eNeuro

*Research Article: New Research | Cognition and Behavior*

# Biological action identification does not require early visual input for development

https://doi.org/10.1523/ENEURO.0534-19.2020

**Cite as:** eNeuro 2020; 10.1523/ENEURO.0534-19.2020

Received: 16 December 2019
Revised: 16 August 2020
Accepted: 27 August 2020

1. **Manuscript title -** Biological action identification does not require early visual input for development
2. **Abbreviated title –** Development of action identification
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6. **Number of figures – 6**
7. **Number of tables – 2**
8. **Number of Multimedia - 0**
9. **Number of words for abstract – 250 (limit 250 words)**
10. **Number of words in significance statement – 112 (limit 120 words)**
11. **Number of words for introduction – 696 (limit 750 words)**
12. **Number of words for discussion – 2107 (limit 3000 words)**
13. **Acknowledgements –** We would like to thank Prof. Balasubramanian for supporting the study at the Hyderabad Eye Research Foundation and the Opticals department at LV Prasad Eye Institute for preparing the trial frames with the Bangerter filters.
14. **Conflict of interests – Authors report no conflict of interest**
15. **Funding sources –** The study was funded by the European Research Council grant ERC-2009-AdG 249425-CriticalBrainChanges and DFG Ro 2625/10-1 to Brigitte Röder.

Abstract:

Visual input during the first years of life is vital for the development of numerous visual functions. While normal development of global motion perception seems to require visual input during an early sensitive period, the detection of biological motion (BM) does not seem to do so. A more complex form of BM processing is the identification of human actions. Here we tested whether identification rather than detection of BM is experience dependent. A group of human participants who had been treated for congenital cataracts (of up to 18 year duration, CC group) had to identify ten actions performed by human line figures. In addition they performed a coherent motion (CM) detection task, which required identifying the direction of coherent motion amidst the movement of random dots. As controls, developmental cataract reversal individuals (DC group) who had undergone the same surgical treatment as CC group were included. Moreover, normally sighted controls were tested both with vision blurred to match the visual acuity of CC individuals (vision matched (VM) group) and with full sight (sighted control (SC) group). The CC group identified biological actions with an extraordinary high accuracy (on average ~85% correct) and was indistinguishable from the vision matched control group. By contrast, CM processing impairments of the CC group persisted even after controlling for visual acuity. These results in the same individuals demonstrate an impressive resilience of biological motion processing to aberrant early visual experience and at the same time a sensitive period for the development of coherent motion processing.

**Significance statement:**

Biological motion is a crucial aspect of human vision, which has been shown to emerge early in human ontogeny. Here we report an astonishing high accuracy in identifying human actions in a unique group of individuals who had regained vision later in life (until the age of 18 years) after being treated for congenital cataracts. By contrast the same individuals were markedly impaired in another non-biological motion tasks requiring the detection of motion coherence in dot kinematograms, even after visual acuity impairments were taken into account. Thus, the present study demonstrates a remarkable resilience of complex biological motion processing capabilities such as the identification of human actions to aberrant early visual experience.

**Introduction:**

Sensory input during early years of life is essential for normal development of sensory systems (Wiesel and Hubel, 1965). In humans, studies in individuals treated for congenital cataracts (CC) have revealed incomplete recovery in many visual functions, including visual acuity (Ellemberg et al., 1999), stereovision (Tytla et al., 1993), visual feature binding ( Putzar et al., 2007; McKyton et al., 2015), global motion processing (Ellemberg et al., 2002; Bottari et al., 2018), and face processing (Le Grand et al., 2001; Röder et al., 2013) while functions such as color discrimination (Brenner et al., 1990; Pitchaimuthu et al., 2019) seemed to emerge independently of early visual experience. Biological motion (BM) processing, e.g. the ability to detect the movement of biological figures with sparse information (Johansson, 1973), has been shown to recover well following early visual deprivation (Hadad et al., 2012), that is, both detection thresholds as well as neural signatures have been observed to be indistinguishable between a CC group and normally sighted controls (SC group) (Bottari et al., 2015, 2016).

However, it is unclear yet whether more complex aspects of BM processing, such as the identification of human actions, require early visual experience. BM detection, as studied with point light displays of walkers, requires the extraction of the spatial configuration of point lights and its congruent change over time (Theusner et al., 2014). In contrast, action identification involves knowledge of the meaning of human postures and how they change over time. Action identification is further complicated by the large variance from different agents performing the actions and the different viewpoints from which actions are observed. Action identification, thus, requires extracting action invariant features.

In the present study, we tested individuals with a history of pattern vision loss due to bilateral, total, dense congenital cataracts on their ability to accurately perceive human actions performed by line figures. For this purpose, we used the test battery (BMLtest battery) developed by Saunders and Troje (2011)). Three potential confounds were additionally investigated: first - unspecific effects related to cataract surgery; second - the timing of visual deprivation, that is, whether the visual deprivation

existed at birth or emerged later in development; third -the overall lower visual acuity typical for individuals with a history of early cataracts. In previous studies both of these confounds have been simultaneously controlled for by including individuals who had lower visual acuity compared to typically sighted individuals due to cataract onset later during development (e.g. individuals with reversed developmental cataract (DC); Lewis and Maurer, 2009; Röder et al., 2013). Alternatively, the persisting visual impairments have been controlled for by blurring visual stimuli for normally sighted controls (e.g. - McKyton et al., 2015). If a sensitive period exists for the development of a specific function, once visual acuity (VA) is controlled for, the CC group, but not the DC group is expected to show impaired performance. The normally sighted age matched controls were tested with full sight and with the visual acuity matched using specialized translucent filters called Bangerter filters, which have been regularly used in amblyopia therapy (Agervi, 2011). All participants were tested in two tasks of the BMLtest battery (Saunders and Troje, 2011): (1) an action identification task, in which subjects had to name the action performed by an actor shown as stick figures; (2) a coherent motion (CM) detection task, in which participants judged the direction of the coherent motion of dots among a set of randomly moving dots (CM task).

