Report

Current Biology

Grip Constancy but Not Perceptual Size Constancy Survives Lesions of Early Visual Cortex

Highlights

- Computing object distance is crucial for size constancy and grasp aperture scaling
- We tested both size and grip constancy in M.C., who has damage to early visual cortex
- When object distance varied, her estimates of size co-varied with retinal-image size
- Under the same viewing conditions, her grasps remained sensitive to real-world size

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In Brief

Like perceptual size constancy, grasping goal objects entails compensatory processing for changes in the retinal image with viewing distance. Does early visual cortex support both grip constancy and perceptual size constancy? Whitwell et al. show that damage to early visual cortex spares grip constancy while disrupting traditional size constancy.

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Grip Constancy but Not Perceptual Size Constancy Survives Lesions of Early Visual Cortex

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SUMMARY

Object constancies are central constructs in theories of visual phenomenology. A powerful example is "size constancy," in which the perceived size of an object remains stable despite changes in viewing distance [1–4]. Evidence from neuropsychology [5], neuroimaging [6–11], transcranial magnetic stimulation [12, 13], single-unit and lesion studies in monkey [14–20], and computational modeling [21] suggests that re-entrant processes involving reciprocal interactions between primary visual cortex (V1) and extrastriate visual areas [22–26] play an essential role in mediating size constancy. It is seldom appreciated, however, that object constancies must also operate for the visual guidance of goal-directed action. For example, when reaching out to pick up an object, the hand's in-flight aperture scales with size of the goal object [27–30] and is refractory to the decrease in retinal-image size with increased viewing distance [31–41] (Figure 1), a phenomenon we call "grip constancy." Does grip constancy, like perceptual constancy, depend on V1 or can it be mediated by pathways that bypass it altogether? We tested these possibilities in an individual, M.C., who has bilateral lesions encompassing V1 and much of the ventral visual stream. We show that her perceptual estimates of object size co-vary with retinal-image size rather than real-world size as viewing distance varies. In contrast, M.C. shows near-normal scaling of in-flight grasp aperture to object size despite changes in viewing distance. Thus, although early visual cortex is necessary for perceptual object constancy, it is unnecessary for grip constancy, which is mediated instead by separate visual inputs to dorsal-stream visuomotor areas [42–48].

RESULTS

More than a decade before the current study, M.C. had sustained bilateral damage to V1 and most of the occipital cortex, leaving MT^+ intact (see Figure 1) and functional [49]. In one experiment (see experiment 1 in the STAR Methods and Supplemental Information for details), M.C. and a sample of 10 control participants, who had their heads fixed in a chinrest, provided manual estimates of the lengths of rectangular objects of different dimensions (but the same top-surface area) presented at different viewing distances. In a separate set of trials, M.C. and the controls reached out and grasped the same rectangular objects across their length while we recorded their hand movements by using optoelectronic markers.

Consistent with re-entrant accounts, M.C.'s perceptual estimates of object length were severely impaired. In fact, as Figure 2 and Figure S1 illustrate, her judgments of perceived length co-varied with object distance rather than object size: the further away the object the smaller her estimates. In contrast, when M.C. reached out to pick up the objects positioned at different distances, her in-flight grasp aperture co-varied with the real-world size of the objects rather than object distance, revealing spared grip constancy (Figure 2; for statistical details, see Table 1). At the same time, the peak velocity of her reach toward the target object co-varied with its distance (see Figure S2). The fact that M.C. could reliably scale her grip aperture to the length of the goal objects with identical top-surface areas shows that her visuomotor system also remained sensitive to the objects' shape and/or principal axis.

