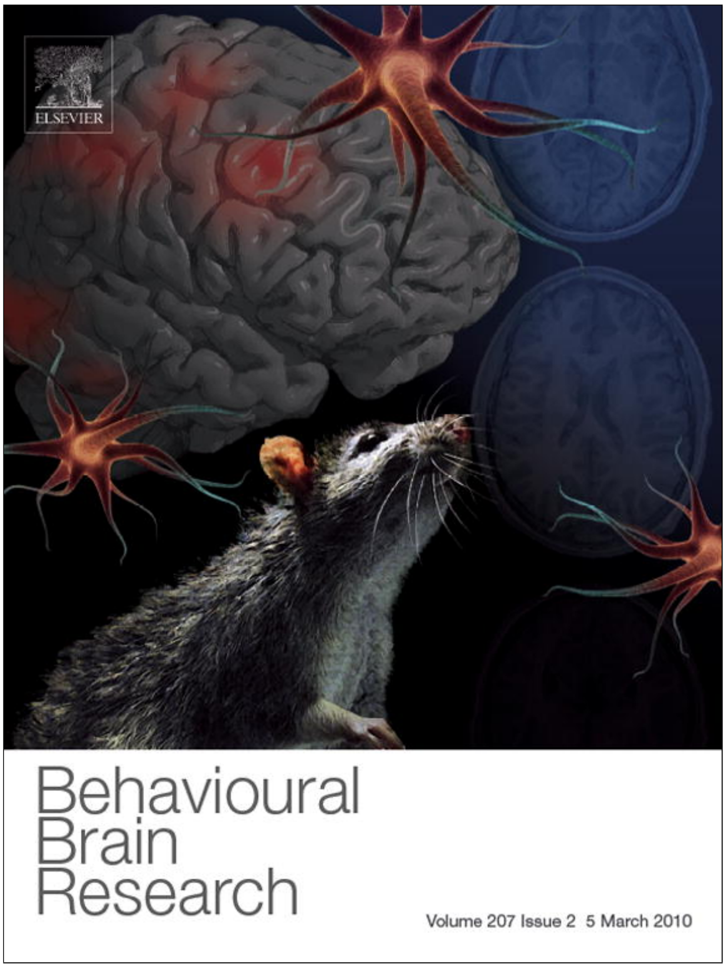
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Visual experience affects handedness

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ABSTRACT

In birds, a lateralised visual input during early development importantly modulates morphological and functional asymmetries of vision. We tested the hypothesis that human handedness similarly results from a combination of inborn and experience-driven factors by analysing sidedness in children suffering from congenital muscular torticollis. These children display a permanently tilted asymmetric head posture to the left or to the right in combination with a contralateral rotation of face and chin, which could lead to an increased visual experience of the hand contralateral to the head-tilt. Relative to controls, torticollis-children had a higher probability of right- or left-handedness when having a head-tilt to the opposite side. No statistical significant relation between head position and direction of functional asymmetries was found for footedness and eye-preference, although the means show a non-significant trend in the same direction as was observed for handedness. Thus, an increased visual control of the hand during early childhood seems to modulate handedness and possibly other lateral preferences to a lesser extent. These findings not only show that human handedness is affected by early lateralised visual experience but also speak in favour of a combined gene-environment model for its development.

1. Introduction

Like all amniotes, birds have a genetically determined embryonic preference for a right head turn [33]. Inside the egg, this head turn brings the right eye close to the translucent egg shell while the left eye is covered by the body and is therefore visually deprived [49]. This asymmetrical visual stimulation importantly affects the just developing visual pathways and modulates the emergence and organisation of visuocognitive asymmetries [33]. Incubation of eggs in total darkness prevents the development of anatomical asymmetries within ascending visual pathways, while abolishing or modulating behavioural left–right differences in object discrimination [6,48,51]. Occlusion of the right eye and exposition of the left eye to light leads to a reversed visual lateralisation pattern [33]. In precocial birds, like chickens, whose visual system is fully mature at birth, this reversal of lateralisation is only possible in embryos in a period of time shortly before hatching [49,50]. In contrast, altricial birds, like pigeons, have a visual system that is highly immature at birth and still develops after hatching. Therefore, it is possible to induce a reversal of lateralisation in pigeons by post-hatching visual stimulation of the left eye and deprivation of the right eye [34]. Just a few days of early asymmetrical light input are enough to shape behavioural asymmetries for the entire lifespan of the individual [33].

