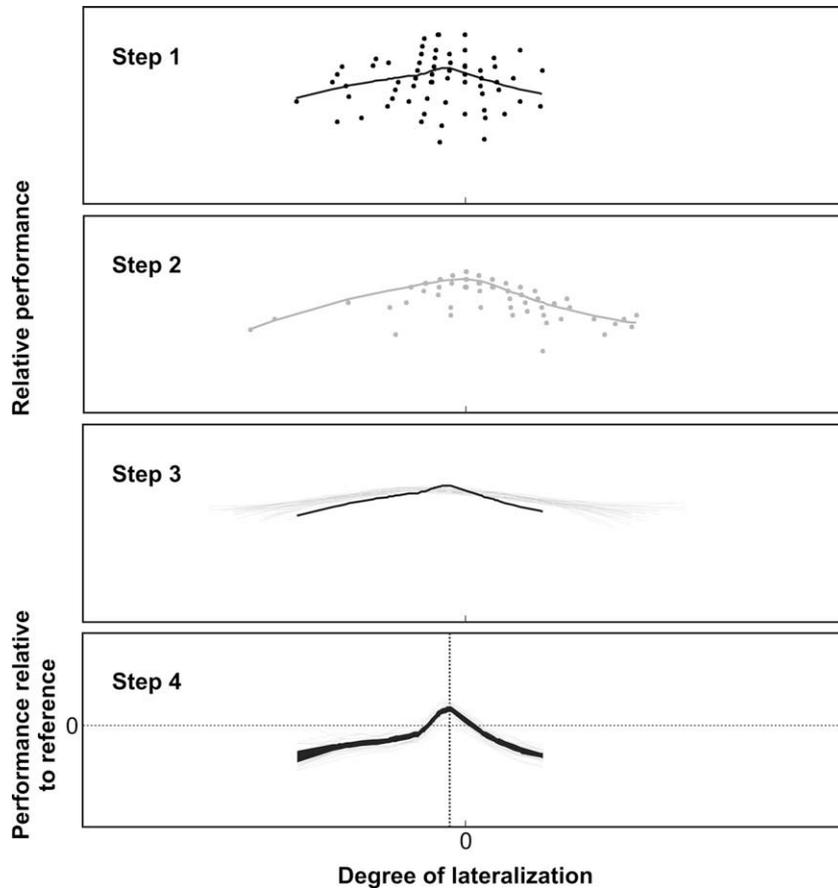


Fig. 1. The alternative approach illustrated by an example. Step 1 shows the empirical data of men in the face-decision task (accuracy). The LI is plotted against the mean performance and smoothed with LOESS. Each dot represents one participant. Step 2 shows an example of a reference model. The empirical RVF data is vertically displaced with respect to LVF so that RVF and LVF do not correlate with each other. Then, the LI is plotted against mean performance and smoothed again with LOESS. Step 3 shows all reference models (gray lines) and the real data (black line) in one plot. Step 4 shows the difference between empirical data and reference models (empirical data minus low-correlation references). Each gray line represents the difference between the empirical data and one reference model. Black lines are 99% confidence bands and serve as an estimate of uncertainty. The LI at which performance is optimal is indicated by a vertical dashed line.

Since the alternative approach is purely descriptive, 99% confidence intervals were computed across all reference models to quantify the differences between the real and modeled data. If the zero line lies outside of the confidence intervals at a given laterality index, it is assumed that the mean performance at this degree of lateralization is either better or worse than implied by the reference models.

3. Results

3.1. Hemispheric asymmetries

A mixed 2×2 ANOVA with VHF (LVF vs. RVF) as within- and sex as between-participants factor was calculated for both tasks and for both accuracy and reaction times. The effect size is given as the (partial) proportion of variance accounted for (partial η^2) throughout. Mean accuracies, response times and LIs across both tasks and both sexes are shown in Table 1.

