Grasping behavior does not recover after sight restoration from congenital blindness

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Summary

We investigated whether early visual input is essential for establishing the ability to use predictions in the control of actions and for perception. To successfully interact with objects, it is necessary to pre-program bodily actions such as grasping movements (feed-forward control). Feed-forward control requires a model for making predictions which is typically shaped by previous sensory experience and interaction with the environment[1]. Vision is the most crucial sense for establishing such predictions[2,3]. We typically rely on visual estimations of the to-be-grasped object's size and weight in order to scale grip force and hand aperture accordingly[4–6]. Size-weight expectations play a role also for perception, as evident in the size-weight illusion (SWI), in which the smaller of two equal-weight objects is misjudged to be heavier[7,8]. Here we investigated predictions for action and perception by testing the development of feed-forward controlled grasping and of the SWI in young individuals surgically treated for congenital cataracts several years after birth. Surprisingly, what typically developing individuals do easily within the first years of life, namely to adeptly grasp new objects based on visually-predicted properties, cataract-treated individuals did not learn after years of visual experience. Contrary, the SWI exhibited significant development. Even though the two tasks differ in substantial ways, these results may suggest a potential dissociation in using visual experience to make predictions about object's features for perception or action. What seems a very simple task -picking up small objects- is in truth a highly complex computation that necessitates early structured visual input to develop.

Keywords

Grasping, feed-forward control, size-weight illusion, cataract-treated individuals, recovery from blindness, sight restoration, visual deprivation, action and perception

Results

Twenty-four young Ethiopian individuals (mean age: 12.5y, range: 8-21y) who suffered from congenital dense bilateral cataracts took part in the experiments. They were surgically treated several years after birth (mean: 11.99y, age range: 8-20y). Before surgery, patients had very limited visual abilities (21 were classified as legally blind according to NIH, see Table S2). Their vision improved significantly after surgery, even though their visual acuity was still reduced compared to normally sighted individuals. Testing took place between 2 days and 3 years after surgery, such that we were able to follow the patients' developmental path.

Cataract-treated patients were compared to two typically developing sighted control groups matched individually for age (sighted controls) and additionally also for post-surgical visual acuity (blurred vision controls). For the latter control group, vision was blurred using optical filters to individually match the patients' reduced visual acuity (see STAR Methods).

Participants were asked to repeatedly grasp and lift one of three objects differing in size (width=25, 40, and 55 mm) as naturally as possible using a pincer grip. We recorded their grasp duration (movement time and pick-up time), their hand opening during approach, and their applied force when lifting the object. The three objects were manipulated to either have an identical weight (constant weight condition) or a constant density, such that their weight increases with size in a natural way (constant density condition).

Starting from the first few lifts, both control groups presented short movement and pick-up times (Figure 1A), and they scaled grip aperture to the size of the object. This was evident from the linear relationship between grip aperture and object width (i.e. slope of maximum grip aperture / object width) in both control groups when the slope was tested for difference from zero (sighted controls: $t(62)=9.23$, $p<0.001$, mean ± SEM: 0.40 ± 0.04, 95% CI[0.31,0.48]; blurred vision controls: $t(62)=7.49$, $p<0.001$, mean ± SEM: 0.31 ± 0.04, 95% CI[0.23,0.39], both slopes are significantly larger than zero; Figure 1B). Similarly, for grip force rate the slope (i.e. slope of maximum grip force rate / object width) was significantly larger than zero for both control groups in both, the constant weight and the constant density condition (constant weight condition: sighted controls: $t(707)=7.89$, $p<0.001$,b=0.02, 95% CI[0.01,0.02], mean ± SEM: 0.73 ± 0.10; blurred vision controls: $t(708)=6.65$,$p<0.001$,b=0.01, 95% CI[0.01,0.02], mean ± SEM: 0.70 ± 0.10; constant density condition: sighted controls: $t(45)=4.31$, $p<0.001$, b=0.01, 95% CI[0.01,0.02], mean ± SEM: 0.74 ± 0.18; blurred vision controls: $t(44)=4.84$, $p<0.001$, b=0.01, 95% CI[0.01,0.02], mean ± SEM: 0.78 ± 0.18; Figure 1C). These results suggest that control participants applied feed-forward controlled grasping. The two control groups differed only in the Pick-up time, but not in any of the other variables (see Table S1).

The control's perfomance is in stark contrast to the patients' behavior who exhibited significantly longer movement and pick-up times than sighted controls (difference in movement time: $t(45)=4.47$, $p<0.001$, b=0.44, 95 % CI[0.20;0.69]; difference in pick-up time: $t(95)=5.86$, $p<0.001$, b=0.41, 95% CI[0.24,0.58]) or blurred vision controls (difference in movement time: $t(45)=3.12$, $p=0.006$, b=0.31, 95% CI[0.06,0.55]; difference in pick-up time: $t(96)=3.30$, $p=0.003$, b=0.23, 95% CI[0.06,0.40]; Figure 1A). Patients lifted all differently sized objects with the same maximum grip aperture ($t(46)=1.46$, $p=0.15$, mean ± SEM: 0.07 ± 0.05, 95% CI[-0.03,0.16], slope not different from zero; Figure 1B) and with the same grip force rate (constant weight condition: $t(707)=0.96$, $p=0.34$, b=0.02, 95% CI[-0.002,0.005]; mean slope ± SEM: -0.003 ± 0.10; constant density condition: $t(45)=1.75$, $p=0.09$, b=0.005, 95% CI[-0.0007,0.01], mean ± SEM: 0.21 ± 0.18; both slopes not different from zero; Figure 1C). This suggests that the patients were unable to control their grasping movements in a feed-forward manner. Importantly, when debriefed after the experiment all participants were well able to perceptually discriminate the three object sizes using vision. To better quantify their perceptual ability to discriminate object size, the Just-noticeable difference (JNDs) was measured in a subset of 10 patients, yielding an average threshold of 4.4mm (SD=2.2mm, range=1.4-7.7mm),

which is well below the 15 mm size difference of the grasped objects. That is, patients' impaired motor behavior could not be ascribed to a possible inability to properly visually identify object size. The possibility that patients' impairment is simply due to poorer visual acuity was further ruled out by the finding that blurring vision in controls did not cause such detrimental effects.
In order to investigate whether there is any improvement in the patients' grasping ability after the eye surgery, we followed their developmental path for several years. Strikingly, the scaling of their grip aperture ($t(721)=0.80$, $p=0.42$, $b=-7e-05$, 95% CI[-3e-04,1e-04] and grip force rate (constant weight condition: $t(390)=0.03$, $p=0.97$, $b=-2e-07$, 95% CI[-1e-05,1e-05]; constant density condition: $t(216)=1.19$, $p=0.24$, $b=9e-06$, 95% CI[-6e-06,2e-05]), was not correlated with time since surgery indicating that even years after surgery their grasping behavior did not develop to normal levels (Figure 1B and 1C). To further emphasize this stagnation in development, a subset of participants was re-tested in a follow-up experiment: the first test occurred less than 7 months after surgery, the follow-up more than one year after the first test. Scaling of grip aperture ($t(370)=0.35$, $p=0.72$, $b=-0.03$, 95% CI[-0.18,0.13]) and grip force rate (constant weight condition: $t(304)=0.55$, $p=0.59$, $b=-0.002$, 95% CI[-0.01,0.005]; constant density condition: $t(86)=0.65$, $p=0.52$, $b=-0.006$, 95% CI[-0.02,0.01]) in this follow-up test did not differ significantly from the initial test (Figure 1B and 1C). However, there were some changes in grasping behavior with the progression of time, as both movement time and pick-up time decreased with time after surgery (Movement time: $t(200)=7.65$, $p<0.001$, $b=-0.002$, 95% CI[-0.002,-0.001]; Pick-up time: $t(272)=6.34$, $p<0.001$, $b=-0.00009$, 95% CI[-0.0001,-0.00006). They were also both significantly shorter in the follow-up test as compared to the initial test (movement time: $t(152)=6.66$, $p<0.001$, $b=0.68$, 95% CI[0.48,0.87]; pick-up time: $t(818)=8.94$, $p<0.001$, $b=0.10$, 95% CI[0.07,0.12]; Figure 1A). Duration did no longer differ from the time needed by the blurred vision controls (Movement time: $t(18)=0.96$, $p=0.35$, $b=0.17$, 95% CI [-0.17, 0.50]; Pick-up time: $t(46)=0.48$, $p=0.64$, $b=0.008$, 95% CI [-0.02, 0.04]). However, shorter grasping durations in the follow-up experiment are most likely the result of an overall greater confidence in using vision for handling objects including identification of the object location during hand transport (Movement time), placement of fingers on the object or grasping, and object lifting (Pick-up time). Qualitatively, grasping in the follow-up test did still differ massively from grasping in healthy, age-matched participants (see Figure S1), suggesting that patients are still impaired in their feed-forward control of grasping.
To test for the perceptual effects of using visual expectations, we additionally assessed the size-weight illusion (SWI). To this end we asked participants to simultaneously hold the equally-weight smallest and largest objects and report which of the two felt heavier or lighter. 91% of the participants in each control group and 74% of the patients experienced the size-weight illusion reporting the smaller object felt heavier (effect in both groups significantly above chance level: patients: $z=2.19$, $p=0.03$, $b=1.04$, 95% CI[0.16,2.06], both control groups: $z=3.18$, $p=0.002$, $b=2.35$, 95% CI[1.13,4.18]; Figure 1D). To follow the development of the SWI we assessed a subset of patients multiple times: Some were tested before surgery (n=5), some less than 7 months after surgery (n=14), and finally more than one year after the first test (n=14). Before surgery and in the first post-surgical test, they did not differ from chance (40% SWI, $z=0.44$, $p=0.66$. $b=0.41$, 95% CI[-2.43,1.39 and 71% SWI, $z= 1.55$, $p=0.12$, $b=0.92$, 95% CI[-0.18,2.21], respectively). However, in the second post-surgical test (mean time since surgery 1.4 years) 86% experienced the SWI, which was significantly above chance ($z=2.35$, $p=0.02$, $b=1.79$, 95% CI[0.49,3.65]) and very close to that of healthy controls (Figure 2).