In a follow-up experiment (for methodological details, see experiment 2 in the STAR Methods), we presented M.C. and 8 controls with glow-in-the-dark spheres in a darkened room with their head fixed in a chinrest, so that only accommodation, stereo, and vergence cues were available for computing distance [3]. Spheres of different diameters were matched for retinal image size by positioning them at different distances. M.C. and control participants were asked to estimate the diameter of the spheres and to grasp them in separate blocks of trials. Note that as the reaching movement unfolds in the grasping task, kinesthetic and proprioceptive feedback about target distance becomes available. To provide similar information about distance in the estimation task, participants were instructed to

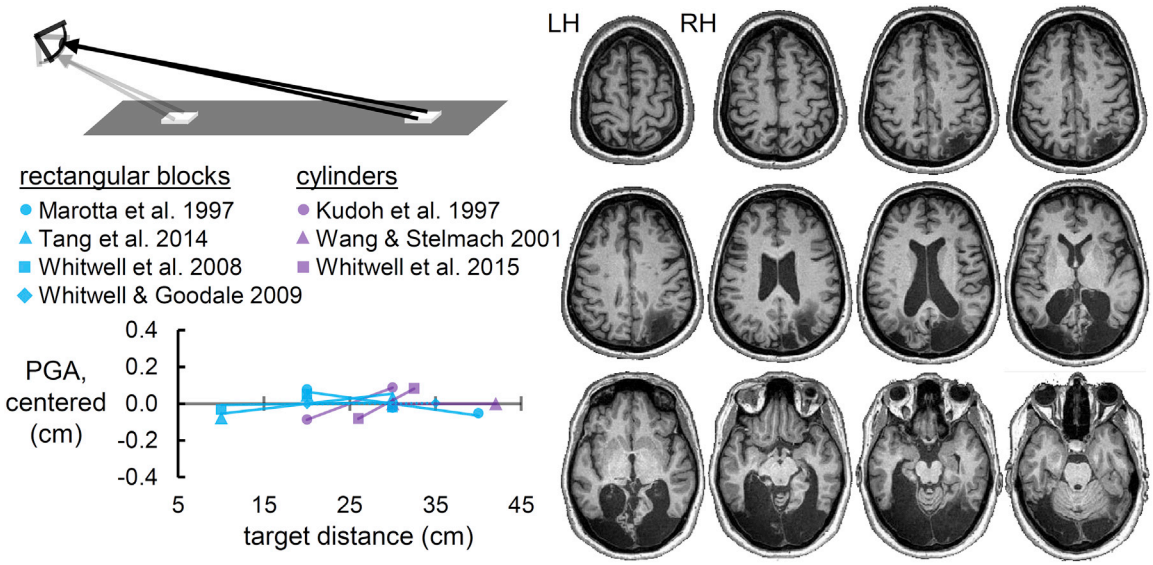

Figure 1. Grip Constancy and Successive Horizontal Sections through M.C.'s MRI Scan

Left: grip constancy, as reflected in a largely invariant mean peak of the in-flight grip aperture (PGA) as neurotypical participants reach out with their right hand to pick up target objects positioned at different distances on a tabletop. The mean centered PGAs are illustrated as linear functions of target distance for each study listed. (Note the difference in scale between the x and y axes.) Shown on the right are horizontal sections through M.C.'s MRI scan reveal large bilateral lesions in the occipital cortex that include V1 and encroach upon the temporal lobe and the right parietal lobe (see also 49). Abbreviations are as follows: LH, left hemisphere; RH, right hemisphere. For clinical details, see STAR Methods.

touch the side of the sphere with their left index finger before providing a manual estimation of its diameter with their right hand. M.C.'s estimates failed to co-vary with the real-world size of the spheres (Figure 3). In contrast, her in-flight grip aperture during grasping scaled with the real-world size of the spheres (Figure 3). These results confirm that grip constancy operates independently of perceptual size constancy and that M.C.'s perceptual impairment is not compensated for by advance proprioceptive information about object distance. For statistical details, see Table 1.

DISCUSSION

Our findings have two main implications. First, they reinforce reentrant theories of stable perception, in which V1 and ventral-stream structures with which V1 is reciprocally connected are posited play a central role [22–26]. With respect to size constancy, a recent EEG study has shown that early signals in V1 reflect the retinal-image size of visual stimuli, whereas later signals in V1 reflect their perceived, real-world size [6]. Similarly, a recent TMS study has demonstrated that stimulation of the lateral occipital cortex, a ventral-stream structure, disrupts size perception ahead of stimulation of the occipital pole [13]. Thus, given damage to V1 and much of the ventral stream, M.C.'s size perception should be severely compromised. Indeed, our findings show that her estimates of the size of objects presented at different distances are correlated with retinal-image size rather than real-world size.