We predicted that complex aspects of biological motion, such as the identification of human actions, would depend less on early visual experience than coherent motion perception. Thus, we hypothesized that any group difference between the CC group and SC group in the action identification task can be accounted for by visual acuity differences. By contrast, for the coherent motion task we predicted that impairments specific for the same CC group emerge even after controlling for visual acuity. Thus, the present study is aimed at providing non-confounded evidence for a sensitive phase in early development for global motion processing while showing in the same individuals a high resilience of complex biological motion functions as the identification of human actions to aberrant early visual experience.

Methods:

Participants:

The group of individuals with a transient phase of congenital cataracts (CC group) was comprised of 12 participants (mean age: 16 years, range: 7-34 years; 3 females; all right handed; mean age at surgery: 66.8 months, range: 2-220 months; mean duration since surgery: 120 months, range: 6-396 months; for detailed demographics of participants refer table 1) who had undergone treatment for bilateral, dense, congenital cataracts in both eyes. These participants were recruited from LV Prasad Eye Institute, Hyderabad, India. Congenital cataract individuals qualifying for the present study were identified among a larger number of patients with the diagnosis "congenital cataract" based on the following criteria: (1) All patients suffered nystagmus which is often the result of a lack of pattern vision for longer than 10-13 weeks after birth (Rogers et al., 1981; Gelbart et al., 1982). Such a nystagmus persists after surgery, and was present in all CC individuals. (2) The lenticular opacity for CC individuals was dense prior to surgery which resulted in an inability to have a view of the fundus during clinical examination (except participants with partially absorbed cataracts). Additionally, (3) a positive family history of congenital cataract. (4) Esotropia resulting from equal visual deprivation in both eyes was used as additional classification criteria. This information was available from the detailed medical records available at LV Prasad Eye Institute, Hyderabad, India. Patients with an ambiguous clinical profile were not included. Although a 100% confidence of having included only congenital cataract-reversal individuals with a history of bilateral, total, dense cataracts is not possible in a retrospective classification of participants, the likelihood of achieving an accurate CC classification was maximized in the present sample by having access to extensive clinical data allowing for the use of strict criteria.

In order to ensure that any observed difference between congenital cataract-reversal individuals and normally sighted controls was not the result of trivial causes such as the experience of a surgical procedure at the eyes, and to understand the effects of vision loss immediately after birth vs. later in

childhood, we tested a group of control participants whose form vision was preserved at birth and who developed cataracts later during childhood. These participants had undergone the same surgical procedure as the CC group; 3 out of these 12 individuals had congenital but non-dense cataracts. These participants were subsumed as developmental cataract group (DC). Similar to the CC group, these participants had undergone treatment for cataract (mean age at surgery: 116 months, range: 24-434 months; mean time since surgery: 37 months, range: 2-183 months). We tested 12 DC participants (mean age: 12.6 years, range: 8-37 years, 4 females, all right handed) who were recruited from LV Prasad Eye Institute, Hyderabad, India. They were classified based on the medical records of the place of testing (will be revealed later). The clinical diagnosis of developmental cataract was mostly based on a number of criteria such as the parents' or patients' report of the age of poor vision onset, lack of nystagmus and a lack of family history of congenital eye pathologies. Additionally, individuals with incomplete congenital cataract, suggesting preservation of early pattern vision were included in the DC group (for complete description see table 2).

To control for VA and thus to isolate the effects of prevailing VA loss at the time of testing, a second control group of 12 participants with normal vision (mean age 15.3 years, range: 8-32 years; 6 females; all right handed; for the exact visual acuities refer table 1) was tested. Similar to the CC and DC participants, these individuals were also recruited from Hyderabad, India. They were matched for age with the CC group (CC) (+/- 1 year, for one adult CC participant -2 years, see Table 1). This control group performed the task twice: once with normal vision and the second time with the VA being individually matched to one of the CC individuals. With their vision reduced using the Bangerter filters, these participants served as the vision matched control group (VM), and without the filters the same participants served as normally sighted controls (SC). Hence, with their reduced vision, the control group was matched for age and visual acuity with that of the CC group.

Participants in all three groups (CC, DC, VM/SC) were healthy (expect the history of cataracts in CC and DC individuals) with no history of physical problems by self-report (VM/SC group) and by physical

158 examination (CC and DC groups). The study was approved by the institutional ethics boards of
159 University of Hamburg, Hamburg, Germany and LV Prasad Eye Institute, Hyderabad, India. Informed
160 consent was obtained from participants, and from legal guardians for minors before the beginning of
161 experiments. The quality of healthcare received by the participants was not affected by their
162 willingness to participate in our experiments.

163 Stimuli and apparatus:

164 Visual acuity matching using Bangerter filters:

165 Bangerter filters are translucent light diffusers that can be attached to spectacles and are capable of
166 causing degradation in vision due to the resultant attenuation of higher spatial frequencies (Pérez et
167 al., 2010). Although, these filters can reduce the visual acuity in steps on 0.1 logMAR in healthy eyes,
168 (Odell et al., 2008; Agervi, 2011; Rutstein et al., 2011) an intended degradation of more than 1.0
169 logMAR of visual acuity cannot be obtained even by the manufacturer's recommendation. Since our
170 participants required visual acuity reduction of up to 1.3 logMAR, we used a combination of filters to
171 achieve visual acuity reductions beyond 1.0 logMAR. For this purpose, we attached the filters to zero
172 power wide field trial lenses typically used in optometric eye examinations. Similar to the use of trial
173 lenses during an eye examination to arrive the correct refractive correction, combinations of these
174 "trial filters" were in turn used to arrive at the desired visual acuity. Using the manufacturer's
175 recommendations and previous reports (Odell et al., 2008) as starting filter strengths, different
176 combinations of filters were tried until the desired visual acuity was obtained. Although not tested
177 with Bangerter filters, the neural system is generally prone to blur adaptation (Clifford et al., 2007;
178 Webster, 2015), and hence, the participants were asked to stay with the filters for a few minutes for
179 the visual system to get adapted to the blur, and visual acuity estimation was repeated after
180 adaptation. If the pre and post visual acuity varied widely, the filter strength was assessed again until a
181 stable filter strength was obtained. While combining multiple filters, the "microbubbles" (Pérez et al.,
182 2010) of a given filter aligning with that of the preceding/following one might potentially be an

important factor in maintaining image degradation. But in our experience, we noticed that the alignment was robust to small variations in head movements. All visual acuity measurements were done using the Landodt's C optotype of the Freiburg Visual Acuity Test (FrACT) (Bach, 1996). The optotypes were shown on a 20" Dell monitor with a resolution of 1600X900 (refresh rate 60 Hz) and a testing distance of 240 cm controlled by a Dell laptop.

