8th North Sea Laterality Conference on Brain Asymmetry

Abstracts

Effects of aging on lateralized auditory processing

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The processing of complex acoustic stimuli such as speech requires the involvement of auditory cortex (AC) in both hemispheres and thus interhemispheric interaction. In older adults, this interhemispheric interaction seems to be reduced. The present study shows how younger (18-38 years) and older adults (56-75 years) differ in auditory processing when tasks require different levels of interhemispheric interaction. One task was the categorization of frequency modulated (FM) tones according to their FM-direction which mainly involves the right AC. The other task was the sequential comparison of the same tones according to their FM-direction, which requires the involvement of both hemispheres and thus a higher degree of interhemispheric interaction. The level of difficulty of the tasks was adjusted to achieve similar individual performance across participants. For investigating hemispheric involvement, we used functional magnetic resonance imaging with the contralateral noise procedure. Contralateral noise had a greater overall effect on AC activation in older adults than in younger adults, suggesting greater AC involvement in task processing in the former group. This effect varies between the hemispheres depending on the task. Diffusion tensor imaging data suggest reduced interhemispheric interaction in the older participants due to changes in the microanatomy (reduced fractional anisotropy), particularly of the posterior corpus callosum. This reduced interaction probably complicates the processing of complex auditory stimuli for elderly. Stronger activity in frontal and parietal regions in the older participants may indicate compensatory processes. This suggests that older participants require more cognitive resources to achieve the same performance as younger participants.

Strategizing Verbal Rehearsal and Visual Imagery Effects on Memory Recall Between the Cerebral Hemispheres

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The left hemisphere of our brains typically controls language functions, while the right controls visuospatial functions. Focus on either language or visuospatial stimuli should then lead to differential engagements i.e., language rehearsal should engage the left hemisphere, and imagery the right. A study by Seamon and Gazzaniga (1973) used this to postulate that using imagery to encode language should engage both hemispheres and produce faster recall. The aim of the present study was to conceptually replicate the findings of this paper; participants are asked to hold probe words in their memory using either verbal rehearsal or imagery, while probe images are flashed to either the left or right visual field, and participants respond (yes/no) as quickly and accurately as possible to whether they had been encoding a word representative of that image or not. Experiment 1 ran an online replication (N=52), and replicated the main interaction effect between Condition and Hemifield ($p < .001$). Experiment 2 was an in-lab replication (N=55), and produced no significant results on the main interaction effect of Condition and Hemifield initially. Later additional exploratory analyses revealed a significant three-way interaction between Condition, Hemifield, and Order of Condition. This implied that Condition Order had a moderating effect on the main interaction. Findings suggested that the cerebral laterality effect proposed by Seamon and Gazzaniga (1973) does exist, but with limitations, and moderating effects.

Examining cognitive benefits for the typical pattern of verbal and nonverbal cerebral asymmetry: A systematic review

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We've long known that the cerebral hemispheres differentially specialise for information processing. The left hemisphere is specialised for verbal information (e.g., language) and the right hemisphere is specialised for nonverbal information (e.g., visuospatial judgements). This is the Typical pattern of cerebral asymmetry, but four atypical patterns exist: (1) Reverse, left for nonverbal, right for verbal; (2) Crowded, where both processes specialise to the same hemisphere, (3) Mixed, where one process is specialised but the other is not specialised – equivalent activation in both hemispheres; and (4) Bilateral, where neither process is specialised. Whilst theories pose an evolutionary advantage for a Typical pattern, the evidence for a cognitive advantage appears mixed. Here we report on a systematic review to determine whether there is a cognitive advantage to the Typical pattern of cerebral asymmetry. Following PRISMA guidelines, we identified 14 studies that assessed verbal and nonverbal cerebral asymmetry in association to cognitive abilities. Group studies suggest an advantage of the Typical pattern for verbal abilities, whereas case studies suggest a disadvantage for both verbal and nonverbal abilities—that is, an advantage of Crowded, Mixed, and Reversed patterns; patterns that are underrepresented in group studies. We discuss future directions to better address the question.

Short shrift for right shift theory? Explorations of handedness and ability in schoolchildren

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The question as to whether manual (or cerebral) laterality relates to cognitive ability has been looked at by many investigators but the issue remains largely unresolved. While some researchers have reported that sinistrals are at an intellectual disadvantage relative to dextrals, the converse has rarely been reported. On the basis of data collected from British schoolchildren and university students Annett argued that strong dextrality is associated with relative weakness in overall ability and in certain tests of English, maths and visuo-spatial skills (for reviews see Annett, 1995; 2002). She explained the pattern of her findings in terms of a "balanced polymorphism with heterozygote advantage" (BP+HA). Despite Annett's misleading use of the term BP+HA (because she was not referring to a biological fitness advantage), the findings she reported are intriguing but have rarely been replicated in a form that allows direct comparison with her own work. In this paper we report the results of an attempt to directly replicate some of her findings in a sample (N>500) of schoolchildren comparable in age to those studied by Annett.

Do stickleback parents influence the development of personality and brain laterality in their offspring?

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Parental influences on offspring phenotype occurring through pathways other than inherited DNA are known as parental effects (i.e. epigenetic modifications). Such effects have been demonstrated to affect two traits that are very widespread and of fundamental importance in the animal kingdom with clear fitness consequences: laterality of brain and behavior and personality traits. For example, reproducing groups of adult sticklebacks exposed to predation cues produce offspring with decreased antipredator behavior and reduced activity levels. This study investigated the impacts of parental effects on the development of brain lateralization, personality traits and somatic growth of offspring. Groups of reproducing sticklebacks were treated with a combination of several predator cues or lack thereof during egg production. Soon after laying, eggs were removed and a part of the clutch was reared in standard conditions until 12 weeks post hatching, whereas the other part was used for maternal hormone analyses of steroid in the androgenic and cortisol pathway. Results are currently being analyzed. So far we found that offspring from predator-exposed parents were smaller than control offspring likely due to the ecological stressor of the predation consistent with the possibility that these eggs contained elevated levels of corticosteroids. We expect to find that our results support the hypothesis that stickleback parents influence the development of lateralized behavior, personality traits and growth of their offspring via eggs to match their future environment

How acute stress modulates hemispheric asymmetries: investigating the role of endocrinological and affective parameters