3.1.1. Word-matching task

Accuracy: Participants responded more accurately in the RVF ($92.1 \pm \text{SEM} = .62$) than in the LVF ($86.6 \pm .83\%$) as indicated by a significant main effect of VHF ($F(1,227) = 68.66, p < .001, \eta^2 = .23$). Moreover, a significant interaction between sex and VHF emerged ($F(1,227) = 4.93, p = .027, \eta^2 = .02$) with the RVF advantage being

more pronounced for women (RVF: $92.0 \pm .77\%$, LVF: $85.0 \pm 1.04\%$) than men (RVF: $92.3 \pm .97\%$, LVF: $88.2 \pm 1.30\%$). The main effect sex did not reach significance ($F(1,227) = 1.75, p = .187, \eta^2 = .01$). **Reaction times:** Since the analysis revealed neither a significant main effect nor an interaction for response times (all $F(1,227) < 1.93, p > .166, \eta^2 < .01$), it was excluded from further analyses of the relationship of lateralization and cognitive performance.

3.1.2. Face-decision task

Accuracy: Participants responded more accurately in the LVF ($80.5 \pm .73\%$) than in the RVF ($74.3 \pm .72\%$; $F(1,227) = 80.35, p < .001, \eta^2 = .26$) indicating a strong right-hemispheric advantage. Neither the main effect of sex nor the interaction between sex and VHF became significant (all $F(1,227) \leq .32, p \geq .565, \eta^2 \leq .001$). **Reaction times:** Participants responded faster in the LVF ($967.4 \text{ ms} \pm 15.7$) than in the RVF ($1006.8 \text{ ms} \pm 15.7$; $F(1,227) = 27.79, p < .001, \eta^2 = .11$), again indicating a strong RH advantage. The main effect of sex ($F(1,227) = .49, p = .485, \eta^2 = .002$) and the interaction between sex and VHF ($F(1,227) = 3.59, p = .06, \eta^2 = .016$) failed to reach significance.

Taken together, both tasks revealed robust hemispheric asymmetries in the expected direction. Moreover, women demonstrated a slightly more pronounced asymmetry than men in the word-matching task, albeit the effect size was very small ($\eta^2 = .02$).

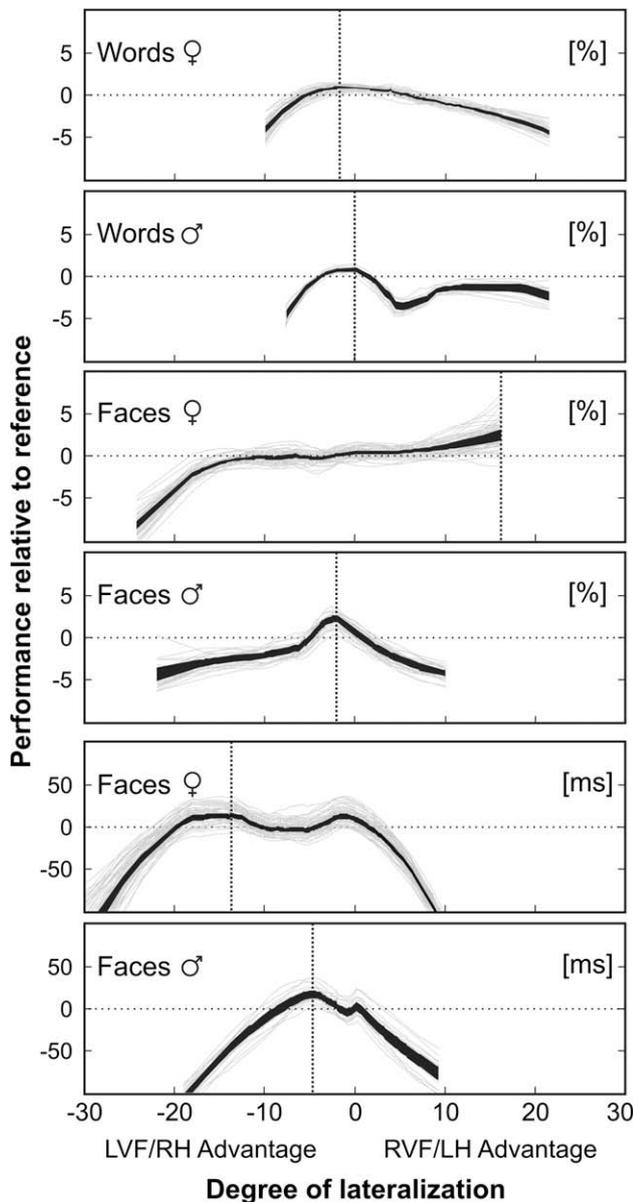


Fig. 2. Degree of lateralization across performance (relative to reference) in the word-matching (words) and face-decision (faces) task for men and women. The dotted horizontal line represents a relative performance of zero, that is, no difference between real data and references. Values above zero indicate higher accuracy and shorter reaction times and values below zero indicate lower accuracy and longer reaction times (relative to reference). Each gray line represents the difference between the empirical data and one reference model (empirical data minus low-correlation references). Black lines are 99% confidence bands and serve as an estimate of uncertainty. Positive LIs indicate a RVF/LH advantage, negative LIs a LVF/RH advantage.

