

University of Groningen

## Testing the Darwinian function of lateralization

Zickert, Nele; Geuze, Reint H; Beking, Tess; Groothuis, Ton G G

*Published in:*  
Neuropsychologia

*DOI:*  
[10.1016/j.neuropsychologia.2021.107884](https://doi.org/10.1016/j.neuropsychologia.2021.107884)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2021

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Zickert, N., Geuze, R. H., Beking, T., & Groothuis, T. G. G. (2021). Testing the Darwinian function of lateralization: Does separation of workload between brain hemispheres increase cognitive performance? *Neuropsychologia*, 159, [107884]. <https://doi.org/10.1016/j.neuropsychologia.2021.107884>

### Copyright

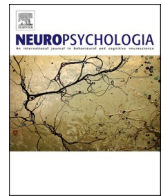
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

*Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.*



## Testing the Darwinian function of lateralization. Does separation of workload between brain hemispheres increase cognitive performance?

Nele Zickert<sup>a,\*</sup>, Reint H. Geuze<sup>b</sup>, Tess Beking<sup>b</sup>, Ton G.G. Groothuis<sup>a</sup>

<sup>a</sup> University of Groningen, Faculty of Mathematics and Natural Sciences, GELIFES — Groningen Institute for Evolutionary Life Sciences, Groningen, the Netherlands

<sup>b</sup> University of Groningen, Faculty of Behavioural and Social Sciences, Department Clinical & Developmental Neuropsychology, Groningen, the Netherlands

### ARTICLE INFO

#### Keywords:

Brain asymmetry  
fTCD  
Language  
Spatial orientation  
Dualtasking

### ABSTRACT

Brain lateralization is a fundamental aspect of the organization of brain and behavior in the animal kingdom, begging the question about its Darwinian function. We tested the possibility that lateralization enhances cognitive performance in single- and dual-tasks. Previous studies reported mixed results on this topic and only a handful of studies have measured functional brain lateralization and performance independently and simultaneously. We therefore examined a possible positive effect of the strength and direction of lateralization on two demanding cognitive tasks: A visuospatial task (mental rotation MR), and a language task (word generation WG), executed either as a singletask or as dual-task. Participants ( $n = 72$ ) performed these tasks while their single-task brain lateralization was assessed with functional Transcranial Doppler for both tasks. From these measurements we determined strength and direction of lateralization for both tasks and the individual pattern of lateralization (contralateral or ipsilateral) was derived. These factors, along with sex, were used in a GLM analysis to determine if they predicted the respective performance measure of the tasks. We found that for MR there was a significant medium effect of direction of lateralization on performance with better performance in left-lateralized (atypical) participants (partial eta squared 0.061;  $p = .039$ ). After correction for outliers, there was a significant effect for strength ( $p = .049$ ). For the dual-task, there was a significant positive medium effect of strength of lateralization on performance (partial eta squared 0.062;  $p = .038$ , respectively) No other association between direction or strength in either tests were found. We conclude that there is no evidence for hemispheric crowding, and that strength of lateralization may be a factor that contributes to the evolutionary selection of functional brain lateralization. Pattern of lateralization does not, explaining the large inter-individual variation in these traits.

### 1. Introduction

After the discovery of Broca's and Wernicke's areas, which indicated the lateralization of language, many additional lateralized brain functions have been found in humans (Toga and Thompson, 2003). Later, evidence of lateralization of other brain functions and behavior was found in a wide variety of other taxa, from molluscs and insects over birds, and mammals (Frasnelli et al., 2012a; Ocklenburg et al., 2019; Vallortigara et al., 1999; Vallortigara and Rogers, 2005). Lateralization of brain and behavior is now established as a fundamental aspect of the organization of the brain throughout the animal kingdom (Blum and Ott, 2018; Frasnelli et al., 2012b; MacNeilage et al., 2009). This begs the questions about its evolution and Darwinian function. Several theories have been proposed to explain the advantages and disadvantages of hemispheric specialization.

The specialization of one hemisphere for a particular function (such as language) would reduce the need for processing information in both hemispheres and in turn the need for communication between the hemispheres via the corpus callosum. This would then allow for quicker processing speed and decision making by avoiding time-consuming cross-talk (MacNeilage et al., 2009). Indeed, when we take motor control as an example, in chimpanzees it has been found that stronger behavioral lateralization results in better task performance that may have a fitness benefit: Individuals who more strongly preferred one hand over the other for ant fishing were more efficient in this task (McGrew and Marchant, 1999). Specialization of cognitive functions could hold the same benefit and it would allow for better *dual-tasking* in case the simultaneous execution of two tasks is processed in different hemispheres. This has been shown in an experiment in which lateralized - as compared to unlateralized - chickens were more efficient in feeding

\* Corresponding author.

E-mail address: [n.zickert@rug.nl](mailto:n.zickert@rug.nl) (N. Zickert).

while simultaneously monitoring their environment for predators (Rogers et al., 2004).

Of course, one could argue that task division within hemispheres would have the same beneficial effect as task division between hemispheres. However, it is likely that division between hemispheres would have a greater impact as most cognitive functions require activity of larger networks, which have a larger chance on interference when executed in the same hemisphere. This is called crowding. Moreover, the organization of the brain in two hemispheres might have developed from the organization of primitive neural systems with two lateralized ganglia leading to task divisions between rather than within hemispheres, as having a dominant hemisphere for a task avoids conflicts between the hemispheres in decision making (Crow et al., 1998; Vallortigara and Rogers, 2005). Thus, an individual who, due to stronger brain lateralization, can perform cognitive tasks more efficiently, needs less time and brain capacity, resulting in better performance and more capacity for additional tasks, which might ultimately increase Darwinian fitness.

Although not always realized, the term lateralization encompasses two different aspects: Its direction and strength. Where the direction describes the dominant side of a function or behavior, the strength describes how strong this dominance is. The so called pattern of lateralization refers to how different brain functions are distributed over the left and right hemisphere. This can result in a so called typical pattern (language left, visuospatial right), a mirrored pattern (language right, visuospatial left), or ipsilateral left/right patterns (both functions lateralized to the left or right hemisphere only).

Not only at the individual level, but also on the population level, strong lateralization of behavior can be beneficial, as it allows individuals to adjust their behaviors to each other, which is particularly important for swarming, schooling or herding animals (Rogers et al., 2004; Vallortigara and Rogers, 2005). Interestingly, the fact that movements are more predictable for opponents or predators if a species has a biased laterality, also gives individuals with less or opposite lateralization a possible advantage, because it makes them less predictable and thus more successful. The increased predictability, and therefore potential cost of lateralization, together with increased vulnerability for brain damage in one hemisphere that cannot be easily compensated for by the other, supports the idea that evolution favoured brain lateralization because it has clear benefits on Darwinian fitness that outweigh the costs. However, evidence, especially for humans, is still not convincing.

Nevertheless, from several previous studies there is some evidence concerning the advantages of brain lateralization for cognitive performance in humans, most of which are taken as evidence for a beneficial effect of stronger lateralization on task performance (Hirnstein et al., 2014; for a review see Tzourio-Mazoyer et al., 2017). A majority of the research, however, is based on the use of paradigms that address either language processing and/or spatial processing since these functions show consistent lateralization (but opposite) biases towards one hemisphere in healthy participants; typically, the left hemisphere is dominant for language and the right hemisphere for visuo-spatial processing. In a developmental study in children and adolescents ( $n = 20$ ), Everts et al. (2009) found that the laterality index (fMRI) for language, being a mixture of both direction and strength of lateralization, positively correlated with verbal and non-verbal performance. With age, the lateralization of language and visuo-spatial functions strengthened. When assessing lateralization with fTCD as done by Knecht et al., (2001), a positive correlation between hemispheric asymmetry and verbal fluency, spoken foreign languages, and academic achievements was found in a sample of healthy volunteers ( $n = 326$ ). Mellet et al. (2014) investigated the relation between strength and direction of language lateralization in a sample of 297 adults, half of which were left-handed. They compared the subgroups of participants with language being lateralized to the left hemisphere, to the right hemisphere or ambilateral, based on the fMRI lateralization index. No difference in

verbal and spatial performance was found between left and right lateralized participants. Only the ambilateral group performed worse in comparison, indicating an effect of strength, not direction of language lateralization (Mellet et al., 2014). Gerrits et al. (2020) determined the lateralization of five different brain functions by means of fMRI and assessed cognitive performance in their participants. They found that the more a participant deviated from the typical organization pattern of the four functions, the poorer they performed in the cognitive assessment. There is also some support for the hypothesis that the distribution of two brain functions over different hemispheres allows more efficient processing – and hence better performance: Powell et al. (2012) found in a sample of 82 participants that when language and spatial ability were located in the same hemisphere, performance of each corresponding task was significantly decreased. Nonetheless, there is also evidence that stronger lateralization corresponds to a decrease of performance since a study in 230 participants found an inverted U-shaped relationship between performance and laterality when using a visual half-field task, a word-matching task, and a face-matching task (Hirnstein et al., 2010).

