

Experience-dependent emergence of functional asymmetries

Elena Nava¹, Onur Güntürkün², and Brigitte Röder¹

¹Biological Psychology and Neuropsychology, University of Hamburg, Hamburg, Germany

²Institute for Cognitive Neuroscience, University of Bochum, Bochum, Germany

Right head-turning preference is assumed to be a developmental default. This motor asymmetry seems to influence the development of other lateralised behaviours—such as handedness—as a consequence of orienting vision towards the right side of the body. To document the role of visual experience in promoting lateralised functions we assessed head-turning preference and handedness in a group of congenitally blind human adults. We found a left-side preference for head turning but a clear right-handedness in the same individuals. This asymmetric relationship suggests that absence of visual experience can alter head-turning preference and that handedness can emerge without visual orientation towards the right side. Our findings shed new light on the role of visual sensory experience in shaping functional asymmetries and suggest that single-gene models and environment alone cannot fully explain the emergence of functional asymmetries in humans.

Keywords: Functional asymmetries; Head turning; Handedness; Blindness; Experience.

A preference for right head-turning appears to be one of the earliest lateralised behaviours reported in human foetuses (Ververs, de Vries, van Geij, & Hopkins, 1994) and human newborns (Liederman & Kinsbourne, 1980; Michel, 1981). Interestingly, this lateralised pattern persists into adulthood, as documented by Güntürkün (2003), who observed kissing side preference in couples in public places, and by Ocklenburg and Güntürkün (2009) who documented the same right-sided head turn preference in young adults asked to kiss a life-sized mannequin in a controlled setting.

Address correspondence to: Elena Nava, University of Hamburg, Biological Psychology and Neuropsychology, Von-Melle-Park 11, 20146 – Hamburg, Germany. E-mail: elena.nava@uni-hamburg.de

This right head-turning preference has been associated with the development of other right-sided asymmetries, such as handedness, which was suggested to be caused by increasingly orienting vision towards the right side of the body (Coryell, 1985; Michel, 1981; Ocklenburg et al., 2010). For example, in a recent study Ocklenburg et al. (2010) investigated the development of hand preference in children suffering from inborn muscular torticollis (a condition by which the head is tilted to one side due to muscular spasm, so that vision is continuously oriented towards the contralateral side of the head-tilt), and found that torticollis children tended to develop right- vs left-handedness according to their side of head-tilt (i.e., children with left head-tilt that forces a right-sided visual orientation are more right-handed than right head-tilted children). Ocklenburg et al.'s (2010) results speak in favour of the role of visual experience in shaping functional asymmetries, although the authors themselves suggested that a combined gene–environment interaction could best explain their findings.

As a matter of fact, the predominant view on handedness has favoured genetic models, such as the right shift theory (Annett, 2002) which proposes that there might be a gene responsible for left cerebral hemisphere dominance that would shift the probability distribution for handedness to the right. In the absence of such gene, hemispheric dominance and handedness would be randomly distributed between left and right.

Overall, the debate as to what extent experience vs genetic programmes contribute predominantly to the development of different functional asymmetries has not reached definite conclusions.

A new approach for solving this debate could come from studies investigating lateralised functions in congenitally blind individuals. Observing whether inborn blindness affects the development of functional asymmetries could shed new light on the role of experience in fostering lateralisation. If visual orientating towards the right side strongly biases the emergence of right-sided motor asymmetries, we would expect blind individuals to be less right-handed. To date only a few studies have assessed handedness in blind individuals (Caliskan & Dane, 2009; Ittyerah, 1993, 2000), while others have investigated ear (Larsen & Håkonsen, 1983) and language (Röder, Stock, Bien, Neville, & Rösler, 2002) asymmetries. Interestingly, these latter studies have suggested that blind individuals may engage both hemispheres during auditory and language tasks, thus recruiting the right hemisphere more for functions that are usually predominantly left-lateralised in right-handed sighted controls. For example, Röder et al. (2002) presented sentences to a group of congenitally blind individuals while recording their brain activity with functional magnetic resonance imaging (fMRI) and found that these participants activated, in addition to the classical perisylvian language areas of the left hemisphere,