M.C.'s impairment in perceptual size constancy was evident not only in experiments 1 and 2 but also in an earlier exploration of her perceptual deficits (see Initial Assessment in the STAR Methods for details), in which we found that her estimates of size co-varied reliably with changes in retinal image size when the real-world size of the object was fixed and viewing distance varied (see Table S2). Importantly, however, this impairment cannot be due to a failure to translate retinal and extra-retinal information into perceptual estimates of the distance of the target object, because her estimates of distance were reasonably accurate under the same viewing conditions, i.e., when the real-world size of the object was fixed and viewing distance varied (see Table S2). In short, M.C. seems unable to integrate information from the retinal image of the perceived object with information about its perceived distance. Instead, her perceptual judgments of size appear to flow from a combination of retinal image size (or estimates thereof) and strategic guesswork about what the range in the size the objects might be.

The second main implication of our findings is that subcortical routes to dorsal-visual-stream structures independent of thalamic inputs to V1 and a functioning ventral stream can support the integration of the retinal image and viewing distance to compute the real-world size and shape of a goal object for the planning and execution of smooth and accurate grasps. This implication is bolstered by the fact that the target's retinal image size and shape were held constant whereas its real-world size and distance were varied. In everyday life, goal-directed grasps require the *de novo* integration of object size, shape, orientation, and distance, so that a target object, regardless of its position in reachable space, can be mapped into effector-based spatial reference frames to plan and execute accurate grasping movements.

M.C.'s structural MRI shows that the dorsal-stream structures in her left hemisphere that would enable the visual guidance of goal-directed grasping with her right hand are intact. Furthermore, M.C.'s functional MRI shows that the middle-temporal