The most frequently observed and extensively studied behavioural asymmetry in humans is handedness. In contrast to the development of behavioural asymmetries in birds, it is widely assumed that environmental factors do not play a large role in determining individual handedness and a number of different single-gene models have been proposed to explain the distribution of left- and right-handedness [1,9,27,28,35,36]. Recently it has been reported that the gene LRRTM1 on chromosome 2p12 is the first identified genetic influence on human handedness [17], a claim that is heavily discussed since it has been publicised [10,16,37].

Nevertheless, it is relatively undisputed that handedness is, to a large extent, genetically determined. However, there are some observations that cannot be readily explained by means of a purely genetic model of handedness and therefore highlight the importance of also integrating non-genetic factors into models of handedness. For example, the frequent observation of discordant handedness in monozygotic twins [19] can only be explained when environmental factors are taken into account [46], since exclusively genetic models would predict genetically identical twins to have identical handedness. Moreover, in societies where use of

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the left hand is associated with bad luck or being unclean, such as most Muslim African countries, there is a lower incidence of left-handedness than in more liberal countries [12,53], showing that cultural factors also influence handedness. Furthermore, in an meta-analysis of a number of studies concerning handedness as a function of period of birth Jones and Martin [26] found a significantly higher incidence of left-handers among persons born in spring and ensuing months (March to July in the northern hemisphere) than among persons born during the rest of the year. A number of explanations have been suggested for this phenomenon, ranging from differences in patterns of nutrition and disease to seasonal variations in prenatal exposure to testosterone [26,42].

Historically, there has been the suggestion that genetic variation does not have a significant role in causing left- or right-handedness and that left-handedness is due largely to environmental influences [41,47]. However such purely non-genetic models of handedness are unable to explain the dominance of right-handedness (despite culture-dependent variations) in all human societies [32]. Therefore, taken together, the most promising approach seems to be an integrative model that takes genetic as well as environmental or cultural influences on handedness into account. Laland et al. [31,32] developed such a gene-culture model of handedness and suggested that, in addition to genetic influences, culturally transmitted biases, primarily through parental influences have an impact on handedness. According to this model, familial handedness has an influence on individual handedness through model learning or direct instruction.

Interestingly, another possible process in which non-genetic influences can shape handedness has been proposed. Humans are amniotes just like birds are and, comparable to them, they also display a preference for a right head turn before and after birth [24]. Indeed, it has been suggested that a right-sided bias in infants may contribute to right-handedness by generating an asymmetry in visual experience of the hands [39]. This theory is supported by findings that infants' preferential head-turning direction correlates with hand use [29]. Although this strong infant right-turning bias of the head has been reported to disappear at 15 weeks of age [25], a similar turning bias is still visible in adults [18] and correlates with adult handedness [43]. Even though these studies suggest a relationship between head-turning bias and functional lateral preferences, they do not yield a causal proof. In principle, the observed head–hand relation could also be explained by a central asymmetry of motor organisation without further causal links between its constituents. The best way to test the influence of a skewed visual control on the development of handedness would be to test children that are born with a permanent motor bias of the head which subsequently increases the probability to visually follow one hand. Children with congenital muscular torticollis provide this opportunity. In this congential orthopaedic condition, the sternocleidomastoid muscle is shortened on the involved side leading to an ipsilateral tilt and a contralateral rotation of face and chin [13,20]. The head-tilt can be either to the left or the right side and a head-tilt to the right is combined with a rotation of face and chin to the left and vice versa. It has therefore to be noted that this condition is not directly comparable to the right-sided head-turning bias in healthy infants [39]. Michel [39] assessed supine head-orientation preferences in infants and in a supine position, a head-orientation preference to the right side would clearly result in an increased visual experience of the right hand. In torticollis children, however, the head-tilt in combination with the rotation of face and chin to the opposite side results in an increased visual experience of the hand contralateral to the head-tilt (see Fig. 1).

In adults, no link between handedness and left or right torticollis has been found [52]. However, in this study, adult patients were tested without asking if the condition was congenital or for how long it existed. Since it is possible to acquire torticollis as a symptom of an underlying muscular, osseous, ocular, psychiatric, or neurologic disorder [30] at a later age and animal studies clearly reveal an early sensitive period of plasticity for asymmetry [33], it is vital to only incorporate participants for whom the condition exists since delivery. Therefore, we assessed hand-, foot- and eye-preference in children diagnosed with congenital muscular torticollis with a right or left head-tilt and compared them to healthy controls. We assume that children with a head-tilt to the right have a stronger left-sided bias than the controls, whereas children with a tilt to the left have a stronger right-sided bias than the controls.

