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A unified view of lateralized vision

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A UNIFIED VIEW OF LATERALIZED VISION

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A unified view of lateralized vision

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and in accordance with
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by

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General introduction

CHAPTER 1

With this thesis, I aim to provide a unified account of lateralized processing of various types of visual information. The work in this thesis describes the search for veridical instances of lateralized vision, and the investigation of mechanisms underlying lateralized visual processing. I conclude by considering how we should go forward in trying to characterize and understand patterns of lateralized visual information processing.

The two hemispheres of the human brain are functionally lateralized, which means that each of them is differentially specialized for a range of processes. Two examples are the left hemisphere's specialization in spotting individual elements within a larger whole (e.g., seeing the trees that comprise a forest; Martin, 1979), and the right hemisphere's specialization in recognizing facial expressions (Christman & Hackworth, 1993). It may seem odd that we, as seemingly symmetric animals (i.e., consisting of roughly two halves mirrored around the sagittal plane), would develop such lateral asymmetries, while the natural world we live in is devoid of systematic left-right differences (Corballis, 2017). Yet, lateral asymmetries are common throughout the animal kingdom (Vallortigara & Rogers, 2005; Rogers, Vallortigara, & Andrews, 2013). For example, seed-eating birds use their right eye (projecting to their left hemisphere) to search for food on the ground, and use their left eye (projecting to their right hemisphere) to simultaneously monitor the sky for predators (Rogers, 2012). This behavior follows from their left hemisphere's specialization in distinguishing elements belonging to different categories (e.g., pecking at grains but not at pebbles), and their right hemisphere's specialization in detecting novel stimuli that demand immediate attention.

As illustrated by this example of bird vision, a reason for the seemingly odd asymmetric organization in symmetrical organisms may lie in an evolutionary pressure to develop specialized routines for complex processes (Corballis, 2017; Vallortigara, Rogers, & Bisazza, 1999). By reducing redundancy – for example by way of preventing two brain halves from duplicating functionally, an animal can arrive at an optimal use of its brain (Rogers & Vallortigara, 2015). It is clear how having a lateralized brain leads to efficient processing in birds: it enables the bird to perform two complex tasks that are vital to its survival (distinguishing food from non-food on the ground and spotting predators in the sky) simultaneously (Rogers, 2000). But what of humans? When grocery shopping, do we spot food items with our right eye and grumpy cashiers with our left? While not exactly being the case, it is not as far-fetched an idea as it may seem.

In contrast to birds, the eyes of humans are not placed laterally, but both face forward. In a bird, everything on the right side of visible space (the right visual field, or RVF) is captured by its right eye, from which nerve fibers project directly to the visual areas of its left hemisphere (LH). Conversely, everything to the left of the bird (the left visual field, or LVF) is captured by its left eye, and projected to the right hemisphere (RH). In humans, with eyes facing the front, a large part of the right side of visible space (a person's RVF) is captured by both eyes, and likewise for the left side (a person's LVF). However, due to the wiring of the visual cortical system in humans, both eyes feed information from the RVF to the occipital areas of the LH, and from the LVF to those of the RH (see Figure 1), just like in birds.

Returning to the two examples of functional specialization, or *lateralization*, of the two hemispheres in humans given above –the LH's specialization in spotting individual elements within a larger whole and the RH's specialization in recognizing facial expressions, an interesting conclusion can be drawn. Following the organization of the human visual system, lateralized processing of these types of information predicts that we will more rapidly spot a sought item in a complex array when it is present in our RVF, and more rapidly notice an angry-looking person when he is present in our LVF. In that sense, we may in fact be walking through the grocery store in a manner not unlike that of birds navigating their habitats. Intriguingly, the above examples are just two out of a sheer multitude of claimed instances of visual lateralization in humans.

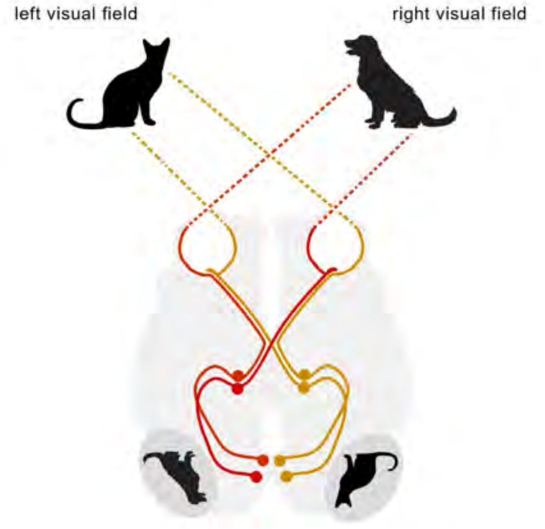

Figure 1. Organization of the human visual system.

Previous research on human lateralized vision

About 50 years of research on lateralization in humans has accumulated into a substantial body of studies showing lateral asymmetries, among which a large array in the domain of visual perception. Examples include the LH-lateralization of processing visually presented words (Willemin et al., 2016), local elements (Yovel, Yovel, & Levy, 2001), and relatively high spatial frequencies (i.e., representing featural information and fine detail) (Peyrin, Mermillod, Chokron, & Marendaz, 2006), and RH-lateralization of processing faces (C. Gilbert & Bakan, 1973; Levy, Heller, Banich, & Burton, 1983), global form (Yovel et al., 2001), and relatively low spatial frequencies (i.e., representing global information like shape) (Kauffman, Ramanoël, & Peyrin, 2014). Furthermore, the RH is believed to govern spatial attention (Linnell, Caparos, & Davidoff, 2014).

Already in 1973, Allen Newell reflected on the state of experimental psychology by pointing out that after years of studying specific phenomena, it was time to start putting things together. However, my impression is that the rate at which further novel phenomena and effects have been described has been much higher than the rate at which unifying theories have been proposed. This has been no different for the field of laterality research; much of previous research on visual lateralization has been devoted to studying single, isolated functional processes. While this has greatly advanced our understanding of lateralized processing of these distinct types of information, the relation between different lateralized processes remains largely unknown (Vingerhoets, 2019). For example, as stated above we know that both visual words and high spatial frequencies in most people are processed predominantly by the LH. We, furthermore, know that these processes are not unrelated, as recognition of visual words requires perception of featural information, relying strongly on the high end of the spatial frequencies range (Woodhead, Wise, Sereno, & Leech, 2011). Nevertheless, studies investigating lateralization of visual word processing rarely take into account lateralization of high spatial frequencies, barring a more encompassing understanding of the role of the LH in visual perception. In other words, and mirroring Newell's point; we have been looking at the trees but neglecting the forest.

Theoretical principles of lateralization

While only few studies have investigated the relation between different instances of lateralization, the preliminary findings of these studies do suggest a number of possible principles that may help explain the organization of lateralized processes. These principles can be referred to as the statistical complementarity; causal complementarity; and input asymmetry principles. These principles each offer a different perspective on whether and how lateralization of one process, once instantiated, can relate to lateralization of another, that is, of lateralization patterns.

The statistical complementarity principle (Badzakova-Trajkov, Corballis, & Häberling, 2016) proposes no mechanistic or functional explanation for why certain different processes are performed by either the same or by different hemispheres, and instead proposes that different processes become lateralized independently from each other. In contrast, the other principles all assume that lateralization of one type of information is dependent on that of another. To start, the causal complementarity principle (Andresen & Marsolek, 2005; Badzakova-Trajkov, Corballis, & Häberling, 2016; Cai, Van der Haegen, & Brysbaert, 2013; Gerrits, Van der Haegen, Brysbaert, & Vingerhoets, 2019) proposes that processes that can in principle take place bilaterally in homologue areas of the left and right hemispheres can be forced into one hemisphere if the other hemisphere becomes engaged with processing of a newly learned type of information. This then results in complementary lateralization of two processes to homologue areas of the two hemispheres. An example is the suggestion that the RH becomes lateralized for processing facial information only once the LH becomes lateralized for visual word processing (Behrmann & Plaut, 2015). The input asymmetry principle (Andresen & Marsolek, 2005) proposes that lateralization of a certain type of information depends on lateralization of a related type of information earlier in the processing cascade. For example, if perception of faces is dependent on low spatial frequency processing (Goffaux & Rossion, 2006), then the former may become lateralized to the RH because the latter already is.

A thorough evaluation of these principles is as of yet missing. In order to study the relations between different instances of lateralized information processing, one would have to assess these within individuals. However, before doing so, it is important to verify that the derived dependent measures (i.e., 'lateralization indices') indeed reflect lateralized processing of the type of information under study. There is reason to question whether this is the case for certain instances of lateralized vision that have been reported in the literature of the past 50 years.

Task and stimulus factors

For a number of the previously reported indices of visual lateralization, uncertainty exists as to what type of information they actually show lateralized processing to occur of. Reason for this is the observation that the choice of specific stimuli (Sergent & Hellige, 1986) and/or tasks (Hellige & Sergent, 1986) can strongly affect the obtained results. With regard to stimuli, a case in point is the common use of hierarchical letters (i.e., larger letters built out of numerous smaller letters) to study lateralization of local and global processing. The reason why the use of letters might limit the interpretation of such effects in terms of differences in global and local processing relates to another well-known instance of lateralization in humans, namely that of LH-dominance for language in the majority of right-handed individuals (Knecht, 2000). The latter phenomenon poses a challenge to the interpretation of the numerous reports of LH-lateralization for local element processing and RH-lateralization for global form processing, as most previous research used hierarchical letters, which are themselves linguistic in nature. This raises the question whether results obtained with such stimuli reflect lateralization of global and local processing, or can be explained by the LH's language-dominance allowing for better recognition in case of the local letters that are more difficult to see because they are smaller.

Reliability of lateralization indices

The multitude of instances of visual lateralized processing that have been reported in the research field of laterality suggest that the two hemispheres of the human brain are each specialized for a wide range of visual processes. However, some of these findings are not reported consistently, and may have low reliability (Voyer, 1998). A publication bias towards positive findings and the pressure for researchers to publish with high frequency and in esteemed journals may have led to an overrepresentation of chance findings in the literature. This in fact denotes a complex problem that is not specific to laterality research, but is faced by psychological science as a whole (Pashler & Wagenmakers, 2012). In order to arrive at a more unified view of lateralized vision, it is important to first separate spurious and genuine instances of lateralized visual processing.

Interim summary and thesis aims

We now have a number of ingredients informing us on the current state of knowledge regarding human lateralized vision. From this follows a set of aims of this thesis with the intention to advance our understanding of the lateralized processing of visual information.

First, previous research suggests that the human brain is lateralized for a multitude of visual processes, likely developed under evolutionary pressure to optimize the efficient use of cortical space and energy. However, at present, the literature may be cluttered with irreproducible instances of lateralization. This brings us to the first aim of this thesis: to establish veridical indices of visual lateralization, by attempting to reproduce previously reported instances of lateralization (Chapter 2).

Second, doubt exists as to whether some of the often-reported instances of lateralization are indicative of lateralized processing of specific types of visual information, or the result of using specific stimuli. As noted above, this is particularly true for two of the most intensively studies visual-field asymmetries, namely those related to processing global and local visual information. Accordingly, the second aim of this thesis is to elucidate whether lateralization indices for local and global processing reflect lateralization of visual information, or of language (Chapter 3).

Third, to better understand lateralization as an organizational property of the brain, it will be insightful to know how lateralization of one process relates to lateralization of another, that is, how patterns of lateralization can be characterized. Some theoretical principles propose circuits to link together lateralization of distinct processes. However, the empirical testing of these principles and their predictions has been scant. In order to do so, it is necessary to look at the relationship between lateralized processing of several types of information in a sample of participants who can be expected to differ in their lateralization for different functions. The final aim of this thesis, therefore, is a rigorous test of the principles proposed to explain the organization of lateralized visual processing (Chapter 4).

Methods

In this thesis, the visual half-field paradigm and variations thereof will be used to assess lateralized processing of different types of visual information. Furthermore, in analyzing the data, we included Bayesian statistical tests. I will shortly introduce these experimental and statistical methods.

Visual half-field paradigm

Previous studies of lateralized vision have used lesion, electroencephalography (EEG), and neuroimaging techniques, but the majority used behavioral approaches, as these are easily carried out and associated with low costs. Behavioral studies of visual lateralization often use the visual half-field paradigm, which makes elegant use of the organization of the visual system (Figure 1). In this paradigm, participants are required to fixate a small central stimulus (e.g., an asterisk or plus sign) on a computer screen. Then, a stimulus is briefly presented to the right or to the left of this central fixation mark. Because of the brief presentation time (in the studies described in this thesis, never longer than 200 ms), participants do not get the chance to move their eyes, and as a result the stimulus is presented in either the RVF or LVF. Consequently, we control whether the stimulus information arrives first in the LH or RH, respectively. From differences in the error rates and reaction times in response to RVF- and LVF-stimuli, we can deduce which of the two hemispheres processes this type of stimulus better and/or faster. This behavioral paradigm has been validated as a method to assess lateralized processing (e.g., Hunter & Brysbaert, 2008), whereby special caution should be taken in the set-up of the experiment (Bourne, 2006) (e.g., by using a chin rest to ensure a stable viewing distance and head position). The resulting visual-field asymmetries (i.e., difference scores between LVF and RVF performance measures) will be used as dependent measures throughout this thesis.

A variation of the visual-half field paradigm is the free-viewing paradigm. In this paradigm, viewers are not required to fixate the center of the screen and stimulus duration is not restricted to 200 ms. It is believed that the stimulus itself induces that the right and left parts of the image are shown in the RVF and LVF. This would, for example, be the case when viewing faces (Voyer, Voyer, & Tramonte, 2012). The free-viewing paradigm is another behavioral method used in this thesis (Chapters 2 and 4).

Bayesian statistics

Null-hypothesis significance testing (NHST) is the most frequently used statistical approach in most scientific fields (Silva-Ayçaguer, Suárex-

Gil, & Fernández-Somoano, 2010), but comes with a drawback: when the outcome of a test is 'non-significant', no conclusions can be drawn with regard to the absence of a certain effect. Consequently, using NHST, the researcher will never be able to accept the null-hypothesis, or in other words, confirm that a hypothesized effect is absent based on the data at hand. Given the earlier mentioned uncertainty regarding reported findings that may have arisen by chance, this is an undesirable limitation: NHST will never allow us to conclude that a replication attempt for an earlier shown effect produced evidence in favor of the absence of this effect. In contrast, Bayesian statistical analyses do allow for conclusions regarding both the absence and the presence of effects (Dienes & McIatchie, 2017). Therefore, we report the outcomes of such analyses alongside the more traditional null-hypothesis testing throughout this thesis. Rather than refraining from reporting NHST statistics, we chose to report both, so as to render our results comparable to previous and future findings, and to allow for the inclusions of our results in future meta-analyses.

Data, analysis scripts and stimulus presentation scripts of the work presented in this thesis can be found at the Open Science Framework (https://osf.io/yv9gz/).

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Reproducibility of visual-field asymmetries

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Abstract

Numerous behavioral studies suggest that the processing of various types of visual stimuli and features may be more efficient in either the left or the right visual field. However, not all of these visual-field asymmetries (VFAs) have been observed consistently. Moreover, it is typically unclear whether a failure to observe a particular VFA can be ascribed to certain characteristics of the participants and stimuli, to a lack of statistical power, or to the actual absence of an effect. To increase our understanding of lateralization of visual information processing, we have taken a rigorous methodological and statistical approach to examine the reproducibility of various previously reported VFAs. We did so by performing (near-)exact replications of nine representative previous studies, aiming for sufficient power to detect the effects of interest, and taking into consideration all relevant dependent variables (reaction times and error rates). Following Bayesian analyses –on our data alone as well as on the combined evidence from the original and replication studies– we find precise and reliable evidence that support VFAs in the processing of faces, emotional expressions, global and local information, words, and in the distribution of spatial attention. In contrast, we find less convincing evidence for VFAs in processing of high and low spatial frequencies. Finally, we find no evidence for VFAs in categorical perception of color and shape oddballs, and in the judgments of categorical and coordinate spatial relations. We discuss our results in the light of their implications for theories of visual lateralization.

Introduction

Depending on the nature of visual information, presenting it in either the left (LVF) or right (RVF) visual field can influence the efficiency with which observers process it. Behavioral experiments in which visual stimuli are presented to the LVF and RVF have, for example, shown that the majority of observers show LVF-advantages for face information, while they show RVF-advantages for words. The visual-field asymmetries (VFAs) resulting from such visual half-field or free-viewing tasks have been suggested to reflect differential hemispheric specialization, or lateralization, of the processing of different types of visual information (Beaumont, 1982; Bourne, 2006; Voyer, Voyer, & Tramonte, 2012).

Over the past decades, behavioral experiments have demonstrated VFAs for a variety of stimulus types, and these phenomena have in turn formed the basis for a number of theories regarding lateralization of visual information processing (for overviews, see Hellige, 1995; Dien, 2008; Hellige, Laeng, & Michimata, 2010; Karim & Kojima, 2010). Importantly, however, there is reason for concern about the reliability of some of these findings. Specifically, a number of VFAs extracted in such studies tend to have a relatively low test-retest and split-half reliability, when compared to behavioral asymmetries in the auditory domain (Voyer, 1998), and the results of different studies on the same types of visual information often lack consistency in their outcomes. As a case in point, consider the results of studies investigating the lateralization of global and local information processing of hierarchical stimuli. While the general assumption is that there is an RVF-advantage when processing of the local elements is task-relevant, and an LVF-advantage when processing the global form is task-relevant (Van Kleeck, 1989), most studies using visual half-field tasks with hierarchical stimuli have found evidence for only one of these two VFAs (for a recent review, see Brederoo, Nieuwenstein, Lorist, & Cornelissen, 2017). Concomitantly, the interpretation of such failures to demonstrate a particular VFA is often difficult because it is unclear whether a null result can be taken as evidence for the null hypothesis or as evidence that the study did not have sufficient power to detect the effect of interest.

The inconsistent findings have promoted the approach of using convergent evidence from, for example, patient and neuroimaging studies, to arrive at insights about the extent to which the left (LH) and right (RH) hemispheres might be specialized for processing certain types of visual input. While this approach provides insight into whether lateralization occurs at the implementational, neural level, the investigation of which aspects of lateralization also produce reliable behavioral effects is an important enterprise in its own right, for several reasons. To start, the availability of reliable behavioral manifestations of lateralization can be of practical importance in distinguishing between clinical populations (Luh & Gooding, 1999) and in studying the effects of aging (Lux, Marshall, Thimm, & Fink, 2008). Secondly, behavioral studies are usually cheaper and easier to implement than patient or neuroimaging studies, and they therefore provide a highly useful means to examine how various factors influence the lateralized processing of visual information. Lastly, insight into the behavioral manifestations of lateralization is also of importance for practical reasons when it comes to designing applications aimed at maximizing the efficiency of visual information processing. For these reasons, verifying the reliability of behavioral indices of lateralization of visual information processing is valuable for the field.

In the current study, we investigated the reliability of several behavioral manifestations of lateralized visual information processing by determining whether we could replicate the earlier-found VFAs. The importance of replication research has received growing emphasis by the scientific community in recent years. Researchers (e.g., Pashler & Wagenmakers, 2012; Schmidt, 2009) and journal editors (Wagenmakers & Forstmann, 2014) have been encouraged to improve reproducibility of scientific findings by engaging in replication research, of which the large-scale replication project of the Open Science Framework is an example (Open Science Collaboration, 2015). This project raised awareness of the importance of studying reproducibility of effects in psychological science, and stressed that “Replication can increase certainty when findings are reproduced and promote innovation when they are not.” (Open Science Collaboration, 2015, p. 7). With this goal in mind, we attempted to replicate nine studies that yielded evidence for lateralization of visual information processing in behavioral outcomes, with each targeting a different type of visual information.

In selecting our targets for the replication studies, we aimed to arrive at a representative set of tasks that have previously been found to yield VFAs for various types of visual features and stimuli. Specifically, our selection included several phenomena that have dominated the field of visual lateralization research over the past 50 years (i.e., VFAs for neutral and emotional faces, global and local visual information, high and low spatial frequencies, categorical and coordinate spatial relations, the distribution of spatial attention, and visually presented words), as well as some that have resulted from more recent studies (i.e., VFAs showing categorical effects in the perception of colors and shapes). Importantly, this selection of phenomena also entailed the inclusion of studies employing different presentation conditions (e.g., free-viewing and visual-half field paradigms) and exposure durations (from 30 ms to 10 s) for a wide diversity of tasks and outcome measures (i.e., target detection, target identification, S1-S2 matching, choice bias), thereby yielding a broad range of phenomena that can be said to be representative of previous studies examining the behavioral manifestations of lateralized visual information processing. Accordingly, our study not only allowed for an examination of the reproducibility of a large number of VFAs found in previous studies, but it also enabled us to examine how reproducibility varied across VFAs for different types of visual information and tasks.

In designing our replication studies, we strove to replicate the original experiments as exactly as possible –either by copying the original methods or by using the original experiment programs when possible– and we conducted a priori power analyses to ensure that our sample sizes would be large enough to have sufficient power to observe the effects of interest. In addition, we examined both error rates (ERs) and reaction times (RTs), so as to allow us to exclude the occurrence of a speed-accuracy trade-off as an alternative account of any observed lateralization effect. Furthermore, in addition to a more conventional analysis using null hypothesis significance testing (NHST), we used Bayesian analyses, as these enable an assessment of the extent to which a non-significant outcome provides evidence in favor of the null hypothesis (Dienes & Mclatchie, 2017). Lastly, we also calculated a meta-analytical Bayes factor (Rouder & Morey, 2011), which is a novel Bayesian analysis method that combines results of several studies in order to arrive at a more robust estimate of the presence or absence of a particular effect.

General methods

Tasks

Each of the to-be replicated tasks had been described in more than one earlier published study. For our replication studies, we selected those studies that were pioneering, or were an updated version of pioneering tasks, based on more recent findings. The tasks used were the Face Similarity Task (FST) (C. Gilbert & Bakan, 1973), Face Emotionality Task (FET) (Levy et al., 1983), Hierarchical Letter Task (HLT) (Yovel et al., 2001), Picture Matching Task (PMT) (Peyrin, Mermillod, et al., 2006), Color Oddball Task (COT) (A.L. Gilbert, Regier, Kay, & Ivry, 2006), Shape Oddball Task (SOT) (A.L. Gilbert, Regier, Kay, & Ivry, 2008), Cross-dot Matching Task (CMT) (Van der Ham & Borst, 2011, 2016), Landmark Task (LT) (Linnell et al., 2014), and Lexical Decision Task (LDT) (Willemin et al., 2016).

Participants

Participants were recruited from the student population of the University of Groningen. All participants were right-handed as assessed by self-report (LT), measured using the Edinburgh Handedness Inventory (Oldfield, 1971) (LDT), or measured using the Flanders handedness questionnaire (Nicholls, Thomas, Loetscher, & Grimshaw, 2013) (all other tasks). All participants had normal or corrected-to-normal vision, which was measured using a Snellen test (PMT), or based on participants' self-report (all other tasks). Participants received course credits or a monetary compensation in exchange for their participation. The ethical committee of the Psychology Department of the University of Groningen approved all experiments, and participants always gave written informed consent before the start of an experiment.

To determine the minimum number of participants needed to find the smallest effect of interest in the original study with 80% power (at α = .05, one-sided), we conducted power analyses using the G*Power 3.1.9.2 software (Faul, Erdfelder, Lang, & Buchner, 2007), based on the original study's effect sizes (Cohen's d_z). The achieved power for each of the effects of interest is reported below, in the subsections where we report the results of each study.

Procedure

The experiments took place in a dimly lit and sound-attenuating cabin. Stimuli were presented on a 22" (1280 x 1024, 100 Hz, Iiyama Vision Master Pro 513) or 19" (1024 x 768, 100 Hz, Iiyama Vision Master Pro 454) CRT-monitor. In each experiment the distance to the monitor was fixed using a chin rest. The experiments were implemented in DMDX (Forster & Forster, 2003) (LDT), or E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA) (all other tasks), running on a Windows 7 operating system. Responses were collected using a QWERTY-keyboard (LT; LDT) or an inhouse manufactured button box (all other tasks).

Statistical analyses

In all analyses, we subtracted performance on RVF-trials from performance on LVF-trials, and therefore any negative test statistic indicates an LVF-advantage whereas any positive test statistic indicates an RVF-advantage. For studies that examined VFAs across different task conditions (HLT; PMT; COT; SOT; CMT), we conducted planned comparisons for the visual-field contrasts even when the repeated measures ANOVA did not show a significant interaction with task condition. The ANOVA tables describing the results of the full models can be found in Appendix A.

In line with the original studies' analyses, we report the outcomes of one-sided dependent samples *t*-tests contrasting LVF- and RVF-performance, or one-sample *t*-tests comparing a VFA to a mean of zero. However, to decide on the success or failure of a replication, rather than using frequentists *t*-tests and focusing on the *p*-value that can be derived from such a test, we used Bayesian *t*-tests (using the BayesFactor package for R). The reason for this is that the frequentist statistical method allows the researcher to reject the null hypothesis, but not to accept it, and as such does not allow the conclusion that a replication attempt has failed. The Bayes factors that we derived from the Bayesian *t*-tests reflect the amount of evidence in favor or against the alternative and null hypotheses, thus allowing us to decide on the success or failure of our replication. To interpret the resulting Bayes factors (BF_{10}) we adopted the classifications proposed by Jeffreys (1961) (i.e., a $BF_{10} > 3.16$, > 10, > 31.6, or > 100 respectively entails substantial, strong, very strong, or decisive evidence for the alternative hypothesis, while a $BF_{10} < .316$, $< .1$, $< .0316$, or $< .01$ repectively entails substantial, strong, very strong, or decisive evidence for the null hypothesis)[1]. In our analyses, we concluded a VFA was successfully replicated when the BF_{10} exceeded 3.16, and we concluded that the replication had failed when the BF_{10} was below .316. When the BF_{10} was within the .316 – 3.16 interval, we concluded that there was not sufficient evidence to decide on the success or failure of the replication.

Effects of interest. The nine studies that we attempted to replicate produced a variety of outcome measures. Specifically, three of the experiments produced a measure of bias towards one of the visual fields (FST; FET; LT), while the effects for the other six experiments were expressed in terms of differences in ERs and/or RTs. Four experiments compared conditions for which opposing VFAs were expected (HLT; COT; SOT; LDT), and two experiments additionally measured the effect of a modulating task factor (PMT) or participant factor (CMT) upon the found VFAs. The effects of interest in the replication studies were restricted to those outcomes that yielded a significant effect (i.e., had a p-value smaller than .05) in the original study.

Additional analyses. Aside from examining the replicability of the effects that were found to be significant in the original studies, we also conducted a number of additional analyses. To start, we examined each VFA in terms of differences in both ERs and RTs. The motivation for examining both ERs and RTs was to determine whether a speed-accuracy trade-off occurred, and whether such a trade-off could explain any discrepancy between the effects found in the original study and in our replication attempt (Hellige & Sergent, 1986). In addition, a test of both RTs and ERs appeared to be warranted by logic, as any beneficial effect of hemispheric specialization could in principle surface in both accuracy and processing time.

A second point of departure from the original analyses derived from the fact that each of the studies that tested the LVF-RVF contrasts under different task conditions (HLT; PMT; COT; SOT; CMT) failed to find some of the predicted VFAs. Since four of these studies used relatively small sample sizes ($N < 17$), these studies may have been underpowered to detect all predicted VFAs. Therefore, we additionally examined the VFAs that were predicted based on theory, but not found in the original studies.

Combined evidence. Finally, for each of the predicted VFAs (significant and non-significant) in the original studies, we calculated a combined Bayes factor based on the statistics of the effect in the original and replication studies. This meta-analytic Bayes factor (Rouder & Morey, 2011) allows the assessment of the total amount of evidence for the predicted VFAs under study (i.e., the effects of interest as well as those effects addressed with the additional analyses).

General results

Data exclusion

Data of participants whose accuracy did not exceed 50% were excluded from the analyses. This resulted in exclusion of 18 of the 322 (i.e., 5.6%) tested participants (HLT: 7; PMT: 2; COT: 1; SOT: 6; CMT: 2). The ensuing descriptions of the participants in each of the replication studies pertain to the remaining participants who were included in the analyses.

For all analyses of RTs, we first subjected the data to the outlier removal procedure described by Van Selst and Jolicoeur (1994). The percentage of trials removed as a result of this procedure ranged between 1.6% and 2.7% over studies.

Replication studies

In the following sections, we describe the experimental set-up, methods and results for each of the nine replication studies and we provide a short discussion of the results. In cases in which we did not successfully replicate an effect, we discuss whether differences between the original and replication studies might have caused this. The presentation of the nine replication studies is ordered by the publication dates of the original studies.

Face Similarity Task (FST)

Faces have been suggested to be the most widely studied type of visual stimulus (Yovel, Wilmer, & Duchaine, 2014). The first to show an LVF-bias for face processing in a group of healthy adults were C. Gilbert and Bakan (1973). They asked participants to judge the similarity of construed symmetric face images to the original face images. Specifically, participants had to choose between a symmetric face image that was made by mirroring the left half of the original face, and a symmetric face that was made by mirroring the right half of the original face. The right-handed participants more often found the left-side symmetric composite to resemble the original face than the right-side symmetric composite. This finding was interpreted to indicate a bias towards the LVF in perceiving faces, caused by RH-dominance in face processing (C. Gilbert & Bakan, 1973). This free-viewing face paradigm and adaptations of it have been widely used since (for an overview, see Voyer, Voyer, & Tramonte, 2012). The current study is a replication attempt of the pioneering Face Similarity Task (FST) used by C. Gilbert and Bakan (1973; Experiment 4 [subsample of right-handed participants]).

Methods.

Participants. Thirty-four participants (17 women) performed the FST. Their mean age was 20 years (range = 18-27).

Stimuli. Fifty-three neutral face images (28 female and 25 male) photographed in straight view were selected from the Karolinska Directed Emotional Faces (KDEF) face database (Lundqvist, Flykt & Öhman, 1998). For each of the original images, we also created two mirror images in which the face was mirrored along the vertical axis. By using both the original and the mirrored images, we aimed to prevent any asymmetries in the features of the model's face to influence choice behavior. The symmetric faces were created in Adobe Photoshop, by mirroring half of a face over the midline, and softening the break line; one consisting of twice the left half of the face (left-side composite), and one consisting of twice the right half (right-side composite).

Procedure. On each trial, a blank screen lasting 250 ms was followed by the stimulus consisting of three versions of the same face: the original (or mirrored) face at the top, and the symmetric versions at the lower left and lower right (Figure 2). The participants were instructed to indicate which of the two lower faces resembled the upper face most by pressing a corresponding button. In making this judgment, participants were asked to go with their first instinct, and to base their decision solely on the face of the person. The next trial started after the participant had made a response, or after a response period of 10 s (in 0.3% of trials no response was recorded). The pictures were shown in randomized order, and presented on a grey background. Symmetric left- and right-side composites were randomly presented at the left or right side of the screen.

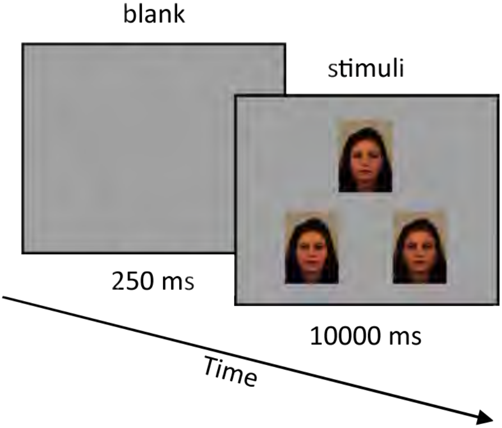

Figure 2. Timeline of a trial in the Face Similarity Task.

Participants started the experimental session with a block of the FST, followed by the FET (see p. 31), and another task including face stimuli that will not be described here. They concluded the test session, which lasted about 45 min in total, with a second block of the FST. Half of the participants saw the original symmetric faces in the first block and their mirror images in the second block, and vice versa for the other half of the participants.

Methods.