Discussion

Reaching and grasping objects is an ability emerging early in life. Already fetal hand movements have been reported to be goal-directed to some extent[9]. At 4-5 months, infants are

able to successfully grasp objects, and by the age of 9 months hand aperture starts to be adjusted to the size of the grasped object[10]. The first anticipatory strategy in adjusting grip forces to an expected object weight emerges around two years, when children start taking the object weight of a previous lift into account[11]. At the age of three, children start using the size of an object in a predictive way to adjust the required grip forces[12]. It is surprising that after sight restoration, the patients tested here are impaired in making similar weight predictions or scaling their grip aperture to the object's size. This is not only true shortly after surgery, but also in patients tested many months after cataract removal and in the ones who were tested again in a follow-up test more than 1 year after surgery. Although these patients regularly grasp and lift objects during their everyday life, they showed no improvement in their scaling ability. It can be ruled out that the described difficulties are due to an inability to visually identify the different object sizes, as patients were well able to visually discriminate between the objects' sizes. It is also unlikely that the absence of force scaling in patients can be ascribed to an impaired weight discrimination ability since previous studies showed that blind individuals are equal or even superior in weight perception compared to sighted individuals[13].
Previous studies in similar populations suggest that there is considerable plasticity in the visual system. Children or adolescents treated for bilateral cataracts late in life have been reported to be able to use their newly gained vision within days or months for various tasks, such as distinguishing between objects based on their size[14], shape or color[15] and they are even susceptible to illusions, such as the SWI[16], the Ponzo illusion, and the Müller-Lyer illusion[17]. There are also some anecdotal observations that cataract-treated children are able to point towards target objects and reach for and grasp objects, although their movements often seem inept and clumsy[15,18]. Still, it is well known that early and long-term visual deprivation leads to impaired visual and neural development and severe deficits in the use of vision even when sight is restored later in life[15,19–22]. Cataract-treated patients suffer in many cases also from other visual dysfunctions, such as reduced visual acuity[23], nystagmus[24], strabismus[23], and amblyopia[15]. The latter conditions are linked to impaired binocular vision, which in turn has been found to affect grasping behavior to some degree[25–27], although not preventing the scaling of grip force and aperture completely[27–29]. Therefore, the potential impairment of binocular vision in the cataract-treated group might have also contributed, to some degree, to the patients' impaired performance.
Feed-forward control of grasping during typical development supposedly emerges via sensorimotor experience with natural objects in the world, in which, statistically, object weight increases with object size[30]. However, this expectation can be altered with experience[31]. Repeatedly lifting objects with an inverted size-weight relationship (i.e. smaller objects are heavier) finally leads to an adaptation of the grasping forces and also a reversal of the SWI. Interestingly, typical participants adjust the grip forces quickly to the weight of the inverse objects, while it takes several thousands of lifts of the inverted density objects to reverse the SWI.
The patients tested here apparently experienced severe difficulties in making use of the general (statistical) relationship between the size and weight of objects when they had to produce the required grasping forces based on visual apparent object properties. In contrast, they were well able to build a (short-term) sensory-motor memory of the required grasping forces after just a few lifts with the same objects, as shown by their within-experiment learning ability (see Figure S1). It is reasonable that the sensory-motor memory takes effect quickly if weight expectations during grasping are not met, (i.e. the required grasping forces are over- or underestimated). Long-term learning the general relationship between size and weight of objects and using it more generally to make predictions about the possible weight of an object, however, seems to be a task that requires abundant experience and might take years to develop.

It has been proposed that grasping can be divided into two distinct components: bringing the hand to the object (transport component) and actually picking up and lifting it (grip component). While the first one is hypothesized to be based on extrinsic object properties (e.g. location) and does not require further knowledge about the object, the latter one requires information about an object's intrinsic properties (such as its size or weight)[36,37] and thus deeper object knowledge. Note that such a division between extrinsic and intrinsic object properties is not as clear and unambiguous as it might seem[37,38], however there is some neuroscientific evidence that at least some separate cortical structures are involved in processing hand transport and grip[38,39]. This might explain why the patients tested in our study do improve in certain aspects of grasping but not others: movement duration is mostly influenced by correctly estimating extrinsic object properties, i.e. the location of the object. Scaling grip aperture and grip force, however, require the correct prediction of intrinsic object properties such as size and weight. We show that while the first one might be much easier and quicker to learn after sight recovery (speeding up grasp duration), the latter one seems not to improve much or at least might take years of visual experience to develop.

As described above, cataract-treated patients are well able to reach for and lift objects, and thus in some sense successfully solved the given task. However, their grasping behavior differs severely from healthy participants which is also immediately visible when casually observing the participants (c.f. Video S1), as they likely rely more on feedback control of action. However, the successful outcome, even when not achieved in an adept, fine-controlled manner, might preclude them from adapting their behavior to a more efficient, feed-forward controlled grasping strategy. One may speculate that in case of missing to achieve the goal of the task (i.e. mislocalization during a pointing task), a faster development is prompted by a distinct error signal[40].

Most patients tested in our study, even years after having been surgically treated, navigate very cautiously through their environment, at times use their hands instead of their vision to feel obstacles, and their interaction with the world often seems ungainly. Almost all of them still attend schools for the blind. Similar informal observations have been made before[15]. Moreover, recently, we have shown that cataract-treated patients are less precise than controls in their pointing behavior and their ability to recalibrate their sensorimotor system to distortions is impaired right after surgery and shows a limited and slow development over time[40]. Thus, in contrast with the often quick development of certain perceptual abilities, the development of action-related capabilities that are required for a smooth interaction with the world seems to proceed slowly. Reasons for such a divide might be manifold: For instance, there are reports about the neural separation in action and perception tasks[32–35] . However, action tasks often differ from perceptual tasks also in several other aspects: for example, action tasks typically involve many more degrees of freedom (i.e. the control of hand movements involves 27 DoF[41]) than perceptual tasks and are thus more complex. Such difficulty due to complexity is mirrored in robotics and artificial intelligence where many perceptual tasks are usually easier to solve (e.g. distinguishing between objects in an image), while teaching a robot to grasp an arbitrary object is still difficult these days. Still, there are also several perceptual tasks in which sight recovered children show a very slow development. It is striking that those slowly developing abilities often involve motion[42–44], or depth perception[15] and are thus tasks which perceptually also require an inference process that includes a world model to be solved.