homologous right hemispheric structures, thus showing a bilateral distribution of cerebral activation during a speech comprehension task. It should be noted that the blind individuals in the study were all right-handed, suggesting that hand preference does not accompany a cerebral dominance for language, as proposed by neuroimaging studies (Knecht et al., 2000) as well as genetic models (McManus, 1985). Thus, it appears that the development of hand preference might be independent from the emergence of other functional asymmetries. It could be argued that the differences in hemispheric activity between blind participants and sighted controls in the fMRI study (Röder et al., 2002)—given its linguistic material—might reflect the use of Braille. In fact the authors speculated that the use of Braille could result in a bilateral organisation of language (even in tasks where reading is not directly involved). However, the blind participants were mixed with regard to preferred Braille reading hand, thus further corroborating the absence of relation between handedness and cerebral dominance for language.

Hand preference in congenitally totally blind individuals has reached conflicting results. For example, while Ittyerah (1993, 2000) found a right hand preference in both groups of blind and control children aged between 6 and 15 years, Caliskan and Dane (2009) reported a higher incidence of left-handers in a group of blind children aged between 7 and 12 years. These mixed results could derive from the sample of blind participants tested. On the one hand, Ittyerah (1993, 2000) tested congenitally totally blind children, while Caliskan and Dane (2009) reported results from both congenitally totally blind children and children with different visual acuity (i.e., “poor” and “very poor”). Indeed, they found that children with higher visual acuity also had a higher rate of left-handedness. On the other hand, Caliskan and Dane (2009) tested over 1000 children (among whom 831 were congenitally totally blind), while Ittyerah (1993, 2000) observed hand preference in 100 children, thus having a reduced number of left-handers.

To further explore whether the role of visual experience shapes lateralised functions, we tested a group of congenitally blind human adults on a supposed innate functional asymmetry, such as head turning, and observed its relation to other motor asymmetries, such as handedness and footedness. We hypothesised that if visual experience plays a crucial role in shaping lateralised functions, then congenitally blind individuals would show no or less-clear direction in their functional asymmetries. More specifically, if right head-turning is an innate default and the development of right-handedness symmetrically follows this pattern, then we would have expected our participants to have a right head-turning preference accompanied with a randomly distributed right vs left hand preference.

METHOD

Participants

A total of 17 blind adults (6 females, mean age = 38 years; range: 24–54 years; all proficient Braille readers) were recruited to take part in the experiment, and 26 participants (15 females, mean age = 35 years, range: 25–63 years) with normal or corrected to normal sight served as controls.

All blind participants were blind since birth (i.e., blindness was diagnosed immediately after birth). In all cases, blindness was due to peripheral deficits and was not associated to other impairments (see Table 1 for details about the blind participants). Twelve blind participants were totally blind (i.e., no perceptual residual), while five reported minimal light sensitivity but they were not able to functionally use this sensation nor had they pattern vision. In other words, their rudimentary light sensitivity did not allow them discriminating any object or face around them. Since the data of these participants did not differ from those of the totally blind individuals we did not treat them as separate group.

The study was approved by the ethical committee of the German Society for Psychology.

TABLE 1
Blind participants

<i>ID</i>	<i>Gender</i>	<i>Age</i>	<i>Cause of blindness</i>	<i>Age of onset</i>	<i>Visual perception</i>	<i>Handedness</i>
1	M	32	Eye cancer	birth	none	right
2	M	49	Retrolental fibroplasia	birth	none	right
3	M	25	Genetic causes	birth	none	right
4	M	34	Glaucoma	birth	diffuse light (*)	right
5	F	48	Optic atrophy	birth	none	right
6	F	30	Leber's congenital amaurosis	birth	none	right
7	F	47	Retrolental fibroplasia	birth	none	left
8	F	31	Genetic causes	birth	none	right
9	F	29	Retrolental fibroplasia	birth	none	left
10	M	35	Retrolental fibroplasia	birth	none	right
11	M	39	Congenital Retinitis pigmentosa	birth	none	right
12	F	40	Retinal degeneration	birth	diffuse light (*)	right
13	M	47	Retinal degeneration	birth	none	right
14	M	54	Unknown peripheral defect	birth	diffuse light (*)	right
15	M	29	Retrolental fibroplasia	birth	none	right
16	M	48	Infection (+)	birth	diffuse light (*)	right
17	M	24	Infection (+)	birth	diffuse light (*)	right

(*) = rudimentary sensitivity for brightness but no pattern vision; (+) = unspecified type of infection transmitted from the mother to the developing foetus during pregnancy.