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Differences between the left and right hemisphere in processing certain stimuli, tasks and internal states are known as functional hemispheric asymmetries (FHAs). The degree of functional asymmetry depends, among other things, on inhibition through the corpus callosum and can be influenced by different hormones and early life events. For example, early life stress has been shown to affect the development of motor asymmetries. Moreover, certain mental and neurodevelopmental disorders are associated with chronic stress as well as atypical lateralization patterns. However, it has not been investigated whether acute stress also affects FHAs. Acute stress acts on different areas in the brain and affects structures involved in affective processing and the endocrine stress response. We performed four studies on the influence of endocrinological and affective parameters of the stress response on FHAs. Here, we could demonstrate that acute stress and the related increase in cortisol do not influence dichotic listening performance but affect interhemispheric integration of information as well as frontal alpha asymmetries in EEG. To differentiate between possible effects of stress and stress hormones, we repeated the experiments with administration of hydrocortisone instead of stress induction. As we could not find any differences between hydrocortisone and placebo treatment, our results suggest that an increase in cortisol alone does not influence dichotic listening performance and interhemispheric integration on a behavioral level. These results indicate that acute stress does not affect FHAs. More likely, long-term changes in cortisol levels and early life stress affect the development of atypical asymmetry.

Unfolding of lateralized neural responses to facial information

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Facial information has been shown to be processed more accurately when presented in the left (LVF) than in the right (RVF) visual field. To elucidate the temporal development of neural processes underlying lateralized face processing, we employed a visual EEG-paradigm in which faces could appear as standards or deviant half-faces in the LVF or RVF, while participants performed a task on a centrally presented series of symbols.

Results from 32 right-handed participants (16 women) show that at the very earliest processing stage (100-130ms) deviant face stimuli invoke more notable negative deflections when presented in the LVF than when presented in the RVF, over both hemispheres. During the next face processing stages (160-180ms and 200-300ms), face deviants in the LVF again induce differential activation, but the effect dissipates over the left hemisphere. During the later processing stage (300-500ms), face deviants invoke negative deflections regardless of whether they are presented in the LVF or RVF, and as measured over both hemispheres. However, at this stage the activation is still strongest for faces presented in the LVF and as measured over the right hemisphere.

This suggests that specifically at more advanced processing stages, right cortical regions process deviances in facial information more rapidly than their left homologues. The timing differences in the observed deflections, reflecting cortical activity over the side that processed the deviant (i.e., changing) facial information, suggest a faster recruitment of cortical regions that are relevant to the processing of the deviant face information for the LVF-deviant compared to RVF-deviant.

The Biases that Matter: How Motor-Sensory Laterality Relates to Complex Cognition

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All brains are bound by natural selective processes, adapting existing neural architecture to accommodate new behaviours. Therefore, although the modern human behavioural repertoire may appear unique, it is supported by more general neural sensory-motor processing selected to drive adaptive behaviours in our ancient ancestors. Comparative research has established that motor-sensory dominances are a fundamental principle of the two hemispheres of the vertebrate brain. The 'divided brain' affords adaptive survival behaviours for evolutionarily urgent situations. The right hemisphere is dominant for keeping the organism safe from predation while the left hemisphere simultaneously allows the organism to find nourishment. While this 'standard' brain profile remains the most common brain organisation at the population level for humans, it is unclear if the strength and/or direction of these biases afford any modern cognitive performance benefits. Here, we explore the variation in behavioural biases in a large, cross-sectional, heterogenous sample of human participants (n=1661). Our results reveal significant associations between motor-sensory biases (the manifestation of inferred left-right brain dominances) and cognitive performance during childhood that diminish with age. A 'standard' behavioural laterality profile appears most frequently in the sample, while a 'reversed' profile occurs least frequently and is associated with increased social-communication difficulties and a higher rate of neurodevelopmental diagnoses. We hypothesise that the same lateral brain dominances that service primitive survival functions in ancient vertebrates, still support the development of cognitive abilities in modern humans highlighting the importance of developmental research that incorporates an evolutionary framework.

Explaining human handedness: combining kin selection and parent-of-origin effects

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The frequency of left-handedness in human populations is low but substantial (around 10%). Previous studies have shown human handedness is heritable, but only 25% of the heritable variance could be explained by known genetic factors, raising a question of "missing heritability". The maintenance of left-handedness has been suggested to imply negative frequency dependent selection, for example owing to a "surprise" advantage of left-handers in combat situations when most opponents are more used to fighting against right-handers. In such social interactions, selection acting upon handedness could be mediated by genetic relatedness between social partners, i.e. kin selection. Here, we develop a kin-selection model to explore the evolutionary forces shaping handedness. Using the combat hypothesis as an illustration, we show that (1) higher relatedness favours a lower frequency of left-handedness; (2) differential relatedness of males and females to their social partners may favour a sex difference in handedness; (3) differential relatedness of maternal-origin versus paternal-origin genes to their carrier's social partners may generate an intragenomic conflict over handedness; and (4) this intragenomic conflict may drive the evolution of parent-of-origin-specific gene effects (i.e. "genomic imprinting") – and associated clinical disorders – in relation to handedness. These parent-of-origin effects might hold the key to detecting the missing genes for handedness.

Hand to Mouth: Does Structured Motor Action Support Syntax?

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Language is a human-unique capability that relies on the production of structured motor sequences. While the expression of language (whether spoken or signed) requires the individual to perform complex motor action sequences, the field of developmental psychology has most generally investigated language acquisition in isolation of motor development. Neuroscientific research suggests that goal-focused manual action sequences and expressive language are supported by a shared neural mechanism which gives rise to a syntactic structure. Indeed, evolutionary theory posits that tool-using and making behaviours performed by our ancestors acted as a neural catalyst for language in modern humans. However, precious little empirical evidence exists regarding how language develops from preverbal skills in healthy individuals. This investigation adopts an evolutionary theoretical framing to test the associations between language development and the complexity of hierarchically structured object manipulation in typically developing children (n=46). Our results reveal that manual problem-solving tasks involving physical syntactic structure elicit a population level right-hand bias in nursery school children (aged 2-5 years). Hand dominance strengthens with tool-use and also with increasing syntactic complexity. Importantly, we reveal that children's physical syntactic skills associate with their expressive language syntax complexity, suggesting a common underlying left hemisphere motor sequencing neural generator. We hypothesise that during a process of 'developmental exaptation', extensions of an early object-related physical syntax provide a critical foundation developmental stage preceding the emergence of language's internal syntax.