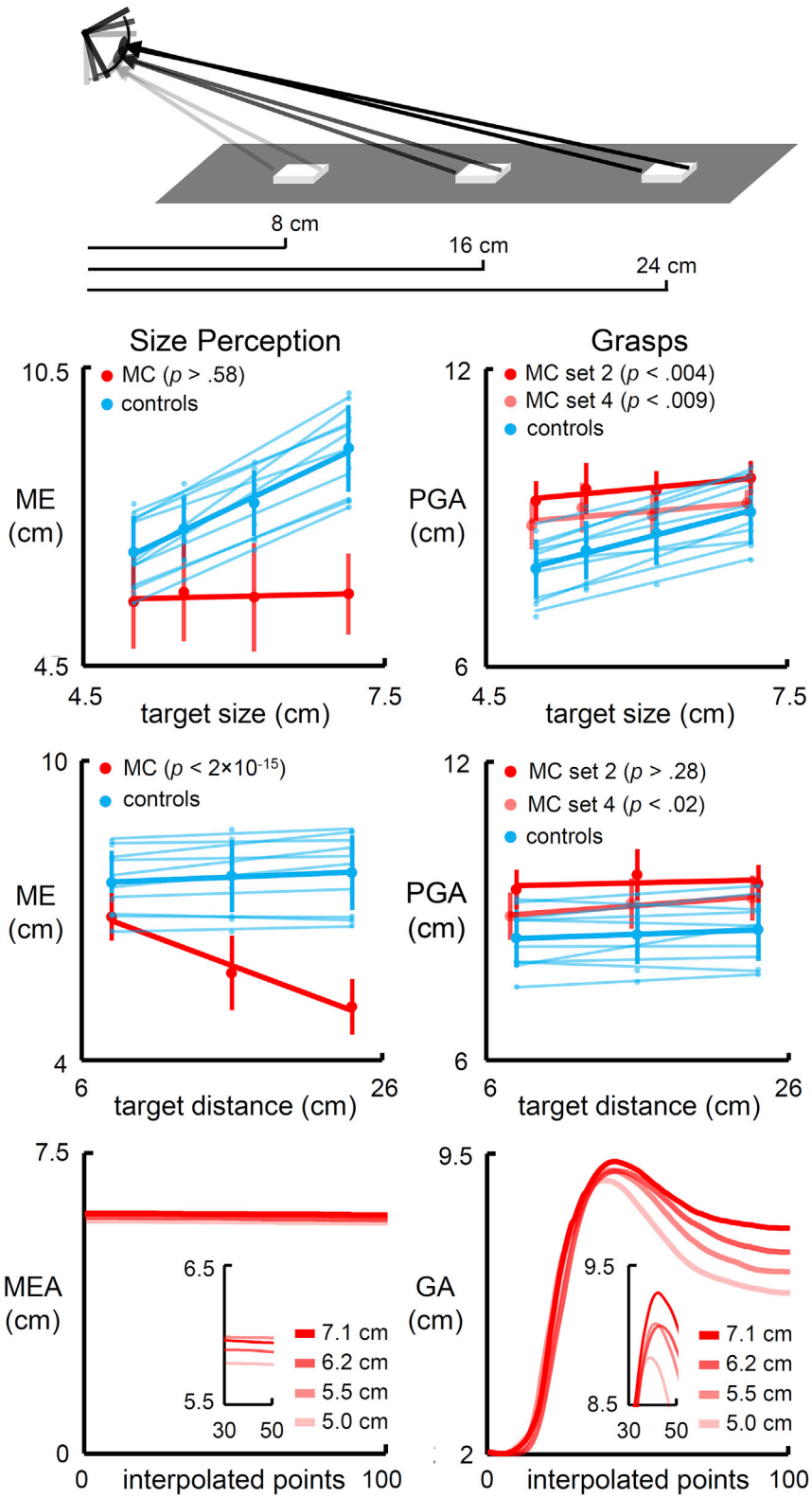

Figure 2. Main Results from Experiment 1

The sensitivity of the manual estimates of perceived size (left) and the grasps (right) to the length of the rectilinear objects (target size), aperture profiles for the manual estimates and grasps (middle), and the modulatory influence of viewing distance on target size sensitivities (bottom). A schematic of the setup depicting one of the objects at three different distances is shown at the top of the figure. Shown in the top pair of graphics are the controls' manual estimates (MEs) and peak grip aperture (PGA) scaled with target size. M.C.'s MEs did not scale with target size, but her PGAs did in both sets of trials in which target distance was varied (the second and fourth set of trials: see also Figure S1). Shown in the middle pair of graphics are the control's estimates of target size (ME) were essentially accurate. Their grip apertures (PGA) were also completely insensitive to target distance; i.e., they showed perfect grip constancy. In contrast, M.C.'s perceptual estimates of target size *decreased* with target distance (note the different axes scales). M.C.'s grip aperture, however, was unrelated to target distance in the first set of grasp trials and showed a slight *increase* with target distance in the second. That is, she showed excellent grip constancy. Furthermore, the peak speed of M.C.'s reach scaled with target distance just as well as the controls' did (see Figure S2). Shown in the bottom pair of graphics: M.C.'s mean interpolated profiles of the manual estimate aperture (MEA) and grip aperture (GA) for each target size. M.C.'s MEAs are steady, indicating she followed task instructions; yet, they do not scale with target size. In contrast, the peaks of her GA (PGA) scale with target size when she reached out to pick up the targets (see also inset). M.C.'s PGA occurred, on average, 511 ms after movement initiation, and a stable grip aperture suitable for lifting the object was achieved, on average, 650 ms later. Where illustrated, error bars reflect SD. The p values for the t tests of M.C.'s regression coefficient relating target size to ME and PGA are listed in parentheses. For statistical details, see Table 1.

Table 1. Descriptive and Inferential Statistics for the Main Results from Experiment 1 and Experiment 2