Procedure

To assess the typical pattern of right-side preference we tested sighted controls (who were not blindfolded) on a series of lateralised tasks, including head turning, handedness, footedness, and eye preference. Head-turning preference was assessed by asking participants to kiss a life-sized mannequin (torso and head only) positioned on a table and adjusted at the participant's head height. Participants were asked to stay right in front of the mannequin, so that the experimenter could observe from behind the kissing movement and report its side (right, left, no preference). We adopted this measure to assess head-turning preference from previous studies (Güntürkün, 2003; Ocklenburg & Güntürkün, 2009).

Foot preference was assessed by making participant put their preferred foot on a foot-step. Eye preference was measured by asking participants to look into a door lock (i.e., of the door of the experimental chamber) with their preferred eye. Finally, handedness was assessed by asking participants to answer a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield, 1971).

Blind individuals performed all tasks with the exception of eye preference. Blind individuals were helped to move in front of the mannequin for the head-turning task; they were moved in front of the footstep to assess their foot preference, and they were helped to move towards the door to assess their ear preference. In addition, to perform the kissing task, blind participants were allowed to touch the mannequin's face before kissing it to enable them to direct the kiss towards the correct location (i.e., the lips).

In accord with Güntürkün (2003) all tasks were performed once to ensure a spontaneous motor response.

RESULTS

Figure 1 shows percentage of right and left preference separately for group and task. Controls were found to have the typical right-side preference, in that they showed a right preference for head turning ($\chi^2 = 3.8$, $p = .05$), handedness ($\chi^2 = 18.6$, $p < .001$), footedness ($\chi^2 = 7.5$, $p = .006$), and eye preference ($\chi^2 = 3.8$, $p = .05$).

In addition, of the 17 sighted right-kissers, 89% were right-handed, 78% were right-footed, and 83% had a right-eye preference. Of the 9 left-kissers, 100% were right-handed, 75% were right-footed, and 38% had a right eye preference.

In contrast, blind individuals showed a strong left preference for head turning ($\chi^2 = 9.9$, $p = .002$), which was accompanied by a clear right-handedness ($\chi^2 = 9.9$, $p = .002$). On footedness, blind individuals showed a trend towards a right preference as well ($\chi^2 = 2.9$, $p = .09$). Out of the 15

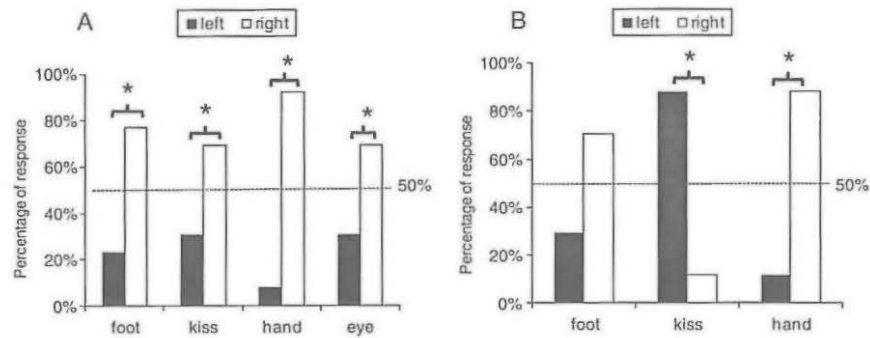


Figure 1. Percentage of right vs left responses as a function of task, separately for (A) controls and (B) blind individuals.

left-kissers, 87% were right-handed and 67% were right-footed. Finally, no preference for hand used during Braille reading was found in the blind participants ($\chi^2 = 1.5$, $p = .5$).

When comparing the relative frequencies of lateralised functions between groups, we found that head-turning preference differed between blind individuals and sighted controls ($\chi^2 = 18$, $p < .001$), while both handedness and footedness did not differ between groups ($p = .6$).