Table 1

Mean accuracy, mean reaction times and corresponding mean laterality indices (LIs) in both the word-matching and face-decision task across both sexes and both visual half-fields (SD in brackets). Positive LIs indicate a RVF/LH advantage, negative LIs a LVF/RH advantage.

	Word-matching task						Face-decision task					
	Women (N = 140)			Men (N = 89)			Women (N = 140)			Men (N = 89)		
	LVF	RVF	LI	LVF	RVF	LI	LVF	RVF	LI	LVF	RVF	LI
Accuracy [%]	84.98 (12.71)	92.02 (9.54)	4.30 (6.24)	88.19 (11.48)	92.26 (8.47)	2.50 (5.84)	80.35 (10.39)	73.81 (10.53)	-4.31 (7.02)	80.75 (11.43)	74.88 (10.91)	-3.75 (6.44)
Reaction times [ms]	1010.9 (256.3)	1014.1 (247.4)	-.23 (4.72)	957.8 (287.6)	974.0 (283.6)	-.92 (5.46)	998.8 (229.4)	1033.0 (235.0)	-1.68 (4.84)	936.0 (233.4)	980.6 (224.3)	-2.47 (5.39)

3.2. Relationship between laterality index and mean performance

Instead of examining the mean LVF/RH and RVF/LH performance one can also correlate the individual performances of the LVF/RH and RVF/LH with the LI. An analysis of these individual performances, however, did not differ substantially from the mean performance. In terms of brevity and to compare the data more directly to the data of Boles et al. (2008), only relationships between lateralization and the mean performance are thus reported subsequently.

3.2.1. Traditional approach

Correlation coefficients between LI and mean performance are shown in Table 2. The p-level was adjusted to $p < .01$ because of the relatively high number of regression analyses. There were five principal findings:

1. Relationship between degree of lateralization and mean performance does exist: Regression analyses revealed significant relationships particularly for the word-matching task in accuracy (only), which were almost identical for males and females. Only one significant relationship was found in the face-decision task (response times), indicating a significant quadratic relationship between the degree in lateralization and overall reaction time in this task for men.
2. (Extremely) High degrees of lateralization are detrimental: All significant relationships for the word-matching task in accuracy were negative, suggesting an increased overall performance when the RVF/LH advantage in this task was low. Significant

Table 2

Linear and quadratic regressions between LI (absolute and directional) and mean performance (measured with accuracy or reaction times) in the word-matching and face-decision task across both sexes. Positive values in quadratic regressions indicate a U-shaped, negative values an inverted U-shaped curve. Optimal LI indicates which LIs were associated with optimal performance. Positive LIs indicate a RVF/LH advantage and negative LIs a LVF/RH advantage.

	Accuracy		Reaction Times
	Word-matching <i>r</i> (optimal LI)	Face-decision <i>r</i> (optimal LI)	Face-decision <i>r</i> (optimal LI)
<i>Directional</i>			
Linear			
Women (N = 140)	-.45***	.08	.002
Men (N = 89)	-.35**	.01	.12
Quadratic			
Women (N = 140)	-.56*** (-.01)	-.20 (-1.25)	-.17 (-2.14)
Men (N = 89)	-.41*** (-1.32)	-.22 (-4.55)	-.32** (-4.85)
<i>Absolute</i>			
Linear			
Women (N = 140)	-.59***	-.18	.13
Men (N = 89)	-.49***	-.17	.19

** $p < .01$.
*** $p < .001$.

quadratic regressions in the word-matching task revealed that optimal cognitive performance was achieved with rather low negative LIs (females: optimum at LI = -0.01, range -9.88 to 21.72, mean = 4.30; males: optimum at LI = -1.32, range -7.67 to 21.77, mean = 2.50). The quadratic regression in the face-decision task also revealed an optimal performance at an LI = -4.85 nearby the mean (mean = -2.47, range -19.21 to 9.29). Overall, the analyses suggest that extremely large LIs (negative or positive) are related to lower performance.