Effects of interest. Following the original study, we computed a measure of LVF-bias by comparing the proportion of choice for the left-side composite in the block using the original face images, to the proportion of choice for the right-side composite in the block using its mirror images. Because one block used the original face images and the other used its mirror images, a choice for the left-side composite in one block and for the right-side composite in the other block is twice a choice for the same symmetric composite face. By making the comparison as we did (following C. Gilbert and Bakan, 1973), we controlled for participants' choosing a composite based on some specific feature that is present in the model's one face half. For example, a model may have a specific feature (e.g., a birthmark) on one of the sides of the face that is particularly striking to a participant and leads them to choose the composite containing it. In the block using mirrored images, this participant will then likely choose the same composite, containing the specific feature. However, if participants' choices are most strongly influenced by an LVF-bias in face perception, they will choose the composite face that reflects what they see on the left side of the face more frequently. Hence, the hypothesis was that the proportion choice for the left-side composite would be higher in the block using original faces images than the proportion choice for the right-side composite in the block using mirrored face images, indicating an LVF-bias.

Based on the original study's finding of an effect size of $d_z = -.943$ we had more than 99% power to detect this VFA with our sample size. No additional analyses were planned.

Differences with original study. Our version of the FST is a partial replication of C. Gilbert and Bakan's Experiment 4 from their 1973 paper, with differences pertaining to the stimulus set and testing procedure. The original study used 14 face pairs, of which printouts were presented to the participants. No details were provided about how participants were required to make their response, and how much time was allowed for this. Our replication attempt used 53 face pairs, which were digitally presented, with a maximum viewing time of 10 s. We used different face images than those used in the original study, but their symmetric versions were constructed in the same manner. In the original study, participants received the block using mirrored (original) images immediately following the block using the original (mirrored) images, while in the replication attempt these blocks were separated by two other tasks involving face stimuli.

The original study compared performance in left- and right-handed participants, finding a diminished LVF-bias for left-handed participants (C. Gilbert & Bakan, 1973). We tested only right-handed participants, and we thus relate our results to the right-handed group of the original study.

Results. We replicated the LVF-bias in the FST (BF_{10} = 5,858, t[33] = -5.34, p < .001, d_z = -.916). Participants more often judged the left-side composite face to resemble the original most in the block using the original face images (59%), than that they judged the right-side composite face to resemble the (mirrored) original most in the block using mirrored face images (47%) (mean choice for left-side composite over blocks = 56%, SD = 6.7%). Combining the original and replication studies' results, we found decisive evidence for the presence of an LVF-bias (BF_{10} = 189,722,311).

Discussion. Our replication attempt for the finding of a behavioral manifestation of lateralized face processing in the FST was successful. Specifically, we replicated the original study's LVF-bias, as participants more often chose the composite face that was constructed from the left half of the original face. When combining the original study's results and the results of our replication study in a meta-analytic Bayes factor, the evidence is decisive in demonstrating an LVF-bias in the FST. Furthermore, the effects in the original and replication studies were comparable in terms of direction and size, while the studies used different face images. This suggests that the likelihood of observing an LVF-bias for face processing in the FST is robust to different face images.

Face Emotionality Task (FET)

In 1983, Levy et al. devised a free-viewing face task using chimeric faces with half the face showing an emotional expression and the other half showing a neutral expression. This Face Emotionality Task (FET) is a widely used task to study lateralization of processing emotional expressions (e.g., Coronel & Federmeier, 2014; Innes, Burt, Birch, & Hausmann, 2016). We attempted to replicate Levy et al.'s 1983 study.

Methods.

Participants. The same thirty-four participants that completed the FST also performed the FET.

Stimuli. Images from the KDEF (Lundqvist et al., 1998) were adapted to form a set of 39 emotional chimeric faces; one half of the face showed an emotional expression, while the other half showed a neutral expression (T. Beking, personal communication, 2014). For each image, we created a version with the emotion showing in the left half of the face and a version with the emotion showing in the right half of the face (its mirror image). Twenty images showed the emotion happiness (10 female and 10 male models), and 19 images showed the emotion anger (10 female and 9 male models) in one half of the face.

Procedure. On each trial, following a blank screen of 250 ms, the participant was shown an emotional chimeric face and its mirror image, one above the other (Figure 3). The participant was asked to indicate which of the two faces showed the strongest emotional expression, by pressing one of two buttons. The next trial started after the participants' response, or after 10 s (in 0.6% of the trials no response was recorded). The 39 stimuli were presented in randomized order, on a white background. The location of the face with the emotional expression on the left side was randomized over trials.

Effects of interest. The effect of interest was whether participants more often judged the face with the emotion on the left side as more emotional than the face with the emotion on the right side (i.e., LVF-bias). Based on the original study's effect size of d_z = -.689 for right-handed participants, we had 99% power to detect this VFA with our sample size. No additional analyses were planned.

Differences with original study. Our version of the FET is a partial replication of the study by Levy et al. (Levy et al., 1983), with differences pertaining to the stimuli and procedure. The original study used 36 pairs of 9 male actors showing the emotion 'happy', and the images were presented to the participants on slides. No details were provided with regard to response procedure, or how much time was allowed to make a response. The replication study used 39 pairs of male (19 items) and female (20 items) actors, showing the emotions 'happy' (20 items) or 'angry' (19 items), which were presented digitally. In the replication attempt we used different face images than those used in the original study. Furthermore, the original study allowed the response ‘can’t decide’, while in the replication study we asked participants to make a choice on each trial. If a participant had not responded within 10 s, it was considered a miss and these trials were not included in our analysis.

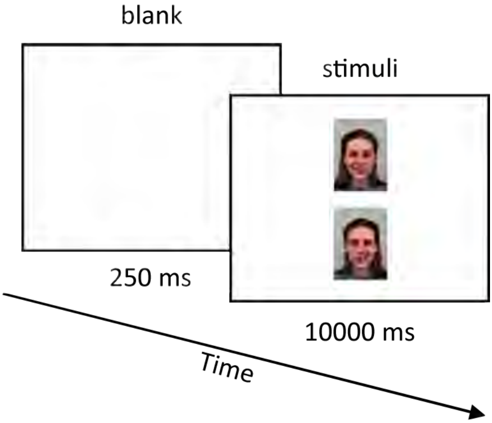

Figure 3. Timeline of a trial in the Face Emotionality Task.

The original study compared left- and right-handed participants, and found the left-handed participants to show a weaker LVF-bias (Levy et al., 1983). We tested only right-handed participants, and we accordingly relate our results to those of the right-handed participants in the slide presentation group of the original study.

Results. We replicated the LVF-bias in the FET (BF_{10} = 2,824, t[33] = -5.07, $p < .001$, $d_z = -.870$). Participants more often judged faces to have a stronger emotional expression when the left side expressed the emotion (bias = 65%, SD = 18%). When combining the effects found in the original and replication studies, there is decisive evidence for the presence of an LVF-bias (BF_{10} = 2.88647E+12).

Discussion. The results of this replication attempt were successful in replicating the original study’s LVF-bias for emotional face processing. As was the case for the FST, the meta-analytic Bayes factor indicates that the evidence combined across the original and replication studies is decisive in demonstrating an LVF-bias in the FET. While the original study used only male faces with ‘angry’ expressions, we found highly similar results using male and female faces with angry and happy expressions. Accordingly, we can conclude that the LVF-bias observed in the FET is robust to different emotional expressions and the actors’ sex.

Hierarchical Letter Task (HLT)

In 1979, Martin studied VFAs in processing the global and local elements present in so-called Navon letters. Using a Hierarchical Letter Task (HLT), she found an RVF-advantage for processing of local information, which was complemented by an LVF-advantage for processing of global information in a later study (Sergent, 1982b). While these asymmetries have been replicated, there has also been a substantial number of studies that did not show a significant LVF-advantage for global processing and/or RVF-advantage for local processing (e.g., Boles, 1984; Boles & Karner, 1996; Van Kleeck, 1989). Discrepancies between these studies were argued to be due to differences in stimulus- and task-characteristics (Yovel et al., 2001). Yovel et al. addressed the influence of a number of stimulus and task factors on the surfacing of VFAs in ERs and RTs using an HLT. Their results showed that requiring participants to divide attention over equally salient local and global stimulus levels produced more robust VFAs than other versions of the HLT. Accordingly, we selected this improved paradigm (Yovel et al., 2001, Experiment 1C) for our replication attempt.

Methods.

Participants. Twenty-one participants (9 women) with a mean age of 20 years (range = 18-23) performed the HLT. The presented data are a subset of a larger data set (Brederoo et al., 2017).

Stimuli. Stimulus letters were T and H (targets), and Y and N (distractors). All stimuli were incongruent, that is, the identity of the letters presented at the global level always differed from that of the letters shown at the local level. The global stimulus was comprised of local stimuli placed within a 5 x 5 grid, with a global/local ratio of 0.14. The hierarchical letters were presented in black on a white background, and they subtended 3.5° of visual angle, with their inner edges positioned at 0.5° from the central fixation point. The mask consisted of a 5 x 5 grid of hash tags. During unilateral presentation blocks, one hierarchical letter was presented, in either the LVF or RVF. During bilateral presentation blocks, one hierarchical letter appeared in the LVF and another in the RVF, but only one of them contained the target.

Procedure. A trial started with the presentation of a central fixation asterisk that was present for a duration jittered between 540-600 ms (Figure 4). Next, a single stimulus was presented in the LVF or RVF, during unilateral presentation blocks, or two stimuli were presented, one in each visual field, during bilateral presentation blocks, for 120 ms. This display was followed by a blank screen of 120 ms during unilateral blocks and of 220 ms during bilateral blocks. After the blank, one or two masks were presented in place of the stimuli, for 110 ms. Participants were required to identify the target letter as quickly as possible, regardless of the level at which it appeared, or on which side it appeared. They did so by pressing one of two buttons using their index or middle finger. As in the original study, finger-response mapping and response hand were counterbalanced over participants. The next trial started after the participant had made a response, or after the response period of 2 s was over.

Participants completed four blocks of 80 trials, amounting to 320 experimental trials in total. They were allowed to take self-paced breaks between the blocks. Throughout the experiment, target letters appeared either at the global or the local level, of only one stimulus. In the first two blocks, unilateral stimuli were presented, while in the last two blocks bilateral stimuli were presented. Within blocks, the target appeared in the LVF and RVF equally often, and on the global and local level equally often, in a randomized manner. Before the start of the unilateral as well as the bilateral blocks, participants were given sixteen practice trials. Twelve of the participants completed 706 trials in a similar task using hierarchical figures, before starting this task. The results are no different for these participants than for the nine participants who only completed the HLT[2].

Effects of interest. The effects of interest were the RVF-local advantage in ERs (based on the original study's effect size of $d_z = .716$, we had 94% power to detect the effect with our sample size), and in RTs (original d_z = .557, 80% power), and the LVF-advantage for global processing in RTs (original d_z = -.835, 98% power).

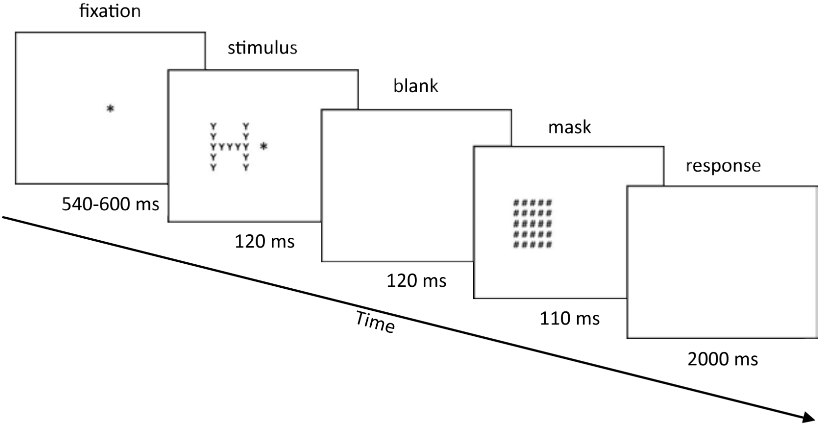

Figure 4. Timeline of a trial (unilateral presentation, global target) in the Hierarchical Letter Task.

Additional analyses. The only additional effect we examined was the LVF-advantage for global processing in ERs which was not found to be significant in the original study.

Differences with original study. Our version of the HLT is a partial replication of the original study (Yovel et al. 2001; experiment 1C), with slight changes regarding the stimuli and trial procedure. Specifically, we chose to replace the E and F of the original study by a T and H, because these are symmetric around the midline, thus preventing an asymmetric stimulus from causing different effects depending on the visual field of presentation. In the original experiment, level saliency of the stimuli was modulated by varying the global/local ratio (288 trials in total). As the equally salient stimuli were shown to produce more robust effects in the original study, we only used equally salient stimuli in our replication attempt (352 trials in total). In place of the manipulation of level saliency, we introduced two blocks using bilateral stimulus presentation, in addition to the unilateral stimulus presentation that the original study employed. We chose to include these blocks with bilateral stimuli because previous research (e.g., Boles, 1987) suggests that VFAs should be expected to be larger when both visual fields are stimulated. Thus, to increase our chance of producing VFAs with the HLT, we additionally included bilateral trials. Furthermore, the original study reported to have placed the local elements in a 3 x 5 grid, but we chose a 5 x 5 grid, because the N and Y could not be produced in a 3 x 5 grid. The original study used a 9 x 8 grid of small letters as a mask, but since no information was provided about the identity of the letters used for the mask, we used a 5 x 5 grid of hash tags. In the original study, the stimulus duration was 100 ms, and the duration of the mask was 1000 ms. Based on a pilot study we changed the durations of the stimuli and masks (see p. 35).

Results. As predicted, the VFAs were present during both unilateral and bilateral presentation blocks, but they were larger during bilateral presentation than during unilateral presentation (see Appendix A). To assess our success of replication, in the following analyses we take into account all trials, as this gives us the greatest degree of power to detect the VFAs.

Effects of interest. We replicated the RVF-advantage in local processing in ERs (BF_{10} = 26.8, t[20] = 3.36, p = .002, d_z = .733) (LVF: 27%, SD = 17%; RVF: 21%, SD = 18%), and in RTs (BF_{10} = 8.39, t[20] = 2.75, p = .006, d_z = .600) (LVF: 845 ms, SD = 134 ms; RVF: 805 ms, SD = 137 ms) (Figure 5). We replicated the LVF-advantage in global processing in RTs (BF_{10} = 409, t[20] = -4.69, p < .001, d_z = -1.023) (LVF: 741 ms, SD = 115 ms; RVF: 809 ms, SD = 150 ms).

Additional analyses. In ERs, we found substantial evidence for an LVF-advantage in global processing (BF_{10} = 237, t[20] = -4.43, p < .001, d_z = -.967) (LVF: 16%, SD = 9.7%; RVF: 24%, SD = 13%).

Combined evidence. When combining the results of the original and replication studies, there is decisive evidence for the presence of an RVF-advantage for local processing in ERs (BF_{10} = 329) and for the presence of an LVF-advantage for global processing in RTs (BF_{10} = 10,124). There is very strong evidence with regard to the RVF-advantage for local processing in RTs (BF_{10} = 40.7).

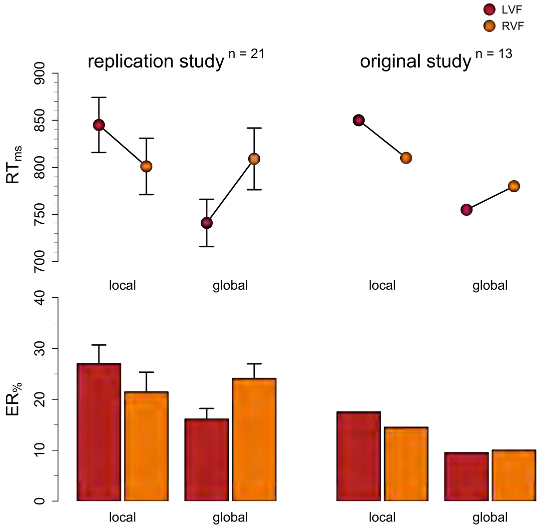

Figure 5. Error rates (lower panels) and reaction times (upper panels) of the replication (left panels) and original (right panels) studies' Hierarchical Letter Task. The means of the original study are estimated from the bottom-left panel of Figure 5 in Yovel et al. (2001, p. 1375). Error bars represent standard errors of the means.

Discussion. The outcome of this replication attempt of the HLT was successful as it yielded the expected behavioral manifestations of lateralized processing of global and local information. Specifically, our results were similar to those of the original study, in showing an RVF-advantage for local processing in both ERs and RTs, and in showing an LVF-advantage for global processing surfacing in RTs, and additionally in ERs. Accordingly, the meta-analytic Bayes factor also yielded strong support the presence of an RVF-advantage for local processing and an LVF-advantage for global processing, as measured with the HLT. It is of further interest that, in line with predictions (Boles, 1987; Hunter & Brysbaert, 2008), the VFAs were larger during the bilateral than the unilateral presentation blocks.

Picture Matching Task (PMT)

The idea that the two hemispheres differentially process high spatial frequencies (HSF) and low spatial frequencies (LSF) was first put forward by (Sergent, 1982c), who used the results in an HLT (see p. 34 for task description) to arrive at these conclusions. In 1992, Kitterle, Hellige, and Christman more directly tested the role of spatial frequencies by assessing VFAs in response to gratings, and reported that HSF gratings were more easily classified when presented in the RVF, whereas LSF gratings were more easily classified when presented in the LVF. As pointed out by Peyrin et al. (2003), much of the theory regarding lateralization of spatial frequency processing was based on studies using hierarchical stimuli, rather than on studies that explicitly demonstrated differing VFAs by manipulating the spatial frequency content of stimuli. One exception is the study by Kitterle et al. (1992), which used gratings to show an LVF-advantage for LSF processing and an RVF-advantage for HSF processing. However, these VFAs were found in only one of four task conditions, and the study used a sample of only 5 participants. Peyrin et al. (2003) introduced a Picture Matching Task (PMT) in which more complex stimuli were used than the gratings used by Kitterle et al. (1992). Using unfiltered and filtered images of natural scenes, Peyrin et al. successfully produced LVF-advantages for LSF processing and RVF-advantages for HSF processing (Peyrin et al., 2003; Peyrin, Chokron, et al., 2006). In addition, Peyrin, Mermillod, et al. (2006) showed that the time allowed for processing of the filtered stimuli affected the surfacing of the VFAs. Acknowledging the importance of processing time as a potential modulator of VFAs in spatial frequency processing, we attempted to replicate the 2006 study of Peyrin, Mermillod, et al.

Methods.

Participants. Thirty-one participants (15 women) performed the PMT. Their mean age was 21 years (range = 18-25).

Stimuli. The stimulus set comprised four black-and-white images of natural scenes (a city, a highway, a beach, and a mountain), two filtered versions of each of these images, and a backward mask. The HSF filtered images were created using a high-pass filter with a cut-off of 24 cycles per filter. The LSF filtered images were created using a low-pass filter with cut-off of 16 cycles per image. The size of the images was 4.8° x 4.8° of visual angle, and they were presented on a grey background at either the center of the screen, in the LVF, or RVF. When presented in the LVF or RVF, the inner edge of the image was positioned at a distance of 2° from the center. The mask contained a mean frequency typical of that of the set of natural scene images from which the stimuli had been selected (see Peyrin, Mermillod, et al., 2006).

Procedure. Each trial began with a centrally presented fixation point for 500 ms (Figure 6). Subsequently, one of the four unfiltered images (S1) was presented centrally. The S1 was presented for 30 ms or 150 ms, after which it was replaced by the mask, which remained on the screen for 30 ms. Immediately following the mask, a second image (S2) was presented for 100 ms. The S2 could be either an HSF or LSF filtered image of the S1, or of one of the other images, and was presented in the LVF or RVF. After 100 ms, the mask replaced the S2 and it was again shown for 30 ms. From the offset, participants had 2 s to indicate whether the S2 depicted the same natural scene as the S1. They did so by pressing two buttons simultaneously with their index fingers each time when they detected a match, as quickly as possible. They were instructed not to press any buttons on no-match trials. After the 2 s response interval the next trial started automatically.

The participants started the task with three practice blocks. First, they performed 32 trials in which the S2, like the S1, was an unfiltered image and presented centrally. Next, they performed 64 trials in which the S2 appeared either in the LVF or RVF, but was still an unfiltered image. The final practice block consisted of 64 trials during which the S2 again always appeared in the center of the screen, but was either an HSF or LSF filtered image[3]. After the practice blocks, participants completed four experimental blocks of 64 trials in each of the S1 duration conditions, with self-paced breaks between blocks. Within each block, HSF and LSF trials, and match and non-match trials, occurred equally often, and both types of trials were randomized. Half of the participants started with the 30 ms condition, followed by the 150 ms condition, and vice versa for the other half.

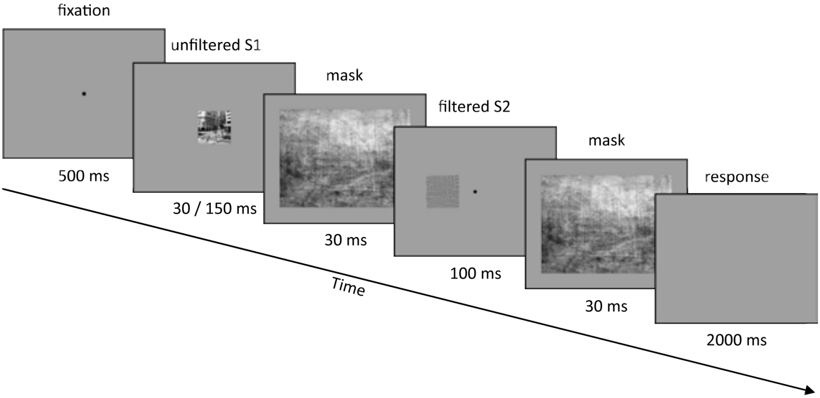

Figure 6. Timeline of a trial (high spatial frequency S2) in the Picture Matching Task.

Effects of interest. The four effects of interest all pertained to RTs. Specifically, the original study showed a LVF-advantage for LSF trials regardless of S1 duration (based on the original study's effect size of d_z = -1.06, we had more than 99% power to detect the effect with our sample size), and this effect was also found to be significant for each duration condition (short duration: d_z = -1.20, more than 99% power; long duration: d_z = -.647, 97% power). In addition, the original study found a significant RVF-advantage for HSF trials in the short duration condition only (original d_z = .615, 96% power).

Additional analyses. In addition to examining the above-mentioned effects of interest, we also analyzed the RVF-advantage for HSF trials in the long duration condition, and we also tested the significance of this VFA averaged across the two duration conditions, in RTs. Furthermore, we analyzed each of the six effects' counterparts in ERs.

Differences with original study. The PMT is a full replication of the original study (Peyrin, Mermillod, et al., 2006), as the first author of the original study shared the experiment E-Prime file and stimulus image files, which we adjusted for Dutch participants (the original included French instructions). The only difference between the original study and our replication study concerned the number of trials. In the original study, participants completed 256 trials in total. Because of the use of a go/no-go procedure, this amounted to 16 trials per condition for analysis. In our replication experiment, we chose to double the number of trials (Brysbaert & Stevens, 2018).

Results.

Effects of interest. We failed to replicate the LVF-advantage for LSF images in the short duration condition in RTs, indicated by substantial evidence against its presence in our data (BF_{10} = .116, t[30] = .78, p = .779, d_z = .140) (LVF: 674 ms, SD = 182 ms; RVF: 663 ms, SD = 146 ms) (Figure 7). For the long duration condition, our results were inconclusive with regard to the presence of this VFA (BF_{10} = .594, t[30] = -1.14, p = .132, d_z = -.205) (LVF: 581 ms, SD = 135 ms; RVF: 591 ms, SD = 131 ms), and the average across duration conditions likewise failed to produce convincing evidence for this VFA (BF_{10} = .789, t[30] = -1.36, p = .093, d_z = -.243) (LVF: 613 ms, SD = 120 ms; RVF: 622 ms, SD = 122 ms).

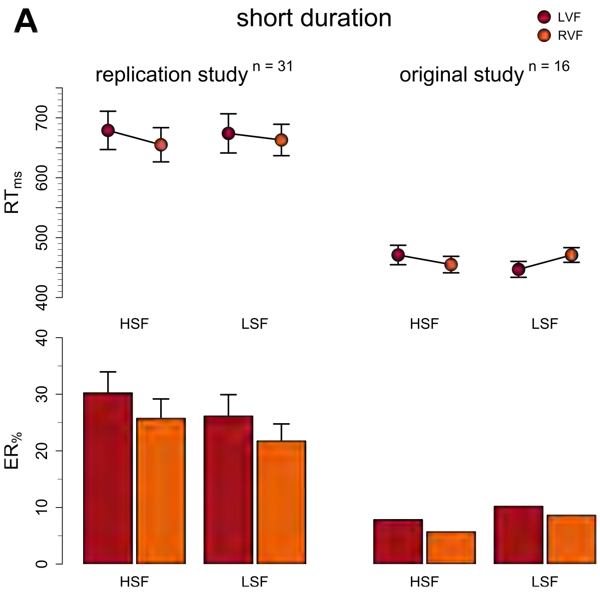

Figure 7. Continues on the next page.

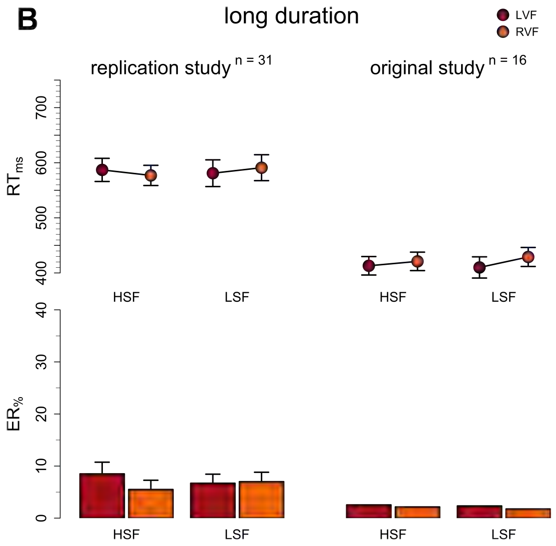

Figure 7. Error rates (lower panels) and reaction times (upper panels) of the replication (left panels) and original (right panels) studies' Picture Matching Task, of the results in the short S1 duration (30 ms) condition (A), and the results in the long S1 duration (150 ms) condition (B). The means of the original study are copied from Table 1 in Peyrin, Mermillod, et al. (2006, p. 128). Error bars represent standard errors of the means.

There was also indecisive evidence with regard to the RVF-advantage for HSF image processing in the short duration condition in RTs (BF_{10} = 1.30, $t[30] = 1.70$, $p = .050$, $d_z = .305$) (LVF: 679 ms, SD = 178 ms; RVF: 655 ms, SD = 159 ms).

Additional analyses. We did not find conclusive support for the presence of an RVF-advantage for HSF images in RTs, when combining the short and the long S1 conditions (BF_{10} = 3.03, t[30] = 2.20, p = .018, d_z = .395) (LVF: 623 ms, SD = 121 ms; RVF: 607 ms, SD = 110 ms), or when considering the long duration condition only (BF_{10} = .744, t[30] = 1.31, p = .100, d_z = .236) (LVF: 587 ms, SD = 117 ms; RVF: 577 ms, SD = 102 ms).

In the ER data of the replication study we found substantial evidence for an RVF-advantage for HSF image processing when combining the short and the long S1 duration conditions (BF_{10} = 5.97, $t[30] = 2.56$, $p = .008$, $d_z = .460$) (LVF: 19%, SD = 14%; RVF: 16%, SD = 12%), as well as in the long duration condition only (BF_{10} = 4.83, *t*[30] = 2.45, *p* = .010, d_z = .440) (LVF: 8.5%, SD = 13%; RVF: 5.5%, SD = 9.9%). In the short duration condition alone, the evidence for this VFA was inconclusive (BF_{10} = 1.29, *t*[30] = 1.69, *p* = .050, d_z = .304) (LVF: 30%, SD = 21%; RVF: 26%, SD = 19%). With regard to the LVF-advantages for LSF image processing in ERs, we found substantial evidence against the presence of this VFA when combining the short and the long S1 duration conditions (BF_{10} = .087, *t*[30] = 1.40, *p* = .915, d_z = .251) (LVF: 16%, SD = 12%; RVF: 14%, SD = 11%), in the short duration condition only (BF_{10} = .081, *t*[30] = 1.58, *p* = .938, d_z = .284) (LVF: 26%, SD = 21%; RVF: 22%, SD = 17%), and in the long duration condition only (BF_{10} = .230, *t*[30] = -.23, *p* = .411, d_z = -.041) (LVF: 6.7%, SD = 9.7%; RVF: 7.0%, SD = 10%).

Combined evidence. When combining the original and replication results, there is substantial evidence for an RVF-advantage for HSF processing in RTs in the short duration condition (BF_{10} = 9.04), but substantial evidence against the presence of this VFA in the long duration condition (BF_{10} = .230).

Combining the original and replication results further shows there to be strong evidence for the presence of an LVF-advantage for LSF processing in RTs (BF_{10} = 19.3), substantial evidence for this VFA in the long duration condition alone (BF_{10} = 3.52), and inconclusive evidence for this VFA in the short duration condition alone (BF_{10} = .592).

Discussion. We were not successful in replicating the expected VFAs for processing of high and low spatial frequencies using the task that was introduced by Peyrin et al. (2006). However, two LVF-advantages for LSF processing and one RVF-advantage for HSF processing were in the expected direction, and combining the evidence for these VFAs in meta-analytical Bayes factors (Rouder & Morey, 2011) resulted in at least substantial evidence for their presence. We additionally found evidence for an RVF-advantage for HSF processing that was not predicted based on the original study's results (Peyrin, Mermillod, et al., 2006), but could be expected based on the theory regarding lateralization of spatial frequency information.

Given the large difference between the original study's and replication study's effect sizes, and the larger error margin on the former than the latter, it seems likely that the effects in the original studies were an overestimation of the true effect sizes, which is not an uncommon problem in replication research (Anderson & Maxwell, 2015). Consequently, while the effects may in fact have been present, our study may not have had enough power to detect them. Furthermore, the notion that the LH is specialized in processing HSF information while the RH is specialized in processing LSF information is supported by neuroimaging data (for a review, see Kauffmann, Ramanoël, & Peyrin, 2014), which suggests that behavioral methods may be less sensitive to measure lateralized processing of this type of visual information, especially with a limited sample size.

Color Oddball Task (COT)

Using an oddball task, A.L. Gilbert et al. (2006) showed that participants were faster to detect colored targets when these had different color names than the distractors, supporting the notion of categorical perception for colors. Importantly, they found that this effect was only present for targets presented in the RVF. In contrast, participants were faster to detect colored targets that had the same name as the distractors, when these were presented in the LVF compared to the RVF. The authors concluded that language affects visual processing of colors in the RVF, but not in the LVF, and called this the 'lateralized Whorf effect'. Since the appearance of this paper, many more publications have followed, supporting and extending this finding (e.g., Daoutis, Pilling, & Davies, 2006; Drivonikou et al., 2007; Siok et al., 2009; but see Brown, Lindsey, & Guckes, 2011; Witzel & Gegenfurtner, 2011), but often using different tasks. We attempted to replicate the Color Oddball Task (COT) described in the original study of A.L. Gilbert et al. (2006; Experiment 2 (no-interference block)).

Methods.

Participants. Thirty-two participants (17 women) performed the COT. All participants had normal color vision, and their native language was either Dutch or German. Mean age was 20 years (range = 18-25).

Stimuli. The stimulus colors were chosen to resemble those used by A.L. Gilbert et al. (2006). We used two shades of green (G1 and G2), and two shades of blue (B1 and B2). The interstimulus distances in CIEL*a*b* space were ΔE = 4.6 for the G1-G2 pair, ΔE = 3.6 for the G2-B1 pair, and ΔE = 5 for the B1-B2 pair. A stimulus array consisted of a ring with a diameter of 8.5° of visual angle, of twelve 1° colored circles, presented on a grey background. Eleven of these circles had the same color, and one circle, the oddball, was colored differently. The oddball could appear in one of eight positions; four on the left and four on the right side of the ring. The two uppermost and two lowermost circles were never oddballs. The color of the oddball was either from the same category as the distractors (i.e., G1-G2, or B1-B2), or from a different category (i.e., G1-B1, G2-B1, or G2-B2).