Is it left or is it right? A machine learning framework for studying hemispheric differences

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The comparison between regions or tracts in the left and right hemispheres grants insight into local asymmetries as one characteristic feature of brain organization. These pairwise comparisons, however, are reminiscent of a localists' view and come with several caveats when assessing multiple asymmetries. To overcome some of the limitations set by conventional statistical comparisons, we recently introduced a novel machine learning-based framework for studying hemispheric differences. In a recent proof-of-principle study, we showed the capability of machine learning-based classification to distinguish the hemispheres based on voxel-wise features. Using a Boruta feature-selection algorithm allowed the mapping of voxels that were important for correctly classifying a given hemisphere. Furthermore, relating these maps of hemisphere-determining voxels with volumetric asymmetries validated our approach for mapping lateralized brain structure. In this talk, I will highlight our framework for studying hemispheric differences and present ongoing work on possible applications.

Brain functional segregation in people with situs inversus totalis: a replication-extension study

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Decades of neuroscientific research support the existence of a stereotypical functional division between the hemispheres. Usually, one hemisphere is dominant for speech and high-level processes involved in skillful manual action (praxis), while the other is dominant for face recognition and visuospatial processes. A previous study ran by our lab investigated whether this arrangement was reversed in situs inversus totalis (SIT), a rare condition in which the positioning of the internal organs is completely mirrored. People with SIT (N=15) and typical visceral asymmetry (situs solitis, SS, N = 15) completed four fMRI tasks tapping into different lateralized functions (speech, praxis, spatial attention and face recognition). While people with SIT showed similar population-level hemispheric dominance as controls with typical visceral asymmetry (situs solitus, SS), arrangements departing from the typical pattern of hemispheric segregation were observed relatively more often in SIT. The current study revisited the question whether hemispheric segregation is more variable in SIT by recruiting a new and bigger sample, and once again using fMRI to determine hemispheric segregation involving the same four functions. The higher rate of atypical segregation in SIT was replicated. Moreover, by combining the new and the previous datasets, we could now reveal that this effect was driven almost entirely by a specific subpopulation whose SIT is idiopathic in origin. By contrast, patients with visceral reversal in the context of primary ciliary dyskinesia had similar rates of atypical segregation as controls. Implications for the potential link between functional brain lateralization and visceral lateralization are discussed.

Testing the relationship between lateralisation on sequence-based motor tasks and language laterality using an online battery

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Studies have highlighted an association between sequence-based motor laterality and speech production laterality. It is thought that common demands for sequential processing may underlie this association. However, most studies in this area have relied on relatively small samples and have infrequently explored the reliability of the tools used to assess lateralisation, making it difficult to draw firm conclusions on the matter. We, therefore, established the validity and reliability of an online battery measuring sequence-based motor laterality and language laterality before exploring the associations between laterality indices on language and motor tasks. The online battery was completed by 521 participants, 51 of whom returned to complete the battery a second time. The three novel motor tasks included in the battery showed good between-session reliability ($r \geq .76$) and were lateralised in the predicted direction within each hand preference group. The Verbal Visual Half-Field (vVHF) Task, used to measure laterality for speech production, was left lateralised at population level as predicted, but reliability was less satisfactory ($r = .63$). We found no evidence of an association between sequence-based motor laterality and language laterality (when assessed using either a speech perception task or a speech production task). Those with a left-hand preference were more strongly lateralised on motor tasks that required participants to operate across the midline; this effect was not observed in right-handers. Given our reports of a lack of association, it can be concluded that there is little evidence of the co-lateralisation of language and sequence-based motor skill.

Left-handedness as a valid Social Identity category

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To most people, handedness is the (right) hand they write with, but for 10% of people their handedness has a more fundamental influence on their sense of 'who they are'. As a group, left-handers have the potential to identify themselves as a 'different' (minority) sub-group in society (Westmoreland, 2016), but there has been little work trying to establish both the extent of this and the possible implications. Social identity is the extent to which a group is meaningful to our concept of self (the degree we self-identity or align with the grouping) and consists of shared values and characteristics to which we identify with to a greater or less extent (Tajfel & Turner, 1979; Haslam et al., 2011). Much of this work has been carried out with some of the most salient human characteristics, such as race or gender and we now focus our attention on handedness. Here we explore the social identity that left-handers self-report and present some preliminary data using established measures of strength of social identity. Initially we will present data from a Thematic Analysis (Braun & Clarke, 2019) of online interview data from a sample of self-reported left handers. This will cover aspects of identity and their experience of living life as a left-hander, looking at the extent that elements of a left-handed identity are found in the data. The second part will look at some quantitative measures of identity, to examine the extent that a left-handed social identity is endorsed by a sample of left-handers.

Turn the other cheek: Comparing the expression and perception of emotion between neurotypical and autistic samples

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It has been suggested that humans intuitively emphasise their left cheek when expressing emotion, and turn their left cheek away when hiding emotion. This left cheek posing bias has been studied extensively in an adult population. However, there has been no research on how posing biases shift across the lifespan, nor on how these biases may differ in persons with and without autism spectrum disorder (ASD). The present study examined how the posing biases shift across the lifespan in both a neurotypical and ASD sample. Participants were asked to imagine themselves in three different situations (good, bad, and neutral condition) and to pose for photographs to depict their facial expressions in these events. Their photographs were coded based on whether they turned their head to show their left cheek or their right cheek. They also completed a judgment task wherein they rated the emotionality of left- and right-turned faces. Preliminary results demonstrate differences in these tasks between the neurotypical and autistic samples, and suggest that the expressed cheek bias in the photograph task may differ based on valence. These findings have implications for how altered laterality in neurodiverse populations may influence the expression and perception of emotion.