3. *Quadratic or linear relationship:* The relationship between degree of lateralization and mean performance slightly favored a quadratic model, at least when directional asymmetries were considered. Across all conditions/measures, correlation coefficients for quadratic regressions were consistently higher than those for directional, linear regressions, as indicated by a Wilcoxon-test across all correlation coefficients in quadratic and linear regressions ($Z = 2.37, p = .018$). Also, in the face-decision task (reaction times in males), it was only the quadratic regression which revealed significance. These differences however seem to disappear when absolute, linear regressions were compared to directional, quadratic regressions ($Z = 1.26, p = .21$; equal number of significant relationships).
4. *The optimal degree of lateralization:* The existence of a quadratic model implies that a task-specific optimum in the degree of lateralization exists. Surprisingly, the optimal degree of lateralization was always related to a small RH advantage in both tasks. This observation was particularly unexpected for the word-matching task, because the vast majority of participants had a RVF/LH advantage in the word-matching task. This finding, however, might be similar to the linear analyses, which localize the optimum in the degree of lateralization close to an LI = 0.
5. *Sex difference?* Although previous studies (and the present study) revealed a sex difference in the degree of lateralization, the relationship between degree in lateralization and mean performance was very similar between males and females. The only exception occurred in the face-decision task (response times), in which the quadratic regression was significant in males but not in females.

3.2.2. Alternative approach

The results can be found in Fig. 2. Each gray line represents the difference between the empirical data and one reference model (empirical data minus low-correlation references). Black lines are 99% confidence bands and serve as an estimate of uncertainty. Performance peaks and lows refer to the confidence bands.

3.2.2.1. Word-matching task. Accuracy: In line with the traditional approach, males and females showed optimal mean performance (compared with reference lines) when the degree of lateralization was low (and slightly shifted towards the RH, men: LI = 0; women: LI = -1.68). Mean performance drops with increasing degrees in lateralization. For men only, an additional drop in performance occurred at around LI = 5.21.

3.2.2.2. Face-decision task. Accuracy: Highly negative LIs (LVF/RH advantage) were associated with poor accuracy in men and women. But while men also showed low accuracy with highly positive LIs (RVF/LH advantage) and an optimum at LI = -2.02, women in fact showed an upswing at around LI = 5.00. There were marginal differences between real data and reference lines between both LIs, indicating no specific relationship with mean performance within this LI range.

Reaction times: Men had a single mean performance optimum at LI = -4.68, while women had two optima at LI = -1.19 and LI = -13.61. Mean performances between both peaks were indifferent (i.e., only marginal differences between real and reference

lines). Highly positive (LVF/RH advantage) and negative LIs (RVF/LH advantage) resulted in a steady mean performance decline.