Procedure. Each trial started with the presentation of a fixation cross, with presentation duration jittered between 800-1000 ms (Figure 8). With the fixation cross remaining on screen, the stimulus ring was presented for 200 ms. Next, a blank screen was presented during which participants could make their response; a left index finger button press if the oddball had appeared on the left side of the ring, and a right index finger button press if it had appeared on the right side of the ring. Participants were asked to respond as fast and accurately as possible. The next trial started after the participants' response, or after 5 s if no response was made.

Each of the oddball-distractor combinations and oddball-positions occurred equally often. Participants completed four blocks of 80 trials, and were allowed to take self-paced breaks between blocks. The experimental session started with a naming task to establish participants' green-blue lexical boundary, on which inclusion of their data in the analyses was based. In this task, one circle was presented centrally on a grey background, for 200 ms. Each of the four possible colors (G1, G2, B1 and B2) was presented ten times, in a randomized order. Participants were asked on each trial to indicate whether the colored circle had been green or blue, by pressing the G-key or B-key on a QWERTY-keyboard. They were not required to respond as fast as possible, but were encouraged to go with their first intuition. The lexical green-blue boundary was defined as the estimated value where blue would be reported half of the time. After the naming task, the participants were given 32 practice trials in the COT before the experimental trials started. Participants received all instructions in their native language.

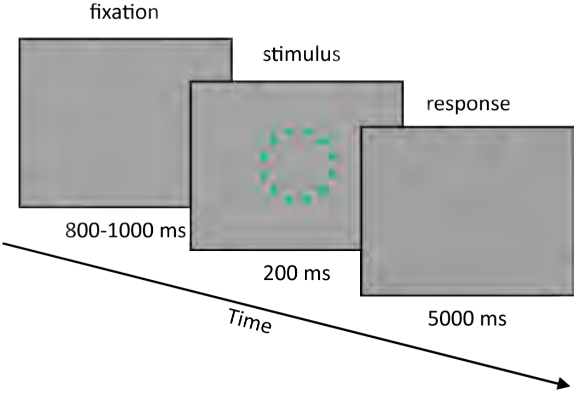

Figure 8. Timeline of a trial (between-category) in the Color Oddball Task.

Sixteen of the participants completed the SOT (see p. 51), before starting the COT, and vice versa for the other 16.

Effects of interest. The effects of interest were the RVF-advantage for between-category discrimination in RTs (based on the original study's (no-interference blocks) effect size of d_z = .742, we had 99% power to detect the effect with our sample size[4]), and the LVF-advantage for within-category discrimination in RTs (original d_z = -.684, power 97%).

Additional analyses. Additionally, we analyzed the two effects' counterparts in ERs.

Differences with original study. The COT is a partial replication of A.L. Gilbert et al.'s (2006) Experiment 2 (no-interference block). The replication experiment differs from the original study on a number of aspects. Firstly, the appearance of the stimuli in the replication study was not identical to that in the original study. Because A.L. Gilbert et al. did not report the specific color values in a way that makes them reproducible, the specific colors of the stimuli used in the replication experiment were likely different from the original color values. Furthermore, in the original study, the stimulus ring consisted of colored squares. However, since using squares leads to differences in the distance from the center to the inner edge of the stimulus depending on its position in the ring, we chose to use colored circles instead. Another possible difference with regard to the appearance of the stimuli is the size of the stimulus ring. Because A.L. Gilbert et al. do not report on its size in their 2006 paper, we chose to use the ring size that they report in their 2008 paper (A.L. Gilbert et al., 2008) on a variation of the oddball task using shapes (see p. 51)[5].

Secondly, in the original study participants completed on average 500 trials in an oddball task (250 of which in the no-interference block), and in the replication study participants completed on average 560 trials in an oddball task (320 of which in the COT). The exact number of trials depended on the order of the three task conditions in the original study, and on the ordering of the COT and SOT tasks[6] in the replication study.

Thirdly, we excluded the two uppermost and two lowermost positions in the ring as potential oddball positions. As it has been suggested that a strip of 1-3° along the vertical meridian of the visual field is projected bilaterally, rather than in a lateralized fashion (Bunt & Minckler, 1977; Jordan & Paterson, 2009; but see Ellis & Brysbaert, 2010), the stimuli in these positions are likely projected to both hemispheres. The COT is used with the assumption that the oddballs are projected to the hemispheres contralateral to the visual fields, rendering the uppermost and lowermost positions unsuitable oddball locations.

In the original study, the authors showed that a verbal interference task could disrupt the surfacing of VFAs. As the focus of these replication studies lies in the reproducibility of VFAs, we did not use any interference tasks, and relate our results only to the no-interference block of the original study.

Results. Three of the participants put the blue-green boundary between G1 and G2, and one put it between B1 and B2, and these participants' data were excluded from analyses. The remaining 28 participants (15 women) put the blue-green boundary between G2 and B1.

Effects of interest. We failed to replicate the LVF-advantage for within-category discrimination, as the evidence against the presence of this VFA was substantial ($BF_{10} = .077$, $t[27] = 1.89$, $p = .965$, $d_z = .357$) (LVF: 475 ms, SD = 71 ms; RVF: 463 ms, SD = 78 ms) (Figure 9). There was inconclusive evidence with regard to the RVF-advantage for between-category discrimination in RTs ($BF_{10} = .490$, $t[27] = .95$, $p = .176$, $d_z = .179$) (LVF: 441 ms, SD = 58 ms; RVF: 436 ms, SD = 66 ms).

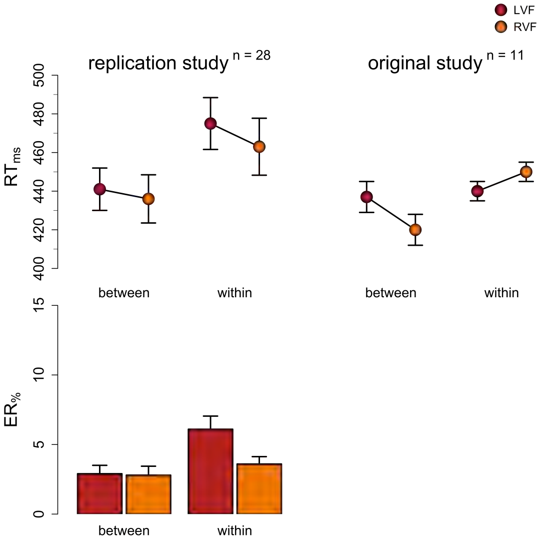

Figure 9. Error rates (lower panel) and reaction times (upper panels) of the replication (left panels) and original (right panel) studies' Color Oddball Task. The mean reaction times of the original study are estimated from Figure 2B in A.L. Gilbert et al. (2006, p. 491) (error rates were not reported for each of the conditions). Error bars represent standard errors of the means.

Additional analyses. In ERs, we found substantial evidence against the presence of an RVF-advantage for between-category discrimination (BF_{10} = .224, t[27] = .14, p = .445, d_z = .027) (LVF: 2.9%, SD = 3.2%; RVF: 2.8%, SD = 3.4%), and we found strong evidence against the presence of an LVF-advantage for within-category discrimination (BF_{10} = .054, t[27] = 3.41, p = .999, d_z = .644) (LVF: 6.1%, SD = 5.0%; RVF: 3.6%, SD = 2.8%). The latter effect indicates that participants in fact seemed to perform better on within-category discrimination when the oddball was presented in the RVF than when it was presented in the LVF.

Combined evidence. When combining the results of the original and replication studies, there is substantial evidence against the presence of an LVF-advantage for within-category discrimination (BF_{10} = .125), and inconclusive evidence regarding the presence of an RVF-advantage for between-category discrimination (BF_{10} = 1.87), in RTs.

Discussion. We did not succeed in replicating the lateralized Whorf effect for color perception. The combined evidence of the original and replication studies indicates evidence against the presence of an LVF-advantage for within-category discrimination, and the combined evidence is inconclusive with regard to the RVF-advantage for between-category discrimination. We will now consider whether the differences between the original and replication studies could account for the differences in results.

Although the original (A.L. Gilbert et al., 2006) and replication studies differed in the specific color values used, we do not consider this difference detrimental to the comparability of the results. First, while the exact color values may differ, we used the same selection criteria as the original study did, resulting in a color set with similar characteristics. Specifically, like in the original study, the colors formed two within-category pairs and one between-category pair, as confirmed by the naming task. Additionally, like in the original study, the colors' interstimulus distances in CIEL*a*b* space were larger for the within-category pairs than for the between-category pair, and participants' performance was worse for within-category discrimination than for between-category discrimination (see Appendix A). Second, the lateralized Whorf effect has previously been found with different color sets (Drivonikou et al., 2007; Roberson, Pak, & Hanley, 2008), and even with stimuli outside the color domain (A.L. Gilbert et al., 2008, see also p. 51). In sum, we do not consider differences in the exact color values to be a potential cause for the differences in results between the original and replication studies. While the shape of the stimuli may have affected their processing, we would expect this to have been the same for stimuli in the LVF and RVF, and as such not to have affected the VFAs.

The original study used on average 12% more trials than the replication study (COT and SOT combined). However, we showed that in the replication study, the order of the tasks, and hence, the number of completed trials in an oddball task, did not affect the VFAs for categorical color perception. A.L. Gilbert et al. (2006) also do not report that the order of tasks affected the VFAs in their experiment. We, therefore, do not regard this difference in the number of trials as a potential explanation for the differing results between the original and replication studies.

In conclusion, rather than lateralized categorical color perception, our replication study supports a general RVF-advantage for color discrimination (see also Appendix A). This RVF-advantage is, contrary to predictions, larger for within-category discrimination than for between-category discrimination, in ERs. This is in direct contrast to the results of A.L. Gilbert et al. (2006), who report an LVF-advantage for within-category discrimination, and has certain implications for the likeliness that there is lateralization of the influence of color categories on color discrimination. We return to this point in the General Discussion (p. 66).

Shape Oddball Task (SOT)

In 2008, A.L. Gilbert et al. showed that the lateralized Whorf effect generalized to stimuli other than colors. Specifically, they showed that categorical perception of cat and dog shapes produced an RVF-advantage for between-category discrimination, and an LVF-advantage for within-category discrimination. This study has been less influential than A.L. Gilbert et al.'s 2006 study, but given the important theoretical implications of a lateralized Whorf effect beyond the realm of colors, we chose to also attempt to replicate the Shape Oddball Task (SOT) (A.L. Gilbert et al., 2008; Experiment 1).

Methods.

Participants. Twenty-seven participants (14 women) who performed the COT also completed the SOT. Their mean age was 20 years (range = 18-25).

Stimuli. The two black shapes of dog figures and two black shapes of cat figures as used in the original study of A.L. Gilbert et al. (2008) were copied from their article. The radius of the stimulus ring was 8.5° of visual angle.

Procedure. The procedure of the SOT is identical to that of the COT (see p. 45) (Figure 10), with two exceptions. Firstly, the SOT used animal shapes instead of colored circles. All the stimulus shapes faced the center of the screen. There were four between-category pairs (combining a dog shape with a cat shape) and two within-category pairs (combining two dog shapes or two cat shapes). Secondly, participants completed 384 trials, which were divided over 4 blocks of 96 trials, and preceded by 32 practice trials. Participants were allowed to take self-paced breaks between blocks.

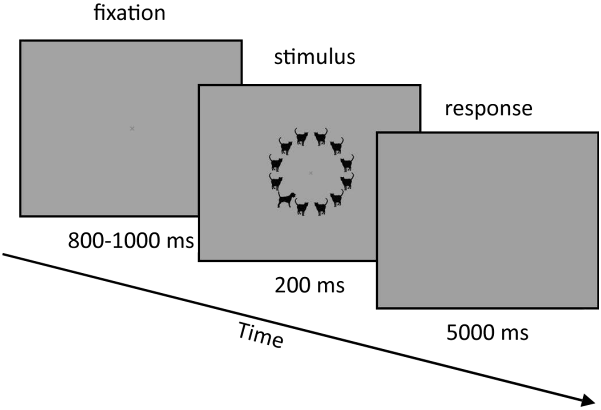

Figure 10. Timeline of a trial (between-category) in the Shape Oddball Task.

Thirteen of the participants completed the COT (see p. 45) before starting the SOT, and vice versa for the other 14 participants.

Effects of interest. The effects of interest were the RVF-advantage for between-category discrimination in RTs (based on the original study's effect size of $d_z = .525$, we had 83% power to detect the effect with our sample size[7]), and the LVF-advantage for within-category discrimination in RTs (original $d_z = -.6$, 91% power).

Additional analyses. We additionally investigated the effects of interests' counterparts in ERs.

Differences with original study. In the original study, the next trial would only start after the participant had made a response, but in the replication study we limited response time to 5 s (in 0.6% of the trials no response was recorded). Like in the COT, we did not use the two uppermost and lowermost positions in the ring as potential oddball locations. Finally, the original study used 864 trials, while participants in the replication study performed 585 trials on average in an oddball task (depending on whether they had started with the COT or the SOT[8], see section above on the COT).

Results. One participant regarded one cat shape as a dog, and this participant's data were excluded from the analyses. The remaining 26 participants (13 women) correctly categorized the cat and dog shapes.

Effects of interest. In RTs, we failed to replicate the LVF-advantage for within-category discrimination, finding substantial evidence against the presence of this VFA (BF_{10} = .126, t[25] = .79, p = .782, d_z = .155) (LVF: 758 ms, SD = 207 ms; RVF: 748 ms, SD = 206 ms) (Figure 11). Our data do not allow a conclusion to be drawn regarding the RVF-advantage for between-category discrimination (BF_{10} = .908, t[25] = 1.41, p = .085, d_z = .277) (LVF: 712 ms, SD = 174 ms; RVF: 698 ms, SD = 180 ms).

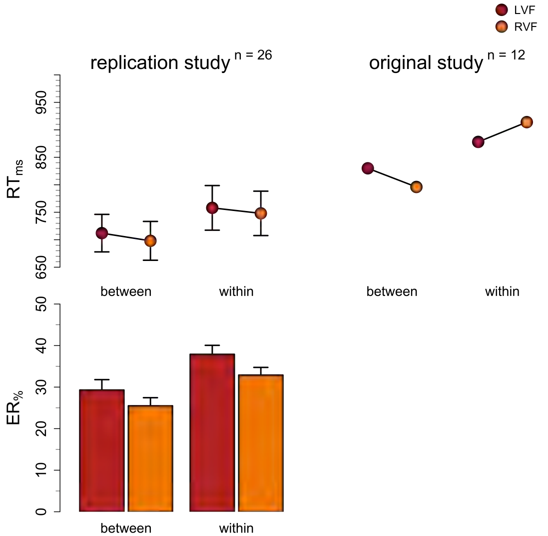

Figure 11. Error rates (lower panel) and reaction times (upper panels) of the replication (left panels) and original (right panel) studies' Shape Oddball Task. The mean reaction times of the original study are estimated from the bottom-left panel of Figure 4 in A.L. Gilbert et al. (2008, p. 93) (error rates were not reported for each of the conditions). Error bars represent standard errors of the means.

Additional analyses. In ERs, we found strong evidence against the presence of an LVF-advantage for within-category discrimination (BF_{10} =

.087, t[25] = 1.65, p = .944, d_z = .324) (LVF: 38%, SD = 12%; RVF: 33%, SD = 10%). The evidence was inconclusive with regard to an RVF-advantage for between-category discrimination in ERs (BF_{10} =. 774, t[25] = 1.29, p = .104, d_z = .253) (LVF: 29%, SD = 14%; RVF: 26%, SD = 11%).

Combined results. When taking the original and replication studies' results together, there is substantial evidence against the presence of an LVF-advantage for within-category discrimination (BF_{10} = .243), and inconclusive evidence regarding an RVF-advantage for between-category discrimination (BF_{10} = 2.75), in RTs.

Discussion. We were not able to replicate the lateralized Whorf effects using animal shapes as stimuli. The combined evidence of the original and replication studies indicates evidence against the presence of an LVF-advantage for within-category discrimination, and the combined evidence is inconclusive with regard to the RVF-advantage for between-category discrimination. We will now consider whether the differences between the original and replication studies could account for the differences in results.

In the original study, participants had unlimited time to make their response, while in the replication study we chose to shorten this interval to 5 s. As a result, in the former a response was always recorded, while in the latter 'misses' occurred, in 0.6% of the trials. Although participants in the replication study almost never failed to respond, they did produce a higher number of errors (mean 30%) than participants in the original study (mean 5.6%). While participants in the original study did receive instructions to respond as quickly as possible, the fact that they had unlimited time to respond may have resulted in their putting more weight on accuracy than on speed. In comparison, participants in the replication study may have put more weight on a speedy response, to the detriment of accuracy. Support for this can be seen in the RTs, which are on average lower in the replication study than in the original study (Figure 9). However, given that ERs are the most informative measure when they are relatively high (Hellige & Sergent, 1986), the effects of interest could have been expected to surface in ERs, which was not the case.

Because we chose to combine the COT and SOT in one test session, we limited the number of trials in the SOT to 384 trials. This, however, is only about half the number of trials participants performed in the original study. As a result, we may have had less power to detect the RVF-advantage for between-category discrimination than we calculated based on the original study's effect size and our number of participants. In combination with the Bayes factors indicating that there was inconclusive evidence with regard to the presence of this RVF-advantage in RTs and ERs, we cannot rule out the possibility that the RVF-advantage for between-category discrimination would have been found, had our replication study used more trials. In contrast, as the Bayes factors indicated a sufficient amount of evidence against the presence of an LVF-advantage for within-category discrimination in ERs and RTs, we can be certain that the failure of replicating this effect is not due to the diminished number of trials in the replication study.

In conclusion, the results we found in our replication of the SOT are similar to those of our replication of the COT. We were not able to replicate the RVF-advantage for between-category discrimination, but in the case of the SOT, this may have been a consequence of low power. In addition, we failed to replicate the LVF-advantage for within-category discrimination. We will reflect further on the likeliness that there is a lateralized influence of shape categories on shape discrimination in the General Discussion (p. 68).

Cross-dot Matching Task (CMT)

Kosslyn proposed that the two hemispheres are lateralized with regard to two different types of spatial relation processing (Kosslyn, 1987). For example, a categorical spatial relation judgment (e.g., "the ball is to the right of the table") is more easily made when the stimulus is presented in the RVF, and a coordinate spatial relation judgment (e.g., "the ball is one meter away from the table") is more easily made when the stimulus is presented in the LVF (for reviews, see Jager & Postma, 2003; Laeng, Chabris, & Kosslyn, 2003). The task predominantly used to study lateralization of spatial relation processing is the bar-dot task (Hellige & Michimata, 1989; Kosslyn et al., 1989). However, Van der Ham, van Wezel, Oleksiak and Postma (2007) identified and attempted to overcome two drawbacks of this widely used bar-dot task.

Firstly, in bar-dot tasks, participants show a training effect over trials, resulting in categorization of the coordinate task condition into different categories of nearness. Secondly, the categorical condition of the bar-dot task seemed to be less difficult than the coordinate task condition. Consequently, Van der Ham et al. (2007) reasoned, the possibility that the VFAs had been caused by differences in difficulty between the conditions could not be ruled out. To overcome these problems, Van der Ham et al. (2007) introduced an alternative task to study lateralization of categorical and coordinate spatial relation processing, making use of cross-dot configurations. We chose to replicate the Cross-dot Matching Task (CMT) that includes a self-rating of spatial strategy (Van der Ham & Borst, 2011), as with this study the authors showed that individual differences in spatial strategy can affect the found VFAs.

In the course of this replication attempt, Van der Ham and Borst published a corrigendum to their original research article (2016). This corrigendum stated that a coding error had occurred in the analyses that were reported in the original article. The originally reported VFAs largely disappeared when these errors were corrected for. Nevertheless, we decided to report the outcomes of the replication study here, and we relate our results to the corrected results as reported in the 2016 corrigendum.

Methods.

Participants. Thirty-four participants (17 women) performed the CMT. Their mean age was 21 years (range = 18-28).

Stimuli. The first stimulus (S1) consisted of a centrally presented plus sign (the 'cross' of the cross-dot stimulus) of 0.35° degrees of visual angle, and a dot of 0.15°. The dot could appear at one of forty fixed positions, in relation to the cross. The second stimulus (S2) could either be a match or a non-match to the S1. In the categorical task, a match was defined as the dot appearing in the same quadrant (upper left, upper right, lower left and lower right, with regard to the cross) as the dot in the S1. In the coordinate task, a match was defined as the dot appearing in the same radius (inner ring, first ring, second ring, or outer ring, with regard to the cross) as the dot in the S1. The stimuli and fixation cross were presented in black on a white background, and the inner edge of the S2 was 2.5° from the center.

Procedure. A grey screen lasting 500 ms signaled the start of the new trial, after which a fixation cross was presented for 500 ms (Figure 12). Next, the S1 was presented for 150 ms, followed by a black screen for 1500 ms. Following another fixation cross for 500 ms, the S2 was presented in the LVF or RVF for 150 ms. After this, a black screen appeared and participants had 2 s to make their response. Participants were asked to indicate whether the S1 and S2 were a match or non-match, by pressing one of two buttons with the index or middle finger of their right hand, as fast and accurately as possible. Finger-response mappings were counterbalanced over participants. During the instructions, it was stressed that participants should take into account the position of the dot relative to the cross, and not take into account the positioning of the cross-dot configuration on the screen.

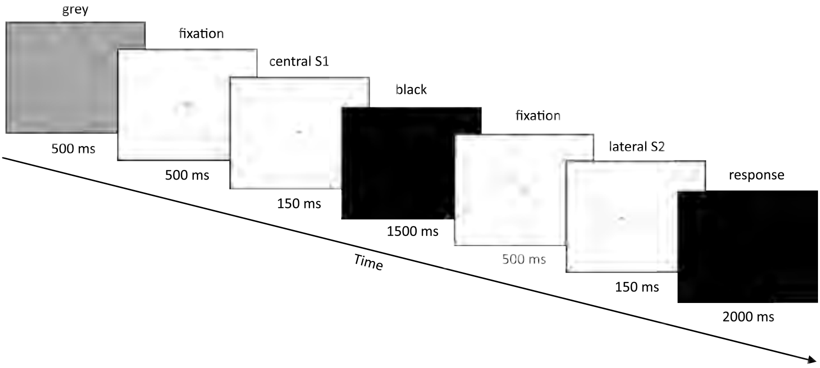

Figure 12. Timeline of a trial in the Cross-dot Matching Task.

Participants completed four blocks of 40 trials in both the categorical and the coordinate task, and each task was preceded by eight practice trials during which participants received feedback on their performance. Match and non-match trials, and LVF and RVF presentations occurred equally often, in a randomized manner. The ordering of the categorical and coordinate tasks was counterbalanced over participants.

At the end of the experiment, participants filled out a questionnaire about the strategy they had used during CMT performance. Participants were asked to rate the degree to which they had used a spatial strategy in the categorical and coordinate tasks, on a seven-point Likert scale.

Effects of interest. The original VFAs that we initially considered to be the effects of interest did not all survive the corrected analyses as reported in Van der Ham and Borst's corrigendum (2016). We relate our results to the effects reported in the corrigendum. Consequently, we had less than 80% power to detect the adjusted effects of interest.

Based on the surviving effects as reported in the corrigendum (2016), the effects of interest became the RVF-advantage for categorical processing in the high spatial strategy group in ERs (based on the original study's effect size of $d_z = .421$, we had 51% power detect the effect with our sample size[9]), the LVF-advantage for categorical processing in the low spatial strategy group in ERs (original $d_z = -.528$, 70% power), the LVF-advantage for coordinate processing in the high spatial strategy group in ERs (original $d_z = -.417$, 50% power) and in the group as a whole ERs (original $d_z = -.304$, 54% power), and the RVF-advantage for coordinate processing in the group as a whole in RTs (original $d_z = .251$, 42% power).

For the analyses, the participants were divided into two groups based on their median scores on the spatial strategy questionnaire, as in the original study (Van der Ham & Borst, 2011).

Additional analyses. In addition, we analyzed the remaining contrasts using the expected directions of the VFAs based on the theory regarding lateralized processing of categorical and coordinate spatial processing (i.e., not based on the unexpected reversed asymmetries found by Van der Ham and Borst (2016)). This resulted in the analyses of the RVF-advantage for categorical processing in the group as a whole, in ERs and RTs, and in the high and low spatial strategy groups in RTs. With regard to coordinate processing, we analyzed the LVF-advantage in the low spatial strategy group in ERs, and this VFA in both high and low spatial strategy groups in RTs.

Differences with original study. The CMT is a full replication of the original study (Van der Ham & Borst, 2011; Van der Ham & Borst, 2016), with the exception of the number of trials. The original study used a selection of 80 of the 160 possible cross-dot configurations, each participant receiving the same fixed-order selection. In the replication attempt, we doubled the number of trials, so that each participant received all possible cross-dot configurations. For each participant, a new randomization of trial order was used. The first author of the original study shared the experiment E-Prime file and stimulus image files.

Results.

Effects of interest. We failed to replicate the RVF-advantage for categorical processing in the high spatial strategy group in ERs (BF_{10} = .238, t[16] = -.06, p = .523, d_z = -.014) (LVF: 21%, SD = 17%; RVF: 21%, SD = 18%) (Figure 13). In addition, our data were inconclusive regarding the replication of the LVF-advantage for categorical processing in the low spatial strategy group in ERs (BF_{10} = .460, t[16] = -.71, p = .245, d_z = -.171) (LVF: 14%, SD = 10%; RVF: 15%, SD = 11%).

We failed to replicate the LVF-advantage for coordinate processing in ERs in the high spatial strategy group (BF_{10} = .326, *t*[16] = -.34, *p* = .370, d_z = -.082) (LVF: 29%, SD = 8.6%; RVF: 30%, SD = 10%), and in the group as a whole (BF_{10} = .221, *t*[33] = -.23, *p* = .409, d_z = -.040) (LVF: 30%, SD = 8.4%; RVF: 30%, SD = 9.4%). We failed to replicate the RVF-advantage for coordinate processing in the group as a whole in RTs (BF_{10} = .102, *t*[33] = -.95, *p* = .826, d_z = -.163) (LVF: 674 ms; SD = 134 ms; RVF: 681 ms, SD = 145 ms).

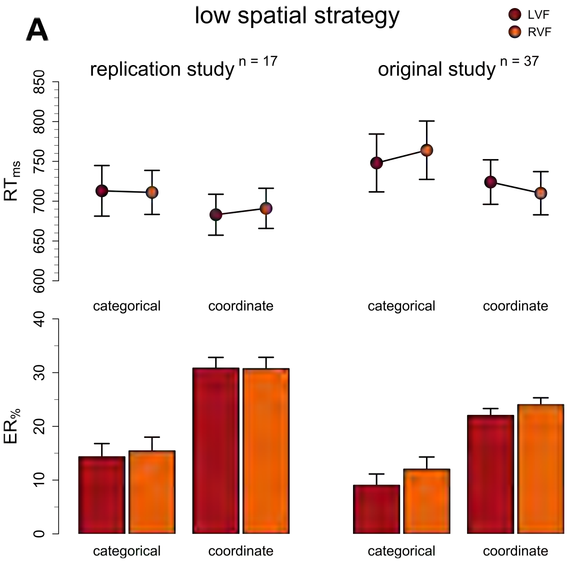

Figure 13. Continues on the next page.

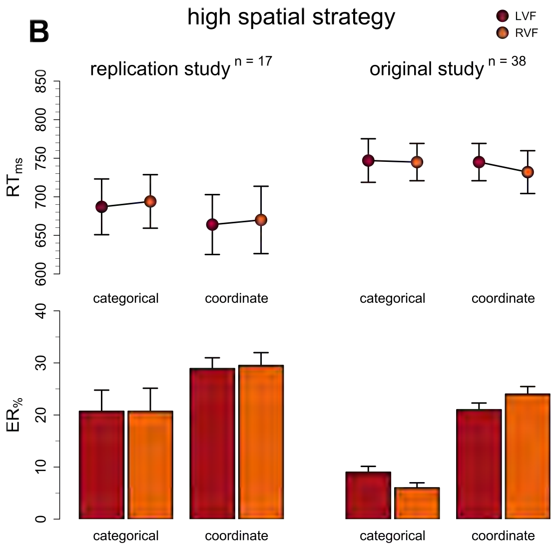

Figure 13. Error rates (lower panels) and reaction times (upper panels) of the replication (left panels) and original (right panels) studies' Cross-dot Matching Task, with the results of the participants in the low spatial strategy group (A), and the results of the participants in the high spatial strategy group (B). The means of the original study are copied from Table 2 in Van der Ham & Borst (2016, p. 41). Error bars represent standard errors of the means.

Additional analyses. We found substantial evidence against the presence of RVF-advantages for categorical processing in ERs in the group as a whole (BF_{10} = .123, t[33] = -.60, p = .722, d_z = -.102) (LVF: 18%, SD = 14%; RVF: 18%, SD = 15%), in RTs in the group as a whole (BF_{10} = .145, t[33] = -.33, p = .629, d_z = -.057) (LVF: 700 ms, SD = 139 ms; RVF: 702 ms, SD = 128 ms), in RTs in the high spatial strategy group (BF_{10} = .153, t[16] = -.79, p = .779, d_z = -.191) (LVF: 687 ms, SD = 149 ms; RVF: 694 ms, SD = 143 ms), and in RTs in the low spatial strategy group (BF_{10} = .202, t[16] = .30, p = .618, d_z = .074) (LVF: 713 ms, SD = 131 ms; RVF: 711 ms, SD = 114 ms). Furthermore, we found substantial evidence against the presence of an LVF-advantage for coordinate processing in ERs in the low spatial strategy group (BF_{10} = .240, t[16] = .05, p = .520, d_z = .013) (LVF: 31%, SD = 8.4%; RVF: 31%, SD = 8.9%), and inconclusive evidence for this VFA in RTs in the low spatial strategy group (BF_{10} = .448, t[16] = -.68, p = .254, d_z = -.164)

(LVF: 683 ms, SD = 106 ms; RVF: 691 ms, SD = 104 ms) and the high spatial strategy group (BF_{10} = .441, t[16] = -.66, p = .259, d_z = -.161) (LVF: 664 ms, SD = 160 ms; RVF: 670 ms, SD = 180 ms).

Combined evidence. When combining the original and replication studies' results, there is strong evidence for an LVF-advantage for categorical processing in ERs in the low spatial strategy group (BF_{10} = 15.1), and inconclusive evidence for an RVF-advantage for categorical processing in the high spatial strategy group in ERs (BF_{10} = 1.87). However, there is strong evidence against the presence of an RVF-advantage for categorical processing in the group as a whole in ERs (BF_{10} = .098) and RTs (BF_{10} = .048).

There is inconclusive evidence with regard to the LVF-advantage for coordinate processing in ERs in the high spatial strategy group (BF_{10} = 3.10), and in the low spatial strategy group (BF_{10} = .351). In the group as a whole, there is inconclusive evidence with regard to the RVF-advantage in coordinate processing in RTs (BF_{10} = .412), and with regard to the LVF-advantage for coordinate processing in ERs (BF_{10} = 2.60). We must note that in the corrigendum, the reported degrees of freedom are not in line with the reported sample sizes[10], so we cannot be certain that the calculated Bayes factors are exact.

Discussion. We were not able to replicate any of the original study's VFAs. Instead, we found substantial evidence against the presence of eight of the VFAs, and inconclusive evidence regarding the other four VFAs. Of note is the fact that when we combined the results of the original and replication studies, we found substantial evidence for the existence of one VFA which was opposite from what we would expect based on Van der Ham and Borst's (2011) predictions. Furthermore, in our replication attempt, the spatial strategy used by the participant did not affect the results as predicted.