The Effect of Prenatal Stress on Laterality in Rats at Different Developmental Periods

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Functional cerebral asymmetry (FCA) is defined as the specialization of the brain hemispheres to control certain functions. For a long time, it was assumed that FCAs are determined by genetic factors and once developed are constant over time. Recently, it has been shown that FCAs have some degree of plasticity and can be influenced by environmental factors and may change over the life span of the individual. In this study, the effect of prenatal stress on FCA was evaluated in rats. In addition, it was investigated if the effect differs between developmental periods (Postnatal days (PD) 21, 40, 60, 90) and if sex has an influence. Seven rat dams were exposed to a restrain stress protocol for 2 hours each day during gestational days 15 to 21 while 6 dams served as controls. Collins test was performed to determine the paw preferences of the offspring on PD21 (F=13, M=13), PD40 (F=14, M=13), PD60 (F=13, M=13), and PD90 (F=12, M=12). In females, the interaction between stress and the developmental periods was found significant with less lateralization in the stressed group increasing with age. In males, the interaction was not significant. These preliminary results demonstrate that prenatal stress may influence the development of lateralization in rats and result in reduced FCA. In addition, it supports the hypothesis that sex hormones may be one of the additional factors which influence FCAs in general. Further validation with a larger number of subjects is required to confirm these conclusions.

Perception of hands and tools in right- and left-handers with left or right cerebral language dominance

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Functional neuroimaging studies report that viewing pictures of either tools or hands induces activation in regions lateralised to the left hemisphere, in right-handed individuals. It has been suggested that this asymmetry for hand and tool perception is because of close links with the action network. This network has been reported to be left hemispheric in most left- and right-handed individuals, but reversed (i.e., right hemispheric) in the minority of individuals with right hemisphere language dominance. It is unknown how the perception of hands and tools lateralise in individuals with right hemisphere language dominance. Here, we examine hand and tool perception in right- and left-handed individuals with right (n = 22) and left (n = 51) hemispheric dominance for language. Brain activity was measured in the 73 participants using functional magnetic resonance imaging whilst viewing pictures of hands and tools, and whilst performing a word generation task used to classify language dominance. Laterality indices were calculated for each participant and task, using the LI toolbox, to quantify hemispheric processing. Most left-handers, regardless of language dominance, processed pictures of tools more with their right hemisphere, and were on average right lateralised. Most right-handers processed tools more with the left hemisphere and were, on average, left lateralised. None of the groups had a population level hemispheric bias for viewing pictures of hands, which generally elicited bilateral brain activation for all three groups. Thus, we did not find that asymmetries in individuals varied similarly to that previously reported for the action network.

The Handedness Profile: a multidimensional standardised assessment for clinical practice and research

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The Handedness Profile (HP) is a standardized diagnostic tool for pediatric practice to determine the degree left or right handedness across several dimensions: untrained and trained preference and proficiency, midline crossing and bimanual cooperation. It has been developed, validated and refined for practice since 1998, and is used in Germany and South Africa to analyse patterns of mixed hand use in children. The HP consists of 7 subtests that are all based on laterality quotients and categorised into 8 handedness groups (explicit left or right handers, moderate left and right handers; mild left and right handers; and variable left and right handers). The seven HP subtest are: (i) 24 Functional Preference items consisting of equal numbers of trained and untrained tasks, as well as unimanual and bimanual tasks; 2 trained proficiency tasks (ii) Tracing and (iii) Dotting; 2 untrained proficiency tasks (iv) Hammering and (v) Tapping; 20 trials of (vi) Midline Crossing; and (vii) Bimanual Cooperation (simultaneous bimanual circle drawing in 4 directions with three levels of speed and visual feedback). In addition to the Handedness Profile, a number of tools summarise the extensive quantitative data with background information such as left handedness in the family, the right-biased socio-cultural influence and possible pathological factors leading to pathological handedness. Based on this, three broad Handedness Types are proposed: inherited degree-based type, motor/pathology-based type and environment-based type, each with several variations. Since the HP has shown to be very useful in clinical practice, it could also make a potential contribution in research, since it offers a comprehensive, multidimensional and standardised approach to handedness assessment.

Modulation of behavioural laterality in wild New Caledonian crows (Corvus moneduloides): Vocalisation, age and function

Cyrielle Mack & Natalie Uomini

The New Caledonian crow (Corvus moneduloides) is known for displaying a unique set of tool-related behaviours, with the bird's bill acting as an individually consistently lateralised effector. However, we still fail to understand how such laterality develops, is modulated or even if its expression is consistent across other behavioural categories. Creating the first ethogram for this species allowed us to examine laterality, vocalisations, and their intersection in a population of wild, free-flying New Caledonian crows using detailed analyses of close-up video footage. We revealed the existence of an overall strong left-sided bias during object manipulation solely driven by the adult crows of our focal population, while the stabilisation of individual preferences appeared to occur during the birds' juvenile years. Individually, at least one crow showed consistent side biases to the right or left for different behavioural categories.

Our findings highlight previously unknown variability in behavioural laterality in this species, thus advocating for further investigation. Specifically, we argue that a better understanding of the New Caledonian crow's biology and ecology is required if one wishes to pursue the promising comparative road with past and present hominids that laterality could be connected to the evolution of tool-making and, perhaps, even uncover new co-evolutionary paths leading to the emergence of language.

Keywords: New Caledonian Crow, Corvids, Object manipulation, Tool behaviour, Limb preferences

Unfolding functional brain lateralization: the asymmetrical priors model

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Functional brain lateralization is widespread in the animal kingdom, and influential theoretical frameworks aim at explaining the phylogenetic and ontogenetic foundations of hemispheric asymmetries. However, what is not well understood is where and how hemispheric dominances arise in the information-processing stream when an organism interacts with its environment. Allocation of hemispheric-specific functions requires detection and functional classification of stimuli, as well as efficient attentional mechanisms that direct relevant information to the specialized hemisphere, which in turn controls major processing steps. Here, we propose a model, which assumes that functional dominance critically depends on feedforward mechanisms at an early level in the perceptual stimulus processing stream whenever the relevant features of a stimulus category are detected. Such stimulus-driven lateralization enables flexible, efficient, and adapted reactions to the environment.

We suggest that simple stimulus configurations (priors) differentially activate left- and right-hemispheric cell population at subpallial level. Because of the endogenously lateralized organization of relevant neuronal networks, spike density in one hemisphere increases and leads to faster signal propagation due to neuronal summation. Top-down and interhemispheric mechanisms maintain or even increase the processing advantage of this hemisphere. As a result, the initially more activated hemisphere can more quickly gain control over motor systems and dominates behavioral responses. Thus, action execution proceeds from a hemisphere according to the winner-takes-it-all mechanism. We will outline this model and illustrate it with examples from human and animal research.