Exp.	Task	Regressor	Controls	M.C.	Test for Deficit
1	manual estimation (set 2)	target size	$\bar{b}$ = 0.95 [.78 1.13]	b = 0.05 [–.13 0.22]	$t = -3.49$, $p < 0.004$
			$t(9) = 12.17$, $p < 7 \times 10^{-7}$	$t(68) = 0.54$, $p > 0.58$	
		target distance	$\bar{b}$ = 0.01 [0 0.02]	$b = -0.11$ [–.13 –.09]	$t = -6.78$, $p < 5 \times 10^{-5}$
			$t(9) = 1.88$, $p > 0.09$	$t(68) = -10.35$, $p < 2 \times 10^{-15}$	
	grasping (set 2)	target size	$\bar{b}$ = 0.55 [.46 0.64]	b = 0.19 [.07 0.31]	$t = -2.66$, $p < 0.02$
			$t(9) = 13.43$, $p < 3 \times 10^{-7}$	$t(66) = 3.07$, $p < 0.004$	
		target distance	$\bar{b}$ = 0.01 [0 0.02]	b = 0.01 [–.01 0.02]	$t = 0.08$, $p > 0.46$
			$t(9) = 1.58$, $p > 0.14$	$t(66) = 1.04$, $p > 0.3$	
	grasping (set 4)	target size	not administered	b = 0.18 [.05 0.31]	N/A
				$t(63) = 2.71$, $p < 0.009$	
		target distance		b = 0.01 [0 0.03]	
				$t(63) = 2.37$, $p < 0.03$	
2	manual estimation	target size	$\bar{b}$ = 0.9 [.8 1.01]	b = 0.07 [–.05 0.2]	$t = -6.43$, $p < 2 \times 10^{-4}$
			$t(7) = 20.6$, $p < 2 \times 10^{-7}$	$t(18) = 1.19$, $p > .24$	
	grasping	target size	$\bar{b}$ = 0.59 [.41 0.78]	b = 0.32 [0 0.63]	$t = -1.57$, $p > .07$
			$t(7) = 7.5$, $p < 2 \times 10^{-4}$	$t(18) = 2.3$, $p < 0.04$	

Slopes (b) and confidence limits of the linear fits relating the *regressors*, target size, and target distance, to M.C.'s manual estimates from the manual estimation task (*size perception*), and her peak grip aperture from the grasping task (grip scaling), for the sets of trials in which both the target size and viewing distance were varied in experiment 1 and experiment 2 (all measurement units in cm). The means of the slopes from the analogous set of linear fits for the controls are also reported ($\bar{b}$), along with confidence limits and tests of whether or not M.C.'s performance was significantly worse than that of the controls (i.e., tests for neurological deficit, see [50–53]), where applicable. Experiment 1: M.C.'s size perception was unreliable. Not surprisingly, the controls exhibited excellent size constancy perception; their mean slope was not statistically different from unitary, $t = -.59$, $p > 0.56$. The test for neurological deficit was positive, highlighting M.C.'s dysfunctional size perception. Despite M.C.'s perceptual deficit, her grip scaling was reliable. The controls' grip scaling was also reliable. Nevertheless, M.C.'s grip scaling was impaired, as indicated by a positive test for neurological deficit. Crucially, the test for differential dissociation [see 51, 54] was positive, $t = -3.04$, $p < 0.02$, meaning that M.C.'s size perception was significantly poorer than her grip scaling, compared to what one would expect from the analogous contrast for the control sample. Increased target distance reliably reduced M.C.'s estimates of target size, suggesting a reliance on retinal image size to inform her estimates of target size. The controls' estimates of target size remained unchanged with increased target distance. The test for neurological deficit was positive, highlighting M.C.'s abnormal reliance on retinal image size to inform her estimates of target size. Remarkably, M.C.'s grip scaling was not influenced by target distance in trial set 2 and *increased* slightly with target distance in the trial set 4, indicating she possesses a reliable degree of grip constancy. The controls' grip scaling was not influenced by target distance, $t = 1.58$, $p > 0.14$. The test for neurological deficit was negative, highlighting M.C.'s intact grip constancy. The test for a differential dissociation was positive, $t = -5.35$, $p < 0.5 \times 10^{-4}$, meaning that M.C.'s size perception more strongly influenced by target distance than was her grip scaling, compared to the analogous contrast for the controls. Experiment 2: the targets were glow-in-the-dark spheres of different diameter, positioned at viewing distances chosen to make their retinal image sizes identical. For the manual estimation task, but not the grasping task, the participants, including M.C., touched the side of the target with their left index finger before estimating its diameter with the index finger and thumb of their right hand. M.C.'s manual estimation slope was unreliable. The controls, however, reliably estimated the target's size very well, with a slope only marginally below unitary, $t = -2.19$, $p > 0.06$. The test for neurological deficit in size perception was positive, again highlighting M.C.'s deficit in size perception. M.C.'s grip scaling, however, was reliable, as was the controls', and the test for neurological deficit was negative, indicating that M.C. possess a degree of grip constancy under these more stringent conditions. Crucially, the test for differential dissociation was positive $t = -3.3$, $p < 0.02$. Thus, M.C.'s size perception was significantly poorer than her grip scaling, relative to what one would expect from the analogous contrast for the control sample.