The fact that the replication study had low power to detect the effects of interest cannot be claimed to have caused the difference in results, as eight of the twelve Bayes factors indicated at least substantial evidence against presence of the VFAs, reflecting that the amount of data was sufficient to support these null hypotheses.

In considering the possible reasons for why our replication study did not replicate the effects found by Van der Ham and Borst (2016), a first possibility might be the fact that we used double the number of trials compared to the original study. To examine whether this may have influenced the results, we repeated the analyses on only the first half of the trials (resulting in 18 participants' categorical blocks and 16 participants' coordinate blocks). The *p*-values and Bayes factors of the effects of interest remained qualitatively unchanged, with the exception two effects in the low spatial strategy group whose evidence for their absence as reflected by the Bayes factors changed from substantial to inconclusive (coordinate processing ERs all trials included: $BF_{10} = .240$; first half of trials: $BF_{10} = .440$; categorical processing RTs all trials included: $BF_{10} = .202$; first half of trials: $BF_{10} = .502$), and for one effect in the high spatial strategy group with the evidence for its absence changing from inconclusive to substantial (coordinate processing ERs all trials included: $BF_{10} = .326$; first half of trials: $BF_{10} = .243$). These relatively unchanged results indicate that the failure of replication of the original results cannot be attributed to the fact that the replication study included more trials.

It remains possible that the differences in selection and randomization of the cross-dot configurations between the original and replication studies caused the differences in results. However, if this were the case, this would imply that the originally found effects depended solely on the sub-set of configurations, and/or their specific order.

We consider it noteworthy that in Van der Ham & Borst's 2016 corrigendum there seems to be a speed-accuracy trade-off for coordinate processing, with an LVF-advantage for this VFA in ERs, but an RVF-advantage in RTs. As such, their data do not seem to support the existence of an LVF-advantage for coordinate processing, as measured by the CMT.

In conclusion, we do not consider the study of Van der Ham and Borst (2016) a strong case for categorical and coordinate lateralized processing, and in that sense the findings of the replication study are in concordance with those reported in the original study's 2016 corrigendum. Based on these results, we conclude that if lateralization of categorical and coordinate spatial relation processing exists, the CMT does not seem to be an adequate task to study them. Alternatively, these results may be taken to suggest that there is low evidence for lateralization of categorical and coordinate spatial relation processing. We return to this point in the General Discussion (p. 68).

Landmark Task (LT)

Observers have a tendency to view the left side of space as being larger than the right side of space, an LVF-bias referred to as 'pseudoneglect' (Bowers & Heilman, 1980), which has been associated with RH-specialization for visuo-spatial attention (Çiçek, Deouell, & Knight, 2009; Zago et al., 2015; Ocklenburg & Güntürkun, 2018). Over the years, pseudoneglect has been studied in several modalities and with a variety of tasks. A review and meta-analysis by Jewell and McCourt (2000) reported that tasks using limited viewing time and a forced-choice response, such as the Landmark Task (LT), produce larger effect sizes than the more often used method-of-adjustment, or line bisection procedures. Manly, Dobler, Dodds and George (2005) devised a computerized version of the LT, after which Linnell et al. (2014) modeled their LT. Given that Linnell et al.'s description of the methods allowed for a full replication attempt, we performed a replication of their study (subsample of British participants).

Methods.

Participants. Forty-three participants (21 women) performed the LT. Their mean age was 22 years (range = 18-31).

Stimuli. A stimulus consisted of a horizontal line of 18.8° of visual angle, presented in black on a white background. The line was transected by a vertical line of 0.8°, positioned at -1.2°, -0.8°, -0.4°, 0.0°, +0.4°, +0.8°, or +1.2° from the midpoint. This resulted in seven conditions: three in which the left part was longer than the right, three in which the right part was longer than the left, and one with equally long left and right parts. Stimuli were equally often presented centrally, or jittered 1.1° to the right or left of the center. The mask consisted of a horizontal line, subtending from the far left to the far right of the screen, with 85 transecting lines across the length of the horizontal line, spaced 0.4° apart.

Procedure. A trial began with the presentation of the stimulus for 1000 ms (Figure 14). After a blank screen of 100 ms, the mask was presented for 1000 ms, followed by another blank screen for 1000 ms. Participants were instructed to indicate which part of the horizontal line was longer; the part left of the transection or right of the transection. The participants responded by pressing the F-key or H-key on a QWERTY-keyboard, using their left or right index finger, respectively. They could make their response from the moment of stimulus presentation to the end of the trial. They were not required to respond as fast as possible, but were asked to respond before the end of the trial.

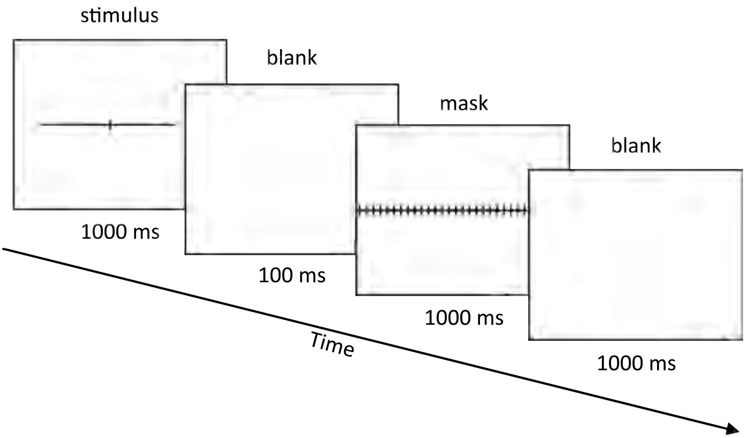

Figure 14. Timeline of a trial in the Landmark Task.

Each transection position occurred 12 times, resulting in a total of 84 trials. Participants were not informed that in one seventh of the trials the line was transected exactly in the middle. Before the experimental task started, participants were given ten practice trials with transections at -1.4° and +1.4°, as seen from the midpoint.

Effects of interest. The effect of interest was whether participants showed an LVF-bias in that they judged the midpoint of the line to be to the left of the veridical midpoint. To assess this, each participant's point of subjective equality (PSE) was derived by finding his or her threshold for deciding that the right part of the line was longer than the left part (Linnell et al., 2014). PSEs are expressed in deviation from the veridical center, in degrees of visual angle. Based on the original study's (British participants) effect size of $d_z = -.361$, we had 75% power to detect this visual field bias with our sample size[11]. No additional analyses were planned.

Differences with original study. The LT was a full replication of the study by Linnell et al. (2014). The stimuli and procedure were identical to those of the original study.

The original study compared pseudoneglect between a group of British participants and a group of Himba participants, to investigate the effect of urbanization on spatial attention distribution. Our replication relates only to the British participant group of the original study.

Results. We replicated the original study's LVF-bias ($BF_{10} = 7.66$, $t[42] = -2.68$, $p = .005$, $d_z = -.409$) (PSE = -.08, SD = .19). When combining the original and replication studies, there is decisive evidence in favor of the presence of an LVF-bias ($BF_{10} = 160$).

Discussion. The results of this replication attempt yield behavioral support for the existence of a lateralized distribution of spatial attention. Specifically, we found substantial evidence for an LVF-bias in spatial attention in our replication attempt and the original and replication studies combined provide decisive evidence for the lateralization of spatial attention distribution.

Lexical Decision Task (LDT)

LH-lateralization for language was the first described instance of hemispheric specialization of the human brain, and is now considered to be one of the most reliably lateralized processes (Hugdahl, 2000). A multitude of ways to study language lateralization has accumulated over the years (e.g., lesion studies, assessing the ear advantage in dichotic listening, neuroimaging combined with word fluency tests), but the Lexical Decision Task (LDT) is an often used way to study lateralization of written language (e.g., Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Hellige & Yamauchi, 1999). The aim of the study by Willemin et al. (2016) was to devise an LDT that could be used in five different languages (French, German, Italian, English, Dutch), and to test it in a French-speaking population. The current replication attempt investigates the reproducibility of the original VFAs in Willemin et al.'s study, in a Dutch-speaking population.

Methods.

Participants. Forty-eight native Dutch speakers (39 women) performed the LDT. Their mean age was 20 years (range = 17-28).

Stimuli. The international word and non-word set described in Willemin et al. (2016) was used in the LDT. This set comprises sixteen 4-, 5- or 6-letter words, which are meaningful in Dutch, German, English, French and Italian. Pseudowords, created by changing two letters from each of the words, were coupled to the words, resulting in sixteen word/non-word pairs. In addition, sixteen non-word/non-word pairs were used. The size of the letter strings was on average 3° of visual angle, the inner edge presented 2° from the center. The height of the stimuli was 0.5°. The letters were presented in Courier New (12 point), in black on a white background.

Procedure. A trial started with the presentation of a fixation cross at the center of the screen, for 1000 ms (Figure 15). Next, the stimulus pair followed, with one letter string in the LVF and the other in the RVF, for 100 ms. After the stimulus pair, a blank screen followed, and participants had 2 s to respond. Participants were required to indicate whether they had seen a meaningful word on the left side, on the right side, or not at all. They did so by pressing the F-key with their left index finger, the J-key with their right index finger, or the space bar with both thumbs, respectively. Participants were asked to respond as quickly and accurately as possible.

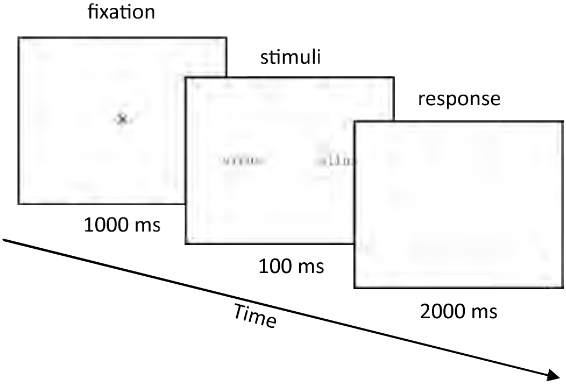

Figure 15. Timeline of a trial in the Lexical Decision Task.

The word/non-word pairs and non-word/non-word pairs were presented in an LVF-RVF and RVF-LVF configuration, four times each. This resulted in a total of 256 trials, which were presented in randomized order. Participants completed these trials in two blocks, with a self-paced break in between.

Effects of interest. The effects of interest were the RVF-advantage in ERs (based on the original study's effect size of $d_z = .88$, we had more than 99% power to detect the effect with our sample size), and the RVF-advantage in RTs (original $d_z = .559$, 99% power). No additional analyses were planned.

Differences with original study. The LDT was a full replication of the original study, with the exception of the native language of the participants. The original experiment DMDX-file was shared by the authors of the original study. As such, stimuli and procedure were identical to that of the original study, but with instructions in Dutch.

The original study examined influences of handedness, sex and multilingualism of the participants on the VFAs, but found no differences between the groups. For this reason, with the replication study we did not address these aspects.

Results. We replicated the RVF-advantage for visual word processing in RTs ($BF_{10} = 282$, $t[47] = 4.08$, $p < .001$, $d_z = .589$) (LVF: 708 ms, SD = 98 ms; RVF: 658 ms, SD = 80 ms), and in ERs ($BF_{10} = 7{,}260{,}758$, $t[47] = 7.26$, $p < .001$, $d_z = 1.05$) (LVF: 36%, SD = 15%; RVF: 19%, SD = 11%) (Figure 16). When combining the original and replication results, there is decisive evidence for the presence of an RVF-advantage in visual word processing in RTs ($BF_{10} = 247{,}259{,}539$) and ERs ($BF_{10} = 1.113278{+}19$).

Discussion. The results of this replication yield behavioral manifestations of, and thus support the existence of, lateralized processing of visually presented words. Specifically, we replicated the original RVF-advantages in ERs and RTs, in a group of native Dutch-speaking participants. Combining the results of the original and replication studies indicated that there is decisive evidence for lateralization of visual word processing.

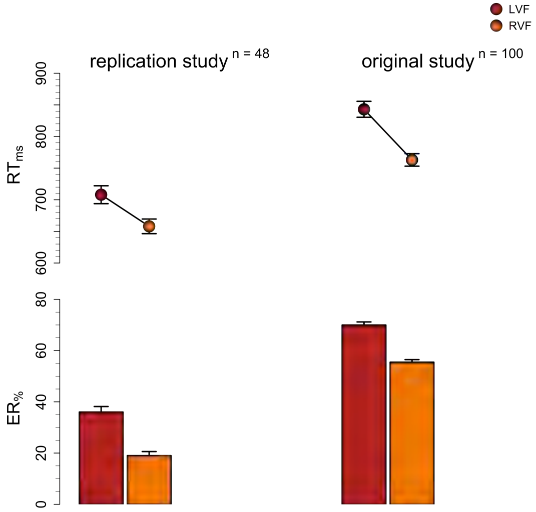

Figure 16. Error rates (lower panels) and reaction times (upper panels) of the replication (left panels) and original (right panels) studies' Lexical Decision Task. The means of the original study are copied from Table 1 in Willemin et al. (2016, p. 10). Error bars represent standard errors of the means.

General discussion

Accurate characterization of hemispheric specialization and the resulting instances of lateralized processing of sensory information is critical to our understanding of how the human brain functions. By allowing for tightly controlled manipulations in powerful within-subject designs, behavioral studies can provide an essential contribution to our understanding of such hemispheric specialization. Importantly, however, a key requirement for such studies to be useful is that they reliably demonstrate differences in behavior or performance when visual targets of a certain type appear in either the left (LVF) or the right (RVF) visual field. In the current study, we took a rigorous empirical and statistical approach in investigating the reliability of a large number of previously found visual field asymmetries (VFAs) by means of a series of replication studies.

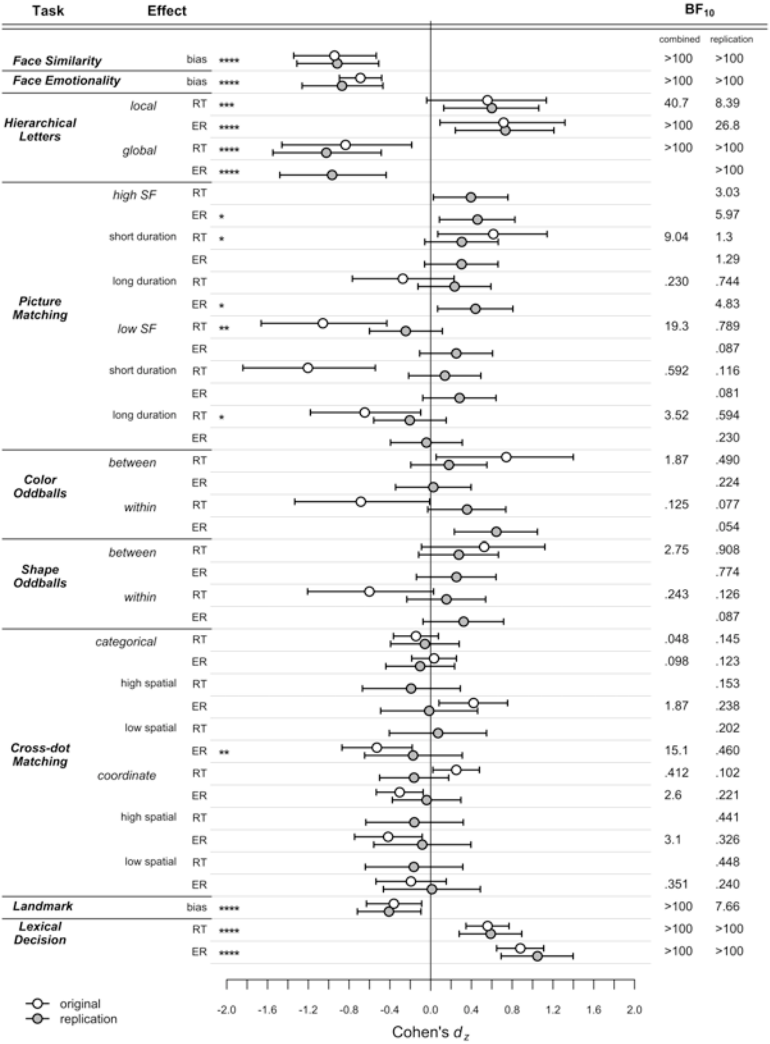

Figure 17. Overview of all original (white) and replication (grey) studies' effect sizes (Cohen's d_z). Error bars indicate 95% confidence interval of the effect size. In the two rightmost columns the Bayes factors of the replication study and the meta-analytical Bayes factors are presented. Asterisks to the left of the effect sizes indicate that either or both of those Bayes factors reflect there to be substantial (*), strong (**), very strong (***), or decisive (****) evidence for the presence of the expected visual-field symmetry.

Summary of results and methodological implications

An overview of our findings can be found in Figure 17. This figure shows the effect sizes and confidence intervals for a total of 41 putative VFAs that could be tested in the nine experiments we included in our replication studies (grey datapoints). In addition, Figure 17 shows for which of these effects the original studies reported the outcomes of a statistical analysis, and it illustrates the outcomes of these statistical analyses in terms of the resulting estimates of effect sizes and their confidence intervals (white datapoints). Moreover, Figure 17 also includes the Bayes factors for the effects we obtained in our replication studies and for our tests of the combined evidence from the original and replication studies, for those cases for which this computation was possible[12]. In interpreting these results, the Bayes factors can be considered to provide an index of the likelihood of the presence of a particular VFA, while the effect sizes and their confidence intervals provide insight into how strong these effects have been estimated to be, and how confident we can be about the precision of these estimates.

In evaluating the evidence depicted in Figure 17, a number of observations can be made. To start, there are five tasks that stand out in terms of producing precise, reliable evidence for moderate to strong effects of lateralization on performance, namely the Face Similarity Task (FST), the Face Emotionality Task (FET), the Hierarchical Letter Task (HLT), the Landmark Task (LT), and the Lexical Decision Task (LDT). Specifically, the FST and the FET yielded clear evidence for an LVF-advantage in perceptual judgments of faces and their emotional expressions. The results of the HLT showed LVF- and RVF-advantages for the processing of global and local levels of hierarchical letters, respectively. Regarding the HLT, it is of note that although the outcomes of the Bayesian analyses produced strong evidence in favor of the presence of the predicted lateralization effects, the confidence intervals were relatively large, and the estimates, therefore, less precise. This indicates that future studies employing this task should use a large sample of participants so as to ensure a reliable estimate of the true effect size. The LT yielded precise and convincing evidence for an LVF-bias in the distribution of spatial attention. Finally, the LDT yielded compelling evidence for an RVF-advantage in the detection of words. Taken together, these results corroborate the existence of hemispheric specialization for the processing of faces and emotional expressions, of the global and local elements of visual stimuli, in the distribution of spatial attention, and in the processing of visually presented words. Furthermore, since the resulting effect sizes are similar to those of the original studies, we consider the current five tasks to offer highly useful, reliable tools to elicit and study the behavioral manifestations of these instances of hemispheric specialization.

A less convincing pattern of results can be seen for the Picture Matching Task (PMT) that was introduced by Peyrin et al. (2006) as a tool to study the putative lateralized processing of stimuli's high (HSF) and low (LSF) spatial frequency content. As illustrated in Figure 17, this task allows for twelve tests of lateralization of which only four were found to reach significance in the original study. Specifically, the original study by Peyrin et al. (2006) only showed evidence for lateralization effects in reaction times (RTs), but not in error rates (ERs), and the observed effects had relatively large effect sizes with relatively large confidence intervals. In comparison, our replication attempt yielded smaller effect sizes with greater precision, and these effects aligned with those of Peyrin et al. (2006) in demonstrating an RVF-advantage for processing of HSF stimuli, albeit in ERs rather than RTs. However, for LSF stimuli, the results were less clear, as the Bayes factors in our analyses were inconclusive and only the combined evidence pointed towards the presence of LVF-advantages in processing LSF stimuli. Accordingly, we conclude that further, high-power replication attempts are needed to establish the usefulness of Peyrin's PMT as a tool to elicit and study the behavioral effects of lateralized processing of high and low spatial frequencies.

Lastly, the current study also included three tasks that did not produce reliable evidence for the effects of brain lateralization on performance. To start, we obtained no evidence for RVF-advantages in detecting color or shape oddballs belonging to different categories than the distractors. For both the Color (COT) and Shape (SOT) Oddball Tasks, our results yielded more precise estimates of the effects than the original studies, and our results failed to replicate the earlier found effects. Secondly, we obtained no evidence for effects of lateralization in categorical and coordinate judgments of spatial relationships in the Cross-dot Matching Task (CMT) (Van der Ham & Borst, 2011; Van der Ham & Borst, 2016), as we did not replicate the effects that survived in the corrigendum by Van der Ham and Borst (2016) and we also did not find evidence for a number of other effects that were predicted for this task in the original report by Van der Ham and Borst (2011). Accordingly, we conclude that the CMT, COT, and SOT do not reliably elicit behavioral manifestations of lateralized information processing.

A generic role for stimulus and task factors?

In view of our large collection of successful and less successful replications of previous findings, an interesting question is whether there are any methodological factors that distinguish the paradigms that do and do not produce reliable behavioral effects of brain lateralization. Indeed, there are many previous studies that have attempted to demonstrate behavioral effects of lateralization and that have concluded that the observation of such effects may depend on various potential modulators (e.g., Bourne, 2006; Hellige & Sergent, 1986; Hunter & Brysbaert, 2008; Yovel et al., 2001; for reviews, see Dien, 2008; Springer & Deutsch, 1998), such as the presentation parameters used in displaying the stimuli (e.g., stimulus duration, presence of masks, bilateral vs. unilateral stimulus presentation), and the nature of the task (e.g., target detection, target discrimination, judging the similarity between two stimuli). Accordingly, we can ask the question whether the current set of results can be understood in terms of the fact that lateralization effects are more likely to surface at the behavioral level when a paradigm has a certain combination of presentation and task parameters. In considering this possibility, we note that the effects that were replicated were obtained in different types of tasks (target detection, target identification, and stimulus matching), using either a free-viewing or a visual half-field technique, and for various presentation durations. Therefore, we conclude that the likelihood of observing a behavioral effect of brain lateralization in one of the currently used paradigms is not related directly to a specific setting of parameters.

Beyond the reliability of specific paradigms: Implications for lateralization

Given that it is difficult to explain our mixed success at replicating previous findings exclusively in terms of methodological factors, an alternative account could be that the success of replication in the current study relates to whether or not a certain type of visual stimulus is indeed processed in a lateralized manner. In this view, the successfully replicated VFAs for faces, emotional expressions, global and local stimuli, spatial attention distribution, and words would be interpreted to reflect the existence of lateralization, whereas the non-replicated VFAs for the influence of categorical processing in detection of color and shape oddballs, and for judgments of spatial relations would be interpreted to reflect the non-existence of lateralized processing in these tasks. In the following sections, we discuss this possibility as we address the relationship between the current findings and those of previous studies that have examined the same instances of lateralization using different behavioral paradigms and more direct measures of brain functioning, such as studies on the effects of lateralized brain injury, and studies employing neuroimaging.

In relating the current findings to the broader context of previous studies investigating the same instances of lateralization with different methods, it becomes clear that the pattern of successful and non-successful replications across the current set of studies resonates well with the amount and consistency of the currently available evidence pertaining to the underlying instances of lateralization. To start, our finding of an LVF-advantage in the FST is consistent with a large body of findings demonstrating RH-specialization for processing faces in patients (e.g., De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994), in neuroimaging studies (e.g., Kanwisher, McDermott, & Chun, 1997), and in behavioral studies (for a recent meta-analysis, see Voyer et al., 2012). The current finding of an LVF-advantage for processing emotional expressions in the FET can likewise be considered to be “unsurprising” in view of the fact that a meta-analysis by Voyer et al. (2012) showed that many previous behavioral experiments using emotional faces have consistently demonstrated this advantage, with a large estimated pooled effect size. At the same time, however, it is not yet clear whether this LVF-advantage should be interpreted as evidence for RH-dominance in processing emotional stimuli, as the results from one meta-analysis of neuroimaging studies showed no support for such generic RH-dominance in processing emotional stimuli (Wager, Phan, Liberzon, & Taylor, 2003), whereas another showed that such lateralization may only pertain to the processing of faces that are difficult to perceive due to masking (Costafreda, Brammer, David, & Fu, 2008). Accordingly, an interesting question for future studies will be to examine whether the LVF-advantage for perceiving the emotional expression of faces in a chimeric face task derives from RH-specialization for processing faces, or from RH-specialization in processing emotional stimuli, under conditions with and without masks.

Likewise, our finding of convincing evidence for an LVF-bias in allocating attention converges with the results of many different types of studies showing RH-dominance in the control of spatial attention (e.g., Rafal, 1998). Lastly, our finding of an RVF-advantage in the LDT converges with a large number of studies which have shown that right-handed participants generally show LH-dominance for language in general (e.g., Vigneau et al., 2006; Springer & Deutsch, 1998), and for processing linguistic visual stimuli in visual-half field studies in particular (e.g., Hunter & Brysbaert, 2008).

While our successful replication of VFAs for faces, spatial attention, and words can be considered an “unsurprising” result in view of the large and consistent body of evidence for lateralized modularity of the neural mechanisms involved in face processing, spatial attention, and language, a different opinion should apply to the lateralization for processing of global and local stimuli and of spatial frequency content. Specifically, an extensive review by Dien (2008) makes it clear that even though research on these instances of lateralization has a long history, the results of neuroimaging and patient studies have not consistently identified the presumed lateralized processing mechanisms, and the results of behavioral studies have likewise been mixed in providing evidence for the predicted VFAs. In light of these observations, the current finding that the HLT introduced by Yovel et al. (2001) produces convincing evidence for RH-global and LH-local processing biases can thus be said to be informative because it provides strong support for the existence of global-local lateralization. However, the current findings demonstrate only limited support for differential sensitivity to HSF and LSF stimuli in the PMT of Peyrin et al. (2006). Accordingly, to sustain the notion of lateralized processing of spatial frequency content would require additional and reliable observations.

Lastly, we consider the implications of the current findings for theories proposing the existence of lateralized influences of stimulus categories on making perceptual judgments. In addressing this matter, we examined the reliability of earlier findings that suggested the existence of an RVF-advantage in making a categorical judgment of the spatial relationship between two stimuli and in oddball detection when the oddball stimulus is categorically distinct from the distractors in terms of its color or shape. Importantly, our results offered little to no support for the reliability of these findings, thereby indicating that our results failed to offer support for theories proposing LH-dominance in categorical spatial judgments (e.g., Kosslyn et al., 1989) and in detecting categorically distinct visual oddballs (A.L. Gilbert et al., 2006; A.L. Gilbert et al., 2008). In considering the broader implications of these findings, it is of relevance to note that previous studies investigating the existence of LH-dominance in categorical spatial judgments have also offered only limited support for this form of lateralization (Van der Ham & Postma, 2010; Van der Ham, Raemaekers, Van Wezel, Oleksiak, & Postma, 2009; Van der Ham et al., 2007). Furthermore, an extensive review by Jager and Postma (2003) shows that behavioral tasks other than the one used in the current study have also produced mixed results, and it indicated that evidence for lateralized categorical and coordinate spatial relation processing from neuroimaging, patient, and computational modeling studies is also variable. Likewise, our failure to find support for previous findings of LH-dominance in detecting categorically distinct visual oddballs converges with the results of previous studies that also did not show evidence for VFAs using different tasks to measure lateralization of categorical color perception (Brown et al., 2011; Efron & Yund, 1996; Witzel & Gegenfurtner, 2011), and it is also consistent with the fact that there is little evidence from neuroimaging studies to support the existence of lateralization in the influence of categorical boundaries on visual search (for a review, see Witzel & Gegenfurtner, 2011). Taken together, we conclude that there is no consistent support for theories that propose a LH-dominance in categorical spatial judgments or in detecting categorically distinct targets in a visual oddball task.

Concluding remarks and recommendations for future studies

Aside from offering insight into the reliability and existence of several previously found instances of behavioral effects of brain lateralization, the current study also suggests a number of more general recommendations for future studies on lateralization. To start, our exposition of the results of previous studies (see Figure 17) shows that there has been considerable tolerance towards selective reporting when it comes to tests that fail to show predicted effects, meaning that non-significant lateralization studies often do not disclose sufficient detail to afford their use in meta-analyses. In light of the many disparate findings that have been obtained for various purported instances of lateralization, such meta-analyses are essential to assess the strength of effects, as well as the influences of modulators and publication bias. Accordingly, a first important general recommendation for future studies on lateralization is to fully disclose the results of all analyses, including those that did not yield statistically significant effects.

A second, related recommendation pertains to the degrees of freedom that researchers have when examining evidence for lateralization in behavioral and neuroimaging studies. On this point, it is noteworthy that a typical study using the visual half field paradigm has at least four opportunities to provide some evidence for lateralization, such that there might be LH- or RH-dominance on either RT or ER outcomes. In view of the degrees of freedom that these options for analysis offer, it seems crucial that researchers preregister their analysis plan so as to clarify which of these effects are predicted to occur in light of the underlying theoretical rationale. In combination with the full disclosure of analyses and findings, such transparency will surely benefit the field by providing the evidence that is needed to identify robust instances of lateralization and to weed out any non-reliable observations and false conjectures.

Finally, we have pointed out a number of paradigms that produce reliable lateralization effects. These paradigms point towards potential underlying neural mechanisms. To establish the scope of the underlying mechanisms, we recommend that future studies should consider replication tests as well as testing variations of these paradigms.

3

Modulation of local and global lateralization

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Abstract

It is often assumed that the human brain processes the global and local properties of visual stimuli in a lateralized fashion, with a left hemisphere (LH) specialization for local detail, and a right hemisphere (RH) specialization for global form. However, the evidence for such global-local lateralization stems predominantly from studies using linguistic stimuli, the processing of which has shown to be LH lateralized in itself. In addition, some studies have reported a reversal of global-local lateralization when using non-linguistic stimuli. Accordingly, it remains unclear whether global-local lateralization may in fact be stimulus-specific. To address this issue, we asked participants to respond to linguistic and non-linguistic stimuli that were presented in the right and left visual fields, allowing for first access by the LH and RH, respectively. The results showed global-RH and local-LH advantages for both stimulus types, but the global lateralization effect was larger for linguistic stimuli. Furthermore, this pattern of results was found to be robust, as it was observed regardless of two other task manipulations. We conclude that the instantiation and direction of global and local lateralization is not stimulus-specific. However, the magnitude of global, —but not local—, lateralization is dependent on stimulus type.

Introduction

Functional hemispheric asymmetry, or *lateralization*, is a particular instance of cortical specialization that enables the brain to use dedicated or optimized processing routines, promoting efficiency in processing of different types of information. The left hemisphere's (LH) dominance for language-related processes and the right hemisphere's (RH) dominance for visuospatial processes are well-known examples of lateralization of the human brain (Cai et al., 2013; Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013; Stephan et al., 2003). In addition, lateralization has been argued to exist for the processing of different aspects of visual information (Hellige et al., 2010). Specifically, studies on patients with unilateral brain lesions (e.g., Delis, Robertson, & Efron, 1986; Robertson, Lamb, & Knight, 1988), and neuroimaging studies with neurologically intact adults (e.g., Fink et al., 1996; Han et al., 2002) suggest that the LH may be specialized in identifying the local elements of visual stimuli, while the RH may be specialized in identifying their global form. These findings have been corroborated by behavioral studies, showing a left visual field (LVF) superiority for global processing and a right visual field (RVF) superiority for local processing, congruent with RH and LH lateralization, respectively (e.g., Hübner, 1998; Van Kleeck, 1989; Yovel et al., 2001).