Importantly, the studies mentioned above, including those that do show a positive relationship, suffer from one or both of two inadequate methods. First, the tasks used to assess functional lateralization differ from the tasks used to measure performance. For example, a word generation task is used during the fMRI procedure, yet a general intelligence or word-recall test is used to assess performance (e.g. Powell et al., 2012; Everts et al., 2009; Mellet et al., 2014). Additionally, often studies inferred lateralization from task performance itself (e.g. Cowell and Hugdahl, 2000; Boles et al., 2008; Chiarello et al., 2009) instead of using an independent measurement of lateralization, such as a lateralization index derived from fMRI or fTCD (functional Transcranial Doppler). Therefore, the interpretation of laterality and performance as if they were directly connected may be incorrect. Furthermore, despite some implicit evidence for an effect of “hemispheric crowding”, that is, when two functions are localized in the same hemisphere they compete for processing capacity (for a review see Badzakova-Trajkov et al., 2015; Cai et al., 2013), there are only very few studies in which participants actually perform two tasks simultaneously.

Lust and colleagues have addressed these issues by using experimental designs that allowed the recording of cerebral laterality during performance of a language and a spatial task using fTCD. They also measured the simultaneous performance of those tasks (Lust et al., 2011a, 2011b, 2011a). They correlated the strength of lateralization with performance, and compared the single and dual-task performance of language and visuospatial functions of four subgroups having distinct lateralization patterns (Fig. 4 Table 1). In both studies single task performance was not related to strength or direction of cerebral lateralization. For dual-task conditions, the first study ( $N = 26$ , right-handers only) reports better performance of typical lateralization and a negative relation between strength of lateralization and performance in participants being non-lateralized for one of the tasks. In the second study ( $N = 71$ , 50% left-handed) no advantage for typical lateralization was found in dual-task conditions, and the right-handed subgroup showed a negative relation between strength and dual-task efficiency for atypical lateralization. Thus, the follow-up study did not confirm that typical lateralization or strength of lateralization is positively associated with better dual-task performance, even though the variation of lateralization patterns was deliberately selected to be more diverse by including 50% left handers (Lust et al., 2011b).

However, one could argue that in the previous studies of Lust et al. no

**Table 1**  
Number of participants in the different laterality groups per task.

	WG left	WG right	Total
MR left	13 (ipsilateral left)	5 (mirror)	18
MR right	41 (typical)	13 (ipsilateral right)	54
Total	54	18	72

relationships between laterality and performance was found because the tasks were too easy to perform. Therefore, in the current experiments we applied a setup, in which we increased the mental load. We argue that, by this, potential benefits of lateralization will be expressed more strongly, which allows for a more robust test whether individual lateralization correlates with performance and with dual-task interference. Dual-task interference is measured as the performance decrease in the dual-task condition compared to the single-task condition.

In the current study visuo-spatial processing was assessed with a right-hemispheric mental rotation task (MR). We chose this task over the previously used tasks by Lust and colleagues (Lust et al., 2011a, 2011b, 2011c) because of its higher complexity. As a language task we selected the word generation task as this shows reliably lateralized activity in the brain (Knecht, 2000). We chose not to exchange the language task with a more complex one as word generation is a widely-used task in many different studies and will allow the results to be more widely comparable with other studies. Additionally, previous to the task selection we have evaluated the performance decrease in the dual-task in the study by Lust et al. (2011a) and found that the line-bisection task only contributed to approximately one fourth, thereby indicating that this was the easier task of the two. Lateralized brain activity during each task was recorded by means of fTCD (see below) during single task performance. Subsequently, the participants performed the two tasks simultaneously. Only during this dual-task, fTCD was not applied as its signal cannot be decomposed in separate task activity and the duration of insonation could have exceeded the recommended safe time window of 60 min in some cases. We also actively recruited left-handed participants in our study in order to obtain a wider variety of different lateralization types, since it has been shown that left-handers more often deviate from the typical lateralization for a task (Floel et al., 2005; Knecht, 2000; Pujol et al., 1999). This means that our sample would not only include the typical laterality pattern (language left, spatial processing right), but also the alternative patterns such as the reversed (mirrored) or unilateral patterns (ipsilateral left or right). In this way, we are able to investigate not only the effect of strength and direction of lateralization on performance, but also the effect of varied patterns of lateralization over both hemispheres.

Based on the above-mentioned hypotheses about the benefits of brain lateralization, we expect that for the strength and direction of lateralization:

- (1) if lateralization is beneficial, stronger lateralization will be associated with better single-task performance.
- (2) if evolution selected for the typical direction of brain lateralization, this typical direction will result in better single-task performance.

For the pattern of lateralization we expect:

- (3) due to less competition for cerebral resources under dual-task conditions, individuals with contralateral brain organization will perform better compared to individuals with ipsilateral brain organization, and this effect will be stronger with increasing strength of lateralization.
- (4) due to less competition within the same hemisphere individuals with contralateral brain organization will experience less dual-task interference compared to individuals with ipsilateral brain organization and hence show better performance. This effect will be more pronounced with stronger lateralization (crowding).

## 2. Material and methods

### 2.1. Participants

In total 72 participants were included in this study. They were recruited from a pool of psychology students, who received credits for

their participation and biology students, who were financially compensated with €10. All participants were Dutch native speakers, healthy, and had normal or corrected-to-normal eyesight (40 women, 32 men, mean (SD) age 21.4 (2.8)). We selected a sample size based on the previous studies of Lust et al. (2011a, 2011b), since we expected a stronger effect due to the more difficult mental rotation task. Aiming for 50% left-handers, we selected participants based on their self-reported hand preference. Their hand preference was subsequently assessed in detail using the Edinburgh handedness inventory adapted for the Dutch language. This questionnaire consists of 10 questions (Strien, 1992) asking which hand one prefers to use in each of ten everyday manual actions on a three-point scale “left” (−1) or “right” (1), or marking both options in case that the participant did not have a preferred hand for this action. From the answers, we calculated the sum score as a lateralization index (EHI) and classified the participants into a group of 28 left-handers (negative sum score; 13 female) and 44 right-handers (positive sum score; 27 female). Participants gave their written informed consent before the start of the experiment.

The protocol of the experiment has been approved by the Ethics Committee of the Psychology Department of the University of Groningen (ppo-011-076).

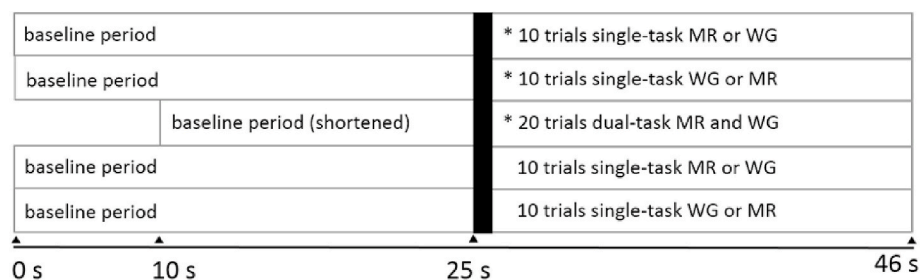
### 2.2. Cognitive tasks & performance measurements

#### 2.2.1. Word generation task

Language performance was assessed with a word generation task in which participants had to name as many words as possible starting with a specific letter during 20s. They were presented with a letter in spoken form (audio stimulus only) preceded by baseline period (25 s, Fig. 1) and a subsequent cue tone (880 Hz, 1000 ms). Based on the Controlled Oral Word Association Test (COWAT) they were informed that personal names, numbers, and names of cities would not be counted as valid answers. Furthermore, successive words starting with the same preposition, numbers, and duplicates were excluded. Correct answers were recorded by two experimenters, who were present in the room. The stimulus letters were balanced according to the number of words occurring in the Dutch language per each of the letters. The lists were composed of the following sets of letters: U, G, L, A, F, K, Z, V, D, H (Set 1); and J, T, N, B, E, O, W, R, M, P (Set 2) (Lust et al., 2011a). The letters were presented twice in a fixed random order resulting in 20 trials of word generation task (see Fig. 1). We used the word generation task in a modified version of the standard procedure, in which participants are instructed only to think of the words starting with the stimulus letter without actually pronouncing them. Since fTCD recording took place during the word generation task all participants were instructed to whisper their answers to avoid vibrations of the vocal chords, which can cause unwanted artefacts in the recordings. After receiving oral instructions by the experimenters and written instructions before the recording of the first set of tasks on the computer monitor, participants were given one practice trial to get accustomed to the procedure of testing (the letter “S”, which was not used during the actual test). The performance measure for word generation was the average number of words per letter generated by the participant. When a participant misheard the stimulus letter, this trial was excluded from the calculation of the average.