area (MT), a visual structure that projects to dorsal-stream structures in the posterior parietal cortex, is functionally intact in both hemispheres [49]. Moreover, the extensive bilateral damage to ventral-stream areas in M.C., including the lateral occipital cortex [49], suggests that any extra-geniculo-striate projections that convey information to these areas are not necessary for grip constancy. It is important to point out, however, that other aspects of the visual control of grasping, such as the deployment of functionally appropriate postures, might depend on these structures [55].

The alternative routes whereby visual input can reach the cerebral cortex have been explored for over 50 years. There are two prominent candidate pathways. The koniocellular layers of the lateral geniculate nucleus receive direct visual input from the retina and indirect visual input from the superior colliculus (SC) and projects directly to area MT [44]. The pulvinar receives input from both the retina and the SC [45, 46] and is reciprocally connected to the dorsal stream's visuomotor networks in the posterior parietal cortex via MT, V6, and V6A [47, 48]. The SC itself receives retinal input, is retinotopically organized [46], and has been implicated in the control of orienting eye and head movements, spatial attention, as well as reaching movements [46, 56]. The inferior pulvinar, which possesses retinal and SC recipient zones [45], contains neurons that respond during visually guided reaching movements and saccades [57] and are sensitive to oculomotor cues such as vergence [58] and visual stimulus features such as shape [59]. Thus, the available anatomical and physiological