A potential caveat to the interpretation of these findings lies in the fact that a preponderance of global-local studies used linguistic stimuli, modeled after the classical hierarchical Navon letters (Navon, 1977). As letters themselves have been shown to induce predominantly LH fusiform gyrus activity (Callan, Callan, & Masaki, 2005; Flowers et al., 2004; Polk et al., 2002), the use of hierarchical letter stimuli to study global-local lateralization introduces a confounding factor. Consequently, results derived using letter stimuli can be interpreted in more than one way. On the one hand, the classic interpretation of local-LH/RVF and global-RH/LVF advantages can be made. This interpretation requires the underlying assumption that global-local lateralization is content-neutral, and as such is not affected by the linguistic nature of the stimuli. Alternatively, the pattern of results can be explained in terms of stimulus-specific lateralization, with linguistic-LH/RVF and visuospatial-RH/LVF advantages. This interpretation assumes that the more taxing local level (as shown by the *global precedence effect*, Navon, 1977) is processed by the hemisphere that is specialized for that stimulus type, predicting local-LH/RVF advantages for linguistic stimuli, but local-RH/LVF advantages for visuospatial stimuli (Fink et al., 1997; Kinsbourne, 1970). In addition, Fink et al. propose that the non-specialized hemisphere processes the global level, as this is the level that is processed by default, resulting in global-RH/LVF advantages for linguistic stimuli, but global-LH/RVF advantages for visuospatial stimuli (Fink et al., 1997).

Whether a content-neutral or stimulus-specific interpretation best explains global-local lateralization cannot be determined based on the available literature. The current study aims to resolve this issue by directly comparing global-local lateralization for linguistic (i.e. letter) and non-linguistic (i.e. figure) stimuli. Before we turn to the present study, we will shortly review the existing theoretical and empirical support for each of the accounts.

Support for content-neutral global-local lateralization

The content-neutral account of global-local lateralization finds support in the theory that perceptual lateralization is the result of hemispheric differences in spatial frequency processing (e.g., Christman, 1989; Han et al., 2002; Kitterle et al., 1992; Musel et al., 2013; Sergent, 1982). This hypothesis forms the basis of the Double Filtering by Frequency (DFF) theory (Flevaris & Robertson, 2016; Ivry & Robertson, 1998). According to the DFF theory, when confronted with visual input, first a spatial frequency range is selected from the incoming spectrum, during which no hemispheric asymmetries are present. Next, this selection is fed forward to each of the hemispheres, where the LH amplifies the high spatial frequency (HSF) range, and the RH amplifies the low spatial frequency (LSF) range of this pre-selection. As a consequence, the HSF amplification in the LH causes a local-LH advantage, and the LSF amplification in the RH causes a global-RH advantage. Thus, the DFF theory predicts that global-local lateralization can be observed for different stimulus types as long as these have similar spatial frequency spectra (for an overview, see Dien, 2008).

Another line of support for the content-neutral account can be found in studies that report the classical global-local lateralization pattern when using non-linguistic stimuli. In such a study, using functional magnetic resonance imaging (fMRI), Martinez et al. (1997) found enhanced activity over the LH occipito-temporal junction during local processing, and enhanced activation of the RH occipito-temporal junction during global processing. Similarly, the classical local-RVF and global-LVF effects have been found in behavioral studies using non-linguistic stimuli (e.g. Hübner & Studer, 2009; Kimchi & Merhav, 1991).

In further support for the content-neutral account, a study that compared global-local lateralization for linguistic and non-linguistic stimuli found the classical pattern of results for both types of stimuli (Bedson & Turnbull, 2002). Using a change detection paradigm, they showed that participants more accurately detected global changes in the LVF, regardless of the nature of the stimuli.

Support for stimulus-specific global-local lateralization

The strongest support for a stimulus-specific account of global-local lateralization comes from two contrasting studies by Fink et al. (1996; 1997). In a positron emission tomography (PET) experiment using linguistic stimuli, they found the LH inferior cortex to be more involved in processing of the local level, and the RH lingual gyrus in processing of the global level (Fink et al., 1996; Fink et al., 1997b). In contrast, when using non-linguistic stimuli in the same paradigm, they found these effects to be reversed to enhanced RH lingual gyrus activity for local processing, and enhanced LH inferior occipital activity for global processing (Fink et al., 1997). In accounting for these results, Fink et al. proposed that processing of the local level of a stimulus is managed by the hemisphere that is specialized for the presented stimulus type. For linguistic stimuli this would entail the LH, and for non-linguistic stimuli the RH. They further proposed that the other, non-specialized hemisphere engages in processing of the global level of the stimulus, this being the default processing mode (Fink et al., 1997).

Also favoring a stimulus-specific account are some of the results of studies by Kéïta et al. In a series of behavioral experiments, they found a local-RVF advantage for linguistic stimuli that was absent (Kéïta et al., 2014), or reversed to a local-LVF advantage (Kéïta & Bedoin, 2011, Experiment 2) when non-linguistic were used.

While the complete reversal of global-local lateralization is, to our knowledge, limited to the experiments by Fink et al. (1997) and Kéïta and Bedoin (2011, Experiment 2), there are also a number of studies that used non-linguistic stimuli and found no lateralization effects. For example, in the behavioral studies by Polich and Aguilar (1990), and Blanca and López-Montiel (2009), no significant global-local lateralization effects were found. However, it must be noted that there also exist studies using linguistic stimuli that failed to find global-local lateralization effects (Boles, 1984; Van Kleeck, 1989), and even one reporting a reversed local-LVF advantage, when stimulus duration was limited (Boles & Karner, 1996).

Confounding factors in letter-figure comparison studies

Aside from presenting mixed results, another problem in interpreting the results from previous studies is that the results might have been suboptimal due to potential confounding factors. Most notably, in the studies that found reversed lateralization for non-linguistic stimuli, the used letter and figure stimuli differed substantially on a number of crucial aspects.

Firstly, the number of local elements that made out one global stimulus was much higher for figures than for letters. The studies by Fink et al. used global letters that were made out of 9 or 15 (example stimuli in Fink et al., 1996), or 11 or 18 (example stimuli Fink et al., 1997b) local letters, while their figure stimuli were made out of 48 local elements (example stimuli Fink et al., 1997). Likewise, Kéïta et al. used letter stimuli that were made out of 16 to 26 elements, while their figure stimuli consisted of 24 to 32 elements (Kéïta & Bedoin, 2011; Kéïta et al., 2014). This might be problematic for the interpretation of their letter-figure comparison, because it has been shown that the number of local elements that a global stimulus is made out of has an effect on lateralization effects. More precisely, stimuli consisting of fewer local elements are more likely to produce local-RVF effects than those consisting of many local elements, and this may be due to the fact that local elements will be perceived as texture, rather than as individual stimuli, when their numbers increase (Christman & Weiner, 1997; Kimchi & Merhav, 1991).

Secondly, the global/local size ratio differed between letters and figures. Letter stimuli in Fink et al.'s studies, for example, had a size ratio of 1/6 or 1/5, whereas it was 1/16 for their figure stimuli. These differences in global/local size ratio might be problematic because it has been shown that lateralization effects are less robust when a smaller global/local ratio is used (Yovel et al., 2001).

Lastly, as explicitly stated by Kéïta and Bedoin (2011), their figure stimuli were more complex than their letter stimuli. This forms a third confounding factor that might play a role in the observed differences in lateralization, as a shift in visual field asymmetries has been shown to be the result of increasing the complexity of stimuli (Fontenot, 1973). In this study by Fontenot, an RVF advantage was apparent for 3-letter nonsense words. In contrast, an LVF advantage was found for figures, but only when these were high in complexity.

In sum, reversals of the classic lateralization pattern might be related to a number of confounding factors, rather than by the modulation of stimulus type.

Present study

In the present study, we set out to provide a more conclusive test of content-neutral versus stimulus-specific global-local lateralization, by avoiding inconsistencies in stimulus material. To this end, we compared global-local processing of linguistic and non-linguistic stimuli in a behavioral experiment, in a within-subjects design. We controlled for potential confounds by using letter and figure stimuli that are comparable in their number of local elements, global/local size ratio, and complexity. Furthermore, we compared lateralization for these letter and figure stimuli across different presentation conditions and tasks, so as to determine the robustness of any possible difference between lateralization for linguistic and non-linguistic stimuli. If global-local lateralization indeed is content-neutral, we predict local-RVF and global-LVF advantages for both letter and figure stimuli. If, alternatively, stimulus-specific lateralization drives the observed global-local lateralization effects, we predict a local-RVF for letters and a local-LVF advantage for figures.

Material and methods

Participants

Seventeen students (7 women, 10 men) from the University of Groningen took part in the experiment for course credits[13]. Mean age was 19.5 years (range 18-23). All participants were right-handed with a mean of 9.6 (range 7-10) on the Flinders handedness survey (Nicholls et al., 2013). All participants reported to have normal or corrected-to-normal vision, which was verified using a Snellen chart. The ethical committee of the Psychology Department of the University of Groningen approved the experiment, and participants gave written consent before the test session began.

Stimuli and apparatus

In half of the trials, hierarchical letters were presented, while in the other half hierarchical figures were presented. Stimulus letters were T and H (targets), and Y and N (distractors). Stimulus figures were a diamond and a plus sign (targets) and a rectangle and a cross (distractors). These stimuli were chosen because the amount of information they convey on the nasal or temporal side does not depend on the visual field of presentation (they are largely symmetrical around the midline). All stimuli were incongruent, that is, the identity of the letters or figures presented at the global level always differed from that of the local level, because such stimuli have been shown to produce visual field effects more reliably (Hübner & Volberg, 2005; Martens & Hübner, 2013).

As directing attention toward and away from salient stimulus attributes has been shown to be a lateralized process itself (Mevorach, Humphreys, & Shalev, 2006a, 2006b), we aimed to ensure that local and global levels of our stimuli were equally salient. As starting point for construction of the stimuli, we used those from the 'equal salience' condition of Yovel et al.'s study in which they compared stimulus and task factors (2001). With this study, Yovel et al. showed that lateralization effects were more robust when using stimuli that have equally salient levels, compared to stimuli that have a more salient global than local level. For both letter and figure stimuli, a global stimulus was comprised of local stimuli placed within a 5 x 5 grid, with a global/local ratio of 0.14. The global letters consisted of 7-13 local letters (mean 10.5), and the global figures consisted of 8-12 local figures (mean 9.5). Figure 18 shows example stimuli.

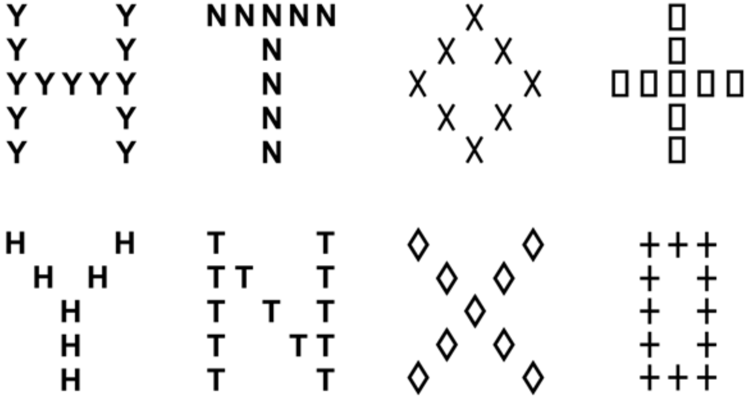

Figure 18. Example of four letter stimuli (left) and four figure stimuli (right), showing targets at the global level (upper), and local level (lower).

The hierarchical stimuli were presented in black on a white background, and subtending 3.5° of visual angle, with their inner edges at 0.5° from the central fixation point. Stimuli were displayed on a 22” CRT monitor (1280 x 1024, 100 Hz, Iiyama Vision Master Pro 513) and viewed from a distance of 57 cm, which was kept fixed using a chin rest. The experimental session took place in a dimly lit and sound attenuating room. The experiment ran in E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA), on a Windows 7 operating system. Responses were collected using an in-house manufactured button box.

Procedure

At the start of the session, participants completed a handedness survey and a visual acuity test. The experiment was divided into two parts, each comprising four blocks that differed in terms of the task and stimuli used. In one of the parts, the stimuli were hierarchical letters while in the other these were hierarchical figures. Nine participants started with the figure stimuli, and eight participants started with the letter stimuli. For each stimulus type, participants first did a target identification task ('target task'), with stimuli displayed unilaterally. Next, they did the same task but with bilaterally presented stimuli. After that, the participants performed a level identification task ('level task'), first with unilateral and next with bilateral stimuli.

During the target task, one of the two possible target stimuli would appear at either the global or the local level. Participants were instructed to indicate which of the two targets they saw, regardless of the level, as fast as possible. They did so by pressing one of two buttons using their index or middle finger. When participants performed the level task, they had to determine whether either target appeared at the global or the local level, or not at all. Participants indicated at which level they had seen a target, by pressing one of two buttons using their index or middle finger, as fast as possible. The participants were instructed not to press a button when they had not seen a target. The no-target-present condition constituted 20% of the trials in this task, and was included to prevent participants from being able to complete the task by monitoring either the global or the local level only.

During a unilateral presentation block, the hierarchical stimulus appeared in the LVF and RVF equally often, in a randomized manner. In bilateral presentation blocks, two hierarchical stimuli would appear simultaneously on every trial, with one in each visual field. When a target was present, this was in only one of these two stimuli, on only one level. A target was present in the LVF and RVF stimuli equally often within in one block. The unilateral-bilateral contrast was included because previous research has shown that bilateral presentation of stimuli can result in larger lateralization effects (Boles, 1987, 1990) (see Appendix B for a discussion).

Each unique task and presentation block consisted of 160 trials. In target tasks, this lead to 40 trials per combination of visual field and level, and in level tasks (where 20% were non-target trials) to 32 trials per combination. Before each of these blocks started, participants were instructed about their task and the response mapping to the buttons, and were given

16 practice trials to get familiar with the new task and stimulus presentation. Finger-response mappings were counterbalanced over participants.

In each of the blocks, a trial started with the presentation of a central fixation asterisk for 540-600 ms, followed by the unilateral stimulus or bilateral stimuli for 120 ms. The stimulus was followed by a blank screen, the duration of which depended on the stimulus presentation condition. The duration of the blank screen was 120 ms in unilateral trials, and 220 ms in bilateral trials, to allow equalized processing time in relation to the amount of information (which was doubled, in case of bilateral stimuli). After the blank, one or two 5 x 5 grids of hashtags were presented at the location of the stimuli, lasting 110 ms, to prevent further persistence of their after images (Bourne, 2006). Participants were required to respond as fast as possible, with a maximum of 2 s to make their response. Nine participants responded using their left hand, and eight using their right hand, to control for any effects due to visual field-hand congruency (Hellige & Sergent, 1986; Wendt, Vietze, & Kluwe, 2007).

Statistical analysis

In analyzing the data, we focused on the results for error rates (ERs), because the use of a short presentation time and masking procedure entailed that ERs were most informative (Hellige & Sergent, 1986)[14]. To examine whether there is evidence for lateralization of global and local processing in our participants' data, we performed repeated measures ANOVAs with within-subject factors Level (global, local), Visual Field (LVF, RVF), Stimulus Type (letter, figure), Presentation (unilateral, bilateral) and Task (target task, level task). In case of higher-order interactions, ANOVAs with factors Level (global, local) and Visual Field (LVF, RVF) were performed separately for each of the levels of the modulating factor, to assess the magnitude of lateralization across different conditions. In case of a significant Level x Visual Field interaction, these ANOVAs were followed up by one-sided paired samples *t*-tests, to examine whether there was an indication for both global-LVF and local-RVF advantages. We did not perform Bonferroni corrections, since the effects were specified a priori, and follow-up *t*-tests were conducted to assess the nature of the significant expected interaction effect. The effect sizes that we report are partial eta-squared (η^2_p) for the *F*-tests, and Cohen's d_{rm} for the *t*-tests (Lakens, 2013).

A global-LVF advantage is defined as a relative reduction in ERs when the global target is presented in the LVF compared to the RVF, while a local-RVF advantage reflects a relative reduction in ERs when the local target is presented in the RVF compared to the LVF.

Results

The average ER over all conditions was 25% (SE = 3%). We found lateralization for global and local processing, with a significant Level x Visual Field interaction ($F_{Level\ x\ Visual\ Field}[1,16] = 28.36$, $p < .001$, $\eta^2_p = .64$), yielding a significant global-LVF advantage (mean LVF advantage= -3.9%, SE = 1.1%, $t[16] = -3.60$, $p = .001$, $d_{rm} = .3$), and a significant local-RVF advantage (mean RVF advantage = 2.5%, SE = .8%, $t[16] = 3.38$, $p = .002$, $d_{rm} = .26$) (Figure 19). There was no significant difference in the magnitude of the lateralization effects seen for the local-RVF and the global-LVF advantages (mean difference = 1.7%, SE = 1.1%, $t[16] = -1.63$, $p = .123$).

Important to our main question, lateralization was modulated by the type of stimulus ($F_{Level\ x\ Visual\ Field\ x\ Stimulus\ Type}[1,16] = 14.00$, $p = .002$, $\eta^2_p = .47$), in the absence of any other modulating effects on lateralization (all *F's* < 3.74, all *p*'s > .07). In separate analyses on letter and figure trials, we found the lateralization effect to be significant for letters ($F_{Level\ x\ Visual\ Field}[1,16] = 43.92$, $p < .001$, $\eta^2_p = .73$), as well as for figures ($F_{Level\ x\ Visual\ Field}[1,16] = 9.98$, $p = .006$, $\eta^2_p = .38$). Each of these lateralization effects consisted of both a global-LVF advantage and a local-RVF advantage (global letters: $t[16] = -3.71$, $p < .001$, $d_{rm} = .46$; local letters: $t[16] = 3.06$, $p = .004$, $d_{rm} = .34$; global figures: $t[16] = -2.29$, $p = .018$, $d_{rm} = .11$; local figures $t[16] = 2.11$, $p = .026$, $d_{rm} = .17$) (Figure 2). The difference between the stimulus types was caused by a significantly larger global-LVF advantage for letters compared to figures ($t[16] = -3.02$, $p = .008$). The local-RVF advantage did not significantly differ in magnitude between letters and figures ($t[16] = .78$, $p = .448$). When comparing the global-local difference of the stimulus types within each of the visual fields, we did not find a difference between letters and figures for the LVF trials ($t[16] = 1.77$, $p = .095$), or for the RVF trials ($t[16] = -.59$, $p = .564$).

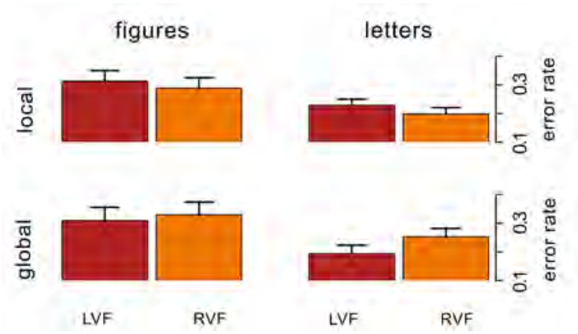

Figure 19. Mean error rates for local (upper panels) and global (lower panels) stimuli for figures (left panels) and letters (right panels). Orange bars depict mean error rates for left visual field trials, red bars depict mean error rates for right visual field trials. Error bars represent standard errors of the means.

We did not observe a general differential lateralization for letters and figures, regardless of level ($F_{Visual\ Field\ x\ Stimulus\ Type}[1,16] = 2.15$, $p = .162$, $\eta^2_p = .12$), as may have been predicted by theories about linguistic LH- and visuospatial RH-lateralization.

Discussion

Our main result showed that global-LVF and local-RVF advantages existed for both letters and figures. This indicates that the direction of global-local lateralization does not depend on the stimulus being linguistic or non-linguistic in nature. In addition, we found that the global – but not the local – lateralization effect was larger for letters than for figures. This pattern of results was robust, as it was observed regardless of whether the stimuli were presented unilaterally or bilaterally, and regardless of whether the task required a response relating to the identity of a target or to the level at which a target appeared. Below, we discuss the implications of these results in detail.

Global-local lateralization is not stimulus-specific

In finding local-RVF and global-LVF advantages for both letters and figures, our results support the notion that the instantiation and direction of global-local lateralization do not depend on LH-lateralization for linguistic stimuli and RH-lateralization for non-linguistic stimuli. Further support for this lies in the fact that we found no overall visual field differences between the two stimulus types. This is consistent with results from a study involving patients with unilateral lesions, showing that there is no overall performance difference for linguistic and non-linguistic stimuli between patients with LH damage and patients with RH damage (Delis et al., 1986).

Our results do not replicate those of reversed lateralization for non-linguistic stimuli by Fink et al. (1997), and Kéïta and Bedoin (2011). A likely explanation for this is that the reversed lateralization effects in those studies are due to differences between their linguistic and non-linguistic stimuli in terms of the number of local elements, the global/local size ratio, or the complexity of the stimuli. The non-linguistic stimuli in Fink et al.'s study (1997) seemed to contain more than double the number of local elements, and have less than half the global/local size ratio compared to their linguistic stimuli (Fink et al. 1996; Fink et al. 1997b). Also in Kéïta and Bedoin's study (2011), the number of local elements in the non-linguistic stimuli seemed to far exceed that of the linguistic stimuli, and the non-linguistic stimuli were reported to be more complex than the linguistic stimuli. These are all factors that have been related to the likelihood of finding global-local lateralization effects (Christman & Weiner, 1997; Fontenot, 1973; Kimchi & Merhav, 1991; Yovel et al., 2001). In the current study, we controlled for these confounds; the number of local elements, the global/local size ratio, and the stimulus complexity were similar for letter and figure stimuli, and reversed lateralization for figure stimuli was found to be absent. Therefore, we can conclude that reversals of visual field effects are most likely driven by other factors than stimulus type, and based on the present results we can argue that the instantiation and direction of global-local lateralization do not depend on stimulus type.

Modulation of global lateralization

Although global-local lateralization is apparent for both stimulus types in the present study, we do see an amplification of the global lateralization effect for letters compared to figures. This finding cannot be explained in terms of the stimulus-specific account of lateralization, since it predicts a reversal of global lateralization, and not a difference in magnitude. We do not have a ready explanation for this modulation of global lateralization, but believe it is worthy of further investigation.

While its cause is not yet clear, our finding of modulation of global lateralization in the absence of modulation of local lateralization suggests that lateralized processing of global information is more susceptible to changes in stimulus characteristics than local lateralized processing. Support for this notion can be found in the fact that a number of previous studies on global-local lateralization report local-RVF advantages in the absence of global-LVF advantages (Boles & Karner, 1996; Christman & Weiner, 1997; Evans et al., 2000; Martinez et al., 1997; Polich & Aguilar, 1990). In contrast, to our knowledge there are no studies reporting global lateralization in the absence of local lateralization[15]. Moreover, in a number of studies that consisted of multiple experiments, local-RVF advantages were more often found than global-LVF advantages (Evert & Kmen, 2003; Kéïta & Bedoin, 2011; Kimchi & Merhav, 1991; Yovel et al., 2001). Notably, of the studies just listed, five used non-linguistic stimuli (Christman & Weiner, 1997; Kimchi & Merhav, 1991; Kéïta & Bedoin, 2011; Martinez et al., 1997; Polich & Aguilar, 1990), and four used linguistic stimuli (Boles & Karner, 1996; Evans et al., 2000; Evert & Kmen, 2003; Yovel et al., 2001). As the majority of global-local studies use linguistic stimuli, there seems to be an overrepresentation of studies using non-linguistic stimuli among those that report the absence of global-LVF advantages. Taken together, this suggests that local lateralized processing is a robust effect, persisting over all kinds of different stimuli used in these studies, and regardless of the linguistic nature of the stimuli. In contrast, the magnitude of the global-LVF advantage may be influenced by specific stimulus characteristics, of which the linguistic nature of the stimulus is a likely candidate.

Additional support for the notion that global and local lateralization could be independently modulated, comes from neuroimaging and lesion data showing that global and local lateralization do not have the same neural underpinnings. Of the studies reporting local-LH and global-RH processing, the involved LH and RH areas were not found to be homologues, except in one fMRI study using non-linguistic stimuli, that showed the involvement of the occipito-temporal junction in both the LH and RH (Martinez et al., 1997). LH areas found to be involved in local processing are the superior temporal lobe (Delis et al., 1986; Robertson et al., 1988), the posterior temporal lobe (Yamaguchi et al., 2000), and the inferior occipital lobe (Fink et al., 1996; Fink et al., 1997b). RH areas found to be involved in global processing are temporo-parietal areas (Delis et al., 1986; Robertson et al., 1988; Yamaguchi et al., 2000), and the lingual gyrus (Fink et al., 1996; Fink et al., 1997b). These findings highlight the fact that global and local lateralization can be regarded as separate processes, that may, therefore, be independently affected by stimulus characteristics.

In sum, we conclude that local lateralization is a robust phenomenon, while global lateralization can be modulated by stimulus type. A distinction between global and local lateralization is supported by behavioral, neuroimaging, and lesion studies.

Future studies

We have shown that the use of non-linguistic stimuli does not reverse global and local lateralization, but that it can lead to diminished global lateralization. Future studies are needed to further delineate the cause of this difference between linguistic and non-linguistic stimuli, and why this affects global but not local lateralization.

One known difference between linguistic and non-linguistic stimuli is that in skilled readers, the processing of the former is more automatic than that of the latter (Lachmann, Schmitt, Braet, & Leeuwen, 2014). A consequence of the automaticity of letter processing is that it could result in better processing of linguistic than non-linguistic stimuli. While not the focus of the present study, we did indeed find participants to make fewer errors in processing letters than figures (p = .006). How an increase in global lateralization, and not local lateralization, could follow from automaticity of processing remains a topic for further study.

Further regarding potential differences between linguistic and non-linguistic stimuli, it has been suggested that local figures will presumably be more readily perceived as texture than local letters will, which in turn may affect their lateralized processing (Christman & Weiner, 1997). It is noteworthy that the number of local elements of the current study's stimuli straddled the boundary of being perceived as individual elements or as texture, according to Kimchi (1992) and Christman and Weiner (1997). Following this, if we presume that in our experiment local letters had been perceived as individual elements, but local figures as texture, this may have contributed to their differing lateralized processing. Again, how this then could have affected global lateralization, but not local lateralization, remains unclear. Future studies should consider manipulating the number of local elements, to compare linguistic and non-linguistic stimuli on how this affects global lateralization.

Finally, in addition to the number of local elements, we have listed two more factors that may have contributed to the reversal of global and local lateralization in earlier studies, namely the global/local size ratio and stimulus complexity. To increase our knowledge of lateralization of global and local processing, and of lateralization in general, it is important to assess how such stimulus factors may cause a 'typical' lateralization effect to reverse completely.

4

Principles of lateralized vision

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Abstract

While functional lateralization of the human brain has been a widely studied topic in the past decades, few studies to date have gone further than investigating lateralization of single, isolated processes. With the present study, we aimed to arrive at a more unified view by investigating lateralization patterns in face and word processing, and associated lower-level visual processing. We tested a large and heterogeneous participant group, and used a number of tasks that had been shown to produce replicable indices of lateralized processing of visual information of different types and complexity. Following Bayesian statistics, group-level analyses showed the expected right hemisphere (RH) lateralization for face, global form, low spatial frequency processing, and spatial attention, and left hemisphere (LH) lateralization for visual word and local feature processing. Compared to right-handed individuals, lateralization patterns of left-handed and especially those who are RH-dominant for language deviated from this 'typical' pattern. Our results support the notion that face and word processes come to be lateralized to homologue areas of the two hemispheres, under influence of the RH- and LH-specializations in global form, local feature, and low and high spatial frequency processing. As such, we present a more unified understanding of lateralized vision, providing evidence for the input asymmetry and causal complementarity principles of lateralized visual information processing. The absence of correlations between spatial attention and lateralization of the other processes supports the notion of their independent lateralization, conform the statistical complementarity principle.

Introduction

Functional lateralization, or the differential specialization of the two cerebral hemispheres, enables the human brain to process a multitude of different types of information in an efficient and optimized manner (Hellige, 1993). At the population level, this division of labor is expressed in 'typical' patterns of lateralization, such as left-hemisphere (LH) dominance for most language-related processes, and right-hemisphere (RH) dominance for face processing (Behrmann & Plaut, 2015). At the same time, individuals can still differ in direction and strength of lateralization to such an extent that some people show RH-dominance for language, whereas others show no clear evidence for either hemisphere being dominant for language-related tasks (Mazoyer et al., 2014; Rasmussen & Milner, 1977). To understand the principles underlying the distribution of functions across the two hemispheres in both typical and reversed or atypical lateralization, the current study examined the relationships between hemispheric specializations for an array of processes including and subserving language and face perception, using a sample of participants that could be expected to show considerable heterogeneity in their direction and strength of lateralization based on variability in their handedness and/or known hemispheric dominance for language.

To date, only few studies have examined the relationships between different lateralized processes –often including measures of language and face processing, and the results of these studies have led to different views on the existence and nature of these relationships. Specifically, previous studies have suggested a number of hypotheses about the principles that may govern patterns of lateralization, which we here summarize as the *statistical complementarity* (Bryden, Hécaen, & DeAgostini, 1983), *causal complementarity* (Bryden et al., 1983), and *input asymmetry* (Andresen & Marsolek, 2005) principles. Each of these three principles assumes that various processes are lateralized, and attempt to explain patterns of lateralized processing.

According to the statistical complementarity principle, each process has a certain probability of being lateralized to one hemisphere, which is independent of the probability that other processes are lateralized to the same or the other hemisphere. Consequently, certain brain processes may show consistent lateralization to contralateral hemispheres at the population level, but there is no causal relation underlying this division of labor. In line with this view are the results of a factor-analytic study of cortical activity during rest, supporting the independence of lateralized brain systems involved in vision, internal thought, attention, and language (Liu, Stufflebeam, Sepulcre, Hedden, & Buckner, 2009). This claim was further corroborated by a review by Badzakova-Trajkov et al. (2016), showing that most evidence supports independent lateralization of different processes, especially with regard to processes that operate on information from different domains. In support of the conclusions from their literature review, the authors additionally present the results of a factor-analysis on neuroimaging data, suggesting independently lateralized systems governing spatial attention, word generation, and face processing (Badzakova-Trajkov et al., 2016).

In contrast to the statistical complementarity principle, the causal complementarity and input asymmetry principles both assume that lateralization of one process does depend on lateralization of others, with the former accounting for *functional segregation* (i.e. lateralization of different functions to opposite hemispheres) and the latter for *co-lateralization* (of different functions to the same hemisphere) (Vingerhoets, 2019). According to the causal complementarity principle, once a certain process is lateralized to a specific cortical area in one hemisphere, there is limited room for specialization of other processes in this area (Andresen & Marsolek, 2005; Badzakova-Trajkov et al., 2016; Cai et al., 2013; Gerrits et al., 2019). As a consequence, other types of information that may initially have been processed by the now occupied area, will become lateralized to homologous areas in the contralateral hemisphere. Support for this notion has been provided by Dundas, Plaut, and Behrmann (2015). In their study, Dundas et al. presented word and face stimuli (both assumed to recruit the middle fusiform gyrus) to a group of 7-12 year-olds, who varied in their word recognition competence, while measuring the electro-encephalography (EEG) response. The results showed that the more LH-lateralized the children were for word processing, the more RH-lateralized they were for face processing, as reflected by the differing magnitudes of the measured event-related potentials (ERPs) in response to word and face stimuli. Aside from this evidence for causal complementarity between face and visual word processing, a number of studies have suggested causal complementarity for face processing and the production of language during speech. For example, Gerrits et al. (2019) showed a correlation between LH-lateralization of brain regions that were active during language production and RH-lateralization of brain regions that were active during face perception.

The question then arises why visual word processing becomes lateralized to the LH and face processing to the RH, rather than the other way around. Behrmann and Plaut (2013) suggest that in order to arrive at efficient word and face processing, there is pressure for intrahemispheric connectivity to areas governing the representation of information necessary for such processing. While word and face processing demand similar resources (such as central vision, a possible reason they both engage the fusiform gyrus [Hasson, Levy, Behrmann, Hendler, & Malach, 2002]), they also differ in the types of information necessary from lower levels in the processing hierarchy. In the case of visual word and face processing, this difference would concern cortical areas devoted to language, which are necessary for processing of the former but not the latter type of visual information. Indeed, previous studies have shown a positive correlation between lateralization for language production (i.e., verbal fluency) and visual language perception (i.e., word reading) (Gerrits et al., 2019; Van der Haegen & Brysbaert, 2018). As such, hemispheric dominance for speech can be seen as a candidate for driving the direction of the complementary lateralization of word and face processing.