#### 2.2.2. Mental rotation task

An adapted version of the MR task described in Shepard and Metzler (1988) was used. We generated six individual figures composed from eight cubes. From each Fig. 3D rotated versions were generated, presenting views at different angles, as well as mirrored images of each. These images were used to produce matching and mismatching stimulus pairs (Fig. 1). Participants were asked to determine if a pair were the same or different 3D figures. The start of the task was preceded by a baseline period of 25 s and the start indicated by a cue tone (880 Hz, 1000 ms), followed by the sequential presentation of 5 stimulus pairs



**Fig. 1.** Scheme of the task block sequence and the timing of the trials. Task blocks of single tasks consist of ten trials, and the dual task of 20 trials. First task blocks are preceded by one practice trial (indicated by asterisk). Single task blocks alternate between MR and WG. Each trial begins with a baseline “resting” period (25 s in single tasks, 15 s in dual tasks), followed by a cue tone (black bar), after which the task must be performed for 20 s. Internal reliability of the task was determined by correlating the lateralization indices of the first and the second block of word generation (Pearson correlation  $r = 0.577$ ,  $p < .000$ ).

within a period of 20 s. Each pair was presented on a monitor for 3000 ms followed by a blank screen (1000 ms) during which participants indicated ‘same’ or ‘different’ by pressing the corresponding button on a device in front of them. This custom-made input device showed two vertically-aligned buttons with a distance of 80 mm – the top green button representing “same shape” and the bottom red one “different shape”. The input device was fixed in place at the center axis of the monitor and the participants were instructed to put both index fingers and thumbs on the top and bottom button, respectively. This arrangement, together with the vertical alignment of the buttons, was chosen to avoid interference from differential activation of the right or left motor cortex during this task as much as possible. The performance of the mental rotation task was measured as the number of correct decisions (range 0–100; 100 being the maximal score). A response was wrong when two shapes were indicated as being the same when they were not, when two shapes were reported as being different while they were rotated forms of each other, or when the participant did not give the response within the set response time.

Participants were given two practice trials to get accustomed to the procedure of testing using cube shaped stimuli that were not shown during the actual testing. Internal reliability of the task was determined by correlating the lateralization indices of the first and the second block of mental rotation (Pearson correlation  $r = 0.794$ ,  $p < .000$ ).

## 2.3. fTCD

### 2.3.1. fTCD setup and analysis of raw data

This technique uses the blood flow velocity in the left and right middle-cerebral arteries, which reflects oxygen demand of the parts of the cortex involved in a task. This is validated as a measurement of hemispheric dominance with both the WADA test as well as fMRI (Knecht et al., 1998, 1999, 1998; Stroobant and Vingerhoets, 2000). fTCD recordings were performed using the ultrasonic Doppler apparatus (DWL Doppler Box, Compumedics Germany) and QL 3.0 software. Two transducer probes (2 MHz) were positioned on the left and right temporal windows of the participant and fixed in a position that allowed the clearest readout of the signal typical of the middle cranial artery (MCA) (for a detailed description of fTCD, see Deppe et al., 2004). fTCD was only recorded during single-task sessions. During the time of dual-task testing the device was switched off but remained on the head of the participant. When no clear MCA signal could be found (due to head shape or other reasons), participants were excluded ( $n = 8$ ).

Analysis of the fTCD recordings was performed using the dopOSCCI m2 software package (Badcock et al., 2012a) to determine hemispheric lateralization of language processing (WG) and spatial processing (MR) with the help of Matlab software package R2011b. Recordings of single-tasks were combined to include 20 trials each for WG and MR, and fed into the dopOSCCI program where the raw data was processed in such a way that artefacts (e.g. effects of heartbeat) were removed and the 20 trials centred on the event of the cue tone so that all baseline and task periods would align. From these aligned trials an average of the change in blood flow velocity relative to baseline is calculated for the right and left MCA, which is a proxy for hemispheric activation. The

baseline period was chosen 15 s before the cue tone even though 25 s were recorded in order to omit carry-over effects from the previous task period. To determine the individual laterality of a task we chose an analysis period (period of interest POI) from 7 s after the cue tone until the end of the task (see Fig. 2). We did not use the time-period right after the cue tone to exclude possible activation effects of the cue and because of the delay in vascular response (see Fig. 3). We chose to use a period of interest (13 s) that is longer than the commonly used peak window (2 s) within a period of interest for the calculation of the laterality index of a participant for a task because this is the relevant period of the cognitive processing of the task and gives a more stable estimate of the lateralization in comparison to the 2 s most lateralized peak window (Knecht et al., 1998). A similar approach has been used successfully by other studies (Petit et al., 2020; Woodhead et al., 2020). The laterality index was automatically calculated by subtracting the average blood flow velocity change of the right MCA from the left MCA, thereby resulting in a negative score when the right hemisphere was dominant for a task and vice versa a positive score for a left-dominant task.

### 2.3.2. Procedure

Participants sat in a quiet room on a comfortable chair in front of a computer screen. Tasks were presented with a behavioral stimulus program (E-prime, Psychology Software Tools, Pennsylvania, USA). In single tasks each trial lasted for 20 s, preceded by a 25 s blank screen for fTCD baseline recording (Fig. 1). Participants were asked to think of nothing or a starry night sky during this resting period. In dual tasks the baseline period was shortened to 15 s since no fTCD recording took place.

Cognitive tasks were administered in two conditions: a single-task condition, in which a word-generation task or a mental rotation task had to be performed separately, and a dual-task condition in which both tasks had to be performed simultaneously. In order to avoid learning effects for the sequence of the task blocks, the first half of both single-tasks were presented before and the other half after the dual-task condition. For example, the sequence was 10 trials single-task WG, 10 trials single-task MR, 20 trials dual-task WG + MR, 10 trials single-task WG, and 10 trials single-task MR. In order to balance the sequence of MR and WG tasks as well as the sets of letters between participants, we administered eight different protocols, each comprised of an individually-balanced randomization of starting task (WG/MR), letter set, and MR stimulus set.

In the dual-task condition after the cue, the spoken letter was presented as well as the sequence of five MR stimulus pairs so that words starting with the stimulus letter had to be whispered while also pressing the correct button for matching versus mismatching pairs. Before the actual recording of the task participants were given two practice trials to get accustomed to the procedure of testing using cube shape stimuli and letters (C and I) that were not presented during the actual testing.

## 2.4. Determination of lateralization strength, direction, and patterns

DopOSCCI software calculated a lateralization index (from here on called fTCD\_LI) and its standard error within the period of interest based

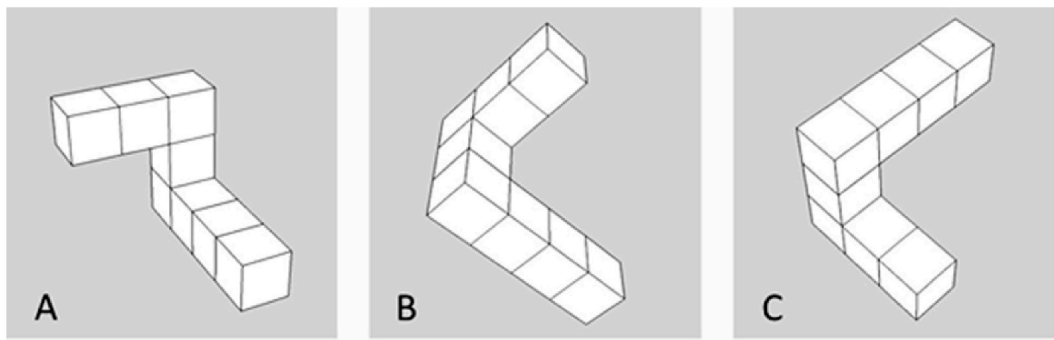


Fig. 2. Examples of cube figures used as stimuli for the mental rotation task. A – original figure, B – rotated matching version, C – mirrored non-matching version.