Stimuli:

The biomotion test battery (*BMLtest*) by Saunders and Troje (2011) was used. The test battery consists of a number of tests, of which we used the "coherence" and "action" experiments. All stimuli were shown on a 20'' Dell IN2030M LCD monitor with a refresh rate of 60 Hz using a Dell laptop with a resolution of 1600 X 900. Participants were seated at a distance of 60 cm from the screen, and viewed the stimuli with their best refractive correction. They were allowed to switch between the segments of their bifocals (in case of the CC and DC participants), and were additionally allowed to get a closer look at the stimuli in cases where the stimuli were not sufficiently visible at the testing distance. For the VM participants the Bangerter filters were placed over their refractive correction.

Procedure:

Coherent Motion task:

The "Coherency test" of *BMLtest* battery, originally based on Newsome and Paré (1988), and used by Bottari et al. (2018) was adapted to obtain global motion coherence thresholds (CM task). In a 10 degree circular field, 15 dots, each of 15 pixel size moved either randomly or were displaced by 0.15 degree in a particular direction (right or left; the direction of motion was randomized on each trial). Each trial lasted 1000 ms and was preceded by a black screen with white fixation cross for the same amount of time. After each trial, participants gave a verbal response indicating the direction of motion (towards left or towards right). Younger children waved the appropriate hand to indicate the direction instead of providing an oral response. In all cases, the experimenter pressed the response button. The

next trial did not start until participants had given a response for the current trial. The test used a QUEST staircase procedure to obtain the threshold for detecting the direction of motion with a likelihood of 82%.

Biological action identification task:

The "Action" subtest of the *BMLtest* battery was used to assess participants' ability to accurately recognize an action performed by a moving line figure (see figure 1). The suite consisted of 10 different actions presented from three different viewpoints – straight ahead (0 degree view angle), oblique (30/45 degree view angle) and profile (90 degrees view angle) totalling to 30 trials. The line figure was formed by connecting 14 dots located at different joints and extremities of a typical human body (see figure 1). Each dot of the line figure was 15 pixels in size with the full figure being 280 pixels in size. The order of these trials was randomized on each participant. Participants were made aware of the 10 possible actions prior to the experiment, but were encouraged to respond intuitively. The 10 possible actions presented were catching, climbing stairs, jumping, jumping jacks, kicking, lifting, running, sitting, throwing, and walking. If participants, particularly children, did not have a word to describe the action performed by the biological motion figure, they were asked to imitate the action. On a number of occasions, participants who found it hard to give a verbal response for an action were able to recognise the action by imitating it, which was still taken as correct response. Participants reported the action verbally in Hindi, Telugu or English, and the experimenter pressed the response button. Reaction times were not recorded.

**Figure 1 to be inserted here**

The CC and DC group performed the coherent motion and biological action identification task in a random order once. The normally sighted controls performed both tasks twice - with (vision matched

control group - VM) and without (sighted control group - SC) the Bangerter filters; again, the order was randomized.

Data analysis:

Visual acuity as measured using FrACT was recorded in logMAR units and the ability to detect coherent motion was measured as the percentage of coherently moving dots needed to achieve 82% correct responses. The "Action" task consisted of 10 actions presented from three different view angles. The number of correct responses obtained out of 30 was used to calculate the proportion of correct responses for each participant. Visual acuity (logMAR units), biological action identification (proportion of correct responses) and coherent motion detection (threshold) were taken as dependent variables for separate group comparisons (CC, DC, VM/SC). One-way analysis of variance (ANOVA) was used to compare the CC group with the DC and VM group. A separate analysis was run comparing the CC group with the DC and the SC group. Planned comparisons between SC and VM groups were run using paired t- test. Homogeneity of data was tested using Levene's test, and when violated, the ANOVA was conducted assuming unequal variance.

The effect of viewpoint on the proportion of correct responses was additionally added as a repeated measurement factor in a 2-way analysis of variance with CC vs. VM as group factor. The number of correct responses was averaged for all the 10 trials from a given viewpoint and the average score was taken as the proportion of correct responses for this view angle. All analyses were done with RStudio (RStudio Team, 2016) using appropriate packages. An effect was considered significant if the resulting p-value for the statistical test was less than 0.05.

Result:

*Visual acuity comparison between groups:*

A one way analysis of variance (ANOVA) comparing the mean visual acuity between the CC, DC and VM groups was not significant $F(2,33) = 1.11$; $p = 0.34$. However, the comparison of the mean visual

acuity between CC, DC and SC groups using a one way ANOVA was found to be significant $F(2,16.45) = 41.2$; $p < 0.001$. Posthoc pairwise t-tests using Bonferroni corrections showed that the visual acuity score for the SC group (mean logMAR VA = -0.13, Standard Deviation (SD) = 0.11) was significantly higher than the visual acuity scores of both the CC (mean logMAR VA = 0.753, SD=0.33; $p < 0.001$) and the DC (mean logMAR VA = 0.556, SD=0.63; $p=0.001$) group. Further, a within group comparison using paired t-test demonstrated the successful match of the Bangerter filters: The SC group had significantly better visual acuity ($t$ (11) = -10.13; $p < 0.001$), than the VM group (mean logMAR VA = 0.82, SD=0.34). (Figure 2)

**Figure 2 to be inserted here**

Biological action identification task: Comparison between groups

The one way ANOVA with participant groups CC, DC, VM as between groups factor and proportion of correct responses as dependent variable found no significant effect of group $F(2,33) = 1.44$; $p = 0.24$, whereas the analogous ANOVA with the participant groups CC, DC and SC groups was found to be significant $F(2,33) = 4.34$; $p = 0.02$. Posthoc pairwise t-tests using Bonferroni corrections for the latter showed that the CC group (mean score = 0.85, SD=0.08) performed significantly worse in the task than the SC group (mean score = 0.95, SD=0.04; p =0.019), but the performance of CC group was not significantly different from the DC group (mean score = 0.91, SD=0.11; p =0.25) (Figure 3a). As seen in Figure 3b, performance varied across action type but the CC group achieved a mean accuracy of 66.7% (SD= 0.3) for the action they were least able to identify.