One limitation of this study is the relatively small sample size, given by the rarity of patients with this condition, and the varying number of participants taking part in the different experimental conditions and in the follow-up experiments. We cannot exclude that the low statistical power, given by the small sample size and the high inter-subject variability, could have contributed to the absence of significant correlations in some of our analyses on the effect of time since surgery. However, the lack of correlation between the tested abilities and time since surgery is confirmed by the results of the follow-up test, which showed no improvement compared to the first test. Another limit of the study is related to the fact that, despite investigating patients' development after surgery, most patients were tested within one year after surgery. Further studies are needed to clarify whether more sensorimotor experience gained after several years from sight restoration could contribute to some development of the feed-forward control of grasping. The SWI was assessed visuo-haptically. We cannot rule out that the haptic size cues that were available to the patients during testing contributed to the presence of the SWI. Nevertheless, we were able to show a development in the presence of the SWI from shortly after surgery (no SWI present) to years after surgery (SWI similar to controls), emphasizing the role of visual experience in its development, independent of how it is assessed.

To summarize, our findings show that early-onset visual deprivation dramatically harms the ability to use visually-estimated features of the object (such as size and expected weight) during grasping after cataract removal. Although the visual experience gained after surgery rapidly helps building perceptual predictions for weight estimation, as in the case of the size-weight illusion, cataract-treated individuals seem to fail to use such predictions for feed-forward controlled grasping. This finding highlights the crucial role of early visual experience in developing appropriate action planning and suggests that there might be sensitive periods in early childhood in which patterned visual input is essential to develop natural grasping behavior. It is highly surprising that after sight restoration surgery the human brain is not able to easily catch up with this very fundamental behavior that we normally adeptly perform hundreds of times during everyday actions.

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Author contributions:

SP: Conceptualization, Methodology, Investigation, Formal Analysis, Visualization, Writing-original draft. IS: Methodology, Investigation, Visualization, Writing-review & editing. DW: Software, Writing-review & editing. IBZ: Supervision, Writing-review & editing. MOE: Conceptualization, Methodology, Visualization, Supervision, Writing-review & editing.

Declaration of interests

The authors declare no competing interests.

Inclusion and Diversity

We support inclusive, diverse, and equitable conduct of research.

Figure 1. Grasping behavior. Three aspects of grasping behavior were analyzed: **A)** Grasp duration: temporal grasping parameters, **B)** Hand opening: grasping parameters including the shape of the hand, and **C)** Applied force: parameters related to the grasping force.
A) Top: time series of a typical reaching and grasping movement of a patient. The duration of the grasp is divided into movement time and pick-up time.
Middle: Three groups were tested: a group of cataract-treated patients (red; see also Methods and Table S1), a sighted control group (purple) and a blurred vision control group (i.e. whose visual acuity was individually matched to that of the patients after surgery, lilac). Movement time is significantly increased in cataract-treated patients compared to both sighted controls (stars always indicate significance levels), and blurred vision controls. Similarly, pick-up time is longer in patients compared to both control groups.
All boxplots contain the following elements: center line, median; box limits, upper and lower quartiles; whiskers, minimum and maximum values smaller than 1.5x interquartile range; black points, outliers.
Bottom: Initial test (2-5 months after surgery, red), follow-up test (1.4 years after surgery, orange). Both temporal grasp parameters significantly decrease with the time passed after surgery when jointly considering initial and follow-up tests. The summary boxplot shows that both temporal grasp parameters in the group of retested participants are significantly smaller in the follow-up test as compared with the initial test. Dashed lines indicate performance of blurred vision controls which was not significantly different anymore in the follow-up test.
B) Top: Schematic illustration of the hand opening (Grip aperture) showing typical grasping behavior of a control participant. Typically, object size and grip aperture are closely related, with (often linearly) increasing maximum grip aperture for larger objects. Grasped object widths: 25mm, 40mm and 55mm.
Middle: No scaling of the maximum grip aperture in patients vs. linear relationship between grip aperture and object width (i.e. slope of maximum grip aperture / object width) in both control groups.
Bottom: Patients' behavior was not affected by time since surgery (tss), nor did it change from initial to follow-up test (summary boxplot: initial test: tss=4 month (red), follow-up test: tss=1.4 years (orange). Dashed lines indicate the slope of blurred vision controls which was significantly larger than patients'.
C) Top: Average applied force profiles for grip force and grip force rate when lifting a small and large object with equal weights, respectively. Left: Average behavior of sighted controls; right: Average behavior of cataract treated patients. Forces first increase to a maximum and then decrease again to reach their final level. If the lifted object is unexpectedly lighter than predicted, the grip force first overshoots the required amount of force before reaching its final level (see large object in controls). Both maximum grip force and grip force rate only scarcely differ between the large and small objects in the group of patients, while they do in controls. See Figure S1B for force profiles for individual, representative participants.
Maximum grip force and grip force rate are closely correlated in both controls and patients (inset plot). Maximum grip force rate was analyzed as representation of participants' weight expectations (see also STAR Methods).
Middle: Patients showed the same maximum grip force rate for lifting the three differently sized objects in both grasping conditions. The linear relationship between grip force rate and object width (i.e. slope of maximum grip force rate / object width) is not present in the patients. Thus, patients did not expect weight differences between objects based on their size. In contrast, both control groups scaled the maximum grip force rate with object size, showing they expected increasing weights with increasing size.

Bottom: Patients' behavior did not change with time since surgery considering all data from initial and follow-up test, nor did it change from initial to follow-up test (summary boxplot, constant weight condition: initial test tss=1 month (red); follow-up test tss=1.4 years (orange); summary boxplot constant density condition: initial test tss=5 month (red); follow-up test tss=1.4 years (orange). Dashed lines indicate slope of blurred vision controls.
See also Figure S1, Table S1 and Video S1.

Figure 2. The Size-weight illusion (SWI)
Percentage of participants in each group perceiving the SWI (percent ± SEM). 74% of patients and 91% of participants of both control groups experience the illusion which is significantly above chance level. Prior to surgery (n=5) participants were only guessing, thus not showing the illusion (i.e. 40% SWI). Fourteen patients were tested again in a follow-up test: initially, 71% of them experienced the illusion (not significantly different from chance; tts=1 month (red)). In the follow-up test, 86% experienced the illusion (above chance; tts=1.4 years (orange)). Stars indicate significance levels. Black dashed line indicates chance performance; lilac dashed line indicates performance of blurred vision controls. All error bars indicate standard errors of the mean. Boxplots contain the following elements: center line, median; box limits, upper and lower quartiles; whiskers, minimum and maximum values smaller than 1.5x interquartile range; black points, outliers.

STAR Methods

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed and will be fulfilled by the Lead Contact, Sophia Piller (sophia.piller@uni-ulm.de).

Materials availability
This study did not generate new unique reagents.

Data availability
Full datasets have been deposited at Mendeley Data at https://doi.org/10.17632/f994nhdctk.1 and are publicly available as of the date of publication. DOIs are listed in the key resources table.

Code availability
All original code has been deposited at Mendeley Data at https://doi.org/10.17632/f994nhdctk.1. and is publicly available as of the date of publication. DOIs are listed in the key resources table.

Any additional information required to reanalyze the data reported in this paper is available from the Lead Contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants
This study included two different grasping conditions (i.e. constant weight and constant density) followed by the assessment of the size-weight illusion (SWI). Due to important medical examinations that had to be carried out during the testing sessions, the differing testing locations, or patients' living situations partly far away from the test infrastructure, not all patients were available to be tested (or retested) in all parts of this study. A total of twenty-four Ethiopian children and adolescents (11 female; mean age: 12.5 years, range: 8-21 years; 23 right-handed; mean time since surgery: 9 months, range: 2 days–3 years) participated in the study (see Table S2 for additional information). All of them were diagnosed with mature, feremature or partially absorbed bilateral cataracts. These were classified congenital (i.e. present at birth or shortly afterwards [45]) as the patients showed nystagmus, a sign of visual deprivation in early life [24]. Additionally, some parents reported that their children had white eyes since birth, and some cases exhibited a high familial incidence, thus were probably hereditary. All patients were ophthalmologically examined and received cataract surgery with an intraocular lens implantation at Referral Hospital in Hawassa, Ethiopia. The target refraction was adjusted for far vision. Surgeries took place years after birth (mean age at surgery: 11.99 years, range: 8-20 years). After the cataract removal, visual acuity was still reduced in patients (see Table S2), which is commonly the case after late cataract treatment [23]. Fourteen patients took part in both grasping conditions (constant weight and constant density), eight participated only in the constant weight condition and two participated only in the constant density lifting condition. Tests for the two conditions were carried out in separate experimental sessions (mean time between sessions: 5.4 months, range: 0 days-12.4 months).