3.2.2.3. Summary of the main findings.

1. *Relationship between degree of lateralization and mean performance does exist:* Similar to the traditional approach, the alternative approach suggests that there is a relationship between degree of lateralization and mean performance. The empirical data differed considerably from the reference lines in all conditions.
2. *(Extremely) High degrees of lateralization are detrimental:* The vast majority of plots suggest that the mean performance did not enhance with an increasing degree of lateralization (for potential exceptions see Point 4 below). On the contrary, participants with extremely high positive or negative LIs usually revealed lowest performances.
3. *Quadratic or linear relationship:* In accordance with the directional quadratic models in the traditional approach, the LOESS procedure led in most cases to lines which came closest to an inverted U-shaped curve (the female reaction times in the face-decision task might even suggest an inverted W-shaped curve). In fact, none of the other plots suggest a linear relationship between LI and mean performance except for women's accuracy in the face-decision task.
4. *The optimal degree of lateralization:* Every plot revealed performance optima at specific degrees of lateralization. At all those specific degrees of lateralization the gray lines in Fig. 2 differed significantly from the zero reference line (one sample t -tests with test value zero: all $t \geq 8.85$, all $p \leq .0001$), indicating that the real data differs indeed from the reference models at these laterality indices. These optimal degrees of lateralization, however, were not necessarily related to the dominant hemisphere in a particular task. For instance, in the face-decision task, where participants showed a LVF/RH advantage, the optimal mean performance in the accuracy rates of males was found in the lower LVF/RH advantage range (negative LIs). Women however, who also showed a LVF/RH bias, were more accurate when showing a strong RVF/LH bias (positive LI), though optimal mean performances in reaction times was also achieved with LVF/RH biases. Performance optima in the accuracy rates of both women and men in the word-matching task were associated with a slight LVF/RH bias despite the fact that both sexes showed a left-hemispheric bias. That means the task-specific degree of lateralization that is characteristic for a particular (sub-) population is not necessarily identical with the degree of lateralization that is associated with optimal performance (compare with Table 1).
5. *Sex difference?* There is some evidence that the relationship between degree of lateralization and mean performance is sex-dependent. Men consistently demonstrated a single optimum and deteriorating mean performances with highly positive and negative degrees of lateralization. Women performed similarly to men in two cases (reaction times in face-decision task and accuracy in word-matching task), but in one case (accuracy in face-decision task) such a single, U-shaped relationship did not emerge. Here, extremely high LVF/RH biases were associated with poor performances and extremely high RVF/LH biases with exceeding performances.

4. Discussion

Most theories about potential evolutionary advantages of hemispheric asymmetries imply that lateralization enhanced cognitive processing and that accordingly a higher degree of lateralization is associated with enhanced cognitive performance in specific cognitive functions. There is indeed empirical evidence coming from

an animal study to support this notion. Güntürkün et al. (2000) found that the more pigeons were lateralized in discriminating grain from grit with either the left or right eye (i.e., the right or left hemisphere respectively due to complete decussation of the optic nerves), the more successful were they in a foveal condition (general performance). The literature on humans however is less supportive. While mathematical models (Kosslyn, Sokolov, & Chen, 1989; Reggia, Goodall, & Shkuro, 1998) and a recent study (Chiarello et al., 2009) are in accordance with this notion, other studies reveal either ambiguous (Birkett, 1977; Boles et al., 2008; Bryden & Sprott, 1981; Springer & Searleman, 1978) or contrary results (Hirnstein et al., 2008; Ladavas & Umiltà, 1983; Leask & Crow, 2006; O'Boyle et al., 2005). The seemingly contradictory findings may well be the result of different functions and different tasks being investigated (let alone different species as in the case of pigeons and humans). For some tasks it might be more advantageous to have a more asymmetrical brain organization, whereas for other tasks a more symmetrical organization might be optimal. Moreover, it cannot be ruled out that some of these studies (e.g. Birkett, 1977; Boles et al., 2008) are confounded with intercorrelations between left and right side performance since the traditional approach was used. The present study combined the traditional and the alternative approach to the present study to overcome the potential limitations of one method with the strengths of the other. The fact that both approaches led to similar findings on a number of occasions provides a strong basis for the interpretation of the data.

4.1. No positive relationship between lateralization and performance

First of all, both approaches revealed that for both tasks a relationship between lateralization and cognitive performance does exist. Our findings are thus in accordance with a number of studies (Birkett, 1977; Boles et al., 2008; Bryden & Sprott, 1981; Chiarello et al., 2009; Leask & Crow, 1997, 2006; Springer & Searleman, 1978) and corroborate the view that cognitive performance might have indeed played a part in why hemispheric asymmetries have developed and why they still persist.

However, taken together both approaches also correspondingly suggest that this relationship does not follow the rule 'the more lateralized, the better the cognitive performance'. On the contrary, high degrees of lateralization led to poor mean performance according to the traditional approach and – perhaps with the exception of women with a strong left-hemispheric bias (see below) – also according to the alternative approach. The fact the bulk of participants had rather moderate degrees of lateralization also rules out that the relatively good performance of less lateralized participants was based on a few outliers. In turn, one might argue that the relatively poor performance of highly lateralized participants is the result of a few outliers. This however seems unlikely, too, since the poor performance emerged consistently across both tasks and measures. Our results are thus in clear contrast to computational models (Reggia et al., 1998), animal data (Güntürkün et al., 2000) and a recent study, which found a positive, albeit weak correlation between visual field asymmetries and reading performance (Chiarello et al., 2009). Hence, one cannot simply generalize our findings of a rather negative relationship and argue that hemispheric asymmetries and cognitive performance in humans are always negatively related to each other. In fact, Boles et al. (2008) have found that in a single dataset of a large number of lateralized tasks, sometimes positive and sometimes negative correlations emerge, which strongly suggests that the relationship between lateralization and cognitive performance is task-dependent. Our data are in accordance with this view. In the traditional approach, for example, all but one significant relationship between degree of lateralization and mean performance were found in the