2. Methods

2.1. Participants

A total of 117 children (54 girls and 63 boys) with a mean age of 8.21 (SD = 1.11, range: 7–11 years) were tested. The EG (experimental group) consisted of 58 children which were newly diagnosed with KISS (Kinematic imbalances due to suboccipital strain) syndrome [2–4], a syndrome that includes congenital muscular torticollis (ICD-10 classification: Q68.0) as the main symptom. Participants were recruited in the private practice of the co-author H.B. and congenital muscular torticollis was diagnosed by means of clinical assessment, shortly (less than half a year) before the testing took place. Therefore the age of diagnosis was between the 7th and 11th year of life (depending on the participants age). To make sure that the condition existed since birth, a diagnostic interview with the parents including an inspection of baby pictures of the participants (if available) for typical signs of congenital muscular torticollis (see Fig. 1), was conducted before testing. The participants in the experimental group had no psychiatric, neurological, muscular or orthopaedic disorders or any injuries that might have caused an acquired torticollis [30] or might otherwise have influenced functional lateralisation.

The experimental group was subdivided in EG Right (27 children with a right head-tilt) and EG Left (31 children with a left head-tilt). The CG (control group) consisted of 59 healthy children recruited from local schools. Parents were present during testing but were instructed not to interfere. All parents gave written informed consent that their children were allowed to participate in the study. The study was approved by the ethics committee of the

Fig. 1. A 4-month old boy with torticollis. The head-tilt in combination with the rotation of face and chin to the opposite side results in an increased visual experience of the hand contralateral to the head-tilt.

University of Bochum and all participants were treated according to the declaration of Helsinki.

2.2. Procedure

To test the children's handedness, footedness and eye-preference, they were asked to perform a number of different behavioural tasks which were based on commonly used questionnaires to assess these lateral preferences in adults. The tasks used to assess handedness were based on the Edinburgh Handedness Inventory (EHI) [44]. Children had to: 1. Write their name on a piece of paper; 2. Throw a ball; 3. Cut-out a nameplate using scissors; 4. Use a toothbrush; 5. Cut a piece of play dough with a knife; 6. Use a spoon to eat puffed rice; 7. Play a C-major scale on a xylophone. To keep testing time and stress for the children to a minimum, the three items 'Drawing', 'Using a broom' and 'Opening a box' of the EHI were excluded from the test, since the remaining seven items are sufficient to provide an internally consistent and valid measure of handedness [14]. Task seven was used to substitute the item 'Striking a match' of the EHI as an assessment of fine motor skills, since the original item seemed unsuitable for children. The tasks used to assess footedness were based on the Waterloo Footedness Questionnaire [15]. Children had to: 1. Kick a soccer ball towards a goal; 2. Stand on one foot; 3. Smooth a carpet with one foot; 4. Step up onto a chair; 5. Stomp on a fast-moving cloth ball; 6. Balance on one foot on a wooden ledge; 7. Pick up a marble with the toes of one foot; 8. Hop on one foot; 9. Stomp on the ground. The tasks used to assess eye-preference were mainly obtained from Porac and Cohen [45]. Children had to sight through a hole in wooden plate and down a kaleidoscope. Moreover, their dominant eye was also assessed with the Miles test [40] and the Dolman test [5]. The order of testing for handedness, footedness and eye-preference was counterbalanced across subjects.

For each behavioural test, a laterality quotient (LQ) was calculated according to the method by Oldfield [44]. The LQ's range was between −100 and +100, with positive values indicating a right-sided preference and negative values a left-sided preference. Participants were considered right-handed if the LQ was larger than zero and left handed if it was smaller than zero. There was no participant with an LQ of zero in the present sample.

3. Results

No differences in gender ($\chi^2(2) = 1.08$; $p = .58$) or age ($\chi^2(8) = 8.06$; $p = .43$) were observed between the groups. All 31 (100%) children in the EG Left were right-handed, whereas in the in the EG Right 21 (77.78%) children were right handed and the remaining 6 (22.22%) children were left handed. In the CG 54 (91.53%) children were right-handed and 5 (8.47%) were left handed (see Fig. 2). Children in EG Left were significantly more often right-handed than those in the EG Right when those two groups were compared directly ($\chi^2(1) = 7.68$; $p < .01$; effect size $\varphi = 0.36$). Also, when all three groups were compared, right-handedness was significantly more prevalent in the EG Left than in the CG and the EG Right ($\chi^2(2) = 8.49$; $p < .05$; effect size $\varphi = 0.27$). For footedness ($\chi^2(2) = 1.69$; $p = .43$) and eye-preference ($\chi^2(2) = 2.33$; $p = .31$) no significant differences between the three groups were observed.