**Figure 3 to be inserted here**

*Effect of viewpoint on biological action identification:*

A mixed ANOVA with the between subject factor group (CC, VM) and the repeated measures factor viewpoint (straight, oblique, profile viewpoints) was run to test for the effect of viewpoint on action identification. There was neither a main effect of group ($F(1,22) = 1.577$, $p = 0.22$; pooled means: CC = 0.85, SD=0.08; VM = 0.89, SD=0.08) nor a main effect of viewpoint ($F(2,44) = 1.18$, $p = 0.317$, pooled means: straight ahead = 0.85, SD=0.11; oblique = 0.89, SD=0.11; profile=0.87,SD=0.09). Further, the interaction of group and viewpoint was non-significant ($F(2,44) = 0.942$, $p = 0.397$) (Figure 4).

**Figure 4 to be inserted here**

*Effect of duration of visual deprivation on task performance:*

A partial correlation between the duration of visual deprivation and the performance in biological action identification task after controlling for the duration of sight recovery following cataract surgery was not significant (Pearson's $r$ (10) = -0.43; $p = 0.18$) (Figure 5a). In contrast, the corresponding partial correlation for the coherent motion task was significant (Pearson's $r$ (10) =0.63, $p = 0.03$) (Figure 5b).

**Figure 5 to be inserted here**

*Effect of visual acuity on coherent motion detection thresholds:*

Detection thresholds for coherent motion were compared between CC, DC, VM groups using a one way ANOVA (Figure 4). The group difference was found to be significant ($F(2,19.1) = 8.87$; $p = 0.001$). Posthoc group comparisons using Bonferroni corrected t-tests showed that the CM threshold for the CC group (mean threshold = 56.9, SD=22.9) was significantly higher than both for the DC (mean threshold = 33.9, SD=25.4; $p = 0.03$) and the VM group (mean threshold = 25.5, SD=11.1; $p = 0.002$), while the DC and the VM group did not differ ($p = 0.98$). In a separate analysis, the one way ANOVA comparing the CC, DC and SC groups revealed a significant group effect ($F(2,33) = 7.95$; $p = 0.001$).

Bonferroni corrected group comparisons found significantly higher CM thresholds for the CC group than for the SC group (mean threshold = 20.9, SD=18.2; $p$ =0.001). Again, the DC group did not significantly differ from the SC group ($p$ = 0.49). Blurring the visual stimuli did not significantly reduce CM thresholds in the normally sighted control group ($t(11)$ = 0.98, $p$ =0.34) as tested using a paired t-test comparing the VM and SC groups. (Figure 6)

**Figure 6 to be inserted here**

Discussion:

Biological motion detection thresholds in sight recovery individuals with a history of congenital cataract have been found to be indistinguishable compared to both typical sighted controls and individuals with a history of developmental cataracts (Hadad et al., 2012; Bottari et al., 2015). In the present study we tested a group of individuals with congenital cataracts (CC group) after cataract removal surgery (a few of whom had had long lasting visual deprivation of up to ~18 years) in a more complex biological motion task, that is, the identification of human actions. Three control groups were employed: to test for unspecific effects of cataract surgery and for the importance of visual pattern input at birth, we ran a group of developmental cataract reversal individuals (DC group); to test for the effects of persisting visual acuity loss, we included normally sighted controls both with (VM group) and without (SC group) a blurring of their sight. Additionally, a coherent motion task was performed by the same individuals. Despite some CC individuals still suffering severe acuity loss after cataract removal surgery they were able to recognize human actions with an impressive precision (mean accuracy of 85%). The VM group's results demonstrated that the slightly but statistically significant lower performance of the CC compared to the SC group could be accounted for by overall lower visual acuities at the time of testing. This finding for action identification was in stark contrast to the results in the coherent motion task: CC individuals performed worse than all three control groups. This

pattern of results in the same individuals provides strong evidence for an impressive resilience of complex biological motion processing, such as recognizing human actions to aberrant visual experience after birth.

Detecting biological motion has been shown to be present in human infants (Bertenthal et al., 1987; Simion et al., 2008) and other animals such as chicks (Vallortigara et al., 2005). Biological motion processing does not seem to rely on typical temporal motion processing areas, since lesions in these areas do not affect participants' ability to perceive biological motion (Vaina et al., 1990), and their ability to identify actions performed by human point light displays (McLeod, 1996). Here we tested specific actions, almost exclusive of human beings such as bipedal climbing stairs and kicking. Neurons responding to biological motion and actions have been observed in a number of brain areas such as F5 of the premotor cortex in macaque monkeys (Giese and Poggio, 2003). In macaques, neurons of the superior temporal sulcus (STS) have been shown to respond to full body movement (Oram and Perrett, 1994), and these neurons have been found to be multisensory (Bruce et al., 2017). The action-related (Grossman et al., 2004) and multisensory nature (Bidet-Caulet et al., 2005; Nath and Beauchamp, 2011) of the superior temporal sulcus (STS) have been demonstrated in humans too. Hence, it could be speculated that during development, these neurons acquire their functional tuning by means of auditory and proprioceptive cues of self-motion. After sight restoration, CC individuals might associate the cues of self-motion from the multisensory neurons with the newly available visual cues, which in turn allows them to learn to recognize visual actions. This idea is compatible with brain imaging studies in congenitally blind humans which observed an activation of premotor and parieto-temporal areas to sounds produced by human actions; the activation overlapped with that found in sighted people for both auditory and visual actions (Ricciardi et al., 2009). Alternatively, it could be argued that the recognition of visual actions is an innate ability of humans possibly due to its high relevance for survival. This idea is expressed in the concept of perceptual life detectors (Troje and Westhoff, 2006). The finding that newborns as young as two days preferentially look at biological movement (Simion et al., 2008) is compatible with this idea. However, detecting biological motion does not mean