The input asymmetry principle captures this co-lateralization principle more generally, in proposing that lower-level processes subserving higher-level processes will drive ipsilateral lateralization of the latter (Andresen & Marsolek, 2005). This principle is, for example, reflected in a theory by Ivry and Robertson (1998), which has its basis in the assumption that the LH selectively processes relatively high frequency information, while the RH selectively processes relatively low frequency information. Any higher-level visual process that operates on a specific range of spatial frequencies, therefore, would also be lateralized to the hemisphere specialized for lower-level processing of that frequency range. As the holistic processing of a face has been shown to be affected by removing low spatial frequency (LSF) but not high spatial frequency (HSF) information

(Goffaux & Rossion, 2006), the strength of RH-lateralization for face processing would thus be expected to depend on the strength of RH-lateralization for LSF processing. Conversely, word processing has been shown to rely on HSF information (Ossowski & Behrmann, 2015), and the strength of LH-lateralization would thus be expected to depend on the strength of LH-lateralization for HSF processing. This idea has been supported by findings of differential sensitivity to spatial frequency information in the LH and RH fusiform gyri (Woodhead et al., 2011). Specifically, they used sine-wave gratings to show that the LH fusiform gyrus –an area specialized in word processing– responds more strongly to the presentation of HSFs, while the RH fusiform gyrus, –specialized in face processing–, responds more strongly to the presentation of LSFs.

In summary, previous studies examining the relationships between different instances of hemispheric specialization have resulted in diverging claims about the existence and nature of these relationships. Specifically, the statistical complementarity principle assumes no relation between lateralization of different processes, while the other two principles do. The causal complementarity principle explains how different processes become functionally segregated to the two hemispheres. Furthermore, the input asymmetry principle proposes that cortical areas devoted to different processes within a processing hierarchy benefit from intrahemispheric connectivity and thus promote co-lateralization of these processes to the same hemisphere. As such, the causal complementarity and input asymmetry account for two sides of the same coin: the former proposing contralateral specialization of processes recruiting similar resources (e.g., faces and words), the arrangement of which in turn is driven by ipsilateral specialization of processes within a processing hierarchy (e.g., faces and low spatial frequencies), as proposed by the latter. As such, the causal complementarity and input asymmetry principles are not mutually exclusive, while both are mutually exclusive with the statistical complementarity principle.

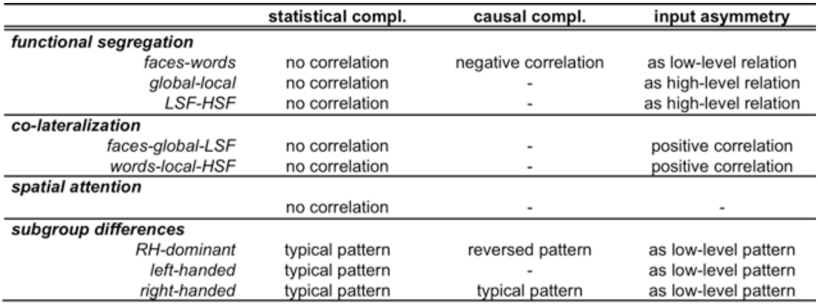
Present study

In the present study, we aim to shed light on these relationships by investigating the lateralized processing of different types of visual stimuli, using a large sample of participants (*n* = 122) who would be expected to show heterogeneity in both strength and direction of lateralization because of variation in, amongst other things, handedness. Specifically, we examined the relationships between behavioral indices of lateralized processing of visual words, faces, global and local elements, high and low spatial-frequency information, and the distribution of spatial attention, using tasks that we had previously found to produce replicable lateralization indices for population-typical lateralization in a sample of right-handed participants (see Brederoo, Nieuwenstein, Cornelissen, & Lorist, 2019). Using this series of tasks we aimed to test previous claims proposing causal complementarity between the processing of words and faces, and to determine whether any such complementarity might relate to hemispheric specialization for lower-level perceptual processes that rely on similar information (i.e., high spatial frequencies and local elements in the case of visual words vs. low spatial frequencies and global form in the case of faces), as proposed by the input asymmetry principle. Furthermore, we will test whether lateralization of these several types of visual information is statistically independent from lateralization of spatial attention, which is often measured in the visual domain with the Landmark Task (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Cai et al., 2013).

In examining the relationships between lateralized processes, we also aimed to determine whether certain processes are consistently mediated by the same or by different hemispheres, irrespective of which hemisphere this might be. That is, we investigated whether people who show population-typical lateralization for one process (e.g., LH-dominance for recognizing visual words) also show population-typical lateralization for another (e.g., LH-dominance for high spatial frequencies), and whether people with reversed lateralization for one process then also show reversed lateralization for the other processes. To be able to address this question, we included a number of participants (all left-handed) whom were known to show RH-dominance for language processing. Such RH-dominant individuals are difficult to find in random samples, which is why we recruited them from a sample of left-handed participants whose language dominance had previously been assessed using functional magnetic resonance imaging (fMRI) and behavioral methods in a study by Van der Haegen et al. (2011). By including a sample of this rarely studied group of participants, our study offered a unique opportunity to determine if consistent patterns of contralateral and ipsilateral specialization can be found for participants who differ in terms of which hemisphere is dominant for language. Previous studies indeed suggested that individuals with RH-dominance for language can show absent or reversed lateralization of other processes, such as face processing (Gerrits et al., 2019) and spatial attention (Cai et al., 2013).

Furthermore, we actively sought to include as many left-handed participants (generally known to be more variable with regard to their lateralization of language [Knecht et al., 2000]) as possible so as to obtain a participant sample that could be expected to be heterogeneous with regard to hemispheric dominance for language. This resulted in subgroups of right-handed, left-handed (for whom language dominance was unknown), and (left-handed) RH-dominant participants.

As such, the present study deviated from many earlier lateralization studies in that the gathering of lateralization indices of a multitude of within-domain processes and the aimed for heterogeneity of our sample allowed for a thorough evaluation of predictions following the three principles of lateralized processing (Table 1). The statistical complementarity principle predicts the absence of correlations between lateralization indices of different processes, and based on this principle there is no reason to assume lateralization patterns other than the ‘typical’ one to occur. If, to the contrary, the lateralization of the investigated processes is not independent, the causal complementarity principle predicts negative[16] correlations between processes governed by homologue areas (i.e., the stronger LH-lateralization for words, the stronger RH-lateralization for faces). Following this prediction, lateralization patterns should be reversed for individuals for whom language dominance is reversely lateralized to the RH. The causal complementarity principle does not allow any predictions regarding lateralization of processes that do not become lateralized to homologue areas. As processing of global form and local features (Chechlacz, Mantini, Gillebert, & Humphreys, 2015) and LSFs and HSFs (Peyrin, Baciu, Segebarth, & Marendaz, 2004) have both been proposed to recruit differing cortical areas, no predictions regarding correlations between lateralization of these processes can be made based on the causal complementarity principle. Furthermore, based on the causal complementarity principle we cannot make any predictions regarding processes that are lateralized to the same hemisphere (i.e., ipsilateral processes such as face and global feature processing). The input asymmetry principle fills this gap by predicting both the direction of correlations and the lateralization patterns of higher-level ipsilateral processes to simply mirror those of lower-level processes. In addition, the input asymmetry principle predicts positive correlations between ipsilateral processes within a processing hierarchy (e.g., the stronger LH-lateralization for local processing, the stronger LH-lateralization for word processing). Based on previous studies on the relation between spatial attention, language production, face processing, and vision more generally (Liu et al., 2009; Badzakova-Trajkov et al., 2016), lateralization of spatial attention is predicted to be statistically independent from that regarding other processing domains.



	statistical compl.	causal compl.	input asymmetry
functional segregation			
faces-words	no correlation	negative correlation	as low-level relation
global-local	no correlation	-	as high-level relation
LSF-HSF	no correlation	-	as high-level relation
co-lateralization			
faces-global-LSF	no correlation	-	positive correlation
words-local-HSF	no correlation	-	positive correlation
spatial attention			
	no correlation	-	-
subgroup differences			
RH-dominant	typical pattern	reversed pattern	as low-level pattern
left-handed	typical pattern	-	as low-level pattern
right-handed	typical pattern	typical pattern	as low-level pattern

Table 1. Predictions regarding relations among lateralization of processes and lateralization patterns, following the three tested principles of lateralized processing. Blank fields imply that no specific prediction follows from the principle.

Methods

Participants

Participant recruitment. Right- and left-handed participants were recruited at the University of Groningen, while only left-handed participants were recruited at the University of Ghent, from an existing left-handed participant pool. Part of the participants in this Ghent participant pool had undergone fMRI scanning in a previous study, establishing their RH-dominance for language (Van der Haegen et al., 2011). The final sample was based on pragmatic considerations, testing as many participants as we could get. Participants in Groningen who had participated in a previous study using the same tasks (Brederoo et al., 2019) were excluded from participation in the current study, to prevent unwanted practice effects or familiarity with the stimuli to influence the results.

Participant sample. In total, 122 (69 women and 53 men) were tested[17]; 99 at the University of Groningen and 23 at Ghent University. Mean age of the participants was 21.3 years (range 17-35 years). All participants were native speakers of Dutch, German, or English, and reported normal or corrected-to-normal vision. Participants were classified as right-handed when they had a positive score on the Flinders Handedness Questionnaire, and as left-handed when they had a negative score on this questionnaire (Nicholls et al., 2013). Twenty-three people from the left-handed Ghent participant pool signed up to participate, of whom 13 had known RH-dominant for language as verified with a verbal fluency task during fMRI scanning (Van der Haegen et al., 2011). Accordingly, our participant sample could be grouped into right-handed participants (*n* = 69), left-handed participants of whom hemispheric dominance for language was unknown (*n* = 40, including the 10 Ghent participants who had not undergone fMRI scanning), and left-handed RH-dominant participants (*n* = 13).

Participants received course credit or a monetary compensation for their participation. The ethical committee of the Psychology Department of the University of Groningen approved the experimental procedure, and all participants gave informed consent before the start of the experiment.

Tasks

Over the past decades of lateralization research, a wide variety of tasks have been devised to measure lateralization of information processing. For the current study, we used a series of tasks that we have previously shown to produce reliable evidence for population-typical visual lateralization in right-handed participants (Brederoo et al., 2019). A detailed description of these tasks and their methods can thus be found in our earlier study. The only general difference to the earlier study is that in the present study an in-house manufactured button box was used to collect responses in all tasks. A short description of each of the tasks will now follow, and the minor differences to the earlier study (Brederoo et al., 2019) will be mentioned.

In the Face Similarity Task (Brederoo et al., 2019) –assessing lateralized face processing–, participants were presented with a neutral face image and two symmetrical composites of that same image: one consisting of twice the left side, the other of twice the right side of the original image. Participants then had to judge which of the two composite faces resembled the original image most. In the Lexical Decision Task (Hausmann et al., 2019; Willemin et al., 2016) –assesing lateralized word processing–, participants saw strings of letters to the left and right of a central fixation point. Participants had to indicate whether the left, right, or neither of the letter strings was a valid word. In the Picture Matching Task (Peyrin, Mermillod, et al., 2006) –assessing lateralized spatial frequency processing–, participants were presented with images of natural scenes. A first centrally presented image (S1) was followed by the same or a different image (S2) to the left or right of central fixation, the latter one being filtered to contain only relatively low or high spatial frequencies. Participants indicated whether the S1 and S2 had depicted the same natural scene. Of note is the fact that in our previous replication study, the Picture Matching Task produced less convincing results than the other tasks used in the current study (Brederoo et al., 2019). We opted to use it nevertheless, as we were unaware of a more suitable task to measure lateralization of spatial frequency processing. In the Hierarchical Letter Task (Brederoo et al., 2017) –assessing lateralized global form and local feature processing–, participants were shown so-called Navon letters, one to the right and one to the left of a central fixation point. A pre-specified target letter could appear as the local elements making up one of the Navon letters, as the global Navon letter, or be absent. Participants indicated whether the target letter had been present. In contrast to the earlier study (Brederoo et al., 2019), only bilateral presentation was used and the presentation durations were slightly different: a trial started with a blank screen, lasting 280 ms, followed by a centrally displayed fixation asterisk for 500 ms, and the Navon letters were presented for 100 ms. In the

Landmark Task (Cai et al., 2013; Linnell, Caparos, & Davidoff, 2014) – assessing spatial attention bias–, participants were presented with a horizontal line that was transected by a vertical line at 0.2°, 0.6°, or 1° to the left or right from the midpoint[18]. Participants had to judge whether the transection occurred to the left or right of the midline.

General procedure

The experiments took place in a darkened and sound-attenuated room. Distance to the monitor (22", 1280 x 1024, 100 Hz in Groningen; 24", 1920 x 1080, 100 Hz in Ghent) was kept fixed using a chin rest to ensure stability of the visual angle. All experimental tasks were run in E-Prime (E-prime Psychology Software Tools Inc., Pittsburgh, USA), and were preceded by the Flinders Handedness Questionnaire to measure handedness and the Dolman Method to measure eye dominance. As eye dominance is not a focus of this study, we will not elaborate further on it.

As the strength of RH-lateralization in the Landmark Task has been suggested to decrease over the course of an experimental session (Manly et al., 2005), participants always completed this task at the start of the session. After that, the participants performed the remaining tasks (Face Similarity; Lexical Decision; Picture Matching; and Hierarchical Letter Tasks), the order of which was randomized and counter-balanced over participants[19].

Data pre-processing

Before analyses, we inspected the data per task to remove the data of participants who performed at chance level. To do so, error rates (ERs) were computed separately for left visual field (LVF) and right visual field (RVF) trials in the visual half-field tasks. A participant's data were removed only when he or she performed at chance level in both the LVF and RVF, assuming that when performance is at chance level in one but not the other visual field this could be considered to reflect lateralization rather than poor performance. Removing data when performance in both visual fields was at chance resulted in missing data of 1 participant for word processing, 1 for LSF processing, 1 for HSF processing, 10 for local processing, and 1 for global processing. Due to a coding error, 2 participants' data were lost for spatial attention.

We used the outlier removal procedure as described by Van Selst and Jolicoeur (1994) to remove outliers in the RT data. This resulted in the removal of 1.64% of the trials in the Hierarchical Letter Task, 2.23% in the Lexical Decision Task, and 2.58% in the Picture Matching Task.

For each of the tasks, we first conducted analyses to confirm that they produced the expected, population-typical lateralization effects. LVF and RVF performance were compared using paired *t*-tests on ERs and RTs to assess lateralized processing of LSF and HSF, global and local, and word processing. Lateralization of face processing and spatial attention were assessed with a one-sample *t*-test, testing the difference of the visual field bias against zero.

The results of these analyses, reported in Appendix C, showed that, except for the Picture Matching Task, all of the tasks indeed produced the expected lateralization effects, thus corroborating the findings of our earlier study (Brederoo et al., 2019).

Correlation analysis

Outcome variables for correlational analyses. The main analysis of interest examined the correlations between lateralization indices of the different processes. To assess the degree of lateralization for each process, we derived a scaled index for the extent to which performance and judgments differed for stimuli shown in the left and right visual fields. For performance-based measures (i.e., error rates and reaction times), this index was computed by subtracting a participant's RVF-performance from his or her LVF-performance, and dividing it by the sum of both. Accordingly, positive values for these indices indicate the presence of an RVF-advantage, suggestive of LH-dominance for the task in question, whereas negative values indicate the presence of an LVF-advantage.

For the Face Similarity Task, an analogue to a performance-based index of lateralization was derived by subtracting the proportion of choice for the right composite face (indicating that participants judged the face based on the facial information on the right side) from the proportion choice for the left composite face (indicating that participants judged the face based on the facial information on the left side). Thus, negative values on this measure of the Face Similarity Task indicate an LVF-advantage in processing faces, while positive values indicate an RVF-advantage.

Lastly, for the Landmark Task, the index of lateralization was defined as the point of subjective equality (PSE), with 0 being assigned to the veridical point of equality. Consequently, negative values for the outcome of the Landmark Task indicate an LVF-bias suggestive of RH-dominance in allocating spatial attention, whereas positive values indicate an RVF-bias indicative of LH-dominance in spatial attention.

Statistical analysis of correlations. To assess the extent to which our data supported the presence (H1) or absence (H0) of the hypothesized correlations (see p. 104), we used Bayesian analyses. An advantage of Bayesian statistics over null hypothesis significance testing (NHST) is that it provides information about the likelihood of the null hypothesis being true, given the data. In contrast, NHST only allows for rejection of the null hypothesis. Specifically, in Bayesian analyses, evidence is based on the relative plausibility of the data under the alternative (H1) versus the null hypothesis (H0) (Wagenmakers et al., 2017). A Bayesian analysis produces a Bayes factor (BF_{10}), where $BF_{10} > 3$ indicates moderate, $BF_{10} > 10$ indicates strong, $BF_{10} > 30$ indicates very strong, and $BF_{10} > 100$ indicates extreme evidence for H1, while $BF_{10} < 1/3$ indicates moderate, $BF_{10} < 1/10$ indicates strong, $BF_{10} < 1/30$ indicates very strong, and $BF_{10} < 1/100$ indicates extreme evidence for H0 (Jeffreys, 1961). When the BF_{10} ranges between 3 and 1/3, the data are said to be inconclusive with regard to the hypotheses. We computed pairwise correlations for each possible pair of lateralization effects using the libDienesBayes package in R, and used a uniform prior (making no specific predictions with regard to the strength of the correlations) with the lowest split-half reliability of the two correlated lateralization indices as upper bound. The reported correlations were corrected by accounting for the split-half reliabilities of both measures ($r_{corrected} = r / \sqrt{[\text{reliability}_1 * \text{reliability}_2]}$). These choices for an upper bound of the lowest split-half reliability in the Bayesian analyses, and for correction of the correlations with the split-half reliabilities, were made on the grounds that a measure cannot show a larger correlation with another measure than it can with itself. Split-half reliability was computed as the correlation between lateralization indices for odd and even trials in each task, corrected for halving the length of the task by means of the Spearman-Brown formula (Appendix C). In each of the tasks, there were equal numbers of LVF- and RVF-trials within blocks, and randomized presentation order per participant, warranting the calculation of split-half reliabilities.

Subgroup-comparisons

We contrasted the lateralization effects for right-, left-handed, and RH-dominant participants. All these paired contrasts were made using one-sided Bayesian *t*-tests, based on the associated hypotheses (see p. 103).

Results

In all tasks, there was substantial evidence for the expected RVF- and LVF-advantages, with the exception of those in the Picture Matching Task, which showed no evidence for the presence of an RVF-advantage for HSF processing (Appendix C). Nevertheless, we did include this non-significant RVF-advantage in all following analyses, as there could still be a relation of HSF-lateralization to lateralization of the other processes and/or differences between subgroups. Split-half reliability of each of the measures was good (all $BF_{10} > 38$), ranging from $r = .45$ for HSF processing to $r = .86$ for word processing (Appendix C).

In the following, for all derived laterality indices and statistics, positive values indicate RVF/LH-lateralization, and negative values indicate LVF/RH-lateralization.

Correlations between lateralization indices

We here report the correlations for which we found at least substantial evidence in favor of their presence (see Figure 20) or absence. For an overview of all correlations, including those for which the data were inconclusive, see Appendix C.

Lateralization of face processing related to lateralization of three other processes. The stronger RH-lateralization for face processing, the stronger (1) LH-lateralization for word processing (RTs)[20] ($r_{corrected} = -.29$, $BF_{10} = 6.12$, $t[119] = -2.42$); (2) LH-lateralization for local processing (RTs) ($r_{corrected} = -.33$, $BF_{10} = 8.76$, $t[110] = -2.55$); and (3) RH-lateralization for global processing (ERs) ($r_{corrected} = .39$, $BF_{10} = 11.15$, $t[119] = 2.53$). There was no correlation between face lateralization and lateralization of HSF or LSF processing (BFs < .303).

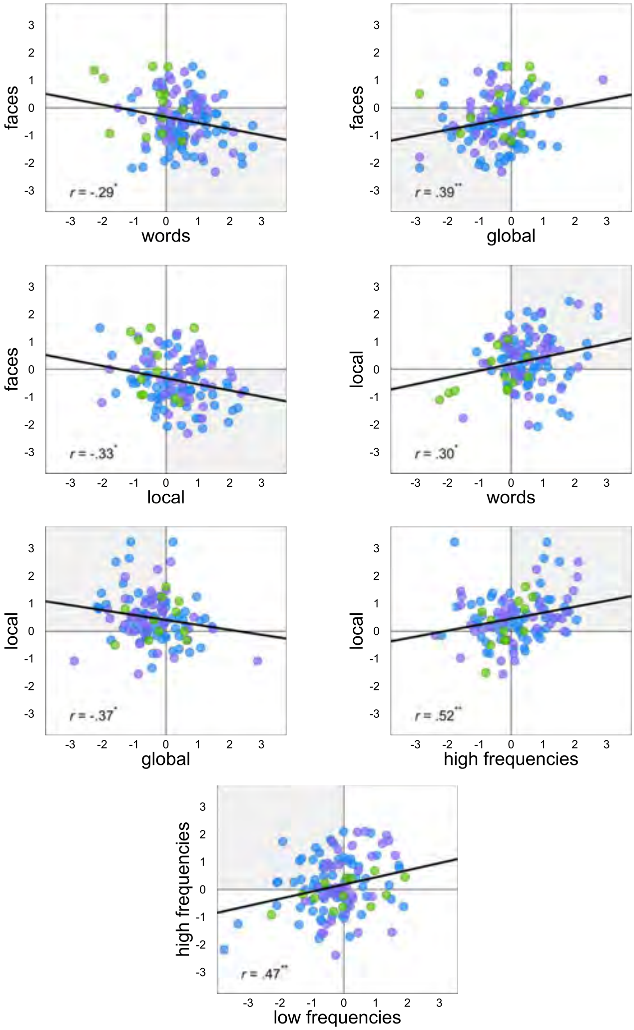


Figure 20. Correlations between scaled lateralization indices of right-handed (blue), left-handed (purple), and RH-dominant (green) participants. In each diagram, the grey-colored area depicts the locus of typical lateralization patterns. Larger positive and negative values indicate larger RVF- and LVF-advantages, respectively. ** $BF_{10} > 10$; * $BF_{10} > 3.16$.

Second, in addition to its relation with face processing, word processing also correlated with local processing: the stronger LH-lateralization for word processing (RTs), the stronger LH-lateralization for local processing (RTs) ($r_{corrected}$ = .30, BF_{10} = 6.49, *t*[109] = 2.47). Stronger LH-lateralization for local processing (ERs) was in turn associated with stronger LH-lateralization for HSF processing ($r_{corrected}$ = .52, BF_{10} = 17.9, *t*[108] = 2.67). In testing the associations between contralateral lateralization for lower-level processes we found that stronger RH-lateralization for global processing (ERs) was associated with stronger LH-lateralization for local processing (ERs) ($r_{corrected}$ = -.37, BF_{10} = 3.01, *t*[109] = -1.92), but that stronger RH-lateralization for LSF processing was associated with weaker LH-lateralization for HSF processing ($r_{corrected}$ = .47, BF_{10} = 29.7, *t*[118] = 2.87). There were no relations between spatial attention bias and lateralization of the other visual processes, with inconclusive evidence with regard to positive relations with lateralization of global processing (BF_{10} = .629, *t*[112] = .945) and that of word processing (BF_{10} = .532, *t*[112] = 1.16), and support for the absence of any relations with lateralization of the other processes (all $BF_{10} < .25$, $|t| < .529$).

Lateralization indices per subgroup

Lateralization indices per subgroup can be found in Figure 21. Right-handed participants as a group showed all typical lateralization effects ($BF_{10} > 4.9$, $|t| > 2.5$), except for inconclusive evidence with regard to LH-lateralization for HSF processing (BF_{10} = .591, *t*[67] = 1.37).

Left-handed participants showed typical lateralization effects ($BF_{10} > 12.76$, $|t| > 2.9$), except for the absence of RH-lateralization for LSF processing (BF_{10} = .104, *t*[38] = .783) and RH spatial attention bias (BF_{10} = .266, *t*[38] = -.5), and they showed inconclusive evidence with regard to RH-lateralization for face processing (BF_{10} = 1.51, *t*[39] = -1.84), and LH-lateralization for HSF processing (BF_{10} = .389, *t*[38] = .862).

RH-dominant participants did not show the expected reversed lateralization effects (all $BF_{10} < 2.37$ for reversed effects), but did not show typical lateralization either, as for all types of processing typical effects were absent or data were inconclusive. Specifically, in RH-dominant participants the evidence supported the absence of RH-lateralization for face processing (BF_{10} = .193, *t*[12] = .571), of RH-lateralization for LSF processing

(BF_{10} = .279, t[12] = -.005), and of LH-lateralization for HSF processing (BF_{10} = .163, t[12] = -.912). Furthermore, LH-lateralization for word processing for RH-dominant participants was absent in RTs (BF_{10} = .113, t[12] = -1.98), and data were inconclusive regarding this effect in ERs (BF_{10} = 1.44, t[12] = 1.61). Similarly, LH-lateralization for local processing was absent RTs (BF_{10} = .161, t[11] = -1.03), and data were inconclusive in ERs (BF_{10} = .747, t[11] = 1.05). With regard to RH-lateralization for global processing, data were inconclusive both in ERs (BF_{10} = 1.13, t[11] = -1.4) and RTs (BF_{10} = .348, t[11] = -.247).

Differences between subgroups. Group-wise comparisons between the three groups showed that right-handed participants had stronger RH-lateralization for face processing than left-handed participants (BF_{10} = 5.43, t[82] = -2.42) and than RH-dominant participants (BF_{10} = 25.49, t[15] = -2.73). Right-handed participants also had stronger LH-lateralization for word processing (RTs) than RH-dominant participants (BF_{10} = 1445, t[16] = 4.24). Finally, they had stronger RH-lateralization for LSF processing than left-handed participants (BF_{10} = 8.38, t[103] = -2.92).

RH-dominant participants, furthermore, differed from left-handed participants in weaker LH-lateralization for word processing (RTs) (BF_{10} = 94.71, t[18] = 3.38), and local processing (RTs) (BF_{10} = 5.21, t[23] = 2.7), and weaker RH-lateralization for global processing (RTs) (BF_{10} = 6.15, t[15] = -2.06).

In addition to the presence of these subgroup differences, we found support for the absence of a number of differences. Right-handed participants did not differ from left-handed participants with regard to lateralization of local processing in ERs (BF_{10} = .258, t[85] = .234) or RTs (BF_{10} = .128, t[86] = -.831), of global processing in ERs (BF_{10} = .186, t[76] = .159) or RTs (BF_{10} = .134, t[92] = .717), of word processing (ERs) (BF_{10} = .243, t[77] = .184), and in HSF processing (BF_{10} = .209, t[67] = -.014). Right-handed participants did not differ from RH-dominant participants with regard to lateralization of global processing (ERs) (BF_{10} = .3, t[14] = .039), or in spatial attention bias (BF_{10} = .255, t[14] = .183). RH-dominant participants did not differ from left-handed participants with regard to lateralization of LSF processing (BF_{10} = .25, t[15] = .265), or in spatial attention bias (BF_{10} = .174, t[17] = .88).

Evidence was inconclusive for all other pairwise comparisons between the subgroups ($BF_{10} > .33 < 2.57$, $|t| < 1.74$).

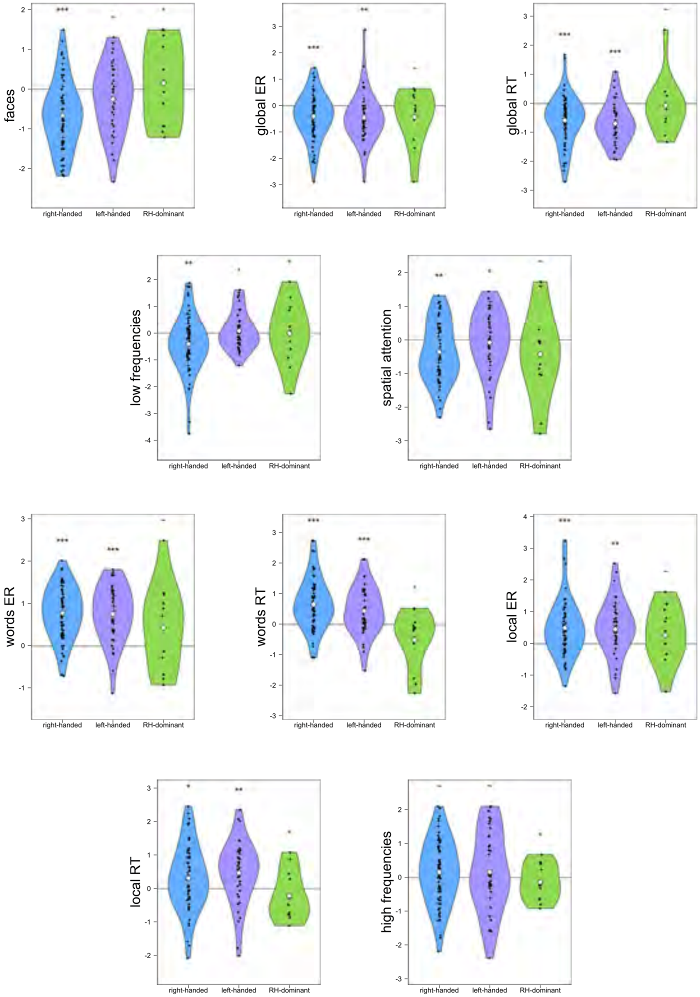


Figure 21. Lateralization indices and accompanying probability densities for right-handed, left-handed, and RH-dominant participants. Represented values are the scaled indices by dividing by the root mean square. White diamonds represent the means, where larger positive and negative values indicate larger RVF- and LVF-advantages, respectively. *** $BF_{10} > 100$; ** $BF_{10} > 10$; * $BF_{10} > 3.16$; ~ $BF_{10} > .316 < 3.16$; x $BF_{10} < .316$, where H_1 is that the mean is higher of lower (depending on the hypothesis) than zero.

Discussion

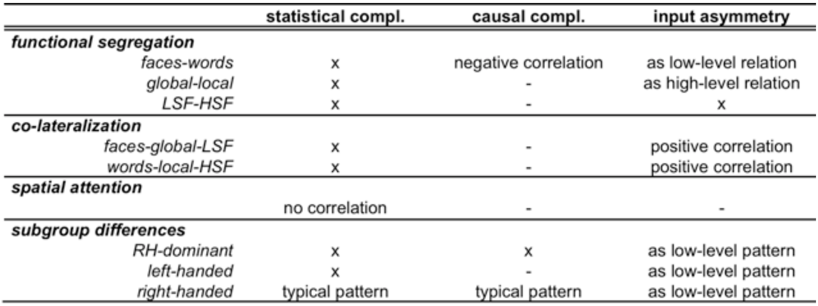
Summary of results

Before evaluating our findings in light of the previously proposed principles underlying patterns of lateralization, we present a short summary of the results. As predicted, group-level analyses indeed gave rise to a ‘typical’ pattern of lateralization: left hemisphere (LH) processing of words and local features; right hemisphere (RH) processing of faces, global form, and low spatial frequencies (LSF), and a RH spatial-attention bias. The evidence for the expected LH-lateralization of high spatial frequency (HSF) information processing was not substantial, confirming neither its presence nor its absence in the group as a whole.

In addition to the group-level analyses, we investigated possible differences between right-handed, left-handed, and RH-dominant participants. We found that, as a group, right-handed participants showed the typical lateralization pattern, with the exception of LH-lateralization for HSF processing. RH-dominant participants did not show the expected reversed lateralization pattern, but their results were characterized by an absence of lateralization effects, with the exception of inconclusive data with regard to RH-lateralization for global processing and RH spatial attention bias. Left-handed participants showed results more similar to right-handed participants than did the RH-dominant participants, but still deviated from the typical pattern. For left-handed participants, RH-lateralization for LSF processing and RH spatial attention bias were absent, and the data were inconclusive with regard to RH-lateralization for face processing and LH-lateralization for HSF. Left-handed participants did show typical lateralization for word, local, and global processing.