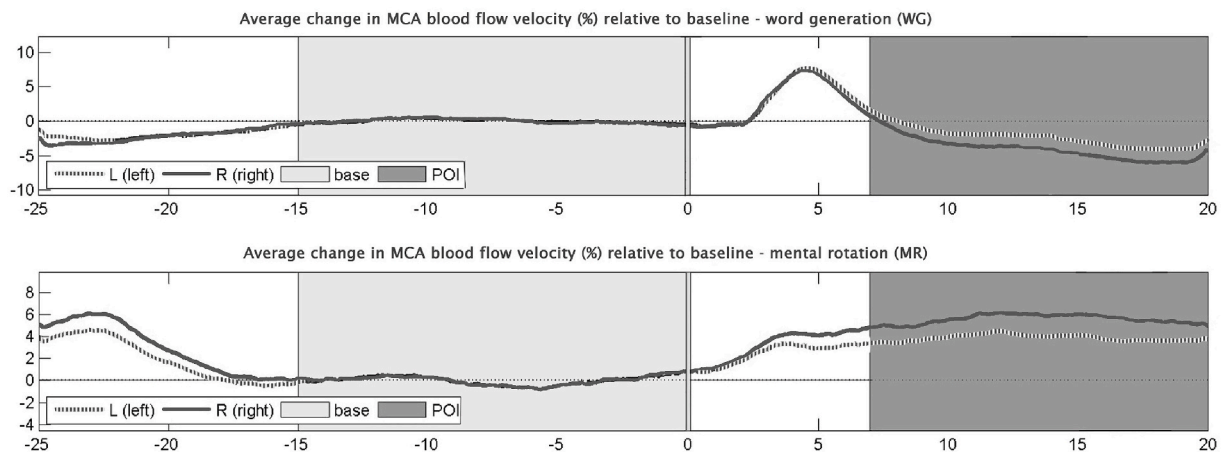


Fig. 3. Functional Transcranial Doppler signals for Word Generation (WG) and Mental Rotation (MR) averaged over trials and participants, showing average change of blood flow velocity relative to baseline in the left (dotted line) and right (full line) middle cerebral artery (MCA). The light grey area depicts the baseline period and the dark grey area the period of interest as used in the analyses. The X-axis represents the timeline of one trial, with task onset at 0 s. The difference in amplitude between the lines represents the direction and strength of lateralization of the task, with a reversed direction of lateralization for the two tasks (Y-axes are different scales for MR and WG).

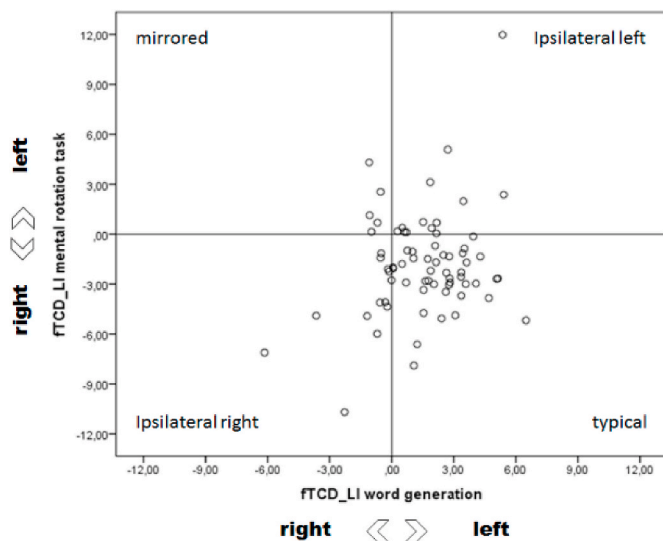


Fig. 4. Lateralization indices of MR and WG task. Negative values indicate lateralization of a task in the right hemisphere; positive values indicate lateralization in the left hemisphere. High values indicate strong lateralization. Accordingly, each quadrant represents a specific lateralization pattern.

on a maximum of 20 epochs and a minimum of 8 epochs. Participants with less than 8 valid epochs were excluded ( $n = 8$ ) (Badcock et al., 2012b). The specific settings used can be found in the [Supplementary \(S1\)](#). To determine the direction of lateralization and thereby assessing which of the two hemispheres was more involved in the task, we recorded the algebraic sign of the ftCD\_LI. Based on this, we assigned participants to different groups based on their laterality per task: left-lateralized (positive score) or right-lateralized (negative score) (Table 1). These classifications were then used to assign participants into one of four groups of laterality patterns that were possible for the dual-task situation: ipsilateral left (both tasks lateralized in the left hemisphere), ipsilateral right, typical (WG left, MR right), or mirrored (WG right, MR left, see Table 1). Since we wanted to include the full spectrum of lateralization strength (see below) in the dataset we did not exclude participants with non-significant lateralization (based on the 95% CI of the ftCD\_LI). An additional analysis of the data using this stricter classification can be found in the [supplementary material \(S3\)](#).

The strength of lateralization is represented by the numeric value of the ftCD\_LI, without algebraic sign. The combined strength of lateralization is calculated by adding up the numeric values of the ftCD\_LI measured for MR and WG.

### 2.5. Statistics

#### 2.5.1. Dual-task performance and interference

Dual-task performance was calculated by adding up the standardized values (z-scores) of the mental rotation task performance score and the

word generation task performance score under dual-task conditions. Dual-task interference was calculated based on the difference in performance between single- and dual-task (a negative score implied dual-task interference, i.e. Dual-Task – Single-task (since higher scores represent better performance)). The z-scores of these differences were summed and averaged for WG and MR to obtain the overall dual-task interference.

2.5.2. Analysis

Statistical analyses were performed using SPSS Statistics software (version 22).

To test hypotheses 1 and 2, i.e. better single-task performance with stronger lateralization and typical direction of lateralization, we conducted general linear models (GLMs), with the respective performance measures for WG and MR as dependent variable. The three main factors in these models were strength of lateralization, direction of lateralization, and sex (strength of lateralization was added as covariate). Furthermore, the interaction term between strength and direction of lateralization was added. In a stepwise backwards regression approach we removed all non-significant factors. The two main terms of the hypotheses (strength and direction of lateralization), remained in the model regardless of their significance level. In order to confirm hypothesis 1, strength of lateralization should show a significant positive influence on the performance score for WG and MR. In order to confirm hypothesis 2, we should find a significant effect of the direction of lateralization on the performance of MR and WG. Furthermore, we predict a significant interaction effect, in the way that strength of lateralization is positively correlated to performance in typically-lateralized participants, but has no or a negative correlation in atypically lateralized participants. Sex was included in the models because of possible sex differences in language and spatial orientation performance (e.g. reviewed in Hyde, 2016).

Under dual-task conditions, we tested our hypothesis 3 as follows: We conducted a GLM, using the combined performance of both tasks as dependent variable, and as factors the pattern of lateralization (contralateral vs. ipsilateral) the combined strength of lateralization (added as covariate), the interaction of those two terms, and sex. For the test of hypothesis 4 we used the same terms including the dual-task interference as dependent variable. We conducted a stepwise backwards regression procedure as described above, removing all non-significant effects while leaving the three main terms of the hypotheses (strength and direction of lateralization as well as their interaction) in the model regardless of their significance level. Based on hypothesis 3 we expect a significant positive effect of combined strength of lateralization and of the pattern of lateralization on dual-task performance (with the contralateral lateralization pattern resulting in better performance than the ipsilateral pattern), as well as a significant interaction between the two terms. For the latter we predicted that strength of lateralization will be positively correlated to performance for contralateral participants but not for ipsilateral participants. Similarly, for interference under dual-task conditions, we expect a significant interaction wherein strength of lateralization negatively correlates to performance decrease contralateral participants.