that infants were able to recognize actions. In particular, actions which involve some artefacts, such as kicking or catching a ball seem to be unlikely innate. A third alternative is that the ability to identify human actions was predominantly visually learned after sight restoration. We did not find a significant correlation between duration of deprivation and performance in the biological action identification task after taking the duration since cataract removal into account (partial correlation Pearson's r (10)=-0.43; p= 0.18). Though we hesitate to interpret a null finding in a relatively small sample size, this finding is at least compatible with the idea that the exact time of vision restoration does not matter for learning to recognize human actions as would be predicted by the existence of a sensitive period. Humans might thus be predisposed to learn biological actions. It might be argued that remaining pre-surgery vision had allowed CC individuals to acquire knowledge of typical biological motion patterns for human actions. However, most CC participants did not have useful pre-surgery vision and the one with useful vision had absorbed lenses (suggesting that the lenses had been dense at birth). Moreover, this participant (CC12) and a second participant with more than light sensation prior to surgery (CC4) belonged to the worst performing CC individuals (76 % and 73 % correct, respectively), likely due to their relatively low post-surgery visual acuity (see table 1).

Another astonishing finding of the present study was the ability of CC individuals to recognize human actions independent of the viewpoint similarly as found for the control groups. This is a remarkable finding, since it has been reported that CC individuals have impairments in recognizing faces from different viewpoints (Putzar et al., 2010; de Heering and Maurer, 2014). In fact, the latter causes a severe impairment in CC individuals in recognizing people by their face in everyday situations. Neuroscience studies have provided evidence that neural systems typically specialized for face processing, including the extraction of face invariant features, lack the functional specificity in CC individuals (Röder et al., 2013; Grady et al., 2014). Since face processing improves with functional differentiation of the fusiform gyrus, a core area of the face processing system (Cantlon et al., 2011), it was speculated that a non-specialized neural system allows for simple functions like face detection and matching but not for the extraction of face invariant features which would allow for the face

identity recognition in different contexts. Interestingly, Bottari et al. (2015) demonstrated in the same CC individuals who did not show a face specific neurophysiological response, a selective event-related potential response for intact vs. scrambled biological motion, suggesting that the neural systems of biological motion processing acquired a functional specialization despite early visual deprivation. These lines of evidence suggest that the neural system for face and biological motion processing can be dissociated. In fact, a recent study in patients with lesions in the ventral temporal cortex including the fusiform gyrus found that they had intact biological motion perception (Gilaie-Dotan et al., 2015) including action identification despite their severe impairments in face processing. Further, controlling for visual acuity, the present study suggests that low vision somewhat attenuates action identification but that action identification is still high even under low visual acuity conditions.

In contrast to biological motion processing, coherent motion processing was impaired in the CC group. In accordance with previous reports (Burton et al., 2015) we found that coherent motion processing threshold did not decrease by blurring the stimuli in the VM group. Thus, the deficit observed in CC individuals cannot be explained by trivial visual acuity differences. Moreover, coherent motion thresholds varied with the age at surgery in the CC individuals: the longer their visual deprivation had lasted, the worse their performance in the coherent motion task. In the context of indistinguishable coherent motion thresholds in the SC and VM group, the present results suggest that the coherent motion processing deficits of the CC individuals must be due to changes in the neural circuits associated with coherent motion processing. In fact, a previous EEG study reported that alpha oscillations which have been associated with global motion processing (Händel et al., 2007) were greatly reduced in CC individuals (Bottari et al., 2016). It could be argued that the selective deficit in coherent motion perception of CC individuals was predominantly due to the presence of nystagmus in this group. Such deficits for nystagmus patients (with other aetiologies than congenital cataract) have mostly been found for slower motion velocities than used in the present study (Neveu et al., 2009; Shallo-Hoffmann et al., 1998). One study (but see Shallo-Hoffmann et al., 1998) observed deficits particular for vertical motion velocity discrimination, that is, motion perpendicular to the direction of

the nystagmus (Neveu et al., 2009). However, vertical motion processing deficits would predict a particular impairment of CC individuals for biological motion tasks as used in the present and in a previous study (Bottari et al., 2016) which unlike the coherent motion task comprised vertical motion components. However, this is not what was found in the present study. Further, despite the presence of nystagmus in all participants coherent motion thresholds considerably varied in the CC group. Therefore, while it is not possible to entirely exclude some effect of nystagmus on coherent motion processing, it seems rather unlikely that the presence of nystagmus could explain the current pattern of results. Finally, given the relatively low number of dots used in the coherent motion detection task, it could be claimed that the CC group did not use motion cues as effectively as the SC group. This is unlikely because the VM group used such cues similarly efficiently as the SC group. Additionally, in order to use a dot size compatible with the participants' visual acuity, the number of dots in the coherent motion display was much lower than in most previous studies investigating the motion coherence thresholds. This may have limited the lowest thresholds that could have been measured in the SC and VM groups. However, the higher thresholds of the CC group would not have been subject to this limitation, and so the difference of coherence thresholds between groups as observed in the present study, if affected, might be an underestimate.