Cerebral polymorphisms: Modelling genetic and phenotypic architectures

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Human brains are laterally polymorphic: most but not all people are right-handed, most but not all people have language in the left-hemisphere, and most but not all people have visuo-spatial analysis in the right hemisphere. A key study by Bryden, Hécaen and De Agostini (1983) showed that aphasia, agnosia and handedness after left or right lesions were statistically independent, all possible combinations occurring. More recent work extends such analyses to six and seven modules, with many combinations being found. Explaining those combinations is the purpose of the present talk, which is based on a long paper I wrote for Sebastian Ocklenburg and Onur Güntürkün's special issue of Symmetry entitled Models of Brain Asymmetry (2022, 14, 814).

A challenge for all modelling in neuroscience is to reconcile ever more complex descriptions of functional phenotypes with polygenic (or even 'omnigenic') influences on those phenotypes, while models remain simple enough to be comprehensible, but rich enough to reflect the remarkable variation in brains and behaviours. At root though, lateralised phenotypes are relatively simple binary characters (right vs left handedness, left vs right language dominance, etc), that simplicity somehow resulting from the interplay of a myriad of genes and developmental processes.

An excellent biological model for lateralisation is Primary Ciliary Dyskinesia (PCD), 50% of individuals showing situs inversus, with the heart on the right rather than the left. The molecular mechanisms of PCD are now well understood, there are many genes involved, but the phenotype remains relatively simple. A polygenic system can therefore act as if it is monogenic for practical purposes.

Behavioral lateralization in Wild American Crows (Corvus brachyrhynchos): Individual differences in eye and foot use bias may develop over time

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What we know of lateralization in birds is greatly influenced by work on domestic chickens (Gallus gallus domesticus). Newly hatched chicks show visual laterality which develops due to late embryonic light exposure of the right eye through the eggshell and gives rise to population-level laterality. This process may apply primarily to precocial birds because, as demonstrated in pigeons (Columbia livia), altricial species including all passerines hatch before the sensitive period. Recent reports of population-level eye use laterality in passerines must mean that post-hatching mechanisms can produce lateralized behaviors. We tested whether a passerine, the American Crow (Corvus brachyrhynchos), exhibits bias in eye and foot use at the population or individual level. Corvids are known for manipulative problem solving including tool use in some species; they use bills and feet to hold and manipulate objects. Lateralization may increase neural efficiency in complex actions. We suggest that such efficiency may develop through practice, explaining individual biases. We scored foot use of individuals in a wild crow population during foraging. We found individual differences in direction and degree of foot use laterality. We did not find evidence of population-level biases of foot use across all ages. We found that on average individuals in the youngest age class show a weak right bias, whereas older individuals show a stronger left bias, suggesting a “practice effect.” This study emphasizes the importance of investigating the underlying mechanisms of laterality, including practice effects and the effects of observational learning, specific task, and individual differences.

Deep phenotyping of hand preference and hand skill in the Dortmund Vital Study: Investigating the role of stress and mental health

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Hemispheric asymmetries are a major organizational principle of vertebrate nervous systems. In humans, handedness is one of the most widely investigated forms of hemispheric asymmetries and it has been associated with many other forms of hemispheric asymmetries. One question that is not well investigated is how stress (early or in later life) is associated with asymmetries. As most large-scale studies only include one dimension of handedness (i.e., “are you right or left-handed”), this shallow phenotyping is prone to underestimation of the prevalence and does often not reflect hemispheric asymmetries correctly. Preclinical and clinical laterality studies, furthermore, point towards stress as a factor affecting asymmetries and mental well-being. Thus, in this study, behavioral data on laterality from the Dortmund Vital study was used to determine asymmetry indices. Both hand preference and hand skill were assessed. Moreover, data on stress exposure and mental well-being was included to determine stress reactivity and a potential association with altered asymmetries. Results show replications of some previously reported associations between handedness and stress and mental health parameters, especially in the affective and social domain, but also substantial influences of phenotyping. This suggests that both hand skill and hand preferences should be assessed in clinical laterality studies.

Navigation asymmetries in a simulated 3D environment

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The two cerebral hemispheres have different capacities for controlling spatial attention. This asymmetry is thought to cause a shift of attention towards the right side of objects located in far space – and a corresponding lack of attention to objects located on the left. As a result of this imbalance, when passing through an aperture, people veer slightly to the right of true centre. The misplacement of centre is related to pseudoneglect and occurs when walking, controlling a wheelchair and operating a toy vehicle. The current study determined whether the bias also exists in a simulated 3D environment. Right-handed participants (n=98) used a joystick to navigate through a virtual 'doorway' or 'corridor' separating two rooms. In both cases, a rightward deviation was observed. The results demonstrate that rightward deviations in the real world generalise to a virtual environment, with implications for the representation of peri- and extra-personal space.

Enhancing ecological validity in laterality research

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The most prominent method to induce emotions in fMRI scanners or EEGs is by showing movies, pictures or music to the participants that elicit positive and negative affect. By application of this method, many studies were conducted to study asymmetries in emotional processing. However, despite the vast number of studies using behavioral, neurophysiological and neuroimaging means to study emotional lateralization in the brain, there is still no conclusive understanding of this phenomenon. A possible reason for the inconclusiveness in the field relates to this method of emotional induction as it has little to do with real-life emotions. Emotions such as fear or love cannot be properly measured if they are merely passively perceived since emotions are inherently connected to behavioral action. Similarly, motor asymmetries are often investigated with finger-tapping tasks, that have little overlap with most real-life motor tasks. In my contribution, I would like to present some ideas and ongoing projects on how to enhance ecological validity in laterality research using mobile EEG, virtual reality, and smartphone-based data collection techniques.

Effect of the environment on the development of laterality and personality in the Three-spined Sticklebacks

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Laterality of brain and behavior has been found to be widespread among animal species. Recently, laterality has been found to be correlated to personality. In addition, the development of both personality and laterality in fish can be influenced by environmental factors: e.g., high perceived predation leads to bolder and more lateralized individuals. Also, in fish, bolder and more lateralized individuals tend to swim in a safer and energetically more favorable position than other individuals while schooling. However, whether this correlative evidence indicates a causal relationship between laterality and personality is yet unclear. Such a causal link will have consequences for evolution, as selection on one may constrain evolution of the other.