For all factors we report the effect size as partial eta squared ( $\eta^2$ ) and interpret it according to Richardson (2011) (0.01, 0.06, and 0.14 for an indication of a small, medium, or large effect).

To confirm the appropriateness of the stepwise backwards progression procedure, residual plots of all final models of each analysis were visually inspected to check whether the model was jeopardized. This was not the case for any of the models. Additionally, we calculated the Akaike information criterion ( $AIC = n \cdot \log(SSE/n) + 2(k+1)$  in which  $n$  = sample size,  $SSE$  = sum of squared errors,  $k$  = number of predictors) for every step of the backwards regression in order to select the best model over all steps (see Supplementary S2).

3. Results

3.1. Lateralization of the participants

In order to describe our study population and thus the basis of the results below, we show the distributions of the various categories of lateralization. Table 1 lists the distribution of participants over the respective lateralization categories showing that the majority of participants adhere to the typical direction of lateralization (WG left, MR right). Resulting from these categories are the 4 different lateralization patterns based on the distribution of the two directions across both hemispheres (represented by the cells of the table). The data yielded sufficient variability in lateralization patterns for analyzing the effect of the lateralization pattern separately from strength of lateralization (Table 1, Fig. 4). In total, of the 72 participants 46 had a contralateral organization (41 were typically lateralized, 5 mirrored) and 26 participants showed an ipsilateral organization.

The individual categories and lateralization indices are displayed in Fig. 4, where the distance from zero represents the strength of lateralization.

3.2. Effect of strength and direction of lateralization on single-task performance

3.2.1. Word generation

As depicted in Table 2, no effects of strength or direction of lateralization on performance of the single word generation task were found. There were no outliers detected in the distribution of the lateralization indices measured under WG. Similarly, excluding participants who were not significantly lateralized for the task (henceforth ‘bilaterals’ – where the 95% CI of the *ftcd\_LI*-score overlaps with 0), resulted in no significant effect of strength of lateralization ( $p = .607$ ) and direction of lateralization ( $p = .480$ , Supplementary table S3).

3.2.2. Mental rotation

Table 3 reports the results of the GLM analysis of single-task MR performance. The final model revealed a significant positive effect of direction of lateralization of MR on performance of MR (Fig. 4), but not of strength of lateralization, although the  $p$  value approached alpha. The interaction of strength and direction are not significant. Sex as a main factor was also not significant. The removal of outliers ( $n = 3$ , strength of lateralization  $\geq 7.9$ ) lowered the  $p$ -value below alpha but did not change the rest of the results qualitatively (direction of lateralization MR  $p = .031$ ; Strength of lateralization MR  $p = .049$ ; sex  $p = .209$ ; Strength of lateralization MR\* direction of lateralization MR  $p = .641$ ). When excluding bilaterals we find a different outcome, i.e. no significant effect of strength of lateralization ( $p = .151$ ) and direction of lateralization ( $p = .198$ , Supplementary table S2).

Table 2

Inferential statistics and effect sizes for Word Generation (WG) performance (average number of words per letter) after stepwise backwards regression. Bold  $p$ -values refer to the final model. Non-bold values indicate the  $p$ -value of the independent variable before removing this factor from the model in the subsequent step in the backward procedure.

Factor	Final model				
	F	df	Last calculated p	Partial eta squared $\eta^2$	B
Direction of lateralization WG	.156	1	<b>.694</b>	.002	-.160
Strength of lateralization WG	1.625	1	<b>.207</b>	.023	.140
Strength of lateralization WG* direction of lateralization WG	.599	1	.442		
Sex	.955	1	.332		

**Table 3**

Inferential statistics and effect sizes for mental rotation (MR) performance (average number of correct decisions) after stepwise backwards regression. Bold *p*-values refer to the final model. Non-bold type indicates the *p*-value of the independent variable before removing this factor from the model in the subsequent step in the backward procedure. The asterisk indicates statistical significance.

Factor	Final model				
	F	df	Last calculated p	Partial eta squared $\eta^2$	B
Direction of lateralization MR	4.450	1	<b>.039*</b>	.061	7.4
Strength of lateralization MR	3.248	1	<b>.076</b>	.045	1.2
Strength of lateralization MR* direction of lateralization MR	.004	1	.953		
Sex	.888	1	.349		

3.3. Dual-task performance

The present study reveals a dual-task performance decrease of 46% as compared to 18% in the previous study of Lust, Geuze, Groothuis & Bouma (2011). Thus, our aim to study dual-task performance and lateralization under more demanding task conditions was met.

For the analyses of dual-task performance, the final model revealed a significant positive effect of the combined strength of lateralization on both tasks ( $p = .038$ ), while the other predictors did not reach statistical significance (see Table 4 and Fig. 5). The removal of outliers ( $n = 2$ , combined strength of lateralization  $\geq 13$ ) did not change the results qualitatively (lateralization pattern  $p = .937$ ; combined strength of lateralization  $p = .036$ ; sex  $p = .504$ ; combined strength of lateralization \* lateralization pattern  $p = .783$ ). Opposed to our findings above, excluding bilaterals did not result in a significant effect of combined strength of lateralization ( $p = .675$ ) Lateralization pattern ( $p = .778$ ) and interaction of the two factors were not significant as well ( $p = .387$ , Supplementary table S4).

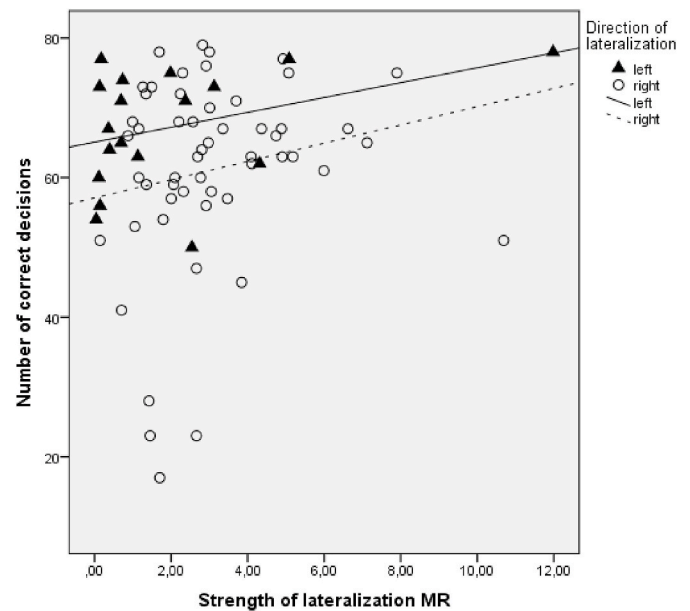
3.4. Dual-task interference

Dual-task interference was not related to strength or pattern of lateralization, or their interaction (see Table 5). The removal of outliers ( $n = 2$ , combined strength of lateralization  $\geq 13$ ) did not change the results qualitatively (lateralization pattern  $p = .642$ ; combined strength of lateralization  $p = .800$ ; sex  $p = .177$ ; combined strength of lateralization \* lateralization pattern  $p = .984$ ). Excluding participants who were bilateral for at least one of the tasks resulted in no significant effect of lateralization pattern ( $p = .509$ ), a significant effect of the combined

**Table 4**

Inferential statistics and effect sizes for combined dual-task performance after stepwise backwards regression. Bold *p*-values refer to the final model. Non-bold values indicate the *p*-value of the independent variable before removing this factor from the model in the subsequent step in the backward procedure. The asterisk indicates statistical significance.

Factor	Final model				
	F	df	Last calculated p	Partial eta squared $\eta^2$	B
Lateralization pattern (contralateral vs. ipsilateral)	.075	1	<b>.785</b>	.001	.153
Combined strength of lateralization	4.482	1	<b>.038*</b>	.062	.105
Combined strength of lateralization *Lateralization pattern	.005	1	<b>.946</b>	<.000	-.007
Sex	.742	1	.392		



**Fig. 5.** Relation between MR performance and strength of MR lateralization for the laterality groups left lateralized – filled triangles, solid line; and right lateralized – open circles, dashed line. Fitted lines are linear, based on subgroups left (solid) and right (dashed).

**Table 5**

Inferential statistics and effect sizes for dual-task interference after stepwise backwards regression. Bold *p*-values refer to the final model. Non-bold values indicate the *p*-value of the independent variable before removing this factor from the model in the subsequent step in the backward procedure.