To assess whether the three groups also differ in regard to continuously measured strength of their lateral preference, mean LQ's for handedness, footedness and eye-preference (see Fig. 3) were compared.

For handedness, the means suggest that the children in the EG Left (90.32) had a higher LQ than those in the CG (79.58), which in turn had a higher LQ than the children in the EG Right (59.22). Children in EG Left had a significantly higher LQ than those in the EG Right when those two groups were compared directly ($t(56) = -2.27$; $p < .05$; effect size Cohen's $d = -0.61$). However, the overall effect when all three groups were tested only approached significance ($F(2,114) = 2.74$; $p = .069$). For footedness ($F(2,114) = 0.72$; $p = .49$) and eye-preference ($F(2,114) = 1.41$; $p = .25$) no significant differences between the three groups were observed.

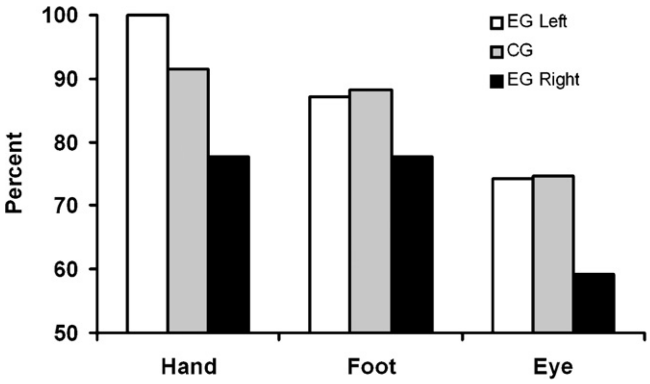

Fig. 2. Percentage of children that have a right-sided hand-, foot- or eye-preference in the EG Left (white bars), the CG (grey bars) and the EG Right (black bars).

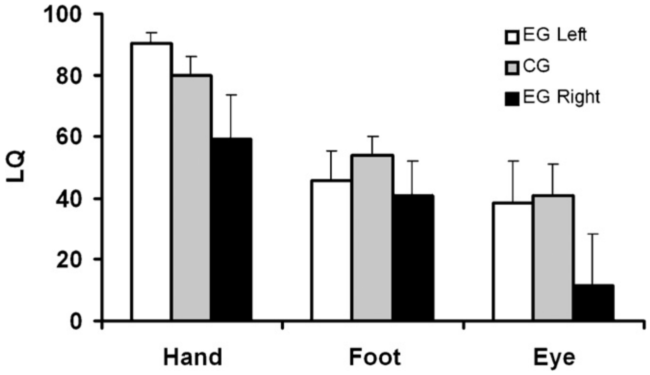

Fig. 3. Mean LQ's for handedness, footedness and eye-preference in the EG Left (white bars), the CG (grey bars) and the EG Right (black bars). Error bars show standard error.

4. Discussion

The primary finding of the present study was that increased visual experience of one hand affects an individual's handedness. Relative to controls, torticollis-children had a higher probability of right- or left-handedness when having a contralateral head-tilt in combination with an ipsilateral rotation of face and chin. In the control group, 91.5% of the children were right-handed which is nearly the same distribution as in the overall population [8]. A higher incidence of right-handedness was observed in children with a head-tilt to the left and a rotation of face and chin to the right, since a remarkable 100% of them were right-handed. In contrast, the probability of being right-handed was reduced to 78% in children with a head-tilt to the right and a rotation of face and chin to the left. Therefore, more than twice as many as the about 10% one would expect in the overall population [8] of the children in this group were left-handed. No statistical significant relation between head position and direction of functional asymmetries was found for footedness and eye-preference. However, it should be noted that the means (see Fig. 2) show a non-significant trend in the same direction as was observed for handedness, at least when the two experimental groups were compared, since there was a higher number of participants with a rightward preference for footedness and eye-preference in the EG Left than in the EG Right.

A similar pattern emerged for the LQ's. Torticollis-children with a head-tilt to the left and a rotation of face and chin to the right had a significantly higher LQ than torticollis-children with a head-tilt to the right and a rotation of face and chin to the left when those two groups were compared directly. Although the overall difference only approached significance when all three groups were compared, there was a non-significant trend that torticollis-children with a head-tilt to the left had higher LQ's than controls and that torticollis-children with a head-tilt to the right in turn had lower LQ's than controls. As for the absolute preferences, no statistical significant relation between torticollis and LQ was found for footedness and eye-preference was observed, but again, there seems to be a non-significant trend in the same direction as was observed for handedness.