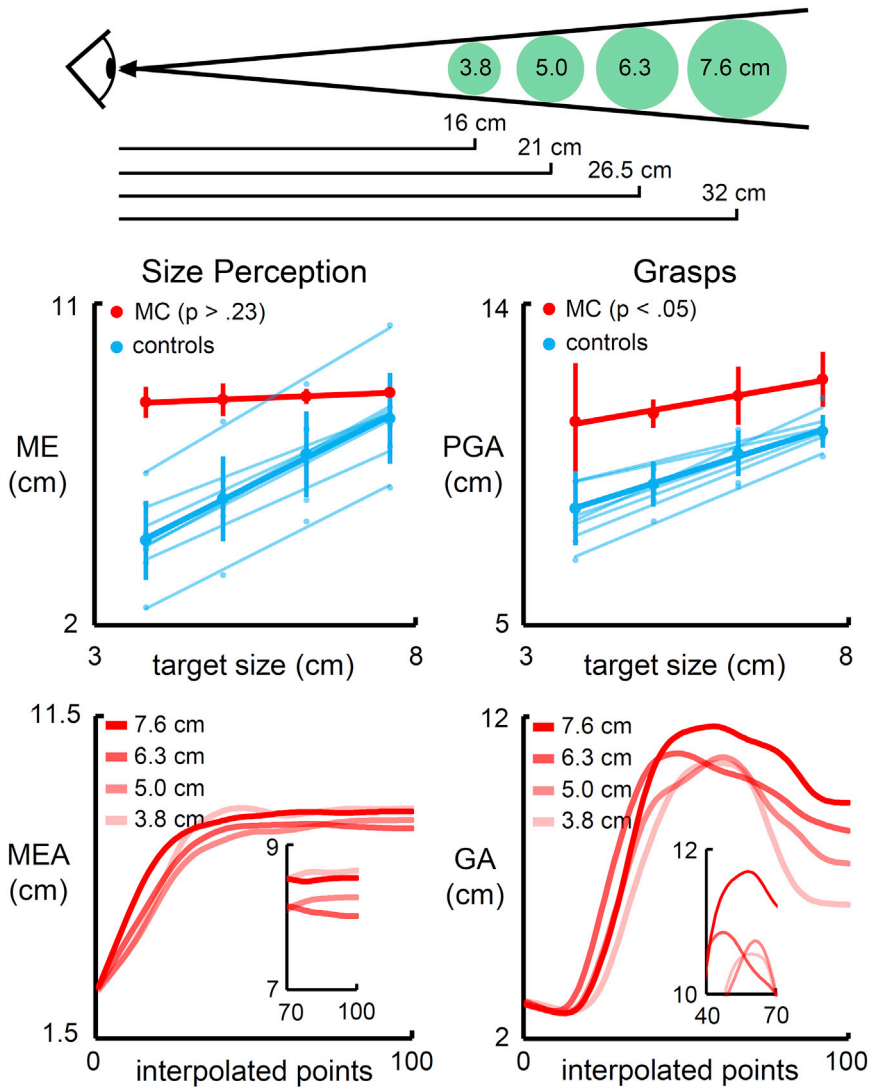

Figure 3. Main Results from Experiment 2

Manual estimation (left) and grasp (right) sensitivity to sphere diameter (*target size*) in experiment 2 when the spheres were matched for retinal image size (see the top schematic), and all participants were permitted to touch the spheres with the index finger of their left hand before responding with their right (dominant) hand. The controls' MEs scaled with target size as did the PGA of their grasps. In contrast, M.C.'s MEs were unrelated to target size, yet, crucially, her PGA scaled with target size. The bottom left graphic illustrates M.C.'s MEAs for each target size standardized temporally from movement start to end. Even though M.C.'s MEAs plateau as expected, indicating that she understood instructions and was satisfied with her final judgment of target size, they bear no relationship to target size. She took, on average, 1,299 ms from the start of her estimate to achieve a stable MEAs. Her unfolding grip aperture (GA), illustrated on the bottom right, is correlated with target size even before the peak grip aperture is achieved and remains so through the peak and afterward as the fingers close down on the target. M.C.'s peak grip aperture occurred, on average, 1,386 ms after movement initiation, and stable grip suitable for lifting the object was achieved, on average, 1,034 ms later. Error bars reflect SD. The p values for the t tests of M.C.'s regression coefficient relating target size to MEs and PGA are listed in parentheses. For statistical details, see Table 1.

evidence indicates that distance and object shape information can be conveyed to visuomotor areas mediating grasping in parietal and frontal cortex, independent of V1. These circuits involving the pulvinar could compute the size of the goal object and/or the spatial locations of stable grasp points on the surface of the object [60]. Indeed, a recent investigation has shown that patients with damage to the pulvinar possess clinical deficits in reaching and grasping [61].

Four studies have shown reliable grasping after focal lesions to V1. Nevertheless, the generalizability of this work to real-world grasping is limited by a number of constraints in their experimental designs. Three of the studies co-varied target size and shape while keeping distance fixed [62–64]. Thus, target distance could have been based on a motor memory that was acquired over many trials, reducing the dimensionality of the problem for the visuomotor system to one of object form and size. In another, perceptual estimates of target size were not measured and, despite trial-to-trial variations in target distance, relied on a categorical analysis of grasp performance (good or bad) without explicitly matching the retinal image size of different-sized targets or measuring the actual scaling of grip aperture to target size [65]. In contrast to this earlier work, we directly examined the relationship between grip aperture and systematic variations in object size and viewing distance—in the absence of V1 and much of early visual cortex, bilaterally. Our findings conclusively demonstrate that subcortical routes from the eye to dorsal-stream visuomotor networks cortex that bypass the geniculo-striate pathway to V1 are capable of supporting the complex visual processing necessary for real-world goal-directed grasping.

Although M.C. showed spared grip constancy, her performance tended to fall toward the lower range of controls. This suggests that projections from V1 to the dorsal stream might modulate or fine-tune grasping movements that are otherwise driven by extra-geniculo-striate projections. Although the nature of that modulation remains unclear, two patients with visual form agnosia who have a relatively intact V1 but bilateral damage to ventral-stream areas show grip scaling that appears to be somewhat better tuned to object size than M.C.'s [66, 67]. Nevertheless, the fact that M.C. shows clear evidence of grip constancy despite extensive bilateral damage to V1 and the ventral stream shows that subcortical routes outside of the geniculo-striate pathway must be capable of conveying the required visual information to the dorsal stream.