Grasping performance in both grasping conditions was assessed by three parameters: grasp duration, grip aperture and grip force rate. Grip aperture could be analyzed in a subset of patients (n=8 of the constant weight condition and n=15 of the constant density condition). For technical reasons movement duration could only be analyzed in the constant density condition (see statistical analyses). Twenty-three patients could be tested in the SWI experiment.

Cataract-treated patients were compared to two typically developing sighted control groups. Thirty-eight participants were individually matched to the patients for age ("sighted controls", 16 female; mean age: 12.6 years, range: 8-21 years; 38 right-handed). Additional 38 participants were individually matched to the patients for post-surgical visual acuity and age ("blurred vision controls", 23 female; mean age: 12.8 years, range: 8-21 years; 35 right-handed, see also STAR Methods). Optical filters were used to blur their vision in order to match the patients' reduced visual acuity. To that aim, we applied semi-transparent blurring foils to glasses worn by the participants. The amount of blur needed to obtain each target visual acuity was determined in a pilot experiment. Nevertheless, to ensure successful matching, we tested the visual acuity of the controls wearing the blurring glasses with the same method used for the patients (see Visual acuity assessment).

All matched control participants took part in the SWI experiment after either taking part in the constant weight (n=22) or the constant density lifting condition (n=16). All controls were recruited and tested in German primary and secondary schools or at Ulm University.

To rule out that any difference found between patients and controls was simply caused by language barriers, 6 typically developing Ethiopian children in the same age-range were tested in the same weight condition and the SWI experiment (all males; mean age: 11.2 years, range: 7-15 years; all right-handed). They did not differ from the German controls in any of the tested parameters. No motor deficits were observed in any of the participants.

We followed the developmental path of 14 patients, who were tested shortly after surgery and then were available on multiple testing occasions. All of them (8 female; mean age: 11.3 years, range: 8-15 years; 13 right-handed) were tested twice in the constant weight condition and the SWI. The initial tests took place on average one month after surgery (range: two days to 4.5 months), the follow-up tests around 1.4 years after surgery (range: 1.1 years - 1.5 years). Four patients (3 female; mean age: 10.6 years, range: 8-15 years; all right handed) were additionally tested twice in the constant density condition. For this condition, the initial test took place on average five months after surgery (range: 3 days – 6.5 months), the follow-up test 1.4 years after surgery (range: 1.1 years – 1.5 years). Moreover, in a subset of eight patients, grip aperture was analyzed multiple times (4 female; mean age: 12.2 years, range: 8-15 years; 7 right handed). The initial test took place 4 months after surgery (range: 3 days - 6.5 months); the follow-up test 1.4 years after surgery (range: 1.1 years – 1.5 years).

All Ethiopian patients and controls were tested either in Hawassa Referral Hospital, in the Shashamane Catholic School for the Blind, or in the Sebeta Blind School in Ethiopia. The ethics committee of Bielefeld University (EUB 2015-139) approved the study. Informed consent was obtained from participants, or from participant's parents, or legal guardians in case of minors. All participants were naïve to the objective of the study.

METHOD DETAILS

Experimental procedure

Participants were tested in two different grasping conditions, that is the constant weight and the constant density condition. In the constant weight conditions, participants lifted a small (60 x 60 x 25mm), an intermediate (60 x 60 x 40mm) and a large object (60 x 60 x 55mm), all weighing 112g. In the constant density condition, participants lifted a small (70 x 70 x 25mm), an intermediate (70 x 70 x 40mm) and a large object (70 x 70 x 55mm) with a coherent size-weight relationship, i.e. the larger the object the heavier it was. Their weights were 191g, 306g and 420g, respectively, resulting in a constant density of 1.56 kg per liter. All testing objects were made from light colored softwood and weighted with metal inlays of different thickness, invisible from the outside, to obtain the desired weight. The inlays were circular in shape, and centrally attached, so that the weight was evenly distributed within each object. The objects could be opened and a removable six-axis force-torque sensor (ATI Mini40), which was used to record lifting forces, could be inserted and held in place at the exact center of the object via small magnets attached to the metal inlays (see Video S1). We decided to place the force sensor within the object (and invisible from the outside) mainly for two reasons: it allowed us to minimize distractions caused by the technical device, and it allowed the participants to place their fingers freely on the sides of the object, instead of a predefined "handle" (which is often used in similar experiments). Investigating grasping in children, and in particular in patients, our aim was to design the grasping task as natural as possible. This design enabled us to measure the diagnostic force applied perpendicular to the object surface (i.e. the grip force), while we refrained from also measuring load force.

The entire scene was filmed from above with two infrared cameras of a Leap motion sensor (Leap Motion, Inc.) to later extract finger aperture from the recorded videos. Duration between movement onset and reaching the maximum grip force was measured and later divided into movement and pick-up time (see Data preparation). Each object was presented once per trial in random order. The experiment consisted of 8 trials, resulting in a total of 24 lifts.

At the beginning of each trial, participants sat at a table in front of the setup, with the thumb and index finger of the dominant hand resting in a closed pinch-grip posture on one small screw equipped with a capacitive sensor. The seat's height was adjusted so that participants' elbow was flexed by about 90° when touching the screw. The table was covered with a black fabric to maximize the contrast between table and objects and to minimize distractions. Participants were presented with one object at the time, at a distance that was adjusted to the arm length of each participant to ensure comfortable reaching (45% of the distance between the acromion and the metacarpophalangeal joint of the middle finger [46,47]). The average distance did not differ between groups. All participants were instructed to reach for and grasp the object with a pincer grip, and lift it a few centimeters above the table. Underneath the object, a force sensing resistor was placed, registering the object's lift-off and triggering an acoustic signal 1.5 seconds later. Participants had to put the object back in place after the acoustic signal. For each lift, data collection was automatically started when the participant released the starting position, by removing the hand from the screw, and started to reach for the object. For each trial, data recording was ended manually by the experimenter after the participant had placed the object back on the table.

After the last lift, the experimenter assessed whether the participant was able to visually discriminate the objects based on their size. For that purpose, two objects at a time were presented one after the other at the same distance as for the grasping task, and the participant had to indicate which of the objects was larger. All pairings were presented once, in counterbalanced order across participants. In the constant weight condition, only three mistakes out of 198 trials were made, two by controls with blurred vision and one by a patient. In the constant density condition one mistake out of 144 trials was made by a blurred vision control participant. In the follow-up tests no mistakes were made.

To measure JNDs, the patients were asked to compare differently sized objects and indicate the larger one (see [14] for more information on the procedure).

Finally, to test for the size-weight illusion, participants were asked to turn the palms of their hands upwards and to lift them off the table, so that hands and arms did not touch the table.

Then, the experimenter simultaneously placed the smallest of the same weighted objects in one hand of the participant, and the largest object with the same weight in the other one in a counterbalanced order across participants. Participants were holding the objects unsupported. With this procedure we ensured that the SWI task was solely perceptual and the estimated weight was not confounded through an active grasping task or motor noise. In half of the cases the experimenter asked the participant which object felt heavier, in the other half which one felt lighter.

Visual acuity assessment

To determine visual acuity in patients and controls with blurred vision, the participants had to indicate the orientation of Gabor patches (19.5 cm Gaussian envelope at 30 cm viewing distance) with sinusoidal gratings of different spatial frequency and contrast on a gamma-corrected LCD display (15.6 inch, 1920x1080 pixel resolution). The viewing distance was occasionally reduced to 15-20 cm for a few participants with extremely poor vision who could not have performed the task otherwise. In these cases, the spatial frequency was adjusted accordingly. During the testing, the participant's head rested on a chin-rest. The patches were either presented vertically or horizontally. Spatial frequencies varied between 0.042 and 10.75 cycles per degree (cpd, i.e. 2 to 512 pixels per cycle at a viewing distance of 30 cm) with the range of frequencies in between spaced evenly on a logarithmic scale, for a total of 9 spatial frequencies. Each spatial frequency was tested separately, starting from the lowest, while the contrast was adjusted according to a psychophysical procedure. To determine the threshold contrast, each block began with a contrast of 100% and with each correct response the contrast was gradually reduced to a minimum of 0.78%. A total of 8 contrast levels, logarithmically spaced, were used. After participants' first wrong answer, the procedure changed to a 3:1 staircase procedure, thus three correct responses were required for the presentation of the next lower contrast level, while each wrong answer resulted in the presentation of the next higher one. After the sixth reversal the procedure ended and the next spatial frequency was tested. The sensitivity (1/threshold) and the spatial frequency were converted to logarithmic scales and plotted against each other. The contrast sensitivity function (CSF) was fitted with an inverse parabola *(18,50,51)* and the cut-off frequency was determined as the highest spatial frequency that was still visible for the participant when presented at 100% contrast. After surgery, patients had an average CSF cut-off frequency of 3.9 cpd(range: 0.04-12.75 cpd; see Table S2) and matched controls with blurred vision obtained an average CSF cut-off frequency of 4.0 cpd (range: 0.19-12.65 cpd).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data preparation