Principles governing patterns of lateralized processing

When considering the implications of the current findings for the previously proposed principles underlying patterns of lateralization, we can conclude that the input asymmetry and causal complementarity principles are best supported (Table 2). These principles are not mutually exclusive, but rather complement each other in explaining how lateralization of related processes comes about.



	statistical compl.	causal compl.	input asymmetry
functional segregation			
faces-words	x	negative correlation	as low-level relation
global-local	x	-	as high-level relation
LSF-HSF	x	-	x
co-lateralization			
faces-global-LSF	x	-	positive correlation
words-local-HSF	x	-	positive correlation
spatial attention			
	no correlation	-	-
subgroup differences			
RH-dominant	x	x	as low-level pattern
left-handed	x	-	as low-level pattern
right-handed	typical pattern	typical pattern	as low-level pattern

Table 2. Summary of results. ‘x’s appear where a prediction is not supported.

Mixed support for causal complementarity. In accordance with the causal complementarity principle (Bryden et al., 1983), which proposes that different processes recruiting similar brain regions will come to be lateralized to homologue areas in opposite hemispheres, our correlational analyses support a relation between LH-lateralization for word processing and RH-lateralization for face processing, where an increase of one co-occurs with an increase in the other. This is in line with a similar correlation found between the strength of LH-lateralization for visual word processing and that of RH-lateralization for face processing in a group of children who were learning to read (Dundas et al., 2016). Our results furthermore corroborate those reported by Badzakova-Trajkov et al. (2010) and Gerrits et al. (2019). In both these neuroimaging studies, LH-lateralization of brain regions activated during language production (i.e., letter fluency task) correlated with RH-lateralization of brain regions activated during face perception.

While the causal complementarity principle further predicts reversed lateralization patterns (i.e., LH-lateralization for face processing and RH-lateralization for word processing) for individuals who are RH-dominant for language, our data did not support such a pattern. Instead, the subgroup of participants who were RH-dominant for language showed an absence of RH-lateralization for face and LH-lateralization for word processing. One possible interpretation of the absence of reversed typical lateralization patterns in RH-dominant individuals is that causal complementarity is not a very strong driving force for functional segregation, resulting in subtle lateralization patterns. As a case in point, Badzakova-Trajkov et al. (2016) suggest that the mirroring of different functions to homologue areas does not take place as absolutely as the causal complementarity principle would dictate. Their results show that while –as predicted by the causal complementarity principle– one part of Broca's homologue in the RH is activated by face stimuli (i.e., the pars opercularis), another part of Broca's RH-homologue (i.e., the pars triangularis) is not. Relating to this, Häberling et al. (2016) entertain the possibility that lateralized brain systems can evolve following the causal complementarity principle (i.e., by competing pressure for cortical space), but once instantiated will go on to develop more independently. As a result, a directly observable relation between the functionally segregated functions will dissipate over the course of evolution.

Alternatively, it is possible that causal complementarity underlies the functional segregation of face and word processing, and that RH-dominant individuals in fact do tend to display reversed patterns, but that our sample of $n = 13$ was too small to detect this. What we can conclude based on our Bayesian analyses, is that in case of the RH-dominant participants the data supported the absence of typical lateralization of face and word processing. Due to practical limitations, we were unfortunately unable to enlarge our sample of RH-dominant participants.

Finally, these findings could indicate that lateralized processing in RH-dominant individuals does not adhere to the same principles as it does in LH-dominant individuals. Given the scarcity (±6%, Knecht et al., 2000) of RH-dominance for language, it is unsurprising that our understanding of lateralization in this group of individuals is limited as of yet (see also Vingerhoets, 2019). Our results can be taken as encouragement for future research to further explore lateralized processing in its atypical as well as typical form.

Support for input asymmetry. In support of the input asymmetry principle, we found the predicted correlations between lateralization of low-level processes and lateralization of associated higher-level processes in the same hemisphere (Andresen & Marsolek, 2005). The only such predicted relation for which we did not find conclusive support was that between lateralization of face and LSF processing. Specifically, as predicted by the input asymmetry principle, we generally found that stronger LH-lateralization for local feature processing was associated with stronger LH-lateralization for word- and HSF-processing. Complementing this, stronger RH-lateralization for face processing was associated with stronger RH-lateralization for global form processing. We further found that stronger RH-lateralization for face processing was associated with stronger LH-lateralization for local feature processing. However, the input asymmetry principle also predicted positive relations between RH-lateralization for face processing and LSF processing, and between LH-lateralization for word processing and HSF processing; relations which were absent in the present study. The input asymmetry principle further predicted the relation of lower-level processes to mirror those of higher-level processes. Indeed, in our data the stronger RH-lateralization for global processing was associated with stronger LH-lateralization for local processing, which is in accordance with the relation between the higher-level face and word processing.

Furthermore, rather than making predictions with regard to typical and atypical lateralization patterns in individuals varying in handedness and hemispheric dominance for language, the input asymmetry principle predicts that whatever is the pattern found for lower-level processes, should be the pattern found for higher-level processes. Indeed, our results support this notion in that (1) typical lateralization of spatial frequencies (with the exception of HSF processing) and global and local processing co-occurred with typical lateralization of face and word processing; and (2) the absence of lateralization of spatial frequencies co-occurred with absence of lateralization of face and word processing in RH-dominant individuals. As such, lateralization patterns, or lack thereof, of higher-level processes mirrors that of lower-level processes.

Statistical complementarity for attention and vision. According to the statistical complementarity principle, the distribution of lateralization of different processes arises by chance (Bryden et al., 1983). Based on a factor analysis of neuroimaging data, Liu et al. (2009) suggested that such independent lateralization is the case for the domains of vision, language, attention, and internal thought. In line with Liu et al. (2009), we showed that spatial attention bias does not relate to lateralization of any of the other processes, and as such can be considered to be statistically independent from lateralization of the remaining visual processes under study. This is in line with the factor-analysis reported in Badzakova-Trajkov (2016), which also suggested the existence of independently lateralized brain systems for face processing and spatial attention. Furthermore, in showing that our handedness groups differed in language lateralization but not in spatial attention bias, we corroborated earlier findings (Badzakova-Trajkov et al., 2010; Karlsson, Johnstone, & Carey, 2019), and provided further support for statistical independence of spatial attention and language lateralization.

However, our results differ from two earlier studies showing support for causal complementarity of spatial attention and language production (Cai et al., 2013; Zago et al., 2015). Specifically, these studies showed reversed typical patterns consisting of LH-lateralization for spatial attention and RH-lateralization for verbal fluency in a group of RH-dominant individuals (Cai et al., 2013), and a correlation between RH-lateralization for spatial attention and LH-lateralization for language production in a group of left-handed participants (Zago et al., 2015). In accommodating these differences with our results, it is important to note that our sample included right-handed as well as left-handed participants, while these results by Cai et al. (2013) and Zago et al. (2015) are based on groups consisting solely of left-handed participants. Zago et al. (2015) separately tested a group of right-handed participants, and found no evidence for a relation between spatial attention and language within this group. In the study by Zago et al. (2015), right-handed and left-handed participants were not pooled together for the analyses, unfortunately precluding a direct comparison with our results. In relation to this, Gerrits et al. (2019) –using a sample of only left-handed participants, failed to show a relation between lateralization for face processing and visual word processing (with $p = .065$), while in our data this correlation was evident. These observations may be taken as a reminder of caution in selecting participants; while in laterality research it is important and fortunately good custom to include left-handed participants, the exclusion of right-handed participants may come with its own price. To prevent the emergence of incomplete or distorted depictions of lateralization patterns, future research on this topic should use participant samples that are maximally heterogeneous with regard to handedness and hemispheric dominance for language.

Finally, we showed that lateralization of processes within the domain of vision are not statistically independent: lateralization of each of the measures of visual information processing was correlated to lateralization of another. Furthermore, the statistical complementarity principle predicts there to be no difference in lateralization patterns between individuals based on their handedness and/or hemispheric dominance for language. As described above, right-handed, left-handed, and RH-dominant participants were in fact shown to differ in terms of lateralization patterns, further discrediting the notion of independent lateralization of the visual processes under study. Taken together, our results support statistical independence of the lateralization of attention and vision, but not within the domain of vision.

Conclusion

In sum, the typical and deviating patterns of lateralization of face, word, global form, local feature, low and high spatial frequency processing can best be explained by the governing principles of input asymmetry and, to a lesser extent, causal complementarity. Our results are partly in line with the notion that processes recruiting similar resources will come to be lateralized to homologue areas in a manner that promotes intra-hemispheric proximity to other cortical areas within their processing hierarchies. In the case of word and face processing, the former will be driven to the LH because of its specialization in language, local feature and high spatial frequency processing, while the latter will be driven to the RH because of its specialization in global form and low spatial frequency processing. We further suggest that statistical complementarity applies to the relation between lateralization of attention and vision.

In the present study, group-level analyses gave rise to typical lateralization patterns, while separate analyses for subgroups differing in terms of handedness and RH-dominance for language provided a more nuanced view. Future research should keep studying lateralized processing in individuals who are expected to deviate from typical patterns, so as to increase our understanding of hemispheric specialization in all its diversity and complexity.

5

Unifying views

CHAPTER 5

Summary of main findings

With the work presented in this thesis I intend to provide a unified view of lateralized vision. Before returning to the central question of this thesis, I will shortly summarize the main findings.

In Chapter 2, I reported the results of a study investigating the reproducibility of visual-field asymmetries, thereby assessing their reliability as behavioral indices for lateralized visual processing. In order to do so, I performed exact or near-exact replications of nine previous 'hallmark' studies using the visual half-field paradigm, together encompassing eleven types of visual information that had been proposed to be processed in a lateralized fashion. Bayesian statistical analyses confirmed the lateralized processing of face expressions and identity, words, global form, local features, and spatial attention. I failed to replicate lateralization of coordinate and spatial relation processing, and of within- and between-category processing of objects and colors. The evidence was inconclusive with regard to the presence or absence of lateralization for processing of low (LSF) and high (HSF) spatial frequencies.

In Chapter 3, I tested whether the linguistic nature of stimuli typically used in global/local tasks is responsible for the previously reported lateralization effects. The expected left visual field (LVF) and right visual field (RVF) advantages for global and local processing were present even when using non-linguistic stimuli, thereby ruling out the possibility that global/local lateralization is in fact language lateralization in disguise. However, the LVF-advantage for global processing was larger for linguistic than non-linguistic stimuli, indicating that stimulus type does play a role in lateralized processing of global form.

In Chapter 4, I examined how we can characterize and understand patterns of lateralized visual processing across different types of tasks. This was done with a series of tasks that I had shown to successfully produce visual-field asymmetries (Chapter 2). By having a sample of right- and left-handed participants perform each of these tasks, I showed that visual processes relate to each other in terms of their direction and strength of lateralization. Specifically, correlational analyses indicated that lateralization strength for faces and words is related, offering support for the causal complementarity principle. Such a relation in lateralization strength was also apparent for other processes at different levels of the processing hierarchy (i.e., HSF, local and word processing; global and face processing), offering support for the input asymmetry principle. Contradicting the causal complementarity principle was the absence of ‘reversed typical’ lateralization patterns, which under this theory had been hypothesized to be present in the left-handed individuals who showed right hemisphere (RH) dominance for language. In addition, the finding of several significant associations of strength and direction of lateralization was used to argue against the principle of statistical complementarity, which states that processes become lateralized independently from each other, and as such should be unrelated in terms of strength or direction.

In sum, in light of existing theoretical principles governing lateralization patterns, the results presented in Chapter 4 lend strong support for the input asymmetry principle, weaker support for the causal complementarity principle, and no support for the statistical complementarity principle, when it comes to lateralized processing of visual information.

A unifying principle of lateralized vision

In Chapter 4 I argued that both the input asymmetry and causal complementarity principles can be viewed as governing the found lateralization patterns. However, on further consideration, the input asymmetry principle seems to be able to account for these and previously reported results, without the need to evoke the causal complementarity principle. Moreover, when taking into consideration other studies performed in humans and animals, the support for the causal complementarity principle even seems to break down.

The input asymmetry principle as described by Andresen and Marsolek (2005) states that asymmetries at lower levels of a processing hierarchy are the root cause of lateralization of higher-order processes in that same hierarchy. The Double Filtering by Frequency (DFF) theory of Ivry and Robertson (1998) is a version of the input asymmetry principle. According to this theory, during any visual task (e.g., reading, face recognition) a selection of the task-relevant spatial frequency band is made, and projected to the higher-order visual processing areas of both hemispheres. Next, selective tuning to spatial frequencies on this selected frequency range ensues, with the left hemisphere (LH) processing the relatively high spatial frequencies, and the RH processing the relatively low spatial frequencies within the selected range. As a result, a particular frequency band may be processed in the RH in one instance, and in the left hemisphere (LH) in another. To illustrate, imagine looking at a forest in front of you. You are standing far enough back to see the group of trees, but near enough to discern some of the nearest trees' individual leafs. In processing the image on your retina, your attentional focus will determine what each of your hemispheres is dealing with. When viewing a single tree as part of the forest, your LH will process this one tree while the RH keeps track of the global form of the forest. When focusing on one leaf on this tree, this distribution will shift: the RH now processes the one tree (in its entirety), while the LH processes the leaf. The spatial frequencies present in the image on your retina, obviously, will stay constant throughout this shifting of focus. It is the changing selection of the relevant frequencies that will determine what type of information each of the hemispheres will take on.

Against causal complementarity

Let us, for a moment, go back to the causal complementarity principle, for which I found support in the form of a relation between lateralization strength for processing faces and words (Chapter 4). Behrmann et al. (2015) proposed that causal complementarity explains why people are typically LH-lateralized for words and RH-lateralized for faces. In an EEG-experiment (Dundas, Plaut, & Behrmann, 2014), they showed that children process faces using both hemispheres up until the moment they learn to read. With improving reading performance, the LH becomes lateralized for visual word perception and the RH for face perception. They take these results to indicate that face processing is 'pushed' to the RH-fusiform area once the LH-fusiform area becomes occupied by word processing.

However, there are a few problems with this interpretation. First, this hypothesis predicts that face processing should be bilateral for those who never learn to read. While indeed it has been shown that cortical areas devoted to face processing of illiterate individuals rearrange when they learn to read (Dehaene, Cohen, Morais, & Kolinsky, 2015), there are reports of RH-lateralization for face processing in animals (see below), which the causal complementarity principle cannot account for. Second, under the causal complementarity principle it should not be possible that face processing is atypically lateralized in an individual if word processing is not also atypically lateralized, as the latter is viewed as the driving force of the former. Contradicting this hypothesis is my finding of the opposite (Chapter 4); the number of left-handed participants who showed atypical face lateralization was larger than the number of left-handed participants who showed atypical word lateralization, corroborating similar findings in a number of previous studies (C. Gilbert & Bakan, 1973; Hellige et al., 1994; Levy et al., 1983). Third, the assumption that lateralization of one function will 'push' another function over to the other hemisphere's homologue area is rather crude. If processes compete for cortical space, it is equally possible that only parts of the homologue areas become specialized (Badzakova-Trajkov et al., 2016). In sum, using the causal complementarity principle to explain functional segregation for words and faces is problematic.

If we refute the causal complementarity principle, we still have to explain the finding presented in Chapter 4 that the more LH-lateralized participants are for visual word processing, the more RH-lateralized they are for face processing. The input asymmetry principle typically explains co-lateralization, but functional segregation can in fact be theorized to be the result of co-lateralization of lower- and higher-level processes. If the lateralization of lower-level processing drives the lateralization of higher-level processing (as predicted by input asymmetry), then strong lateralization of lower-level processes should result in strong functional segregation of word and face processing. Speaking in favor of this proposition is the fact that we found a similar relation for global and local processing (Chapter 4): the more LH-lateralized participants were for local processing, the more RH-lateralized they were for global processing. The causal complementarity principle cannot account for this: global and local processing are not localized in homologue areas, as was reviewed in Chapter 3. However, the input asymmetry can. Strong LH-lateralization for local processing co-occurs with strong LH-lateralization for word processing and strong RH-lateralization for global processing co-occurs with strong RH-lateralization for face processing (Chapter 4). Following this, if local and global processing are strongly lateralized to the LH and RH respectively, word and face processing should similarly be strongly lateralized, without there having to be a direct causal relation between lateralization of word processing and that of face processing in itself.

Changing the point of view

When regarding the input asymmetry principle as best explaining the development of co-lateralization as well as functional segregation of visual processes as set out above, this has some important implications for how we should view lateralization patterns. Specifically, the literature on this subject has been dominated by the view that handedness and language lateralization are the main instantiations of hemispheric asymmetries, and therefore the driving forces behind the lateralization of other functions. This is illustrated by the fact that when 'LH-dominance' or 'RH-dominance' is used in a casual manner, usually LH- or RH-lateralization of language production is implied (of which I too, admittedly, am guilty [Chapter 4]). However, according to the input asymmetry principle, the driving force behind lateralization patterns is not a higher cognitive function such as language, but a lateralization of lower-level perceptual processing. Importantly, while this thesis focuses on visual processing, it should be noted that lateralization of language functioning in the auditory domain can also be understood under the input asymmetry principle. The explanation on spatial frequency processing as given above translates perfectly to that of processing frequencies in the sound spectrum. As speech perception is highly dependent on being able to make fine-grained distinctions in the auditory signal, the LH is the obvious candidate for becoming the language-specialized hemisphere. Note that the DFF (Robertson & Ivry, 1998) is not domain-specific, but indeed provides an account of the development of lateralized processing in both the visual and auditory domains. The fact that lateralized global and local processing seems to have an equivalent in the auditory domain (Wetzel, Ohl, & Scheich, 2008) further supports this.

An additional argument to view lower-level perceptual processing as driving lateralization of higher-order processes such as language, rather than the other way around, is the sheer amount of evidence for lateralized processing in non-human animals. In the introduction to this thesis, I hinted at an explanation of how the brain comes to be functionally lateralized to begin with. It has been suggested that a lateralized brain has greater processing efficiency, as it gives an individual the advantageous ability to perform two complex tasks simultaneously (Rogers, Zucca, & Vallortigara, 2004). In the introduction, I illustrated this using the example of a bird that uses its LH to pick out food whilst using its RH to scan the sky for predators, but lateral asymmetries have been documented in numerous vertebrate (Vallortigara & Rogers, 2005; Rogers, Vallortigara, & Andrews, 2013) and invertebrate (Rogers & Vallortigara, 2015) species. As we share lateralized processing with many other species, phylogenetic development of lateralization implies the root of asymmetries to lie in other functions than language or handedness. An example is LH-lateralization for functions relating to foraging and hunting for prey, which has been shown to exist for a number of animals (see Vallortigara and Rogers, 2005 for a review). Another example is RH-lateralization for predator detection or aggressive responses, which has been demonstrated in birds (Rogers et al., 2004) and lizards (Deckel, 1995), amongst others. In humans, lateralization of 'predator detection' as such has, to my knowledge, never been examined. However, a large body of work exists showing that we are RH-lateralized for processing of stimuli that evoke an emotional response (Gainotti, 2019). In the case of humans, 'predator detection' more likely translates to distinguishing same-species friends from foes. Specifically, facial expressions (Voyer et al., 2012) and emotionally charged language (Godfrey & Grimshaw, 2015) are RH-lateralized in humans. This has also been related to differential lateralization of approach and avoidance behaviors (Rutherford & Lindell, 2011). In a number of domestic animals, lateralized processing of emotion other than predator detection has been shown as well (Leliveld, Langbein, & Puppe, 2013). Furthermore, humans are also RH-lateralized for face recognition in the absence of emotional expressions (i.e., neutral expressions) (Voyer et al., 2012). This RH-lateralization recognition of (non-emotional) faces of other members of our own species is something we share with, at least, chimpanzees (Morris & Hopkins, 1993), sheep (Broad, Mimmack, & Kendrick, 2000), rhesus monkeys and dogs (Guo, Meints, Hall, Hall, & Mills, 2009).

Note that the functions reviewed so far can each be explained in terms of relying predominantly on one end of the frequency spectrum, as they depend either on a global or focal view of the relevant stimuli. This is not undeniably the case for the last lateralized functions to evolve in humans: LH-lateralization for handedness and language. These lateralized functions are not directly observed in other species than humans, but we do share precursors of them with other primates and birds. Hand preferences have been shown in non-human primates (Hopkins, 2006). Manual manipulation of food and tools has been suggested to be LH-lateralized in birds (Rogers, 2002) and primates (Fitch & Braccini, 2013; Meguerditchian et al., 2015), analogous to LH-language and manual lateralization (right-handedness) in humans. Furthermore, some studies indicate LH-lateralization for vocalizations in birds (e.g., Moorman, Gobes, Van de Kamp, Zandbergen, & Bolhuis, 2015).

As literacy is a very recent invention, the neural wiring for visual word recognition will be the result of ontogenetic development (i.e., on the individual level) rather than of phylogenetic development (i.e., on the level of the species). Following the above exposition of the input asymmetry principle, I argue that the ontogenetic development of LH-lateralization for reading has its roots in the phylogenetic development of LH-lateralization for high frequency processing, rather than in the LH-lateralization for language.

In summary, our brains as well as the brains of other animals are prone to utilize both cerebral hemispheres for optimal processing. As a result, the two hemispheres will become differently specialized. Under the influence of lower-level frequency processing asymmetries, differential specializations will develop for higher-order processing of more complex stimuli like words and faces. For humans, a LH that emphasizes relatively high frequencies allows specialized processing of details and, later on in an individual's development, visual word form processing. The RH emphasizes relatively low frequencies, rendering it the designated hemisphere for processing global form and faces. When lower-level processes are strongly lateralized in an individual, higher-level processes in the same processing hierarchy will likewise be strongly lateralized. Similarly, when lower-level processes are weakly lateralized, or lateralized in the other direction than is typical, the same will hold for higher-level processes that rely on it. This will then result in a strong, weak, or reversed functional segregation of visual word and face processing.

While the input asymmetry principle provides a rather encompassing explanation for patterns of lateralized vision, open questions of course remain. Two very basic ones, for example, are why and where the LH-high frequency and RH-low frequency division originate in the first place. Another question is whether the high versus low frequency distinction is the true underlying causal principle. It is imaginable that the driving force is still another one, such as the distinction between ensemble perception, – by exploring statistical regularities in scenes (Alvarez, 2011), versus the perception of individual objects.

A line of research often engaged in when investigating the origins of the functional organization of the brain, is that of genetics. However, most of the genetic inquiries into lateralization have focused on the development of handedness and lateralization for language (for recent reviews, see Esteves, Lopes, Almeida, Sousa, & Leite-Almeida, 2020; McManus, 2019), not vision. Moreover, it is quite likely that the development of lateralization will not only depend on genes, but also on environmental factors, among which are prenatal influences (Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009). Turning again to the animal kingdom, Rogers (1990) showed that in the domestic chick, reversed lateralization for distinguishing food grains from pebbles can be induced by stimulating the (non-preferred) left eye of the chicken embryo inside the egg (although it was not tested whether this also led to reversed lateralization for predator detection with the non-preferred right eye). Recently, Hamaoui et al. (2020) have taken on the task to investigate whether, similarly, intra-uteral position in human fetuses may play a role in the ontogenesis of lateralization. It will be exciting to see if their forthcoming results can inform us on the development of LH-high frequency and RH-low frequency processing.

Concluding, the input asymmetry principle has received less attention in recent years than the statistical and causal complementarity principles. I believe this to be undeserved, as it is the input asymmetry principle that can provide a unifying account of lateralized vision.

Critical asides and future directions

While much of the theory that I present and advocate in this chapter is based on the assumption that spatial frequencies are processed in a lateralized fashion, I was only marginally able to show this in the experiments presented in this thesis. By lack of a better task (see Chapter 2), I used the Picture Matching Task (Peyrin, Mermillod, et al., 2006) to measure lateralized processing for low (LSF) and high (HSF) spatial frequencies. In Chapter 2, I reported support for RH-HSF but not for RH-LSF processing, while in Chapter 4 I found the opposite. There are no obvious identifiable differences between the experiments that could explain these discrepancies. Previous research does support the existence of lateralized spatial frequency processing (Flevaris & Robertson, 2016; Peyrin, Mermillod, et al., 2006). It might, however, be tricky to measure it using a task such as the Picture Matching Task, which due to its complexity can leave unwanted room for noise. Future studies should search for a better suiting task, possibly falling back to earlier paradigms using simple gratings (Kitterle et al., 1992), but optimizing them through careful testing.

Another limitation to the work presented in this thesis is that I have used face processing and processing of emotional facial expression quite interchangeably. The relation between face processing and emotion processing is long-standing and complex (Yovel et al., 2014), but assuming that they are the same in terms of neural underpinnings and –therefore, lateralization, is probably incorrect. In order to deepen the unified view of lateralized vision, the possible distinction between lateralized processing of neutral faces and emotional faces should be investigated.

Beyond vision

Furthermore, the results as presented in this thesis should be extended beyond the domain of vision. Excitingly, recent years have seen an increase in studies assessing patterns of lateralization by acquiring lateralization indices of multiple cross-domain processes within participants. Karlsson, Johnstone, and Carey (2019) performed a large-scale study, testing lateralization of a number of visual and auditory processes, and shedding further light on the relation between handedness and other types of lateralized functions. Gerrits, Verhelst, and Vingerhoets (2020) investigated lateralization of visual, auditory, and motor processing in a sample of participants who were RH-dominant for language. An important finding in their study was that individuals who deviate from typical or reversed typical patterns showed poorer cognitive functioning. Following the theory proposed in this chapter, a fruitful approach for future research could be to group participants based on their hemispheric asymmetries in (spatial and/or auditory) frequency processing, rather than based on their dominant hemisphere for language production. Other interesting avenues for future research are to relate lateralized vision to lateralization of motor-coordination.

Improving reproducibility

Another important consideration for future studies will be the matter of reproducibility. In order for within-subject projects to be optimally valuable, the starting point should always be the selection of tasks that have been verified to produce reliable indices of lateralization. The replication crisis as addressed in Chapter 2 highlights the fact that also the research field of laterality is stained by some spurious effects. As a case in point, consider the so-called 'lateralized Whorf' effect, which was first published in a much-cited paper in the journal PNAS (A.L. Gilbert et al., 2006). We (Chapter 2) and others (Suegami, Aminihajibashi, & Laeng, 2014; Witzel & Gegenfurtner, 2011) later were unable to replicate these findings, showing that the surge of papers in leading journals that had quickly followed the original results had been out of place and likely the result of publication bias. On a similar note, it is alarming that many visual-field asymmetries that can be found in the literature are in fact opposite in direction from what would be predicted based on theory, but not critically evaluated (Peyrin, Mermillod, et al., 2006; Van der Ham & Borst, 2011). Other instances of reversed visual-field asymmetries are explained in terms of stimulus factors (Fink et al., 1997; Kéïta & Bedoin, 2011), but lack thorough argumentation (Chapter 3). Admittedly, I too report two examples of visual-field asymmetries in opposite direction from what was expected in the series of replication experiments in Chapter 2. These unexpected visual-field asymmetries were found using tasks I was unable to replicate (i.e., a task designed to investigate the lateralized Whorf effect and a task designed to investigate lateralized processing of spatial relations). As these visual-field asymmetries in opposite-from-hypothesized directions often are RVF-advantages (where LVF-advantages had been expected), this inspires the question whether there might be something particular about LH-lateralization, for example in relation to task difficulty. Luckily, a simple solution exists to the problem of spurious and unexpected effects, and that is pre-registration of studies. Pre-registration guarantees that null-results are reported (countering publication bias) and forces theoretical interpretation of unexpected results (countering spurious effects to go unexplained), and is becoming more and more common. As I have done in the work presented in this thesis, Bayesian statistics form a further addition to these measures to overcome the replication crisis, and are hopefully the statistics of the future.

For the above reasons, it is reassuring to see that leading scientists in the field of laterality research encourage colleagues to engage in replication research, to pre-register their experiments, and to step away from small samples and single-center studies (Ocklenburg, Berretz, Packheiser, & Friedrich, 2020).

Towards a truly unifying account

The aim of this thesis has been to provide a unified view of lateralized vision, but there have been limitations to the breadth of such a view. Just as our visual fields together span about 180 degrees of the 360 degrees that make up our full surroundings, in presenting this unified account I have turned my back on a number of aspects that will be of importance in arriving at a truly unified account of lateralized processing. Among these is, for example, the role of the corpus callosum and inter-hemispheric connectivity. While the two hemispheres may be functionally specialized, they do not work independently from each other (Gazzaniga, 2000). Furthermore, if indeed a lateralized brain allows for more efficient processing, then being less strongly lateralized would predict performance costs (for a recent investigation of the relation between lateralization direction and cognitive functioning, see Gerrits et al., 2020). Going one step further, links have been made between atypical lateralization and symptoms associated with psychiatric disorders. An example is the role of Broca's right hemisphere homologue in the occurrence and phenomenology of auditory verbal hallucinations (Sommer et al., 2008). Moreover, numerous studies exist that report individual factors –other than handedness and language-dominance, to influence lateralization. To name one, sex hormones are known to play a role both in human (Beking et al., 2018; Hausmann, Becker, Gather, & Güntürkün, 2002) and non-human

(Pfannkuche, Bouma, & Groothuis, 2009) lateralization. Needless to say, the list goes on.

Conclusion

From closely inspecting a number of leafs –the nine individual replication experiments (Chapter 2), to examining the tree of local/global processing and the role of language therein (Chapter 3), I eventually arrived at a view of the forest of lateralized vision in its entirety (Chapters 4 & 5). Here, I have come to the conclusion that patterns of lateralized vision can best be understood as resulting from input asymmetry in lower-level visual processes. The journey could continue by looking at the even larger forest that lateralized vision is merely a part of, and work towards a unified account of brain lateralization in general. However, I foresee the problem that not one person’s right hemisphere will be up to the task of taking such a rigorously global view. A solution to this may be found in the advice Allen Newell gave in 1973, when he said that “Maybe we should cooperate in working on larger experimental wholes than we do now” (Newell, 1973, p. 306). These words are echoed today in a similar address to the community of laterality researchers (Ocklenburg et al., 2020), which I have learned, if anything, is a stimulating community to be a part of.

Appendices

Appendix A

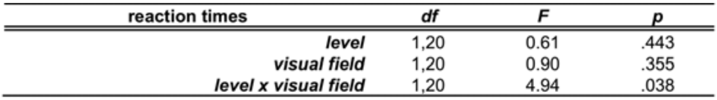
For each of the replication studies that compared visual field performances over different conditions we performed repeated measures ANOVAs, which are reported here. Significant main and interaction effects that do not relate to the VFAs under study are described below the ANOVA-tables. We followed up significant interactions with Bayesian and frequentist t-tests. In a number of these tests, the Bayes factor indicates indecisive evidence, while the p-value is below .05. In these cases, we phrase the results in terms of significant effects to explain the nature of the effects in the ANOVA, but the reader is here alerted to the fact that more data would be needed to substantiate those claims.

Hierarchical Letter Task.

error rates	*df*	*F*	*p*
level	1,20	0.97	.336
visual field	1,20	1.14	.299
level x visual field	1,20	26.9	.000

Table 3. Repeated measures ANOVA on ERs in the Hierarchical Letter Task.

While not the focus of this replication study, we additionally performed an ANOVA including the factor Presentation (unilateral or bilateral blocks), which yielded a main effect (F[1,20] = 9.20, p = .007) indicating that participants performed better in the unilateral presentation blocks (18%, SD = 12%) than in the bilateral presentation blocks (27%, SD = 14%). Furthermore, there was an interaction of Presentation x Level x Visual Field (F[1,20] = 6.28, p = .021). In unilateral presentation blocks, there was indecisive evidence for an RVF-advantage for local processing (BF_{10} = 2.99, t[20] = 2.16, p = .022, d_z = .471) (LVF: 21%, SD = 21%; RVF: 18%, SD = 21%), and an LVF-advantage for global processing (BF_{10} = 1.89, t[20] = -1.87, p = .038, d_z = -.408) (LVF: 14%, SD = 10%; RVF: 18%, SD = 12%). In the bilateral blocks, there was substantial evidence for an RVF-advantage for local processing (BF_{10} = 7.31, t[20] = 2.67, p = .007, d_z = .583) (LVF: 33%, SD = 18%; RVF: 25%, SD = 19%), and strong evidence for an LVF-advantage for global processing ($BF_{10} = 34.7$, $t[20] = -3.47$, $p = .001$, $d_z = -.757$) (LVF: 18%, SD = 15%; RVF: 31%, SD = 19%).