word-matching task and not in the face-decision task. Still, the notion that higher degrees of lateralization inevitably lead to better cognitive performance was disconfirmed.

4.2. Inverted U-shaped curve

As far as directional asymmetries are concerned, both approaches correspondingly suggest that the relationship between lateralization and cognitive performance can be best described by an inverted U-shaped curve. This finding is in accordance with Leask and Crow (2006), who also revealed that performance was optimal at a certain degree of lateralization and deteriorated towards extremely high and low degrees. In contrast to our data, however, where different optimal degrees of lateralization were found across both tasks and both sexes, Leask and Crow (2006) found a single optimal lateralization degree (at about $LI = 10$) across various tasks. Perhaps, multiple optimal degrees in lateralization as observed in the present study might be the result of a rather heterogeneous sample (men and women of different ages) compared to the homogeneous sample (10–11 year old boys) used by Leask and Crow (2006). An inverted U-shaped relationship between hemispheric asymmetries and cognitive performance with a performance peak slightly shifted to either LH or RH would also be in accordance with a recent notion of Corballis (2006, 2005). His notion is based on the Right-Shift Theory, according to which handedness is mediated via a balanced polymorphism for cerebral dominance and cognitive processing (Annett, 1995), which predicts poorer performance at extremes of lateralization, the so-called 'heterozygote advantage'. Corballis has suggested that an extremely symmetrical brain might be disadvantageous, because it is detrimental for complex processes such as language, whereas an extremely asymmetrical brain might be disadvantageous, because it would result in poor sensor analysis or motor control on the sub-dominant side of the body/brain. Therefore, symmetry and asymmetry should be held in balance, to prevent those disadvantages. Our findings, and those of Leask and Crow (2006), fit the notion of Corballis in so far as extreme lateralization seems to be detrimental for cognitive performance. Despite sensorimotor deficits, a rather less lateralized functional brain organization however may contain the advantage of an enhanced cognitive performance.

It also becomes apparent from both the traditional and the alternative approach that the slight advantage of a quadratic over a linear relationship would disappear if analyses were based on absolute and not directional degrees of lateralization. This is in accordance with Boles et al. (2008) who also found consistently higher linear relationships for absolute rather than directional degrees of lateralization. Unfortunately, (Boles et al., 2008) did not provide correlation coefficients of quadratic regressions to test whether they were also higher than directional linear coefficients. Boles et al.'s explanation for higher and more frequent linear correlations in absolute rather than directional degrees of lateralization also holds true for our data, that is, the relationships in the LH ($LI < 0$) and RH scale ($LI > 0$) are almost mirrored with an optimum close to virtual symmetry ($LI = 0$).

If, like in the present study or the study of Leask and Crow (2006), a specific degree of lateralization (i.e., a specific left- or right-hemispheric bias) is associated with optimal performance, it seems reasonable to use directional rather than absolute degrees of lateralization to investigate the relationship between hemispheric asymmetries and cognitive performance. Otherwise information about the side/hemisphere ideally dominating a given function would be lost. However, if the optimal degree in lateralization is close to zero (virtual symmetry), as in the present study, it appears that the directional bias in the localization of the optimum is less relevant.

4.3. Other factors than cognitive processing contribute to hemispheric asymmetries

Finally, both approaches reveal that the average degree of lateralization in a population is not necessarily the same that is required to achieve an optimal performance. The traditional approach revealed that although men and women had a significant bias towards the left hemisphere in the word-matching task, optimal mean performances were even associated with a slight right-hemispheric bias (which might be still in the range of a bilateral functional brain organization, though). The alternative approach revealed a similar pattern for the word-matching task in accuracy for men. If cognitive performance were the only factor that decides about the adaptiveness of the degree in lateralization, one would expect that the vast majority of a population would gather around these optimal degrees of lateralization. However, this does not seem to be the case: many individuals reveal a degree of lateralization which is suboptimal or even detrimental for cognitive performance. One might thus speculate that factors other than cognitive performance also contribute to the adaptiveness of the degree of lateralization. For example, an additional adaptive value of hemispheric asymmetries might be the cerebral susceptibility to harmful events as a functionally less lateralized neural network supporting language, for instance, can be beneficial for compensation after unilateral lesions (Knecht et al., 2002).