Grip force data were sampled at 400Hz. To obtain the grip force rate, the grip force data were first filtered using a fourth-order, low-pass Butterworth filter with a cut-off frequency of 20Hz and then differentiated with respect to time. The peak of the grip force rate was determined based on a visual inspection, separately for each lift. Videos for the analysis of grip aperture were sampled at 60Hz. The maximum grip aperture was manually extracted separately for each lift. To this end, each trial in the video was visually examined frame by frame, the pixels representing the fingertips were manually selected in the camera image and the Leap Motion SDK was used to triangulate the position from the camera rays (taking into account also depth), to calculate the distance between thumb and index finger. The maximal identified

distance was then determined to be the maximum grip aperture. Movement time was defined as the duration between release of the starting position and the moment the applied grip force exceeded the noise of the sensor. For this the threshold was set to 0.05N (i.e. the moment in which the participant started to grasp and lift the object). Pick-up time was defined as the duration between the applied force exceeding the threshold of 0.05N and the reaching of the maximum grip force rate. For the analyses of grip aperture and pick-up time, the data of both experimental conditions was combined, since the experimental set-ups of both conditions were identical and there was no theoretical reason to expect duration or aperture would differ between conditions (and indeed they did not; grip aperture: $t(1432)=1.65$, $p=0.20$; pick-up time: $t(1411)=1.27$, $p=0.26$).
Although maximum grip force and grip force rate are correlated, obtained sensory information (i.e. early/late object lift-off; information about object weight) might affect the maximum of the applied grip force [48,49]. The grip force rate, however, occurs early in the lift (often even before the object's lift-off [49]) and is known to result from feed-forward control processes [48]. It has been found to be accurately scaled to the predicted weight of an object [50] and is thus a better measure of participants weight expectations. Therefore, we used the maximum grip force rate for our analyses. When grasping an object multiple times, after some lifts, grasping forces are adjusted to the actually sensed weight of the object. In comparable settings [48,51] this adjustment takes several lifts. To compromise between measuring initial weight expectations based on visual information and reducing random noise (which is increased in the tested cataract-treated patients compared to normally sighted controls, see also Figure S1B), we used the first four trials for the analyses of the grip force rate. For the analyses of grip aperture and duration all trials were considered.

Statistical analyses

All statistical analyses were performed with R version 3.5.1[52]. Mixed models were calculated with the package *lme4* [53], p-values were calculated based on the Satterthwaite's method with the package *afex*[54]. Post-hoc comparisons are based on the estimated marginal means and were calculated with the package *emmeans* [55]. Effect sizes analyses were performed with the packages *MuMIn*[56] and *effectsize*[57]. The alpha level was set to 0.05. All tests were performed two-sided. Post-hoc comparisons were accounted for by using Bonferroni-Holm corrections for multiple testing. For all dependent variables, values more than 3 standard deviations above or below the mean were defined as outliers and discarded (~1.5%). Duration data (i.e. movement time and pick-up time), grip aperture, and grip force rate were analyzed for each participant with linear mixed models including next to the fixed effects 1) a random intercept or 2) both a random intercept and random slope for object width (see below). In most cases, the simpler model with only the random intercept (1) was sufficient to explain the data according to the Akaike information criterion (AIC). In all other cases this is specified in Table S1. When comparing the two control groups and patients, "Group" entered as a categorical fixed effect predictor into the models. When analyzing maximum grip aperture and maximum grip force rate, "Object width" was additionally added as continuous fixed effect predictor. In order to analyze the effect of time passed since surgery and visual acuity, these variables were added separately as continuous fixed effect predictors to the model. When comparing patients' performance in the initial test with performance in the follow-up test, "time of test" was used as a categorical fixed effect predictor. In the last two cases, only patients but not controls were included in the analyses. Residuals of all requiring tests were visually assessed for normal distribution and homoscedasticity. To obtain normal distribution of residuals, all duration data (i.e. movement time and pick-up time) and force data was logarithmically transformed. In the initial experimental set-up (i.e. the constant weight condition), the temporal resolution for measuring the release of the starting position was too low. This was later modified when the constant density experiment was conducted. Thus, movement time could only be analyzed in the constant density condition. However, although movement time data was transformed with a logarithmic transformation, normal distribution of residuals could not be achieved. Thus, analyses were repeated with a non-parametric Kruskal-Wallis test and a Bonferroni-Holm corrected Dunn test as post-hoc analysis, which confirmed the parametric results.

Missing data

Due to technical reasons (e.g. sensors losing connection or stopping to provide data, power outages causing the loss of a trial), mistakes of the experimenter (e.g. data collection stopped before trial was finished), or participants getting distracted during a trial, some of the data is missing. For grip force rate, this is the case for 38 out of a total of 3168 trials (1%); for grip aperture for 18 out of 1800 trials (1%) and for grasping duration for 209 out of 4416 trials (5%). Missing values were not replaced.

Video S1. Typical grasping behavior of cataract-treated patients, Related to Figure 1.

The video S1 shows the typical grasping behavior of cataract-treated patients taking part in this study.

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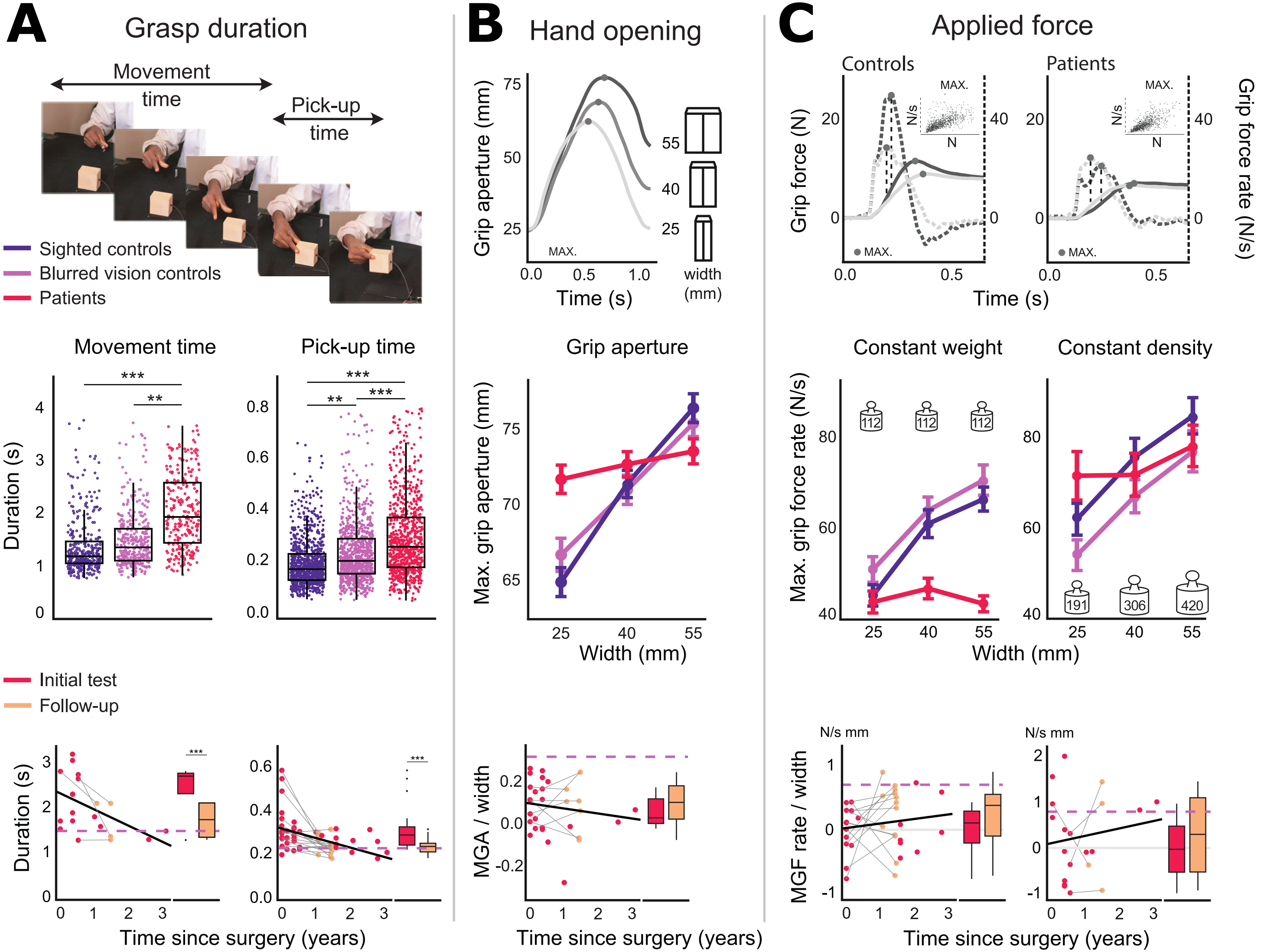
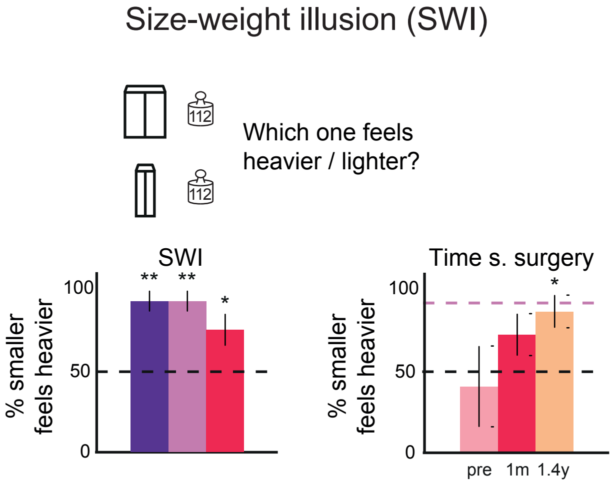