Factor	Final model				
	F	df	Last calculated p	Partial eta squared $\eta^2$	B
Lateralization pattern (contralateral vs. ipsilateral)	.250	1	<b>.619</b>	.004	.156
Combined strength of lateralization	.077	1	<b>.783</b>	.001	.009
Combined strength of lateralization *Lateralization pattern	.003	1	<b>.960</b>	<.000	-.003
Sex	1.692	1	.198		

strength of lateralization ( $p = .049$ ), which was not found in the analysis above, and no significant effect of their interaction ( $p = .790$ , Supplementary table S5).

4. Discussion

In this fTCD study, we examined the influence of brain lateralization on single- and dual-task performance to evaluate the possible Darwinian function of lateralization. We extended on previous studies by successfully applying a more demanding cognitive task. In doing so, we showed that we succeeded to test hypotheses under a higher level of mental load than in previous studies, especially under dual-task conditions. We predicted that under single-task conditions stronger lateralization (hypothesis 1) and typical hemisphere organization (direction of lateralization as being present in the majority of the population, hypothesis 2) would lead to better task performance. Similarly, under dual-task conditions we expected individuals with a (stronger) contralateral lateralization pattern to perform better (hypothesis 3) and to experience less dual-task interference (hypothesis 4).

Single-task performance of a language task (WG) was not



significantly influenced by the strength or direction of lateralization, and the interaction of the two terms (Table 2). Sex was also not found to be a significant predictor, albeit women tended to have slightly better scores (see Supplementary S4), consistent with earlier reports indicating that women generally perform better in language tasks (e.g. Reilly et al., 2016).

Single-task performance was not related to the strength of lateralization in the spatial task (MR), although the p value approached the critical value of 0.05. Moreover, when analyzing the data without outliers the relationship became significant. The absence of an effect of sex in the mental rotation task is typical for the task setup we used (Peters and Battista, 2008). The presence of an effect of strength of lateralization is in disagreement with our previous studies that applied word generation and different visuo-spatial tasks (a dynamic landmark task and a driving simulator task, respectively (Lust et al., 2011a, 2011b)). This discrepancy might be explained by the fact that we made the visuo-spatial task more difficult. Consistent with our second hypothesis, we found that for mental rotation the direction of lateralization had a positive effect on task performance with medium effect size (Table 3). However, contrary to our second hypothesis, it was the atypically-lateralized group (left-dominant for mental rotation), which performed better (Fig. 5).

Interestingly, the effect of a left-lateralized advantage for mental rotation is strengthened by the fact that the association is found equally well in both sexes (supplementary S4, table S6). We have identified several post-hoc potential explanations for this phenomenon, which mostly take into consideration not the argument that there is an advantage for left-lateralized spatial processing per se but rather that the nature of our experimental setup caused this. Mental rotation is recognized as a multidimensional task for the solving of which different strategies can be utilized (Gardony et al., 2017; Lamm et al., 2007). In our case, the task is made more difficult by having the participants input their answer via button-pressing within a very short time frame (4 s). It could be argued that mental rotation in close time proximity to button-pressing involuntarily induces the need for task-switching, which has been shown to recruit the left posterior parietal cortex (Corbetta and Shulman, 2002). Additionally, Lamm et al. (2007) show in an fMRI-based experiment that matching a stimulus and preparing to give the response activates the left hemisphere network as opposed to other steps in mental rotation. Based on this information, we could speculate that we find an advantage for left-lateralized participants since our task setup was focused on matching the stimuli and compressed that response into a short time window asking the participant to make quick and precise decisions repeatedly. Another experiment using actual physical 3D block figures measured the effect of left- or right handed finger-tapping on performance of mental or manual rotations of the 3D figures (Yeary et al., 2002). They found that right-handed finger tapping (loading on the left motor cortex) interfered with mental rotation while right-handed finger tapping interfered with manual rotation thereby providing another incidence of left-hemispheric involvement of mental rotation. Yet another consideration is to ask which sort of visual processing was induced by the specific stimuli used in our setup. Brederoo et al. investigated different visual stimuli and paradigms and their associated patterns of lateralization with respect to different principles of hemispheric organization (Brederoo et al., 2020). They found that the left hemisphere was typically involved in processing local form (detail-oriented, perception of edges, corners, and individual features) while the right hemisphere was responsible for global form (overview, perception of the overall “Gestalt”). Local feature processing might be of advantage for the stimulus type and task we have created, since it features sharp lines, edges, and corners that are essential to solve the task more successfully. However, since we cannot identify the specific cognitive domains which are used by the participants to perform the mental rotation task, this remains speculative. More research with different types of stimuli would be needed to discern if left dominance is an advantage for mental rotation in general or dependent on the specific

task type.

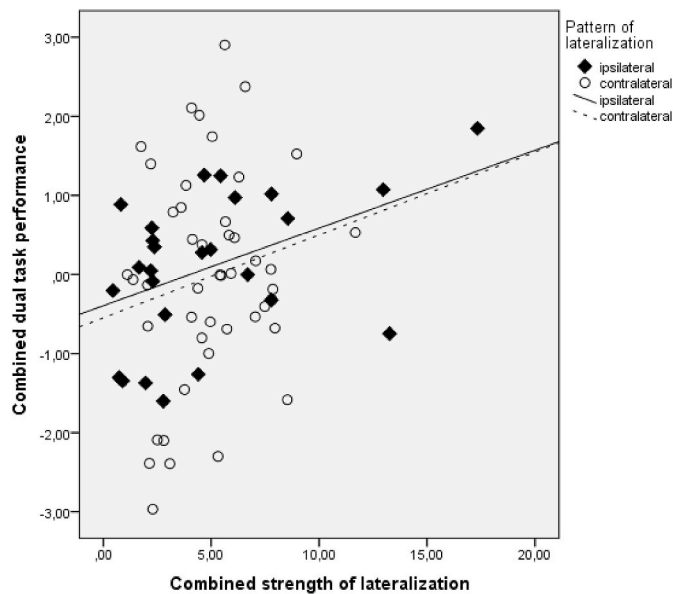
In contrast to hypothesis 1, the strength with which a function is lateralized does not seem to affect performance of the WG task whereas for the MR task the results are indecisive. This is because of the finding that the almost significant positive correlation between strength of lateralization and performance in the mental rotation task can be seen both in typically right- and atypically left-lateralized participants and becomes significant when outliers are excluded. The consistent lack of an effect of typical direction of lateralization on performance suggests that evolution has not prepared specific hemispheres for these specific tasks, explaining perhaps why there is so much variation in patterns of lateralization as indicated in Fig. 3. This is, however, not mutually exclusive with the idea that other – more ecologically relevant – tasks (e.g. facial recognition) could be the target of selection towards a specific hemisphere.

Of the three studies of our research group examining the effect of task lateralization on performance, using fTCD with a visuo-spatial task, and a language task, only one found an advantage of having a typical lateralization pattern (Lust et al., 2011a), however, the two follow-up studies did not find this effect (Lust, Geuze, Groothuis, van der Zwan, et al., 2011; this study). The reason for this discrepancy might be the differences in composition of the samples. The first study of Lust et al. contained right-handers only and no participants with a mirrored lateralization pattern. The follow-up studies (Lust, Geuze, Groothuis, van der Zwan, et al., 2011; this study) had a balanced proportion of right- and non-right-handers (or at least a significant proportion of left-handers) and participants with a mirrored lateralization pattern.

Contrary to our hypothesis, we did not find that in a dual-task participants with contralateral lateralization outperformed those with an ipsilateral organization pattern. The absence of a significant interaction effect between the pattern and strength of lateralization adds detail to this finding by showing that no lateralization subgroup was differentially-affected by the strength of lateralization. By itself, however, strength of lateralization was a significant predictor of dual-task performance with a medium effect size (Table 4), showing a benefit for stronger lateralization irrespective of the actual distribution of the two functions over the hemispheres. This is supporting a Darwinian function of strength of lateralization for a cognitive task assuming that better performance has a positive effect on fitness (similar findings of this effect are reviewed in Tzourio-Mazoyer et al., 2017). Moreover, the fact that strength of lateralization had a positive effect on dual-task performance irrespective of an ipsi- or contralateral organization of the brain (Fig. 6) is an indication against an effect of hemispheric crowding.