The aim of this experiment was to manipulate rearing conditions to see to what extent both laterality and personality are affected together, which would indicate a causal relationship between the two. Three-spined stickleback larvae were therefore reared under predation cues or in the absence of it in small or large groups for 3 months in a two-by-two design, after which their behavior during schooling, social interacting, and predator inspection was recorded in standard tests. We expected that the fish reared under high predation perception and/or in large groups will show a higher tendency to school, a bolder behavior and more lateralized behavior than the control group reared under low predation pressure and small group size. The results are currently being analyzed.

Exploring the cerebral lateralization of writing in relationship to handedness and to risk for dyslexia using functional transcranial Doppler ultrasonography

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It has been established that oral language production is left-lateralized for the majority of individuals. Moreover, both handedness and learning disorders seem to affect the pattern of cerebral lateralization of oral language. Written language has only recently begun to gain attention in terms of cerebral lateralization, despite its importance for communicational, educational, and work purposes. In fact, no study has yet adequately dissociated the linguistic from motor components of writing. Furthermore, certain groups of participants are under-sampled or have not been studied at all; only four studies have sampled left-handers and no study has sampled children, neurotypical or not. In this presentation, we will outline the pre-registration of three studies aiming to compare the cerebral lateralization of the linguistic component of writing as measured using functional transcranial Doppler ultrasonography (a) between left- and right-handed adults, (b) between children at risk for dyslexia and neurotypical children, and (c) in children at risk for dyslexia prior and after receiving a phonological intervention. To disentangle the linguistic and motor components of writing, we will compare the cerebral lateralization during written word generation against the cerebral lateralization during letter copying. We hypothesize that the cerebral lateralization of the linguistic component of writing will be weaker in (a) left-handers compared to right-handers and (b) in children at risk for dyslexia compared to their neurotypical counterparts, and that (c) phonological intervention will result in stronger left-lateralization in children at risk for dyslexia.

Handedness and the corpus callosum: Challenging the Witelson findings

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Inter-individual difference in brain anatomy have traditionally been linked to functional lateralization. For example, evidence for a correlation between hand preference and callosal morphology suggest a role of anatomical connectivity in establishing or supporting and functional hemispheric specialisation. In a series of influential post-mortem studies in the 1980s, Sandra Witelson reinforced the assumption that left-handers have a larger corpus callosum than right-handers. However, critiques towards the validity/reliability of the Witelson studies, as well as mixed success of attempted replications of the studies, has left researchers to question the actual relationship between callosal morphology and handedness. The main aim of the present study is therefore to conceptually replicate (preregistration: https://doi.org/10.17605/OSF.IO/3WS5C) the findings of Witelson, by repeating the study with a larger sample (N>1000) using callosal measures from structural MRI. The results of the study argue against the conclusions drawn by Witelson. Here, we show that the analyses of the midsagittal surface area present no significant main effect of handedness on the total size of the corpus callosum, controlling for both sex and handedness-scorings using different assessments. Also, for the often-indicated isthmus subregion of the corpus callosum, neither a main effect of handedness nor any moderating effect of sex was detected. These findings imply that previous assumptions regarding the relationship between callosal size and handedness should be considered inaccurate. We predict that the present study can contribute to a greater understanding of handedness specifically, as well as laterality in general.

Strength of handedness in twins reared apart

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Approximately one in five twin pairs is discordant for direction of hand preference, such that one cotwin is right-handed and the other cotwin is left-handed. However, direction of hand preference is one of few variables for which the equal environments assumption is violated. That is because early developmental processes that can result in mirror-imaging effects on handedness are unique to MZ twins. Heritability estimates for direction of hand preference derived via the classic twin study paradigm are, thus, likely misleading. However, the same is not true for strength of hand preference, that is strong or weak hand preference, regardless of direction. We present data from the Minnesota Study of Twins Reared Apart (MISTRA) to examine concordance rates for strength of hand preference (unsigned [absolute] laterality index [LI] scores for a modified version of the Edinburgh Handedness Inventory [EHI]), strength of relative hand skill (unsigned LI scores for the Purdue Pegboard [PPB] task), and right- and left-hand speed (right-hand and left-hand task completion speeds for the PPB task). We provide evidence of moderate heritability for right-hand and left-hand speed, and no evidence of heritability for strength of relative hand skill. Unexpectedly, we observed a statistically significant intraclass correlation coefficient for strength of hand preference in DZ twins, but not MZ twins. This finding is challenging to explain, though could reflect the relative lack of available data (particularly with respect to reared-apart DZ twin pairs), the relatively low heritability for this trait, and or unidentified prenatal factors affecting handedness in MZ twins.

Population-level structural asymmetry of the cerebral cortex

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Cortical asymmetry is both ubiquitous and subtly altered in neurodevelopmental disorders and aging. However, no previous study has focused on cortical regions exhibiting robust asymmetry. Consequently, we lack knowledge of how asymmetry development proceeds across life in health, and the extent to which cortical asymmetry may be heritable, interrelated, and moderated by individual differences remains unclear.

We delineated population-level asymmetry in cortical thickness and surface area vertex-wise in 7 datasets, and for the first time tracked asymmetry trajectories longitudinally across life (4-89 years; observations = 3937; 70% longitudinal). We assessed asymmetry interrelationships, heritability, and associations in large-scale data (N=~37,500).

Cortical asymmetry was robust across datasets. We find areal asymmetry is predominantly stable from childhood to old age, whereas thickness asymmetry shows developmental growth and aging-associated decline. Asymmetry interrelationships showed high reproducibility across datasets (min r = .97 [area]; min r = .43 [thickness]). These suggested areal asymmetry correlates in a few specific regions, whereas thickness asymmetry is globally interrelated across the cortex in a pattern suggesting highly left-lateralized individuals tend towards left-lateralization also in population-level right-asymmetric regions (and vice versa). For area, we find replicable patterns of low-moderate heritability, phenotypic correlations are underpinned by high genetic correlations, and highest heritability in leftward anterior insula (max h2SNP ~19%) — wherein leftward asymmetry is reduced in left-handers. In contrast, heritability of thickness asymmetry is low. Finally, we detected an association with cognition and confirm links with handedness and sex.