A
Grasp duration
Movement time
Pick-up time
Sighted controls
Blurred vision controls
Patients
Movement time
Pick-up time
Duration (s)
Initial test
Follow-up
Duration (s)
Time since surgery (years)
B
Hand opening
Grip aperture (mm)
MAX.
Time (s)
width (mm)
Grip aperture
Max. grip aperture (mm)
Width (mm)
MGA / width
Time since surgery (years)
C
Applied force
Controls
Patients
Grip force (N)
Grip force rate (N/s)
MAX.
N/s
N
Time (s)
Constant weight
Constant density
Max. grip force rate (N/s)
Width (mm)
N/s mm
MGF rate / width
Time since surgery (years)



Size-weight illusion (SWI)
112
112
Which one feels heavier / lighter?
SWI
% smaller feels heavier
100
50
0
**
**
*
Time s. surgery
% smaller feels heavier
100
50
0
*
pre
1m
1.4y

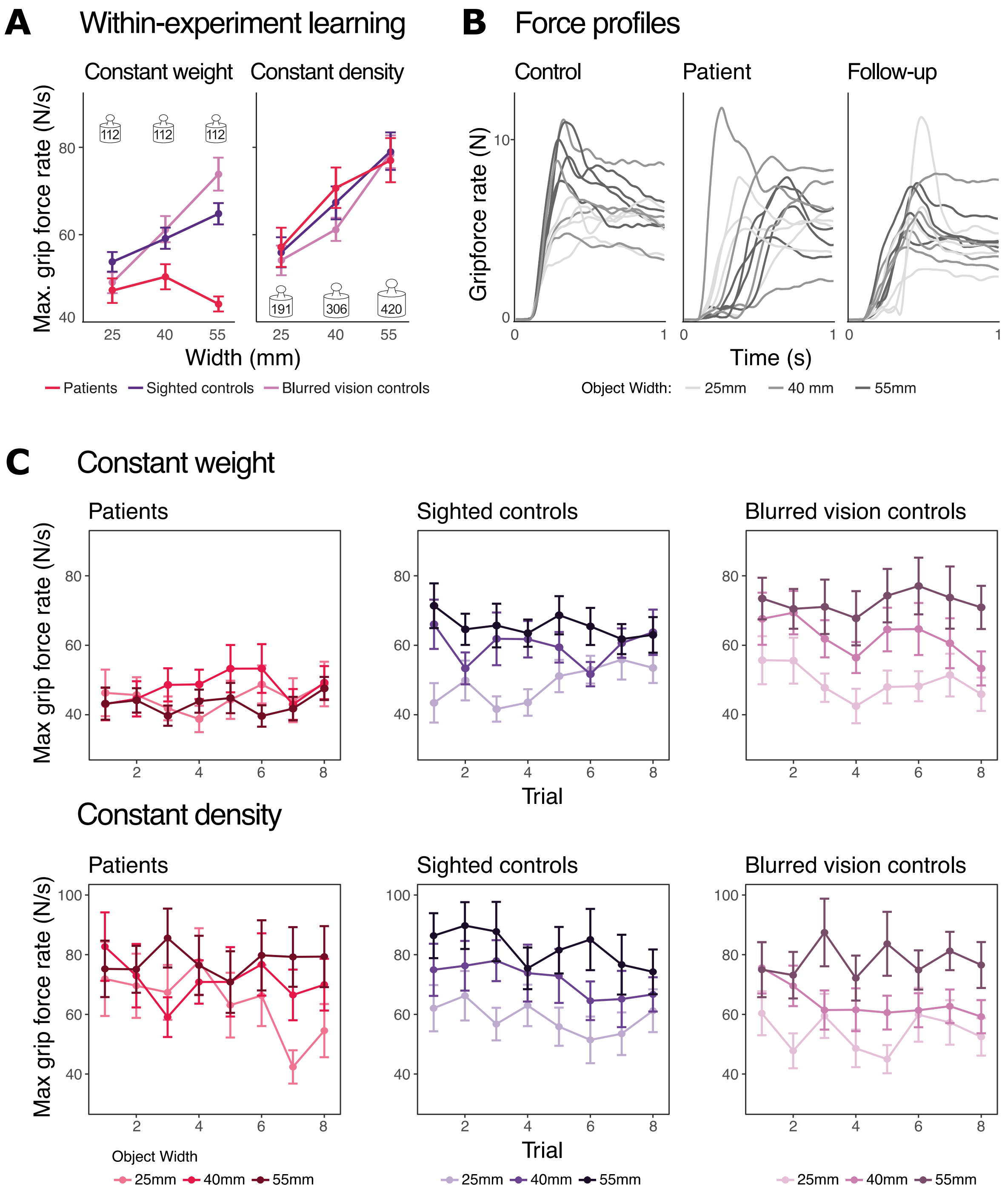


Figure S1. Grip force rate in the constant weight and constant density conditions, Related to Figure 1.

A) Within experiment learning for the constant weight (left) and constant density condition (right). Grip force rate of the last four trials of both grasping conditions was analyzed (cf. first trials in Figure 1C) in order to assess within experiment learning of the participants (i.e. sensory-motor memory). Data of cataract-treated patients (red), a sighted control group (purple) and a blurred vision control group (lilac) is shown. In the constant weight condition, to achieve normal distribution of residuals, the force rate data was logarithmically transformed. The slope of Object width (i.e. maximum grip force rate / object width) is significantly reduced in sighted controls, but not in patients or blurred vision controls, when compared to the initial four trials (sighted controls: t(492)=3.04, p=0.003, b=-0.06, 95% CI[-0.15,-0.03]; blurred vision controls: t(490)=0.30, p=0.77, b=0.01, 95% CI[-0.06,0.08]; patients: t(486)=0.46, p=0.65, b=-0.01, 95% CI[-0.07,0.05]. The slope is larger than 0 in both control groups, but not in patients (sighted controls: *t*(697)=3.90, *p*<0.001, b=0.007, 95% CI [0.003,0.01], blurred vision controls: (*t*(697)=8.73, *p*<0.001, b=0.01, 95% CI[0.01,0.02]; patients: *t*(697)=0.23, *p*=0.82, b=0.0004, 95% CI[-0.003,0.003]). In the constant weight condition, all objects had the same weight. Thus, if learning took place, towards the end of the experiment the same maximum grip force rate should be used for lifting each object. Patients already used the same force rate for lifting the different objects in the initial trials, thus no learning could be expected for this group. These results suggest that, at the end of the experiment, although sighted control participants start to take the haptic weight information into account, they still rely heavily on the expected size-weight relationship predicted from vision and their experience with lifting similar objects. Most likely, participants would require more lifts to adapt the grip force rate to the actual object weight.