It might be argued that the performance in the biological action identification task was at ceiling and thus the task was much easier than the coherent motion task resulting in the simple dissociation observed in the present study. Of course, it is not possible to compare the outcome of the two tasks on the same scale. However, we consider this account for the pattern of results in the present study as unlikely: First, the biological action identification task, unlike the coherent motion task worsened by blurring. Moreover, some items were more difficult than others (e.g. “catching” was the most difficult) demonstrating that performance was not at ceiling. Interestingly, the relative ease or difficulty of action identification for each item was consistent across groups, suggesting the involvement of similar processing mechanisms. Second, the high performance in the biological action identification task of CC individuals was in accordance with indistinguishable thresholds to detect biological motion (Hadad et

al., 2012; Bottari et al., 2015). Third, global motion processing has been shown to be impaired in a number of developmental disorders such as fragile X, preterm infants, dyslexia, amblyopia and hemiplegia (reviewed in Braddick et al., 2017), and these findings have led to the suggestion that dorsal stream functions are highly vulnerable during development (Braddick et al., 2003). The present results of the CC group are in line with this idea. Vulnerability to visual deprivation is the downside of high experience dependence and plasticity. Therefore, we would expect that individuals who particularly rely on visual motion processing from early on, such as congenitally deaf individuals, make use of this enhanced plasticity to acquire an extraordinarily high ability in visual motion processing. In fact, lower thresholds for global motion detection (Neville and Lawson, 1987) and enhanced neural processing (Hauthal et al., 2013; Retter et al., 2018) have been observed in deaf humans (Neville et al., 1983). As suggested by Stevens and Neville (Stevens and Neville, 2009), sensitive periods are a double edged sword: the lack of experience results in permanently impaired functioning and a particularly challenging stimulation results in enhanced functioning.

In sum, we demonstrate an impressive sparing of a complex visual function, that is, the identification of human actions in a group of sight recovery individuals who had suffered a congenital loss of pattern vision for up to 18 years. By controlling for visual acuity as well as for unspecific effects of cataract surgery and the onset of visual deprivation, we furthermore provide in the same individuals strong additional evidence for an experience dependent development of coherent motion processing during a sensitive period in early ontogeny.

Table 1 – Clinical information of the congenital cataract reversal group (CC group) and age/sex matching with the vision matched control group (VM group)

| Participant | Strabismus | Family history | VA at surgery (better eye) | Dense | Nystag-mus | Age at surgery (months) | Duration since surgery (months) | Age at test (years) | VA at test (logMAR) | Sex # | Age VM (years) | VA VM (logMAR) | Sex VM # |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **CC1** | Exotropia | No | Fixates Light | Yes | Yes | 4.5 | 103.5 | 9 | 0.48 | M | 9 | 0.53 | M |
| **CC2** | Exotropia | Yes | Fixates and follows light | Yes | Yes | 5 | 139 | 12 | 0.48 | M | 12 | 0.5 | M |
| **CC3** | Esotropia | Yes | Fixates and follows light | Yes | Yes | 2 | 106 | 9 | 0.3 | F | 9 | 0.39 | F |
| **CC4** | Exotropia | Yes | Finger counting at 0.5m | Yes | Yes | 165 | 27 | 16 | 0.9 | F | 16 | 0.91 | F |
| **CC5** | Esotropia | Yes | NA | Yes | Yes | 24 | 396 | 34 | 0.3 | M | 32 | 0.37 | F |
| **CC6** | No | Yes | NA | Yes | Yes | 72 | 348 | 30 | 1.3 | M | 29 | 1.38 | F |
| **CC7** | Esotropia | No | PL/PR accurate | Yes | Yes | 121 | 11 | 11 | 0.8 | F | 11 | 0.85 | F |
| **CC8** | No | Yes | HM+ | Yes | Yes | 86 | 34 | 10 | 0.5 | M | 11 | 0.55 | M |
| **CC9** | No | No | PL/PR accurate | Yes | Yes | 220 | 6 | 18 | 1.08 | M | 19 | 0.9 | F |
| **CC10** | No | Yes | 1.77 logMAR | Yes | Yes | 74 | 22 | 7 | 1.1 | M | 8 | 1.2 | M |
| **CC11** | Esotropia | Yes | NA | Yes | Yes | 4 | 236 | 20 | 1 | M | 19 | 1.09 | M |
| **CC12*** | No | Yes | Finger Counting at 3m | Yes | Yes | 84 | 12 | 8 | 0.8 | M | 9 | 0.9 | M |

*=subject with partially absorbed cataract; VA – visual acuity; VM – Vision Matched control group; abbreviations used in VA columns: NA - Not available in records; PL = Perception of light; PR – Perception of the direction of light rays; HM – Hand movement close to face; m – metres; #=M=male, F=female

Table 2 – Clinical information of the developmental cataract group (DC group)

| Participant | Strabismus | Family history | VA at surgery (better eye) | Dense | Nystag-mus | Age at surgery (months) | Duration since surgery (months) | Age at test (years) | VA at test (logMar) | Sex # |
|---|---|---|---|---|---|---|---|---|---|---|
| **DC1§** | NA | NA | NA | No | NA | 59 | 45 | 8 | 0.7 | M |
| **DC2** | NA | NA | NA | NA | NA | 102 | 43 | 12 | 0.18 | M |
| **DC3** | Exotropia | No | fixates and follows objects | No | Yes | 24 | 183 | 17 | 0.18 | F |
| **DC4** | NA | NA | NA | NA | NA | 120 | 20 | 11 | 0.18 | F |
| **DC5** | NA | NA | NA | NA | NA | 73 | 48 | 10 | 0.18 | F |
| **DC6** | NA | NA | NA | No | NA | 83 | 44 | 10 | 0.4 | M |
| **DC7§** | NA | Yes | 20/200 | No | Yes | 434 | 9 | 36 | 1 | M |
| **DC8** | No | No | PL+ PR accurate | Yes | Yes | 110 | 10 | 10 | 1.7 | M |
| **DC9** | No | No | 20/100 | No | No | 97 | 6 | 8 | 0 | M |
| **DC10** | NA | No | 20/80 | No | No | 84 | 11 | 7 | 0.3 | M |
| **DC11** | Exotropia | No | CF 2 m | No | No | 96 | 25 | 10 | 0 | F |
| **DC12§** | Exotropia | No | CF 1 m | No | Yes | 105 | 2 | 8 | 1.3 | M |

§ = Individuals with incomplete congenital cataract; VA – visual acuity; VM – Vision Matched control group; abbreviations used in VA columns: NA - Not available in records; PL = Perception of light; PR – Perception of the direction of light rays; HM – Hand movement close to face; m – metres; #=M=male, F=female

**References:**


Agervi P (2011) Treatment with Bangerter filters. *J AAPOS* 15:121–122.

Bach M (1996) The Freiburg Visual Acuity Test—Automatic measurement of visual acuity. *Optom Vis Sci* 73:49–53.