Results suggest areal asymmetry is developmentally stable and arises in early life, whereas developmental changes in thickness asymmetry may lead to directional variability of global thickness lateralization. Our results provide novel insights into normal organization and development of brain asymmetries, and bear enough reproducibility to serve as a standard for future asymmetry studies.

Cerebral lateralisation during typing on computer and smartphone keyboards.

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The cerebral laterality of language processes has been studied to an ever growing extent in the last few decades with most of the studies focusing on oral language production and only a few focusing on handwriting. Handedness differences are present in both modalities, with right-handers showing stronger left cerebral lateralisation compared to left-handers. Word production differs between oral and written language as, apart from the linguistic component that is present in both modalities, writing requires an additional motor component for the formation of the letters. In modern times, writing is performed less in the traditional, handwritten way and increasingly by typing using computers and smartphones. However, there are very few studies on the cerebral lateralisation of language during typing. Typing on a keyboard differs from handwriting as, in the former, the letters are typed by simply pressing a key and without needing to perform elaborate hand movements to form the letters. Also, there is the question of whether the linguistic component of language remains unaffected by the use of electronic devices. In this presentation we will outline the pre-registration of two studies aiming to examine the cerebral lateralisation of language production in left- and right-handers during handwriting compared to keyboard typing on computers and smartphones.

Lateralised behavioral responses in pet dogs during reward expectation and frustration

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Emotional functioning is associated with lateralized activity of the brain hemispheres. However, the precise contribution of each remains unclear. Competing hypotheses include: The Right-Hemisphere-Hypothesis, which claims that the right hemisphere is dominant in all emotional functioning; the Valence- and the Approach-Withdrawal-Hypotheses which assume that either hemispheres may dominate depending on either the prevailing emotional valence (positive vs. negative) or associated action tendencies (approach vs. withdrawal), respectively. Previous non-human research largely fails to discriminate between these hypotheses, therefore we used pet dogs to specifically test different hypotheses.

Dogs were exposed to two experimental conditions differing in valence: Condition 1 (anticipation of a reward); Condition 2 (frustration due to delayed access to a reward) whilst always motivating approach tendencies. Brain lateralization was investigated indirectly by measuring dogs' lateralized behavioral responses at the level of both sensory processing (relative eye use) and emotional expression (tail wagging behavior). Lateralization and its direction were both calculated as a standardized index.

Preliminary data for Condition 1 suggest a population-level right eye/left hemisphere advantage (N=21, p=0.005), whereas no directional population-level lateralization was observed for tail wagging (N=16, p=0.8). This initial result provides relative evidence for the Valence- and the Approach-Withdrawal-Hypothesis for visual processing of an emotional stimulus, but indicates that different components of emotionality (e.g., stimulus inspection, emotional expression) may be associated with different lateralization patterns. Data from both conditions and their combined evidence for different hypotheses will be presented at the conference.

Effects of partial corpus callosum agenesis on laterality and executive functions

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Background: Developmental absence (agenesis) of the corpus callosum (AgCC) in adolescents are associated with problems regulating behavior, attention, and executive functions. Previous studies have shown that adolescents with AgCC often have low-average full-scale IQ scores, with cognitive abilities ranging from extreme low to equally extreme high levels. This may indicate dysfunction of specific cognitive functions due to atypical white matter tracts between the cerebral hemispheres. We will present a case report of an adolescent boy with AgCC tested for laterality for language, attention, and executive functioning using the forced-attention dichotic listening task (DL), as well as for a broad range of neuropsychological functions.

Methods: Structural T1 images were generated from MRI scanning (3T). The DL task and a neuropsychological test battery were administered including measures of intelligence, attention/executive and memory functions, and motor coordination abilities.

Results: The MRI data showed partial AgCC with absence of the anterior part of the corpus callosum and with the posterior commissure intact. The DL results showed a left ear dominance in processing syllables and not a right-ear dominance as expected. The neuropsychological tests showed specific problems performing tasks requiring coordination between the two hemispheres such as in learning new information and with tests requiring coordination between cognitive-demanding processes and motor performance. The results also indicated weaker motor coordination with the left hand (non-dominant). Inhibitory control, attention flexibility, and working memory appeared to be within average age-adjusted scores.

Conclusion: The results from the case report indicated specific difficulties with tasks requiring efficient communication between the two hemispheres.

When Posing in Portraits Turns Cheeky: A Systematic Literature Review of the Left-Cheek Bias

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Since it was first noticed in the 1970s, studies have continued to observe that various types of portraits are often produced with the left side of the face protruding more than the right side of the face. This pose orientation is often preferred by the viewer and the displayed cheek appears to influence the viewer's perceptions of the portrayed individual. This phenomenon has become known as the left-cheek bias. Based on that the right hemisphere both innervates the left hemiface and is considered dominant in emotion processing, a popular explanation for the left-cheek bias is that such a posing orientation better displays emotional qualities. The aim of this systematic review is to provide an overview of the literature concerning the left-cheek bias, both in terms of its occurrence and its effect on the viewers. A systematic literature search was conducted in seven electronic databases: PubMed, Google Scholar, Web of Science, EBSCO Discovery Service, PsychInfo, MEDLINE, and Embase. Two independent raters assessed the resulting 268 articles, of which 65 articles consisting of 91 studies were included. These studies were first divided into whether they assess pose orientation in a set of stimuli (DV-group; k = 57) or how pose orientation affected an outcome measure (IV-group; k = 34), and subsequently divided into subgroups based on type of stimuli or outcome measure. The results of this investigation will be presented.

Revisiting the interhemispheric deficit theory in dyslexia using a lexical decision task

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An impairment in the transfer of information between hemispheres, also referred to as an interhemispheric deficit, has been suggested as a theory of dyslexia. Previous studies have investigated this theory using the visual half-field paradigm (VHF). A well-reported phenomenon is the ability of participants to recognise words presented to the right visual field (RVF) faster and more accurately than words presented to the left visual field (LVF). The extra processing cost for LVF words reflects the necessary callosal transfer of information from the right hemisphere to the language-specialised left hemisphere. Additionally, bilateral presentation of words has shown to yield even better recognition performance, implying cooperative information transfer between both hemispheres during processing.

Based on previous studies by Henderson et al. (2007) and Bradshaw et al. (2020) we hypothesised an increased RVF-LVF difference and a reduced redundant bilateral advantage (RBA) in people with dyslexia, reflecting a deficit in interhemispheric transfer.