When analyzing the dual-task interference (i.e. performance decrease when two tasks are executed simultaneously) as was done by Lust and colleagues (therein called “dual-task efficiency”, Lust, Geuze, Groothuis, van der Zwan, et al., 2011; Lust, Geuze, Groothuis and Bouma, 2011), we could not replicate the results from their first study where the typically-lateralized group was less affected by dual-task interference (Lust et al., 2011a). Our present findings are in accordance with their second study, in which a driving simulator was used as spatial task and where no correlation between the lateralization group or strength of lateralization with interference have been found (Lust et al., 2011b). However, we consider the effect that we found of strength of lateralization on dual-task performance a more relevant target for Darwinian selection than the decrease in performance in dual-tasks relative to single tasks, as this is only a relative measure.

Overall, we found evidence that stronger lateralization increases cognitive performance during the dual-task, and possibly one of the single tasks, while the pattern of lateralization had no effect. We found that the direction of lateralization had a significant effect on task performance albeit the atypical direction had the advantage. The first finding raises the question why there is still so much variation in the strength of lateralization, despite the suggested directional selection for increased strength, at least in dual-task-type situations. Perhaps



**Fig. 6.** Relation between combined dual-task performance and combined strength of lateralization for the laterality patterns ipsilateral – filled diamonds, solid line; and contralateral – open circles, dashed line. Fitted lines are linear, based on subgroups ipsilateral (solid) and contralateral (dashed). Subgroups are based on single-task lateralization.

increased strength of lateralization may lead to potential fitness costs that have not been quantified yet but have been suggested by several authors, such as larger vulnerability for brain damage and too much predictability for predators or social competitors in motor behavior (e.g. Vallortigara et al., 1999; Vallortigara and Rogers, 2005).

The limitations of our study lie in the fact that the tasks we used, cannot be generalized to all cognitive functions of the brain and only represent a small portion of its crucial array of capabilities. Moreover, it needs to be considered that even though the tasks we used are well-established, they only test limited aspects of language and visuospatial function. Secondly, our estimate of lateralization in brain activity in the dual-task condition is based on measurements taken during the single-task due to technical reasons, but ideally, it would be interesting to measure this simultaneously during the performance of the dual-task. The latter might be solved by using fMRI to clearly localize distinct activation patterns during the dual-task itself, and at the same time allowing to examine whether it makes a difference to lateralization if a task is only performed in the mind or has a physical component (e.g. speaking or button-pressing). In future studies it would be interesting to record the fTCD-signal throughout the whole procedure, including the dual-task, to record possible effects on performance and to determine the specific lateralization thereof.

## 5. Conclusion

In our study, we found that atypically leftward lateralization was associated with better task performance in the visuospatial task, but direction of lateralization was not a significant predictor of language task performance. We could not find an effect of strength of lateralization on the performance of a language task but found some evidence for such a relationship for the mental rotation task. The fact that the effect of direction was only present in the MR task and not in WG indicates that the association between lateralization and performance is likely to be task specific. When performing two cognitive tasks simultaneously, we found that increased overall strength of lateralization was associated with better dual-task performance irrespective of lateralization pattern. Interference experienced during dual-task conditions was not associated with strength or pattern of lateralization. From this, we infer that

strength of lateralization serves a Darwinian function, at least in the performance of simultaneous tasks, but that the lateralization pattern typically seen in the majority of humans does not seem to result from evolutionary selection for enhanced performance, explaining the inter-individual diversity of lateralization patterns in our species.

## Credit author statement

Conception or design of the work: Nele Zickert, Reint H. Geuze, Tess Beking, Ton G.G. Groothuis. Data collection: Nele Zickert, Tess Beking. Data analysis and interpretation: Nele Zickert, Reint H. Geuze, Tess Beking, Ton G.G. Groothuis. Drafting the article: Nele Zickert. Critical revision of the article: Nele Zickert, Reint H. Geuze, Ton G.G. Groothuis. Final approval of the version to be published: Nele Zickert, Reint H. Geuze, Tess Beking, Ton G.G. Groothuis.

## Declaration of interest and funding source

There are no known conflicts of interest associated with this publication. This study was funded by the The Dutch Research Council (NWO 022.003.049), that had no involvement in any aspect of the study.

## Acknowledgements

We would like to thank Babet Halberstadt for her help with collecting fTCD and task performance recordings.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2021.107884>.

## References

- Badcock, N.A., Holt, G., Holden, A., Bishop, D.V.M., 2012a. dopOSCCI: a functional transcranial Doppler ultrasonography summary suite for the assessment of cerebral lateralization of cognitive function. *J. Neurosci. Methods* 204, 383–388. <https://doi.org/10.1016/j.jneumeth.2011.11.018>.
- Badcock, N.A., Nye, A., Bishop, D.V.M., 2012b. Using functional transcranial Doppler ultrasonography to assess language lateralisation: influence of task and difficulty level. *Laterality* 17, 694–710. <https://doi.org/10.1080/1357650X.2011.615128>.
- Badzakova-Trajkov, G., Corballis, M.C., Häberling, I.S., 2015. Complementarity or independence of hemispheric specializations? A brief review. <https://doi.org/10.1016/j.neuropsychologia.2015.12.018>.
- Blum, M., Ott, T., 2018. Animal left-right asymmetry. *Curr. Biol.* 28, R301–R304. <https://doi.org/10.1016/j.cub.2018.02.073>.
- Boles, D.B., Barth, J.M., Merrill, E.C., 2008. Asymmetry and performance: toward a neurodevelopmental theory. *Brain Cognit.* 66, 124–139. <https://doi.org/10.1016/j.bandc.2007.06.002>.
- Brederoo, S.G., Van der Haegen, L., Brysbaert, M., Nieuwenstein, M.R., Cornelissen, F.W., Lorist, M.M., 2020. Towards a unified understanding of lateralized vision: a large-scale study investigating principles governing patterns of lateralization using a heterogeneous sample. *Cortex* 133, 201–214. <https://doi.org/10.1016/j.cortex.2020.08.029>.
- Cai, Q., Van Der Haegen, L., Brysbaert, M., 2013. Complementary hemispheric specialization for language production and visuospatial attention. *Proc. Natl. Acad. Sci. U. S. A* 110. <https://doi.org/10.1073/pnas.1212956110>.
- Chiarello, C., Welcome, S.E., Halderman, L.K., Leonard, C.M., 2009. Does degree of asymmetry relate to performance? An investigation of word recognition and reading in consistent and mixed handers. *Brain Cognit.* 69, 521–530. <https://doi.org/10.1016/j.bandc.2008.11.002>.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215. <https://doi.org/10.1038/nrn755>.
- Cowell, P., Hugdahl, K., 2000. Individual differences in neurobehavioral measures of laterality and interhemispheric function as measured by dichotic listening. *Dev. Neuropsychol.* 18, 95–112. [https://doi.org/10.1207/S15326942DN1801\\_6](https://doi.org/10.1207/S15326942DN1801_6).
- Crow, T.J., Crow, L.R., Done, D.J., Leask, S., 1998. Relative hand skill predicts academic ability: global deficits at the point of hemispheric indecision. *Neuropsychologia* 36, 1275–1282. [https://doi.org/10.1016/S0028-3932\(98\)00039-6](https://doi.org/10.1016/S0028-3932(98)00039-6).
- Deppe, M., Ringelstein, E.B., Knecht, S., 2004. The investigation of functional brain lateralization by transcranial Doppler sonography. *Neuroimage* 21, 1124–1146. <https://doi.org/10.1016/j.neuroimage.2003.10.016>.
- Everts, R., Lidzba, K., Wilke, M., Kiefer, C., Mordasini, M., Schroth, G., Perrig, W., Steinlin, M., 2009. Strengthening of laterality of verbal and visuospatial functions