Bertenthal BI, Proffitt DR, Kramer SJ (1987) Perception of biomechanical motions by infants: implementation of various processing constraints. *J Exp Psychol Hum Percept Perform* 13:577–585.

Bidet-Caulet A, Voisin J, Bertrand O, Fonlupt P (2005) Listening to a walking human activates the temporal biological motion area. *Neuroimage* 28:132–139.

Bottari D, Troje NF, Ley P, Hense M, Kekunnaya R, Röder B (2015) The neural development of the biological motion processing system does not rely on early visual input. *Cortex* 71:359–367.

Bottari D, Troje NF, Ley P, Hense M, Kekunnaya R, Röder B (2016) Sight restoration after congenital blindness does not reinstate alpha oscillatory activity in humans. *Sci Rep* 6:24683.

Bottari D, Kekunnaya R, Hense M, Troje NF, Sourav S, Röder B (2018) Motion processing after sight restoration: No competition between visual recovery and auditory compensation. *Neuroimage* 167:284–296.

Braddick O, Atkinson J, Wattam-Bell J (2003) Normal and anomalous development of visual motion processing: Motion coherence and “dorsal-stream vulnerability.” *Neuropsychologia* 41:1769–1784.

Braddick O, Atkinson J, Akshoomoff N, Newman E, Curley LB, Gonzalez MR, Brown T, Dale A, Jernigan T (2017) Individual differences in children’s global motion sensitivity correlate with TBSS-based measures of the superior longitudinal fasciculus. *Vision Res* 141:145–156.

Brenner E, Cornelissen F, Nuboer W (1990) Striking absence of long-lasting effects of early color deprivation on monkey vision. *Dev Psychobiol* 23:441–448.

Bruce C, Desimone R, Gross CG (2017) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J Neurophysiol* 46:369–384.

Burton EA, Wattam-Bell J, Rubin GS, Atkinson J, Braddick O, Nardini M (2015) The effect of blur on cortical responses to global form and motion. *J Vis* 15:1–14.

496 Cantlon JF, Pinel P, Dehaene S, Pelphrey KA (2011) Cortical representations of symbols, objects, and
497 faces are pruned back during early childhood. *Cereb Cortex* 21:191–199.

498 Clifford CWG, Webster MA, Stanley GB, Stocker AA, Kohn A, Sharpee TO, Schwartz O (2007) Visual
499 adaptation: Neural, psychological and computational aspects. *Vision Res* 47:3125–3131.

500 De Heering A, Maurer D (2014) Face memory deficits in patients deprived of early visual input by
501 bilateral congenital cataracts. *Dev Psychobiol* 56:96–108.

502 Ellemberg D, Lewis TL, Maurer D, Hong Lui C, Brent HP (1999) Spatial and temporal vision in patients
503 treated for bilateral congenital cataracts. *Vision Res* 39:3480–3489.

504 Ellemberg D, Lewis TL, Maurer D, Brar S, Brent HP (2002) Better perception of global motion after
505 monocular than after binocular deprivation. *Vision Res* 42:169–179.

506 Gelbart SS, Hoyt CS, Jastrebski G, Marg E (1982) Long-term visual results in bilateral congenital
507 cataracts. *Am J Ophthalmol* 93:615–621.

508 Giese MA, Poggio T (2003) Cognitive neuroscience: Neural mechanisms for the recognition of
509 biological movements. *Nat Rev Neurosci* 4:179–192.

510 Gilaie-Dotan S, Saygin AP, Lorenzi LJ, Rees G, Behrmann M (2015) Ventral aspect of the visual form
511 pathway is not critical for the perception of biological motion. *Proc Natl Acad Sci U S A* 112:E361–
512 E370.

513 Grady CL, Mondloch CJ, Lewis TL, Maurer D (2014) Early visual deprivation from congenital cataracts
514 disrupts activity and functional connectivity in the face network. *Neuropsychologia* 57:122–139.

515 Grossman ED, Blake R, Kim C-Y (2004) Learning to see biological motion: Brain activity parallels
516 behavior. *J Cogn Neurosci* 16:1669–1679.

517 Hadad B, Maurer D, Lewis TL (2012) Sparing of sensitivity to biological motion but not of global motion
518 after early visual deprivation. *Dev Sci* 15:474–481.

519 Händel B, Lutzenberger W, Thier P, Haarmeier T (2007) Opposite dependencies on visual motion
520 coherence in human area MT+ and early visual cortex. *Cereb Cortex* 17:1542–1549.

521 Hauthal N, Sandmann P, Debener S, Thome JD (2013) Visual movement perception in deaf and hearing
522 individuals. *Adv Cogn Psychol* 9:53–61.

523 Johansson G (1973) Visual perception of biological motion and a model for its analysis. *Percept*
524 *Psychophys* 14:201–211.

525 Le Grand R, Mondloch CJ, Maurer D, Brent HP (2001) Early visual experience and face processing.
526 *Nature* 410:890.

527 Lewis TL, Maurer D (2009) Effects of early pattern deprivation on visual development. *Optom Vis Sci*
528 86:640–646.

529 McLeod P (1996) Preserved and impaired detection of structure from motion by a "motion-blind"
530 patient. *Vis Cogn* 3:363–392.

531 McKyton A, Ben-Zion I, Doron R, Zohary E (2015) The limits of shape recognition following late
532 emergence from blindness. *Curr Biol* 25:2373–2378.

533 Nath AR, Beauchamp MS (2011) Dynamic changes in superior temporal sulcus connectivity during
534 perception of noisy audiovisual speech. *J Neurosci* 31:1704–1714.

535 Neveu MM, Jeffery G, Moore AT, Dakin SC (2009) Deficits in local and global motion perception arising
536 from abnormal eye movements. *J Vis* 9:1–15.

537 Neville HJ, Lawson D (1987) Attention to central and peripheral visual space in a movement detection
538 task: An event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Res* 405:268–
539 283.

540 Neville HJ, Schmidt A, Kutas M (1983) Altered visual-evoked potentials in congenitally deaf adults.
541 *Brain Res* 266:127–132.