In the constant weight condition, the best model according to AIC included also a random slope for each participant in addition to the random intercept. To achieve normal distribution of residuals, the force rate data were logarithmically transformed. Here, the slope of Object width (i.e. maximum grip force rate / object width) was now larger than 0 in all groups (patients: t(47)=4.46, *p*<0.001, b=0.01, 95%CI [0.006,0.02]; blurred vision controls: t(43)=5.92 *p*<0.001, b=0.02, 95% CI[0.01,0.02]; sighted controls: t(44)=5.21, *p*<0.001, b=0.01, 95% CI[0.01,0.02]. When running an additional model separately for each group with Initial trials vs. Last trials as fixed effects we found that patients' slope of Object width was significantly increased (t(337)=2.28, p=0.02, b=0.03, 95% CI[0.01,0.15], η2p = 0.02, 95% CI[0.00,1.00]). As expected, for the two control groups the slope did not change significantly (blurred vision controls: t(345)=0.94, p=0.35, b=0.03, 95% CI[-0.03,0.10], η2p = 0.00, 95% CI[0.00,1.00]; sighted controls: t(345)=0.37, p=0.71, b=0.01, 95% CI[-0.05,0.07]. In the constant density condition, both control groups correctly increased their force rate with larger object width. Thus, no learning could be expected during the experiment. The patients, however, did not scale the force rate correctly in the beginning but have learned to scale their force rate correctly after gaining ample sensory-motor experience with the objects. Taken together, we conclude that patients are able to recognize the objects after multiple lifts and use their gained sensory-motor memory to correctly scale the grip force rate towards the end of the experiment. Interestingly, when tested around one year after the initial test in the follow-up test, this sensory-motor memory had disappeared and they started again with not scaling the force rate appropriately. This contrast might be explained by the statistical relationship between size and weight of objects in the environment: while for the majority of graspable objects in the world, the relationship larger equals heavier holds true, there are of course exceptions to this rule for single objects or sets of objects (e.g. full vs. empty boxes or bottles). If weight expectations during grasping are not met, (i.e. the required grasping forces are over- or underestimated), it is reasonable that the sensory-motor memory takes effect quickly to match the present situation: in this case grasping forces are adapted swiftly (often within the first few lifts) accurately predicting the current actual object weight[S1,S2]. Thus, new size-weight expectation for grasping a specific object or set of objects currently handled can be learned relatively quickly as shown by the within-experiment learning ability of the patients in the present this study or for example by Flanagan et al. (2008)[S3]. Long-term learning the general relationship between size and weight of objects and using it more generally to make predictions about the possible weight of an object, however, seems to be a task that requires abundant experience and might take years to develop.

B) Variability in the grip force profiles of representative participants. One sighted control participant, an age-matched patient (four days after surgery), and the same patient in the follow-up test (1.4 years after surgery) are shown. For each participant, the first twelve lifts in

the constant weight condition are shown, four with each of the three objects (widths of 25, 40 and 55mm). Qualitatively, it is possible to observe that, while the control participant shows a consistent pattern, with a highly stereotyped force pattern in each trial, the grip force profile of the patient is much more variable, with force peaks occurring at different times. Even more than a year later, although force peaks start to occur earlier, the applied grip force is still lacking coordination. The pattern shown by the patients resembles that shown by younger typically-sighted children, who tend to show less coordination and a much larger trial-to-trial variation than older participants [S4,S5]. Moreover, we observed a difference in the “overshoot” of the grip force between patients and controls. In feed-forward control of grasping, the force output required to lift an object is programmed prior to touching the object and before obtaining any sensory-motor information about its weight. Thus, visual information is used for estimating the required grip force. The larger the object the more force is applied. If an object is unexpectedly lighter than predicted, the grip force will first “overshoot” the required amount of force before reaching its final level[S1]. In the constant weight condition, this is especially the case for the largest object. As expected, the control participants do exhibit such an overshoot in force, while the patients do not show this consistently (cf. Figure 1C in the main text). Both, the smaller force overshoot and the variable coordination of the force shown by the patients as compared with controls indicate a greater reliance on feedback, instead of feed-forward control for grasping.
C) Trial-by-trial grip force rate in the constant weight condition (upper panel) and the constant density condition (lower panel). For each group (cataract-treated patients, red; sighted controls, purple; blurred-vision controls, lilac) the mean grip force rate in the two conditions is plotted. In each trial, each of the three objects (widths of 25, 40 and 55mm) is lifted once. In neither condition, grip force rate scaling is evident for the cataract-treated patients when considering only the first or the first few trials. This is in contrast to both control groups who do scale the grip force rate to the size of the objects in the first trials. Adaptation of the force scaling in the last trials is evident for sighted controls in constant weight condition (A) and for patients in the constant density condition (B).

Mean (±SD)			
	Patients (Pat)	*Sighted (Sc)*	*Blurred vision (Bvc)*
Movement time (s)	2.04 (± 0.78)	1.34 (±0.60)	1.49 (±0.70)
Pick-up time (s)	0.30 ± 0.19	0.18 (±0.10)	0.22 ± 0.13
Grip aperture (mm)	72.58 (± 11.45)	70.83 (±12.86)	70.93 (±13.74)
Force rate (constant weight, (N/s))	44.08 (± 20.60	57.28 (±27.18)	61.54 (±29.83)
Force rate (constant density, (N/s))	73.88 (± 38.00)	74.25 (±32.39)	65.98 (±32.08)

Results – Main effects					
	F	*df1, df2*	*p*	*η²p*	*95% CI*
Movement time (group)	10.48	2, 45	<0.001	0.32	[0.13, 1.00]
Pick-up time(group)	18.18	2,95	<0.001	0.28	[0.15, 1.00]
Grip aperture (group)	0.08	2,56	0.93	0	[0.00, 1.00]
object width	105.18	1,52	<0.001	0.67	[0.55, 1.00]
group x object width	14.39	2,25	<0.001	0.35	[0.18,1.00]
Grip force rate constant weight	7.01	2,63	0.002	0.18	[0.05,1.00]
object width	80.35	1,707	<0.001	0.10	[0.07,1.00]
group x object width	13.76	2,707	<0.001	0.04	[0.02,1.00]
Grip force rate constant density	0.53	2,45	0.59	0.02	[0.00,1.00]
object width	39.43	1,46	<0.001	0.47	[0.29,1.00]
group x object width	2.63	2,45	0.08	0.11	[0.00,1.00]

Post-hoc Comparisons

Movement time	*t*	*df*	*p*	*b*	*95% CI*
Pat vs. Bvc	3.12	45	0.006	0.31	[0.06, 0.55]
Pat vs. Sc	4.47	45	<0.001	0.44	[0.20, 0.69]
Bvc vs. Sc	1.36	45	0.18	0.13	[-0.11, 0.39]

Pick-up time	*t*	*df*	*p*	*b*	*95% CI*
Pat vs. Bvc	3.54	95	0.001	0.26	[0.08,0.44]
Pat vs. Sc	6.03	95	<0.001	0.45	[0.27,0.63]
Bvc vs. Sc	2.81	98	0.01	0.18	[0.02, 0.34]

Grip aperture	*t*	*df*	*p*	*b*	*95% CI*
Pat vs. Bvc	0.32	57	1	1.00	[-6.61, 8.62]
Pat vs. Sc	0.39	57	1	1.23	[-6.54, 9.00]
Bvc vs. Sc	0.08	57	1	0.22	[-6.85, 7.30]
Pat vs. Bvc (slope)	4.00	52	<0.001	0.24	[0.09, 0.39]
Pat vs. Sc (slope)	5.37	52	<0.001	0.33	[0.18, 0.48]
Bvc vs. Sc (slope)	1.54	62	0.13	0.09	[-0.23, 0.05]
Slope against 0					
Pat	1.46	46	0.15	0.07	[-0.03,0.16]
Bvc	7.49	62	<0.001	0.31	[0.23,0.39]
Sc	9.23	62	<0.001	0.40	[0.31,0.48]

Grip force rate constant weight	*t*	*df*	*p*	*b*	*95% CI*
Pat vs. Bvc	3.51	63	<0.001	0.33	[0.10,0.56]
Pat vs. Sc	2.88	63	0.01	0.27	[-0.04,0.50]
Bvc vs. Sc	0.64	63	0.53	0.06	[-0.17,0.29]