DISCUSSION

In the present study we investigated the role of visual experience in fostering functional asymmetries by testing a group of totally blind human adults. We predicted that, if visual experience plays a crucial role in shaping the direction of lateralisation, our blind participants would have shown no side preference for the motor asymmetries we tested (i.e., head turning, handedness, and footedness). Our results did not match our hypotheses, in that blind individuals, unlike sighted controls, were found to have strong side preferences. They displayed a left head-turning bias and a right hand preference. This atypical relation might have a series of theoretical implications which we discuss in the following, being aware that they are derived post hoc. First, the fact that absence of developmental visual experience alters the typical right head-turning pattern, which has been shown to be robust and thought to be innate (Liederman & Kinsbourne, 1980; Ververs et al., 1994), suggests that this motor bias is greatly affected by sensory input. This novel finding sheds new light on the role of sensory experience in shaping asymmetric behaviours assumed to have a typical right-sided bias.

Second, we have shown that visual deprivation only alters head-turn but leaves other asymmetries unaffected (i.e., handedness). The fact that visual

experience only selectively shapes the direction of some functional asymmetries further suggests that different kinds of left–right biases possibly have different reasons. For example, head-turning preference and handedness might have different degrees of genetic predetermination and experience susceptibility or both might depend on different types of experience. This result has implications for previous studies that have documented the influence of visual experience in fostering functional asymmetries (Coryell, 1985; Ocklenburg et al., 2010), as well as genetic models accounting for the emergence of handedness (for a review, see Corballis, 1997).

Although Ocklenburg et al. (2010) found a strong relation between vision and handedness, they nonetheless concluded that handedness emerges from a combined gene–environment interaction in which handedness cannot be explained with a purely genetic approach, although genetic factors may explain a major aspect of the variance. Consequently, a right-turning bias should increase the incidence and strength of right-handedness since it biases vision towards the right hand. Against this background the lack of a right-turning preference in blind individuals should be expected to decrease right-handedness. This was not the case. Obviously, our sample of blind participants was small and only a strong effect size would have uncovered a significant change in the magnitude of handedness (and footedness) between controls and blind participants. However, the numerically complete absence of a changed left/right handedness ratio in the group of congenitally blind individuals suggests that visual experience does not strongly modify handedness despite its significant influence on head-turn preference, suggesting that either genes or a different type of experience may play a crucial role in the emergence of this specific functional asymmetry. The first option would be in accord with the main models on the emergence of handedness (Annett, 2002; McManus, 1985). In particular, twin studies (for a meta-analysis of the literature, see Sicotte, Woods, & Mazziotta, 1999) have shown that monozygotic twins tend to have same hand preference compared to dizygotic twins, thus supporting the genetic models for handedness. The latter would nevertheless demonstrate that different functional asymmetries do not develop in parallel based on the same types of experiential guidance.

It should be mentioned, however, that the comparison between Ocklenburg et al. (2010) and our study may be susceptible to confound, as total absence of visual experience cannot be completely compared to continuously orienting vision towards one side of the body. For example, people with macular degeneration causing impaired central vision show impaired auditory localisation (Lessard, Paré, Lepore, & Lassonde, 1998), while totally blind individuals show equal or improved auditory localisation skills as compared to sighted controls (Röder et al., 1999). Thus altered vision might affect non-visual functions differently as compared to the total absence of vision. In the same vein it could be speculated that a deviating or total visual deprivation

could differentially influence patterns of lateralisation due to plastic changes that have been observed in the sensory de-afferented brain, possibly related to compensatory mechanisms (for a review, see Merabet & Pascual-Leone, 2010).

Finally it remains to be discussed why an atypical experience, such as blindness, leads to a reversal of head-turning asymmetry. Presently we can only speculate about the reasons for this finding. A hint to what could possibly influence such reversal comes from observation of common patterns of behaviour in most blind individuals. Blind individuals tend to keep their cane in their dominant hand (i.e., right hand), while holding the upper right arm or the right shoulder of their guide with their left hand, so that the interlocutor is kept on the left side. Indeed, all our participants used a cane daily and reported keeping it in their right hand. This particular behaviour could foster selective orienting and head turning towards the left side. Whether other changes in the lateralisation of, e.g., social functions follow from this bias seems an interesting question for future research.

In conclusion, our findings speak in favour of the distinct role of nature (i.e., genetics) and nurture (i.e., environment) in shaping human lateralised functions, and the difficulty of reconciling the emergence of all functional asymmetries to either single-gene or gene–environment interaction models. Further research is needed to shed light on the functional and possibly evolutionary meaning of these distinct roles in explaining human lateralisation.

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