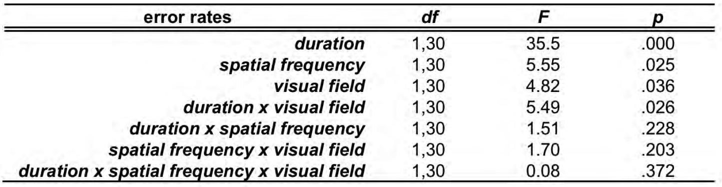


reaction times	*df*	*F*	*p*
level	1,20	0.61	.443
visual field	1,20	0.90	.355
level x visual field	1,20	4.94	.038

Table 4. Repeated measures ANOVA on RTs in the Hierarchical Letter Task.

In an ANOVA including Presentation (unilateral of bilateral blocks), there were no significant effects including this factor (all *F*'s < 3.54, all *p*'s > .073).

Picture Matching Task.



error rates	*df*	*F*	*p*
duration	1,30	35.5	.000
spatial frequency	1,30	5.55	.025
visual field	1,30	4.82	.036
duration x visual field	1,30	5.49	.026
duration x spatial frequency	1,30	1.51	.228
spatial frequency x visual field	1,30	1.70	.203
duration x spatial frequency x visual field	1,30	0.08	.372

Table 5. Repeated measures ANOVA on ERs in the Picture Matching Task.

Participants performed better in the long duration condition (6.9%, SD = 9.7%) than in the short duration condition (26%, SD = 18%). They also performed better in the LSF condition (15%, SD = 11%) than in the HSF condition (18%, SD = 12%), but this was only the case for the short duration trials (short duration: $BF_{10} = 3.99$, $t[30] = 2.70$, p = .011, $d_z = .485$; long duration: $BF_{10} = .197$, $t[30] = .24$, $p = .816$, $d_z = .042$) (short duration-HSF: 28%, SD = 19%; short duration-LSF: 24%, SD = 18%; long duration-HSF: 7.0%, SD = 11%; long duration-LSF: 6.8%, SD = 9.2%). Finally, participants performed better on RVF-trials (15%, SD = 11%) than on LVF-trials (18%, SD = 12%).

reaction times	*df*	*F*	*p*
duration	1,30	17.9	.000
spatial frequency	1,30	0.24	.631
visual field	1,30	1.62	.213
duration x visual field	1,30	0.09	.773
duration x spatial frequency	1,30	2.12	.156
spatial frequency x visual field	1,30	3.88	.058
duration x spatial frequency x visual field	1,30	0.11	.740

Table 6. Repeated measures ANOVA on RTs in the Picture Matching Task.

Participants responded faster in the long duration condition (584 ms, SD = 117 ms) than in the short duration condition (665 ms, SD = 155 ms).

Color Oddball Task.

error rates	*df*	*F*	*p*
pair	1,27	6.86	.014
visual field	1,27	4.30	.048
pair x visual field	1,27	7.12	.013

Table 7. Repeated measures ANOVA on ERs in the Color Oddball Task.

Participants performed better on between-category trials (2.9%, SD = 2.6%) than on within-category trials (4.9%, SD = 3.6%), and better on RVF-trials (2.6%, SD = 2.0%) than on LVF-trials (3.8%, SD = 2.4%).

reaction times	*df*	*F*	*p*
pair	1,27	37.6	.000
visual field	1,27	3.03	.093
pair x visual field	1,27	1.01	.324

Table 8. Repeated measures ANOVA on RTs in the Color Oddball Task.

Participants responded faster on between-category trials (438 ms, SD = 60 ms) than on within-category trials (469 ms, SD = 72 ms).

Shape Oddball Task.

error rates	df	F	p
pair	1,25	54.3	.000
visual field	1,25	2.43	.132
pair x visual field	1,25	0.39	.538

Table 9. Repeated measures ANOVA on ERs in the Shape Oddball Task.

Participants performed better on between-category trials (26%, SD = 11%) than on within-category trials (33%, SD = 10%).

reaction times	df	F	p
pair	1,25	17.4	.000
visual field	1,25	1.80	.192
pair x visual field	1,25	0.09	.771

Table 10. Repeated measures ANOVA on RTs in the Shape Oddball Task.

Participants responded faster on between pair trials (698 ms, SD = 180 ms) than on within pair trials (748 ms, SD = 206 ms).

Cross-dot Matching Task.

error rates	df	F	p
spatial strategy	1,32	0.41	.527
task	1,32	29.1	.000
visual field	1,32	0.33	.571
spatial strategy x task	1,32	2.67	.112
spatial strategy x visual field	1,32	0.02	.902
task x visual field	1,32	0.05	.831
spatial strategy x task x visual field	1,32	0.30	.586

Table 11. Repeated measures ANOVA on ERs in the Cross-dot Matching Task.

Participants performed better on the categorical task (18%, SD = 14%) than on the coordinate task (30%, SD = 8.3%).

reaction times	*df*	*F*	*p*
spatial strategy	1,32	0.22	.641
task	1,32	2.35	.135
visual field	1,32	1.19	.284
spatial strategy x task	1,32	0.00	.958
spatial strategy x visual field	1,32	0.21	.654
task x visual field	1,32	0.19	.663
spatial strategy x task x visual field	1,32	0.30	.590

Table 12. Repeated measures ANOVA on RTs in the Cross-dot Matching Task.

Appendix B

Analyses on reaction times. The results of analyses on the reaction times (RTs) are presented here to illustrate the absence of speed-accuracy trade-offs. The RTs were subjected to the same analyses as the ERs, after removing responses that were identified as outliers (2.1% of the trials), following Van Selst and Jolicoeur's method (1994).

reaction times	
lateralization	$F_{\text{level x visual field}}[1,16] = 15.7, p = .001$
local-RVF	$t[16] = 1.36, p = .096$
global-LVF	$t[16] = -3.68, p = .001$
local-RVF vs global-LVF	$t[16] = -0.95, p = .356$
modulation of lateralization by stimulus type	$F_{\text{level x visual field x stimulus type}}[1,16] = 6.71, p = .020$
lateralization letters	$F_{\text{level x visual field}}[1,16] = 20.6, p < .001$
lateralization figures	$F_{\text{level x visual field}}[1,16] = 0.74, p = .403$
local-RVF letters	$t[16] = 1.96, p = .034$
global-LVF letters	$t[16] = -4.60, p < .001$
local-RVF figures	$t[16] = 0.38, p = .356$
global-LVF figures	$t[16] = -0.53, p = .301$
local-RVF letters vs local-RVF figures	$t[16] = 0.88, p = .392$
global-LVF letters vs global-LVF figures	$t[16] = -3.22, p = .005$
LVF global-local difference in letters vs figures	$t[16] = 1.10, p = .290$
RVF global-local difference in letters vs figures	$t[16] = -2.27, p = .037$
modulation of lateralization by manner of presentation	$F_{\text{level x visual field x presentation}}[1,16] = 5.82, p = .028$

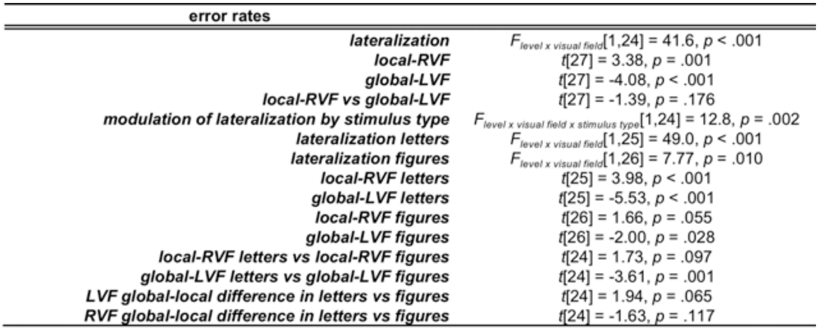
Table 13. Results of *F*- and *t*-tests on RTs, analogous to those on the ERs.

All but a few of the effects that were significant in the ERs were also significant in the RTs. The effects that did not reach significance in RTs (i.e. the general local-RVF advantage, and the lateralization effects in the figure trials), were in the same direction as in the ERs, thus ruling out a speed-accuracy trade-off.

While beyond the scope of Chapter 3, we note that in the RTs there was a significant modulation of the lateralization effects by manner of presentation, yielding significant lateralization effects in the bilateral presentation trials, but not in the unilateral presentation trials. In ERs, the modulation of lateralization by manner of presentation failed to reach significance (p = .071), but seemed to indicate a similar pattern. This corroborates the suggestion by Boles (1987) that bilateral presentation leads to larger and more robust lateralization. A possible explanation for this is that during bilateral presentation, homologue areas are activated in the two hemispheres. This may disrupt the hemispheric transfer of information between these areas (Boles, 1990; 1995), or may induce competition between the hemispheres (Han et al., 2002). It could be hypothesized that unilateral presentation leaves the way open for inter-hemispheric communication, obscuring the product of lateralized processing. When during bilateral presentation the hemispheres have to fend for themselves, this increases the visibility of the hemispheres' disadvantage in processing of their non-preferred levels. However, while most of the studies investigating lateralization of global-local processing used unilateral stimulus presentation, the subset of studies using bilateral presentation yields lateralization effects (Bedson & Turnbull, 2002; Christie et al., 2012; Evans, Shedden, Hevenor, & Hahn, 2000; Kruse & Hübner, 2012; Volberg & Hübner, 2006) as well as null-results (Boles & Karner, 1996; Jiang & Han, 2005). The results of the current study cannot help to resolve this issue, but further highlight the importance of stimulus and task factors in the surfacing of global-local lateralization effects.

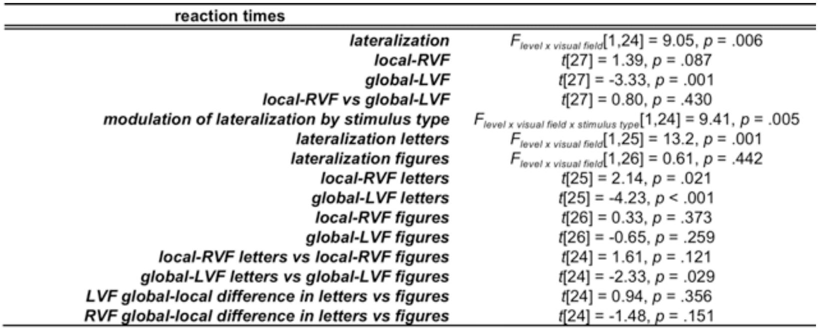
Analyses on complete participant sample. Here we present the analyses on ERs and RTs with the inclusion of all participants' data. Of the 11 participants whose data were left out of the main analyses, some blocks of trials had to be excluded from the analyses presented here, because during these blocks participants (1) largely failed to respond to either the local or global level of the stimuli; (2) mixed up the target and level tasks; or (3) confused the button-response mappings. This led to the exclusion of 42% of these participants' data. Of two participants, all letter blocks had to be excluded, and of one participant all figure blocks. Therefore, these participants could not be included in the grand ANOVA, but they were included in the follow-up tests.

It is likely that we could have prevented the exclusion of participants if we had administered a larger amount of practice trials along with trial-by-trial feedback on responses during these practice trials.



error rates	
lateralization	$F_{level \times visual\ field}[1,24] = 41.6$, $p < .001$
local-RVF	$t[27] = 3.38$, $p = .001$
global-LVF	$t[27] = -4.08$, $p < .001$
local-RVF vs global-LVF	$t[27] = -1.39$, $p = .176$
modulation of lateralization by stimulus type	$F_{level \times visual\ field \times stimulus\ type}[1,24] = 12.8$, $p = .002$
lateralization letters	$F_{level \times visual\ field}[1,25] = 49.0$, $p < .001$
lateralization figures	$F_{level \times visual\ field}[1,26] = 7.77$, $p = .010$
local-RVF letters	$t[25] = 3.98$, $p < .001$
global-LVF letters	$t[25] = -5.53$, $p < .001$
local-RVF figures	$t[26] = 1.66$, $p = .055$
global-LVF figures	$t[26] = -2.00$, $p = .028$
local-RVF letters vs local-RVF figures	$t[24] = 1.73$, $p = .097$
global-LVF letters vs global-LVF figures	$t[24] = -3.61$, $p = .001$
LVF global-local difference in letters vs figures	$t[24] = 1.94$, $p = .065$
RVF global-local difference in letters vs figures	$t[24] = -1.63$, $p = .117$

Table 14. Results of analyses on ERs of the complete participant sample.



reaction times	
lateralization	$F_{level \times visual\ field}[1,24] = 9.05$, $p = .006$
local-RVF	$t[27] = 1.39$, $p = .087$
global-LVF	$t[27] = -3.33$, $p = .001$
local-RVF vs global-LVF	$t[27] = 0.80$, $p = .430$
modulation of lateralization by stimulus type	$F_{level \times visual\ field \times stimulus\ type}[1,24] = 9.41$, $p = .005$
lateralization letters	$F_{level \times visual\ field}[1,25] = 13.2$, $p = .001$
lateralization figures	$F_{level \times visual\ field}[1,26] = 0.61$, $p = .442$
local-RVF letters	$t[25] = 2.14$, $p = .021$
global-LVF letters	$t[25] = -4.23$, $p < .001$
local-RVF figures	$t[26] = 0.33$, $p = .373$
global-LVF figures	$t[26] = -0.65$, $p = .259$
local-RVF letters vs local-RVF figures	$t[24] = 1.61$, $p = .121$
global-LVF letters vs global-LVF figures	$t[24] = -2.33$, $p = .029$
LVF global-local difference in letters vs figures	$t[24] = 0.94$, $p = .356$
RVF global-local difference in letters vs figures	$t[24] = -1.48$, $p = .151$

Table 15. Results of analyses on RTs of the complete participant sample.

The results show that including these participants did not alter the effects in terms of direction and significance. This is with the exception of the local-RVF advantage in ERs of the figure trials, which was significant when excluding the 11 participants (p = .026), and was in the same direction but just failed to reach significance when including these participants (p = .055).

Appendix C

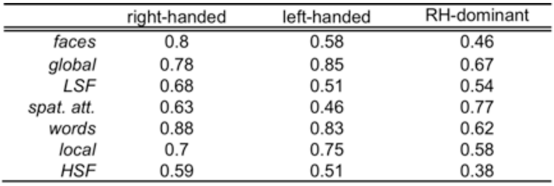
Overview of results.

	mean LVF	mean RVF	BF_{10} LVF-RVF	reliability
words$_{RT}$	849 (124)	803 (108)	5.56×10^5	.8***
words$_{ER}$	45.3 (19.6)	25.7 (15)	1.22×10^{19}	.86***
faces	55.7 (11.9)		49,858	.68***
LSF	669 (118)	677 (115)	1.24	.67***
HSF	683 (122)	677 (119)	0.586	.45**
local$_{RT}$	731 (156)	705 (150)	57.3	.75***
local$_{ER}$	20.2 (13.3)	16 (12.5)	1.99×10^5	.5**
global$_{RT}$	673 (139)	727 (148)	1.96×10^8	.75***
global$_{ER}$	14.9 (9.53)	19.7 (11.3)	1.22×10^5	.49***
spat. att.	-0.05 (0.19)		14	.77***

Table 16. Means and standard deviations for reaction times (ms) and errors rates (%) of the left-visual field (LVF) and right-visual field (RVF) trials for word, local, and global processing; mean proportion (%) of the LVF-choice in face processing; point of subjective equality as indicator of spatial attention bias. Bayes factors for the differences between LVF and RVF means. Split-half reliabilities (Pearson's R correlation) of the LVF-RVF difference, where ** indicates $BF_{10} > 10$; *** indicates $BF_{10} > 30$.

In the Picture Matching Task, in ERs there was no substantial evidence for the presence of the expected visual-field asymmetries in the group as a whole ($BF_{10} < .352$, $|t| < 1.19$), in any of the subgroups ($BF_{10} < 1.48$, $|t| < 1.71$), or for the split-half reliability ($BF_{10} < 1.53$, $|t| < 1.96$) being different from zero ($BF_{10} < 1.16$, $|t| < 1.77$). In RTs, there was, but only for the long duration condition. For these reasons, the analyses on ERs as produced in the Picture Matching Task are not further discussed, and in Chapter 2 all analyses including LSF and HSF processing pertain to those on the RTs of the long duration condition only.

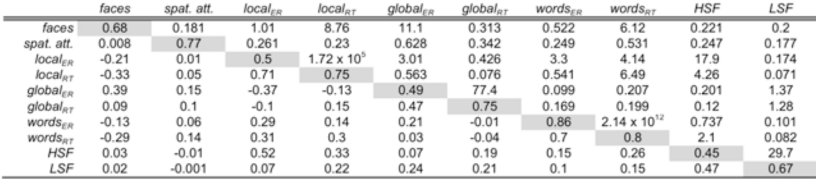
Proportions typical visual-field asymmetries.



	right-handed	left-handed	RH-dominant
faces	0.8	0.58	0.46
global	0.78	0.85	0.67
LSF	0.68	0.51	0.54
spat. att.	0.63	0.46	0.77
words	0.88	0.83	0.62
local	0.7	0.75	0.58
HSF	0.59	0.51	0.38

Table 17. Proportions of participants showing typical visual-field asymmetries within each subgroup (right-handed; left-handed; RH-dominant participants). LVF/RH asymmetries are considered typical for processing of faces, global form, LSF, and spatial attention; RVF/LH asymmetries are considered typical for processing words, local elements, and HSF.

Correlations.



	faces	*spat. att.*	$local_{ER}$	$local_{RT}$	$global_{ER}$	$global_{RT}$	$words_{ER}$	$words_{RT}$	*HSF*	*LSF*
faces	0.68	0.181	1.01	8.76	11.1	0.313	0.522	6.12	0.221	0.2
spat. att.	0.008	0.77	0.261	0.23	0.628	0.342	0.249	0.531	0.247	0.177
$local_{ER}$	-0.21	0.01	0.5	1.72×10^5	3.01	0.426	3.3	4.14	17.9	0.174
$local_{RT}$	-0.33	0.05	0.71	0.75	0.563	0.076	0.541	6.49	4.26	0.071
$global_{ER}$	0.39	0.15	-0.37	-0.13	0.49	77.4	0.099	0.207	0.201	1.37
$global_{RT}$	0.09	0.1	-0.1	0.15	0.47	0.75	0.169	0.199	0.12	1.28
$words_{ER}$	-0.13	0.06	0.29	0.14	0.21	-0.01	0.86	2.14×10^{12}	0.737	0.101
$words_{RT}$	-0.29	0.14	0.31	0.3	0.03	-0.04	0.7	0.8	2.1	0.082
HSF	0.03	-0.01	0.52	0.33	0.07	0.19	0.15	0.26	0.45	29.7
LSF	0.02	-0.001	0.07	0.22	0.24	0.21	0.1	0.15	0.47	0.67

Table 18. Corrected Pearson's R correlations between different measures (below diagonal); accompanying Bayes factors (above diagonal); lowest split-half reliabilities of each measure (on diagonal).

Endnotes

[1] Alternative classifications have been proposed (e.g., Dienes, 2014), but these would lead to a more liberal approach in deciding a replication has failed, rendering them less suitable for the current studies.

[2] We checked whether the length of the task session affected the VFAs in an ANOVA. There showed to be no indication of this (Session Length x Level x Visual Field: $F[1,19] = .721$, $p = .406$ in ERs; and $F[1,19] = .147$, $p = .706$ in RTs).

[3] The original article states that the total practice procedure consisted of eight trials with unfiltered images (Peyrin, Mermillod, et al., 2006). The practice procedure as adopted for this replication, however, is copied from the original experiment E-Prime file, as shared with us by the main author of the study, who confirmed that this in fact was the practice procedure used in the experiment described in the 2006 publication.

[4] With the exclusion of the four participants who failed to put the naming boundary between G2 and B1 (see p. 48).

[5] Pilot studies showed that varying the size of the stimulus ring did not affect the presence of the VFAs.

[6] As a first analysis step we checked whether in our experiment task order (COT or SOT first) affected the VFAs in an ANOVA. There showed to be no indication of this (Task Order x Color Pair x Visual Field: $F[1,26] = .32$, $p = .576$ in ERs; and $F[1,26] = .44$, $p = .513$ in RTs).

[7] With the exclusion of the one participant who failed to put the naming boundary between cats and dogs (see p. 52).

[8] Like for the COT, as a first analysis step we checked whether task order (COT or SOT first) affected the VFAs in an ANOVA. There showed to be no indication for this (Task Order x Color Pair x Visual Field: F[1,24] = .02, p = .878 in ERs; and F[1,24] = 1.84, p = .188 in RTs).

[9] Because we divide the participants into high and low spatial strategy groups based on a median split, there would be 17 participants in each group.

[10] The degrees of freedom were neither in line with the reported sample sizes of the original research article.

[11] We initially performed the power analysis based on the effect size $d = .497$, as reported in the original research article (Linnell et al., 2014), resulting in a required sample size of 27 to reach 80% power. On later inspection, we found this effect size not to correspond to the mean and standard deviation as reported in the article, and to be an overestimation of the actual effect size. We then calculated Cohen's d_z based on the sta-

tistics reported in the article, and refer to this value in the rest of Chapter 2.

[12] We could not compute a meta-analytic Bayes factor for effects for which the original study did not report the outcome of a statistical test.

[13] In total, 28 participants were tested, but the data of 11 participants were not included in the analyses because they failed to follow the instructions during part of the experiment. Analyses including the data of these participants did not alter the results of interest as reported in the main text, and the results of these additional analyses are presented in the Appendix A.

[14] The results of analyses on reaction times are in line with the analyses on the ERs, thus ruling out a speed-accuracy trade-off (Appendix A).

[15] A study by Hübner, Volberg and Studer (2007) reports a significant global-LVF advantage but no local-RVF advantage, in accuracy scores. However, in their reaction time data the local-RVF advantage was nearly significant ($p = .054$), while the global-LVF advantage was absent, indicating speed-accuracy tradeoffs, rather than global lateralization in the absence of local lateralization.

[16] We here adhere to the common calculation of lateralization indices (see p. 109), resulting in values smaller than 0 for RH-lateralization, and larger than 0 for LH-lateralization. Consequently, correlations describing a positive relation in terms of lateralization strength between two processes lateralized to opposite hemispheres, will numerically become negative correlations.

[17] One additional participant was tested in Groningen, but was suspected to be drunk. This participant's data are not included in any of the analyses.

[18] Due to a coding error, participants in Groningen additionally received trials with a transection at 1.4° to the right of the midpoint. These trials are not included in the analyses.

[19] Eighty-six of the participants came back for a second session at the same time of day seven days after they had taken part in the first session. The inclusion of this second session is irrelevant to the purposes of the current study as it served to examine previous suggestions that lateralization effects may dissipate with repeated exposure to a certain task (Jager & Postma, 2003).

[20] We deem ERs and RTs to be reflective of the same lateralized processing –lateralization effects in ERs and RTs of the same processes were always in same direction (for an overview of the full results, see Appendix C) and did not correlate in an opposing manner with other lateralization effects–, and here report the highest of correlations in ERs and RTs, when

lateralization of a process correlates substantially with lateralization of another in both these measures.

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Nederlandse samenvatting

Visuele lateralisatie in één blik

De hersenen van mensen bestaan, net als die van veel andere dieren, uit twee helften. De hersenhelften zien er ongeveer hetzelfde uit, maar wat hun functies betreft verschillen ze van elkaar. Dit noemen we hersenlateralisatie. Eén van die verschillen waar veel mensen wel eens van gehoord hebben is dat de linkerhersenhelft gespecialiseerd is in taal. Jaren van onderzoek heeft laten zien dat er nog veel meer hersenprocessen zijn die in de ene hersenhelft beter of sneller verlopen dan in de andere hersenhelft. In dit proefschrift richt ik me op zulke gelateraliseerde hersenprocessen die te maken hebben met visuele verwerking, oftewel, met dat wat we zien.

De zenuwbanen van de ogen naar de visuele cortex –helemaal achterin de hersenen, lopen deels kruislings. Dat zorgt ervoor dat alles wat we aan de rechterkant zien (het 'rechter visuele veld') door onze linkerhersenhelft wordt verwerkt, en alles dat we aan de linkerkant zien (het 'linker visuele veld') door de rechterhersenhelft. In de experimenten beschreven in dit proefschrift heb ik daar gebruik van gemaakt: door proefpersonen iets in hun rechter of linker visuele veld te laten zien en te meten hoe goed of snel ze hier op reageren, valt af te leiden of het nu juist de linker- of rechterhersenhelft is die het beste met deze informatie overweg kan. Met dat soort experimenten is in de afgelopen 50 jaar bijvoorbeeld aangetoond dat mensen gezichten beter in hun rechterhersenhelft verwerken, en woorden beter in hun linkerhersenhelft. Verder weten we uit onderzoek dat de linkerhersenhelft goed is in het waarnemen van details en de rechterhersenhelft in het zien van het 'hele plaatje'.

Na al die jaren van onderzoek is veel kennis ontstaan over de lateralisatie van afzonderlijke visuele processen, maar wat mist is een holistische blik: we weten weinig over de samenhang tussen de gelateraliseerde verwerking van verschillende typen visuele informatie. Zulke samenhang zou je wel kunnen verwachten, gezien het feit dat visuele processen zelf onderling met elkaar samenhangen. Voorbeelden zijn dat je voor het lezen van woorden op detailniveau moet kunnen zien, en dat we gezichten juist vaak 'als geheel' waarnemen zonder speciaal op de afzonderlijke elementen te focussen. Nu we weten dat zowel woorden als details door de linkerhersenhelft verwerkt worden, ontstaat de vraag of daartussen een verband bestaat. Voorspellingen over zulke samenhang zijn dan ook gedaan, maar nog niet uitvoerig getest. Met de experimenten beschreven in dit proefschrift heb ik me ten doel gesteld grondig onderzoek te verrichten naar de samenhang van gelateraliseerde visuele processen, door die voorspellingen te toetsen.

Er zijn grofweg drie typen voorspellingen. (1) De hersenhelften raken min of meer toevallig gespecialiseerd in het ene of andere type informatieverwerking, en er is dan ook geen samenhang tussen de gelateraliseerde verwerking van verschillende typen informatie. Dit wordt *statistische complementariteit* genoemd. (2) Wanneer een hersengebied in één van de hersenhelften gespecialiseerd raakt in de verwerking van een nieuw type informatie (bijvoorbeeld woorden) is deze niet meer zo snel en goed in het verwerken van al bekende informatie (bijvoorbeeld gezichten), en daar raakt de andere hersenhelft dan automatisch in gespecialiseerd. Er is hierbij dus wel sprake van samenhang tussen lateralisatie van het ene en het andere proces, en dit wordt *causale complementariteit* genoemd. (3) Wanneer de ene hersenhelft gespecialiseerd is in verwerking van een bepaald type informatie, dan zullen andere processen die deze informatie als input gebruiken in diezelfde hersenhelft plaatsvinden, omdat dat efficiënt is. Ook hier wordt dus samenhang tussen de lateralisatie van processen verondersteld, en dit wordt *input asymmetrie* genoemd. De leidende vraag in dit proefschrift is welk van deze drie voorspellingen visuele lateralisatie het best beschrijft.

Om deze voorspellingen te kunnen toetsen heb ik de gelateraliseerde verwerking van een aantal typen visuele informatie onderzocht en met elkaar vergeleken. Echter, voordat ik dit kon doen moest ik me ervan vergewissen dat de onderzochte processen werkelijk gelateraliseerd plaatsvinden. Hierover bestond twijfel, omdat er bijvoorbeeld inconsistenties in de wetenschappelijke literatuur te vinden zijn aangaande lateralisatie van sommige processen. In een reeks van negen replicatie-experimenten (beschreven in hoofdstuk 2) heb ik laten zien voor welke visuele processen er overtuigende aanwijzingen zijn dat deze door één van de hersenhelften beter of sneller verwerkt wordt dan door de ander. Dit betrof de eerder genoemde verwerking van gezichten, woorden, details, en het grote plaatje, maar ook nog drie andere verwerkingsprocessen. Dat zijn het waarnemen van ‘hoge frequenties’ (bijvoorbeeld hele fijne lijntjes die dicht op elkaar zitten) en ‘lage frequenties’ (bijvoorbeeld iets dat er een beetje wazig uitziet), en het richten van visuele aandacht in de ruimte. Met experimenten die lateralisatie van deze zeven visuele processen meten ben ik verder gegaan.

Zoals ik al noemde is bij de meeste mensen de linkerhersenhelft gespecialiseerd in taal. Nu richt ik me met het werk in dit proefschrift op visuele waarneming, maar één van de gelateraliseerde visuele processen die ik onderzocht heb wordt meestal gemeten met experimenten waarin proefpersonen letters te zien krijgen waarop ze moeten reageren. Dit zijn de experimenten waarmee men heeft laten zien dat de linkerhersenhelft gespecialiseerd is in het zien van detail, en de rechter in het zien van het grotere plaatje. Omdat letters talig zijn wisten we eigenlijk niet zeker of de linkerhersenhelft nu wel echt zo goed is in het zien van detail, of vooral goed in het zien van letters. Om deze onduidelijkheid weg te nemen heb ik een experiment uitgevoerd waarin ik de resultaten voor letters en figuren vergeleek (beschreven in hoofdstuk 3). De uitkomsten laten zien dat proefpersonen het beste detail waarnemen wanneer ze daarvoor hun linkerhersenhelft gebruiken, óók wanneer het figuren betreft. Dit toont aan dat de linkerhersenhelft daadwerkelijk gespecialiseerd is in verwerking op detailniveau, en dat dit niet afhankelijk is van taal.

In het laatste experiment in dit proefschrift (beschreven in hoofdstuk 4) keer ik terug naar de drie voorspellingen over de samenhang tussen verschillende gelateraliseerde visuele processen. Om deze te toetsen heb ik in een groep proefpersonen de lateralisatie van zeven verschillende visuele informatieverwerkingsprocessen gemeten en de resultaten aan elkaar gerelateerd. De uitkomsten van deze analyses laten zien dat er sprake is van een systematische samenhang tussen de lateralisatie van verschillende processen, en dat de statistische complementariteitsvoorspelling dus niet standhoudt voor visuele processen. Omdat we zagen dat een sterke specialisatie van de rechterhersenhelft voor gezichten gepaard ging met een sterke specialisatie van de linkerhersenhelft voor woorden konden we de causale complementariteitsvoorspelling wel bevestigen. Ook was er sprake van samenhang in de mate van lateralisatie voor verschillende processen die door dezelfde hersenhelft verwerkt worden, wat ondersteuning vormt voor de input asymmetrie-voorspelling. Door deze resultaten in het licht te stellen van wat we tot dusver weten over de ontwikkeling van lateralisatie bij mensen en andere dieren (hoofdstuk 5), concludeer ik tenslotte dat het input asymmetrie-principe het beste de lateralisatie van visuele informatieverwerking in de hersenen beschrijft. Dit komt er op neer dat onze linkerhersenhelft gespecialiseerd is in het waarnemen van woorden, omdat deze gespecialiseerd is in het waarnemen van bepaalde woordeigen karakteristieken zoals details en fijne lijntjes. De rechterhersenhelft lijkt gespecialiseerd in het waarnemen van gezichten, omdat deze gespecialiseerd is in 'globale' waarneming waarbij we juist minder op details letten.

Al met al leert dit ons ook dat hersenlateralisatie beter begrepen kan worden wanneer er met een holistische blik naar gekeken wordt, al komt men daar pas aan toe nadat eerst de afzonderlijke elementen goed in kaart gebracht zijn. Het onderzoeken van de werking van de hersenen is dus duidelijk een klus voor beide hersenhelften.

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