Pat vs. Bvc (slope)	4.05	707	<0.001	0.012	[0.004,0.0169]
Pat vs. Sc (slope)	4.91	707	<0.001	0.013	[0.007,0.0191]
Bvc vs. Sc (slope)	0.88	707	0.40	0.002	[-0.004,0.009]
Slope against 0					
Pat	0.96	707	0.34	0.0018	[-0.002,0.0054]
Bvc	6.65	708	<0.001	0.0124	[0.0087,0.016]
Sc	7.89	707	<0.001	0.0146	[0.011,0.018]
Grip force rate constant density	*t*	*df*	*p*	*b*	*95% CI*
Pat vs. Bvc	0.90	45	1	0.14	[-0.23,0.49]
Pat vs. Sc	0.02	45	1	0.004	[-0.36,0.37]
Bvc vs. Sc	0.88	45	1	0.13	[-0.24, 0.49]
Pat vs. Bvc (slope)	2.15	45	0.11	0.008	[-0.001,0.017]
Pat vs. Sc (slope)	1.78	45	0.17	0.007	[-0.003,0.016]
Bvc vs. Sc (slope)	0.38	44	0.71	0.001	[-0.008,0.011]
Slope against 0					
Pat	1.75	44	0.09	0.00465	[-0.0007, 0.001]
Bvc	4.84	44	<0.001	0.0124	[0.007, 0.018]
Sc	4.31	46	<0.001	0.0111	[0.0058, 0.016]
Effect of time since surgery	*t*	*df*	*p*	*b*	*95% CI*
Movement time	7.73	188	<0.001	-0.002	[-0.002,-0.001]
Pick-up time	8.29	471	<0.001	-6e-04	[-4e-04,-7e-05]
Grip aperture	0.80	721	0.42	-7e-05	[-3e-04,1e-04]
Grip force rate constant weight	0.03	390	0.97	-2e-07	[-1e-05,1e-05]
Grip force rate constant density	1.19	216	0.24	9e-06	[-6e-06,2e-05]

Table S1. **Summary of the statistical results, Related to Figure 1.**
For each variable (Movement time, Pick-up time, Grip aperture and Grip force rate in the constant weight and density condition, see STAR-Methods for more details), mean values, main effects of the performed analyses, post-hoc comparisons and the effect of time since surgery are reported.
For the analyses of movement time, data was transformed with a logarithmic transformation. However, normal distribution of residuals could not be achieved. Thus, analyses were repeated with a non-parametric Kruskal-Wallis test and a Bonferroni-Holm corrected Dunn test as post-hoc analysis, which confirmed the parametric results: the analyses revealed a significant group effect ($H(2)=15.28$, $p<0.001$, $\eta2=0.30$, 95% CI[0.08,0.55]). Movement duration was significantly longer for patients than for sighted controls ($Z=3.88$, $p<0.001$) or blurred vision controls ($Z=2.37$, $p=0.04$). Grasp duration between control groups did not differ significantly ($Z=1.50$, $p=0.13$). When considering Age as an additional continuous predictor, we found a significant effect, i.e. movement time decreased with increasing age of the participants ($F(1,42)=5.38$, $p=0.03$). However, this effect did not differ between groups (i.e. there was no significant interaction with the factor Group ($F(2,42)=0.63$, $p=0.54$). Patients in the follow-up test differ no longer from blurred vision controls ($t(18)=0.70$, $p=0.49$, $b=0.16$, 95% CI[-0.29,0.61])
Pick-up time data was transformed with a logarithmic transformation. Here, we did not find a significant effect of Age ($F(1,98)=3.61$, $p=0.06$) nor an interaction between Age and Group

(F(2,97)=1.30, p=0.28). Patients in the follow-up test differ no longer from blurred vision controls (t(48)=0.21, p=0.83, b=0.004, 95% CI[-0.04,0.04]).

For the analysis of hand aperture, the winning model, according to the AIC, included also a random slope for Object width, in addition to the random intercept. When considering Age as an additional predictor, we did not find an effect of Age on grip aperture (F(1,62)=2.87, p=0.10) and also no significant interaction between Age and Object width (F(1,1515)=0.09, p=0.76). Visual acuity had no effect on the adaptation of grip aperture to object width. (t(721)=0.50, p=0.61, η2p = 0.00, 95% CI[0.00,1.00]. Patients' behaviour did not change in the follow-up test compared to the initial test (t(370)=0.35, p=0.72, b=-0.03, 95% CI[-0.18,0.13). Moreover, re-tested participants still differed significantly from participants with blurred vision (t(29)=2.65, p=0.01, b=0.22, 95% CI[0.06,0.37].

In the constant weight condition, the force rate data was logarithmically transformed to achieve normal distribution of residuals. When considering Age as an additional predictor, we found a significant main effect, i.e. with increasing Age also peak grip force rates increased (F(1,62)=5.12, p=0.03). However, the ability to scale the force rate to the object's width did not depend on the age of the participants, i.e. we found no interaction between Age and Object Width (F(1,704)=0.05, p=0.83).

In the patient group visual acuity had no effect on the adaptation of grip force rate to object width (t(391)=0.09, p=0.93, b=-4e-05, 95% CI[-8e-04,9e-04]. Patients' behaviour did not change in the follow-up test (t(304)=0.55, p=0.59, b=-0.002, 95% CI[-0.01,0.005].

In the constant density condition, we chose the best fitting model that additionally included a random slope for object width for each participant. To achieve normal distribution of residuals, the force rate data was logarithmically transformed. When considering Age as an additional predictor, we did not find a significant main effect (F(1,40)=0.64, p=0.43) and also no significant interaction between Age and Object width (F(1,41)=2.67, p=0.11). In the patient group visual acuity had no effect on the adaptation of grip force rate to object width (t(211)=0.02, p=0.99, b=-1e-05, 95% CI[-0.001,0.001]). Patients' behaviour did not change in the follow-up test compared to the initial test (t(86)=0.65, p=0.52, b=-0.006, 95% CI[-0.02,0.01], η2p = 0.00, 95% CI[0.00,1.00]).

Patient	Sex	Experiment	Age (years) w/d	Pre-op CSF cutoff (cpd)	Post-op CSF cut-off (cpd) w/d	Time since surgery (months) w/d
1	f	w/d/s	8.0/8.0	0.04	0.04/0.04	0.1/0.1
2	f	w/d/s	8.2/8.5	1.31	6.00/6.19	0.1/4.4
3	f	w/s	9.0	0.04	0.09	0.1
4	m	w/d/s	9.1/9.5	0.71	3.02/5.37	1.9/6.4
5	m	w/d/s	9.2/9.5	1.51	1.41/2.24	0.1/4.4
6	f	w/s	10.0	0.04	0.08	0.1
7	f	w/d/s	10.1/10.5	2.66	4.05/5.30	1.8/6.4
8	f	w/d/s	10.5/10.5	2.84	9.54/9.54	4.3/4.4
9	m	w/d/s	10.6/11.6	3.77	5.31/2.70	19.3/31.2
10	f	d/s	11.0	0.23	0.21	0.1
11	m	w/d/s	11.1/12.1	1.89	2.30/1.43	1.8/14.2
12	m	w/s	11.6	0.06	2.84	19.3
13	m	w/s	11.6	0.72	1.49	19.3
14	m	d/s	13.2	0.39	5.68	0.1
15	m	w/d	14.1/15.1	3.69	6.73/6.59	24.9/37.3
16	f	w/d/s	14.1/14.5	0.88	2.30/4.64	1.9/6.4
17	m	w/d/s	14.2/14.5	6.33	6.03/6.02	0.1/4.4
18	f	w/d/s	15.2/15.6	2.91	4.72/12.75	0.1/4.4
19	m	w/d/s	15.2/15.6	1.50	1.58/1.52	0.1/4.4
20	m	w/d/s	15.2/15.6	0.08	1.30/1.55	0.1/4.4
21	m	w/s	15.8	0.25	1.59	34.0
22	m	w/s	18.1	2.64	2.00	25.3
23	f	w/s	18.9	0.26	11.99	34.0
24	f	w/s	21.1	0.74	1.50	19.3

Abbreviations: *female* f; *male* m; *constant weight condition* w; *constant density condition* d; *size-weight illusion experiment determined always with the w or d condition conducted first* s; *contrast sensitivity function* CSF; *cycles per degree* cpd.

Table S2. Characteristics of the Ethiopian patients and descriptive statistics, Related to STAR-Methods.

Supplemental References

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