4.4. Sex differences

So far, findings were discussed in which there were large overlaps between the traditional and the alternative approach. However, both approaches reveal different results regarding a potential sex difference in the relationship between lateralization and cognitive performance. In the traditional approach (except for a stronger relationship in men than women in reaction times of the face-decision task), relationships overlapped to a large extent, suggesting rather no sex difference. However according to the alternative approach, men consistently showed an inverted U-shaped curve, whereas – at least on one occasion (accuracy in the face-decision task) – women with extremely high left-hemispheric biases demonstrated high mean performances. Possibly, there is a trade-off between reaction times and accuracy in women. For example, in the face-decision task women with extremely high left-hemispheric biases responded slower but also more accurately than expected. Yet, such a (potential) trade-off was not found in men. The traditional and the alternative approach come to different results in this case and it is rather difficult to decide which approach is better. Whether women are more flexible in the relationship between lateralization and performance remains an open question. However, the fact that only the face-decision task showed a sex difference further emphasizes that the relationship between lateralization and cognitive performance is task-dependent.

Apart from sex differences, several other factors that are known to affect hemispheric asymmetries might also have an impact on the relationship between lateralization and performance. For instance, it would be interesting to compare left with right handers or consistent with inconsistent handers to see whether the relationship is subject to handedness.

4.5. Dynamic changes in the relationship between lateralization and performance

Many researchers in this field seem to implicitly assume that the relationship between degree of lateralization and cognitive performance is robust and stable over time. Boles et al. (2008) is among the few who stated that this relationship can differ accord-

ing to neuronal development. He specifically suggests that cerebral functions which lateralize early and late in ontogenesis have a positive relationship and functions which lateralize at intermediate ages have a negative relationship between hemispheric asymmetries and cognitive performance. The authors of the present study believe that changes in the relationship might be not only restricted to specific developmental stages but that an optimal degree in lateralization changes even more dynamically. A large number of studies suggest that the degree in lateralization underlies dynamic changes. These dynamic changes have been observed, for example, for different age ranges (Beste, Hamm, & Hausmann, 2006; Cherry & Hellige, 1999), as a result of hormonal fluctuation (Bayer & Erdmann, 2008; Bayer & Hausmann, 2008; Hausmann et al., 2002; Wisniewski, 1998), emotional and motivational state (Davidson, 1995; Kuhl & Kazen, 2008; Wacker, Heldmann, & Stemmler, 2003), task requirements within a particular task (Czeh, Perez-Cruz, Fuchs, & Flugge, 2008; Hausmann, Kirk, & Corballis, 2004) etc. Why would hemispheric asymmetries be subjected to those dynamic changes if there is only one particular optimum in the degree of lateralization? A possible explanation would be that different degrees of lateralization are associated with different mental states and specific situational requirements other than only optimal cognitive performance.

5. Conclusions

In sum, the present study suggests an alignment with previous studies (Boles et al., 2008; Leask & Crow, 2006) that lateralization is related to cognitive performance and that hence, cognitive performance – alongside with other factors – might have played an important role in the development of hemispheric asymmetries. Moreover, as far as the word-matching and face-decision task are concerned, high degrees of lateralization are detrimental to cognitive performance and the relationship between hemispheric asymmetry and cognitive performance can be best described by an inverted U-shaped curve (with a performance optimum slightly shifted from a zero lateralization degree). Although the relationship between hemispheric asymmetries and cognitive performance is task-specific, this clearly argues against the widely believed notion of a generally positive, linear relationship. In terms of evolution of hemispheric asymmetry, this might imply that initially a small dose of hemispheric asymmetry might have indeed enhanced cognitive performance, but then had to be kept in balance with bilateral symmetry before an overdose became detrimental.

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