542 Newsome W, Paré E (1988) A selective impairment of motion perception following lesions of the
543 middle temporal visual area (MT). *J Neurosci* 8:2201–2211.

544 Odell NV, Leske DA, Hatt SR, Adams WE, Holmes JM (2008) The effect of Bangerter filters on optotype
545 acuity, vernier acuity, and contrast sensitivity. *J AAPOS* 12:555–559.

546 Oram MW, Perrett DI (1994) Responses of anterior superior temporal polysensory (STPa) neurons to
547 "biological motion" stimuli. *J Cogn Neurosci* 6:99–116.

548 Pérez GM, Archer SM, Artal P (2010) Optical characterization of bangerter foils. *Invest Ophthalmol Vis*
549 *Sci 51*:609–613.

550 Pitchaimuthu K, Sourav S, Bottari D, Banerjee S, Shareef I, Kekunnaya R, Röder B (2019) Color vision in
551 sight recovery individuals. *Restor Neurol Neurosci* 37:583–590.

552 Putzar L, Hötting K, Rösler F, Röder B (2007) The development of visual feature binding processes after
553 visual deprivation in early infancy. *Vision Res* 47:2616–2626.

554 Putzar L, Hötting K, Röder B (2010) Early visual deprivation affects the development of face recognition
555 and of audio-visual speech perception. *Restor Neurol Neurosci* 28:251–257.

556 Retter TL, Webster MA, Jiang F (2018) Directional visual motion is represented in the auditory and
557 association cortices of early deaf individuals. *J Cogn Neurosci* 31:1126–1140.

558 Ricciardi E, Bonino D, Sani L, Vecchi T, Guazzelli M, Haxby JV, Fadiga L, Pietrini P (2009) Do we really
559 need vision? How blind people "see" the actions of others. *J Neurosci* 29:9719–9724.

560 Röder B, Ley P, Shenoy B, Kekunnaya R, Bottari D (2013) Sensitive periods for the functional
561 specialization of the neural system for human face processing. *Proc Natl Acad Sci U S A* 110:16760–
562 16765.

563 Rogers GL, Tishler CL, Tsou BH, Hertle RW, Fellows RR (1981) Visual acuities in infants with congenital
564 cataracts operated on prior to 6 months of age. *Arch Ophthalmol* 99:999–1003.

565 RStudio Team (2016) RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.

566 Rutstein RP, Foster NC, Cotter SA, Kraker RT, Lee DH, Melia M, Quinn GE, Tamkins SM, Wallace DK
567 (2011) Visual acuity through Bangerter filters in nonamblyopic eyes. *J AAPOS* 15:131–134.

568 Saunders R, Troje N (2011) A test battery for assessing biological motion perception. *J Vis* 11:686. (The
569 full poster is available at **https://tinyurl.com/y4xx2bq5)**

570 Shallo-Hoffmann JA, Bronstein AM, Acheson J, Morland AB, Gresty MA (1998) Vertical and horizontal
571 motion perception in congenital nystagmus. *Neuro-Ophthalmology* 19:171–183.

572 Simion F, Regolin L, Bulf H (2008) A predisposition for biological motion in the newborn baby. *Proc Natl*
573 *Acad Sci U S A* 105:809–813.

574 Stevens C, Neville H (2009) Profiles of development and plasticity in human neurocognition. In: The
575 new cognitive neurosciences (Gazzaniga MS, ed), pp165–181. Cambridge, England: MIT Press.

576 Theusner S, de Lussanet M, Lappe M (2014) Action recognition by motion detection in posture space. *J*
577 *Neurosci* 34:909–921.

578 Troje NF, Westhoff C (2006) The inversion effect in biological motion perception: Evidence for a "life
579 detector"? *Curr Biol* 16:821–824.

580 Tytla ME, Lewis TL, Maurer D, Brent HP (1993) Stereopsis after congenital cataract. *Invest Ophthalmol*
581 *Vis Sci* 34:1767–1773.

582 Vaina LM, Lemay M, Bienfang DC, Choi AY, Nakayama K (1990) Intact "biological motion" and
583 "structure from motion" perception in a patient with impaired motion mechanisms: A case study. *Vis*
584 *Neurosci* 5:353–369.

585 Vallortigara G, Regolin L, Marconato F (2005) Visually inexperienced chicks exhibit spontaneous
586 preference for biological motion patterns. *PLoS Biol* 3:1312–1316.

587 Webster MA (2015) Visual adaptation. *Annu Rev Vis Sci* 1:547–567.

588 Wiesel TN, Hubel DH (1965) Extent of recovery from the effects of visual deprivation in kittens. *J*
589 *Neurophysiol* 28:1060–1072.

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*Figure legends:*

**Figure 1 -** Still frames from three actions of the biological action identification task. The three actions are walking, climbing and kicking (left to right).

**Figure 2 –** Bar plots displaying the visual acuities of each of group. Shown are the mean VA and the error bars indicate the standard error mean (SEM). CC – Congenital Cataract; DC – Developmental Cataract; VM – Vision Matched controls; SC – Sighted Controls.

**Figure 3 –**Results of the biological action identification task. (a) Bar plots display the proportion of correct responses for each group: CC, DC, VM, SC (see Figure 1 for definition). (b) Same as (a) but proportion correct responses separately averaged for each of the 10 actions. Shown are group mean scores; error bars indicate the standard error of the mean.

**Figure 4 -** Biological action identification task. Bar plots show the proportion of correct responses separately averaged for the three viewpoints and CC- and the VM participants (see Figure 1 for definitions). Error bars indicate the standard error of the mean.

**Figure 5 -** Scatter plot showing the performance of CC group in the (a) biological action identification task and (b) coherence motion detection task as a function of the duration of visual deprivation. Data points indicate single subjects. The data were fitted with a linear regression line (see Figure 1 for definitions).

**Figure 6 –** Coherent motion thresholds. Bars display coherent motion thresholds in each group – CC, DC, VM, SC (see Figure 1 for definition). The Y-axis specifies the percentage of dots moving coherently in order to detect the coherent motion with an accuracy of 82%. Shown are mean scores and the error bars indicate the standard error of the mean.