The finding of an influence of torticollis on handedness in children is in contrast to the findings of Stejskal and Tomanek [52] who did not find such an influence in adult patients. However, these authors did not account for whether the torticollis was congenital or acquired [30] and it is well known from animal studies that there are early sensitive periods of plasticity for asymmetry [33]. It may be possible that some of the participants tested in the Stejskal and Tomanek [52] sample did acquire torticollis at an adult age, when it simply does not have an impact on handedness any more. This indicates that there may be a sensitive period early in life after which torticollis does not have an impact on handedness.

The present results clearly show an impact of a non-genetic, experience based factor on handedness. In principle, this is in line with research on the development of asymmetries and lateralised preferences in other vertebrate species, such as birds in which visual stimulation of one eye during early development is critical for the development of functional and morphological asymmetries [33]. However, it is clear that the mechanism reported here is not identical to that in pigeons or chicks. While the lateralised visual input during early ontogeny in birds alters the visual system of adult individuals and causes changes in functional asymmetries between the two hemispheres of the brain, lateralised visual control of the left or the right hand due to torticollis is assumed to affect the hand motor system in humans and its effects are more likely to be specific to this system.

There is also evidence for an impact of a non-genetic experience based factor on behavioural asymmetries in non-human mammals. For example, pawedness in mice is strongly influenced by an environmental bias that favours a left- or right-sided preference [7]. Only about 10% of the mice in this experiment showed a paw preference inconsistent with the environmental bias. However, in contrast to the classic Collins experiment [7], we expectedly observed a larger genetic than non-genetic effect in the present data, as 78% of the children with a head-tilt to the right and a rotation of face and chin to the left were right-handed, although their visual experience of their hands would favour left-handedness. Therefore, a model incorporating both genetic and non-genetic influences on handedness would be the most suitable one to explain the present data. Such a model has been developed by Laland et al. [31,32]. Following a notation by McManus [35,36], they assume that the probability of becoming left- or right-handed is influenced by two additive alleles D (Dextral) and C (Change) on a single locus. The genetic probability of being right-handed for an individual with two D alleles is than calculated by adding p, a factor that represents the dextralising effect of this genotype, to 0.5, the chance probability of being right-handed. In DC individuals p is weighted by a parameter h specifying the dominance of the two alleles and in CC individuals p is excluded from the formula. In addition, they also assume that parental handedness influences children's handedness. In children with two right-handed parents, a factor α representing the increase in right-handedness caused by having these parental influences is also added to the formula. In children with two left-handed parents this factor is subtracted, whereas in children with parents with mixed handedness a factor β representing the changes in handedness associated with these parental influences is added. The present findings may add to the Laland model as they show that other non-genetic factors than familial handedness have an impact on handedness. Specifically, we would suggest that the values for the factors α and β which represent non-genetic influences on handedness in the model should not exclusively be determined by parental handedness, but also take early asymmetries in visual experience of the hands, as might be caused by head-turning preferences, into account. This view is in accordance with the model of Michel [39] who suggested that side biases in infants' head-turning preferences generate an asymmetry in visual experience of the hands that in turn influences handedness. Also, there is other experimental evidence for this assumption, such as the correlation of infants' preferential head-turning direction with hand use [29] or the finding that preferred head-turning direction during kissing in adults is related to handedness [43].

Remarkably, this relation of head-turning preferences and handedness is not limited to humans. A preference for a right head turn has been observed in infant olive baboons and chimpanzees [11,22] and in chimpanzees it has been reported to be predictive of juvenile hand preferences [23]. Based on these findings in primates, Hopkins [21] developed a gene-environment model of handedness that is very similar to the one we propose, namely that early positioning biases such as head-turning preferences lead to differential stimulation of the two hands and that this, in turn, influences later handedness.

Interestingly, the majority of the adult population demonstrates a very slight head-tilt with about 67% having the left eye higher and 33% the right eye higher [38]. However, it is not possible to assess the exact impact of these minor degrees of asymmetry on handedness in healthy populations based on the present dataset. Torticollis-children exhibit a permanently fixed head-posture, whereas in the overall population a clear head-turning preferences are only evident in specific situations, such as if an infant is brought into a supine position or during kissing. Also, it is not known how often and how long normal adult exhibit the asymmetries in eye height reported by McManus and Tomlinson [38] in everyday life. This probably results in stronger asymmetries in visual experience of the hand in torticollis-children than in the overall population.

Taken together, our findings showed an effect of visual experience of the hands on handedness and possibly on other lateral preferences, which is not possible to explain with a purely genetic approach. Therefore, the present data strongly suggest a combined gene-environment model for the development of human handedness.

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