We used a lexical decision task within a VHF paradigm and tested 45 dyslexic and 55 control participants (aged 18-37 years). Our results showed significant RVF-LVF differences and RBA in RT and accuracy in both groups. However, no significant effects were found in the size of the RVF-LVF difference nor in the RBA between groups. This evidence contradicts the interhemispheric deficit theory of dyslexia and suggests that reading difficulties in people with dyslexia cannot be explained by impairments in information transfer between both hemispheres.

Laterality indices consensus initiative (LICI): Some results of the Delphi expert survey

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Given the substantial variability in how structural and functional asymmetries are recorded, calculated, and reported, an initiative was launched in 2019 to evaluate consensus and stimulate discussion on the use of laterality indices in behavioural and psychophysiological research. Experts were recruited by snow-ball sampling and invited to participate in a three-round online Delphi survey. In Round 0, 106 experts generated 453 statements on what they considered good practice in their field of expertise. A team of moderators organized the statements into a 295-statement survey that the experts then were asked, in Round 1, to independently assess for perceived importance and their readiness to support. Based on these ratings, the same team of moderators removed statements deemed unimportant and reworded others in a new survey of 241 statements that was presented again to the experts in Round 2 together with the group results of the Round 1 ratings. Based on the Round 1 results, experts were given the opportunity to express their agreement or disagreement with the group result, to modify the rating, and to explain their action, using a comment box provided with each statement. In anticipation of a publication on this Delphi survey, we present some of the most striking results from Round 2 and discuss its potential implications for laterality research.

Alterations in hemispheric integration and segregation in clinical (schizophrenia) and non-clinical (bilingual) populations

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While functional laterality in the human brain is commonly investigated by comparing overall magnitude / extent of brain activity in the left and right hemisphere, two distinct forms of functional lateralization have been suggested [1] in that the left hemisphere appears to have a preference to interact more exclusively with itself ("functional segregation"), whereas the right hemisphere tends to interact in a more integrative fashion with both hemispheres ("functional integration").
Here, we examined differences in integration and segregation to compare (a) schizophrenic patients to healthy controls and (b) monolingual to bilingual subjects. In two datasets (COBRE, OpenNeuro), we extracted brain connectivity based on the AICHA atlas, a parcellation based on intrinsic connectivity of homotopic areas [2]. For each ROI, we extracted measures of segregation (difference of within and between hemisphere connectivity) and integration (sum of within and between hemisphere connectivity).
For (a) no significant differences between controls and patients were found with respect to segregation, while integration was significantly more pronounced in healthy participants than in patients across large parts of both the left and right hemisphere. Preliminary results for (b) showed differences between monolinguals and bilinguals with respect to both integration and segregation which were mainly located in medial brain regions while differences in segregation were also found in left lateral frontal cortex.
Altogether, these distinct forms of brain lateralization appear to offer more detailed insights into group differences in the clinical and non-clinical context above what can be achieved by comparing left and right brain activation alone.

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A "failed" fishing expedition for handedness-related differences in corpus callosum morphology

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As the major pathway connecting the two hemispheres, the corpus callosum is thought to have an important role in supporting hemispheric asymmetries. In line with this assumption, Sandra Witelson, in an influential publication in Science from 1985, found that the mid-sagittal corpus callosum was smaller in consistent right handers (cRH) than in non cRH, which is often summarized as "left handers have a larger corpus callosum". However, replication attempts yielded mixed results during the decades that followed, and a recent meta-analysis concluded that the effect is negligible, at least when considering the absolute size of the corpus callosum. Relying on the available published data, the meta-analysis had to leave out a series of factors potentially influencing the outcome, for example, the effect of different definitions of consistent hand preference or using alterative callosal measures. Thus, in the present paper, we utilized the MRI data of the Human Connectome Project (HCP 1200 Young Adults) to reexamine hand-preference related differences in the corpus callosum with the aim to answer the questions remaining after the meta-analysis. We approached this aim using a series of analyses (a) applying the various classification schema of handedness that can be found in the literature, (b) considering both direction and consistency of hand preference, and (c) comprehensively measuring the corpus callosum using several dependent variables (i.e., absolute area and relative to forebrain volume, thickness, and diffusion parameters). Despite of testing a large amount of possible scenarios, we were not able to reveal any convincing evidence of handedness related difference in the corpus callosum.

To press or not to press: Do left- and right-handers differ in responses to ambiguous stimuli?

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Handedness-related differences in approaches to novel ambiguous stimuli have been reported in marmosets, with left-handers less likely to approach, and slower to interact with, an ambiguous target (Gordon & Rogers, 2015). Using a human analogue, we created an online ambiguity task using a Go/No Go paradigm where participants were trained to respond (via a key press) to a target stimulus (either a black or white 'bowl' – counterbalanced across participants) and withhold their response to the non-target. After a training and an experimental phase, an ambiguous grey bowl was presented and participants' reactions to this were recorded. It was hypothesised that left-handers would be less likely to respond to the ambiguous grey stimulus, and if they did respond, left-handers would take longer to do so (than right-handers). Participants were also asked to complete an open-ended question asking why they did/did not respond to the grey stimulus. Results of this exploratory study will be discussed.

Is thickness of the corpus callosum related to the lateralization of functional tasks?

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We tested the possibility of lateralization enhancing cognitive performance in single- and dual-tasks. We have used functional transcranial Doppler (fTCD) to determine individual brain lateralization during the performance of a language task and also for a spatial task (72 participants). From these measurements we determined strength and direction of lateralization for both tasks, from which the individual pattern of lateralization (contralateral, ipsilateral, or mirrored) was derived. When analyzing single- and dual-task performance, we found that for the spatial task and for the dual task, there was a significant positive effect of strength of lateralization on performance, whereas there was no effect for the language task. Direction and typical pattern of lateralization had no significant effect on performance in any task. We concluded that strength of lateralization may be a factor that contributes to the evolutionary selection of functional brain lateralization and that direction or pattern of lateralization does not. As a further promising factor to influence (dual-) task performance we were interested in the structure that connects the two hemispheres with each other – the Corpus callosum (CC). We obtained MRI-scans from a subset of the participants (n=50) and will present our results linking the thickness of the CC at different subsections to task performance and laterality scores.