- during childhood and adolescence. *Hum. Brain Mapp.* 30, 473–483. <https://doi.org/10.1002/hbm.20523>.
- Floel, A., Buyx, A., Breitenstein, C., Lohmann, H., Knecht, S., 2005. Hemispheric lateralization of spatial attention in right- and left-hemispheric language dominance. *Behav. Brain Res.* 158, 269–275. <https://doi.org/10.1016/j.bbr.2004.09.016>.
- Frasnelli, E., Vallortigara, G., Rogers, L.J., 2012a. Left–right asymmetries of behaviour and nervous system in invertebrates. *Neurosci. Biobehav. Rev.* 36, 1273–1291. <https://doi.org/10.1016/j.neubiorev.2012.02.006>.
- Frasnelli, E., Vallortigara, G., Rogers, L.J., 2012b. Left–right asymmetries of behaviour and nervous system in invertebrates. *Neurosci. Biobehav. Rev.* 36, 1273–1291. <https://doi.org/10.1016/j.neubiorev.2012.02.006>.
- Gardony, A.L., Eddy, M.D., Brunyé, T.T., Taylor, H.A., 2017. Cognitive strategies in the mental rotation task revealed by EEG spectral power. *Brain Cognit.* 118, 1–18. <https://doi.org/10.1016/j.bandc.2017.07.003>.
- Gerrits, R., Verhelst, H., Vingerhoets, G., 2020. Mirrored brain organization: Statistical anomaly or reversal of hemispheric functional segregation bias? *Proc. Natl. Acad. Sci. U.S.A.* 117 (25), 14057–14065. <https://doi.org/10.1073/pnas.2002981117>.
- Hirnstein, M., Hugdahl, K., Hausmann, M., 2014. How brain asymmetry relates to performance - a large-scale dichotic listening study. *Front. Psychol.* 4 <https://doi.org/10.3389/fpsyg.2013.00997>.
- Hirnstein, M., Leask, S., Rose, J., Hausmann, M., 2010. Disentangling the relationship between hemispheric asymmetry and cognitive performance. *Brain Cognit.* 73, 119–127. <https://doi.org/10.1016/j.bandc.2010.04.002>.
- Hyde, J.S., 2016. Sex and cognition: gender and cognitive functions. *Curr. Opin. Neurobiol.* <https://doi.org/10.1016/j.conb.2016.02.007>.
- Knecht, S., 2001. Behavioural relevance of atypical language lateralization in healthy subjects. *Brain* 124, 1657–1665. <https://doi.org/10.1093/brain/124.8.1657>.
- Knecht, S., 2000. Handedness and hemispheric language dominance in healthy humans. *Brain* 123, 2512–2518. <https://doi.org/10.1093/brain/123.12.2512>.
- Knecht, S., Deppe, M., Ebner, A., Henningsen, H., Huber, T., Jokeit, H., Ringelstein, E.B., 1998. Noninvasive determination of language lateralization by functional transcranial Doppler sonography: a comparison with the Wada test. *Stroke* 29, 82–86.
- Knecht, S., Deppe, M., Ringelstein, E.B., 1999. Determination of cognitive hemispheric lateralization by “functional” transcranial Doppler cross-validated by functional MRI. *Stroke* 30, 2491–2492.
- Lamm, C., Windischberger, C., Moser, E., Bauer, H., 2007. The functional role of dorso-lateral premotor cortex during mental rotation an event-related fMRI study separating cognitive processing steps using a novel task paradigm. <https://doi.org/10.1016/j.neuroimage.2007.04.012>.
- Lust, J.M., Geuze, R.H., Groothuis, A.G.G., Bouma, A., 2011a. Functional cerebral lateralization and dual-task efficiency—testing the function of human brain lateralization using fTCD. *Behav. Brain Res.* 217, 293–301. <https://doi.org/10.1016/j.bbr.2010.10.029>.
- Lust, J.M., Geuze, R.H., Groothuis, A.G.G., van der Zwan, J.E., Brouwer, W.H., van Wolfelaar, P.C., Bouma, A., 2011b. Driving performance during word generation—testing the function of human brain lateralization using fTCD in an ecologically relevant context. *Neuropsychologia* 49, 2375–2383. <https://doi.org/10.1016/j.neuropsychologia.2011.04.011>.
- MacNeilage, P.F., Rogers, L.J., Vallortigara, G., 2009. Origins of the left & right brain. *Sci. Am.* 301, 60–67.
- McGrew, W.C., Marchant, L.F., 1999. Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates* 40, 509–513. <https://doi.org/10.1007/BF02557586>.
- Mellet, E., Zago, L., Jobard, G., Crivello, F., Petit, L., Joliot, M., Mazoyer, B., Tzourio-Mazoyer, N., 2014. Weak language lateralization affects both verbal and spatial skills: an fMRI study in 297 subjects. *Neuropsychologia* 65, 56–62. <https://doi.org/10.1016/j.neuropsychologia.2014.10.010>.
- Ocklenburg, S., Isparta, S., Peterburs, J., Papadatou-Pastou, M., 2019. Paw preferences in cats and dogs: meta-analysis. *Laterality* 24, 647–677. <https://doi.org/10.1080/1357650X.2019.1578228>.
- Peters, M., Battista, C., 2008. Applications of mental rotation figures of the Shepard and Metzler type and description of a mental rotation stimulus library. *Brain Cognit.* 66, 260–264. <https://doi.org/10.1016/j.bandc.2007.09.003>.
- Petit, S., Badcock, N.A., Woolgar, A., 2020. Finding hidden treasures: a child-friendly neural test of task-following in individuals using functional Transcranial Doppler ultrasound. *Neuropsychologia* 146. <https://doi.org/10.1016/j.neuropsychologia.2020.107515>.
- Powell, J.L., Kemp, G.J., García-Finaña, M., 2012. Association between language and spatial laterality and cognitive ability: an fMRI study. *Neuroimage* 59, 1818–1829. <https://doi.org/10.1016/j.neuroimage.2011.08.040>.
- Pujol, J., Deus, J., Losilla, J.M., Capdevila, A., 1999. Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology* 52, 1038–1043.
- Reilly, D., Neumann, D.L., Andrews, G., 2016. Sex and sex-role differences in specific cognitive abilities. *Intelligence* 54, 147–158. <https://doi.org/10.1016/j.intell.2015.12.004>.
- Richardson, J.T.E., 2011. Eta squared and partial eta squared as measures of effect size in educational research. *Educ. Res. Rev.* 6, 135–147. <https://doi.org/10.1016/j.edurev.2010.12.001>.
- Rogers, L.J., Zucca, P., Vallortigara, G., 2004. Advantages of having a lateralized brain. *Proceed. Biol. Sci.* 271 (Suppl. 6), S420–S422. <https://doi.org/10.1098/rsbl.2004.0200>.
- Shepard, S., Metzler, D., 1988. Mental rotation: Effects of dimensionality of objects and type of task. *J. Exp. Psychol.: Human Percept. Perform.* 14 (1), 3–11. <https://doi.org/10.1037/0096-1523.14.1.3>.
- Strien, J.W. Van, 1992. Classificatie van links- en rechtshandige proefpersonen (Classification of left- and right-handed subjects. *Ned. Tijdschr. Psychol.* 47, 88–92.
- Stroobant, N., Vingerhoets, G., 2000. Transcranial Doppler ultrasonography monitoring of cerebral hemodynamics during performance of cognitive tasks: a review. *Neuropsychol. Rev.* 10, 213–231.
- Toga, A.W., Thompson, P.M., 2003. Mapping brain asymmetry. *Nat. Rev. Neurosci.* 4, 37–48. <https://doi.org/10.1038/nrn1009>.
- Tzourio-Mazoyer, N., Perrone-Bertolotti, M., Jobard, G., Mazoyer, B., Baciau, M., 2017. Multi-factorial modulation of hemispheric specialization and plasticity for language in healthy and pathological conditions: a review. *Cortex* 86, 314–339. <https://doi.org/10.1016/j.cortex.2016.05.013>.
- Vallortigara, G., Rogers, L., Bisazza, A., 1999. Possible evolutionary origins of cognitive brain lateralization. *Brain Res. Rev.* 30, 164–175. [https://doi.org/10.1016/S0165-0173\(99\)00012-0](https://doi.org/10.1016/S0165-0173(99)00012-0).
- Vallortigara, G., Rogers, L.J., 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.* 28, 575–589. <https://doi.org/10.1017/S0140525X05000105>.
- Woodhead, Z.V., Rutherford, H.A., Bishop, D.V., 2020. Measurement of language laterality using functional transcranial Doppler ultrasound: a comparison of different tasks. *Wellcome Open Res* 3, 104. <https://doi.org/10.12688/wellcomeopenres.14720.1>.
- Yeary, S.A., Patton, J.N., Kee, D.W., 2002. Asymmetries in finger-tapping interference produced by mental versus manual rotation of Shepard and Metzler type objects. *Brain Cognit.* 50, 324–334. [https://doi.org/10.1016/S0278-2626\(02\)00536-5](https://doi.org/10.1016/S0278-2626(02)00536-5).