In summary, the current findings (1) reinforce the idea that perceptual object constancies depend on re-entrant processing

involving reciprocal connections between V1 and ventral-stream visual areas and (2) suggest that grip constancy is not mediated by these same processes—but instead depends on visual projections to the posterior parietal cortex that are independent of V1. In short, there is a strong dissociation between the computations underlying accurate size perception and grasping when target size, shape, and distance vary.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- RESOURCE AVAILABILITY
  - Lead Contact
  - Materials Availability
  - Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Participants
- METHOD DETAILS
  - Stimuli and Apparatus
  - Procedure
- QUANTIFICATION AND STATISTICAL DETAILS
  - Data Recording
  - Data Processing and Statistical Analysis

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.07.026.

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AUTHOR CONTRIBUTIONS

R.L.W., I.S., and M.A.G. designed the study. R.L.W., I.S., and G.B. performed the research. R.L.W. and I.S. analyzed the data. All authors contributed to the writing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

RESOURCE AVAILABILITY

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Materials Availability

This study did not generate new unique reagents

Data and Code Availability

Datasets generated during this study are available at OSF: https://osf.io/rk9tm/?view_only=37f41eb41b30471897385b1bc6c12603.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

Patient M.C.

M.C. is a right-handed female who was 43 (and 45) years of age prior to testing. Prior to her injury, she worked as a secretary in a hospital eye clinic. She is intelligent, high-functioning, highly motivated, personable, and cooperative. At age 30, M.C. contracted a respiratory infection which led to a severe stroke resulting in extensive bilateral lesions to her occipital lobes, as well as her ventral temporal cortices, and right posterior parietal cortex (see Figure 1 in main text). Following her extensive lesions, M.C. appeared to be completely blind when tested using static Goldmann perimetry, although she could detect moving targets in some parts of her visual field. Despite her poor performance with Goldmann perimetry, M.C. reliably reports the presence of large high-contrast static stimuli of the kind used in this experiment (for more details about M.C.'s lesions and visual abilities, see Figure 1 and reference 49 in main text). All the protocols described below were approved by the Research Ethics Board at the University of Western Ontario, Canada (Initial Assessment and Experiments 1 and 2) and the Heriot-Watt University, Scotland (Experiment 2). M.C. was naive to the purpose of the studies.

Controls

In order to provide sample estimates of typical performance, we tested 10 self-reported normally sighted, right-hand dominant, gender-matched, and age-appropriate (32 – 53 years old) controls in Experiment 1; eight self-reported normally-sighted, right-hand dominant, gender-matched and age appropriate (37 – 55 years of age) controls in Experiment 2; and seven self-reported normally sighted, right-hand dominant, gender-matched, and age-appropriate (34 – 49 years of age) controls in the initial exploration of her perceptual deficits. The trials and sets of trials were scheduled in the same manner as they had been for M.C. The controls were naive to the purpose of the studies and were tested, in all experiments, at the University of Western Ontario.

METHOD DETAILS

Stimuli and Apparatus

Experiment 1

The targets for size estimation and grasping were wooden blocks painted matte white with the same top surface area (25 cm^2) and height (1.5 cm) but different widths and lengths (w x l: 5 × 5, 4.5 × 5.5, 4 × 6.2, and 3.5 × 7.1 cm). Three infrared emitting diodes (IREDs) were attached to M.C.'s hand, one next to the nail of her index finger, one next to the nail of her thumb, and one on the wrist of her right hand. The positions of the IREDs were recorded by an optoelectronic system, (OPTOTRAK 3020, Northern Digital, Waterloo, ON). For the grasping task, M.C. (and the controls) wore a pair of liquid crystal goggles (*PLATO goggles*, Translucent Technologies, Toronto, Canada) that were used to control her view of the workspace. The goggles were configured to (1) assume a translucent state between trials to prevent an informative view of the workspace and (2) clear (< 6 ms) at the start of the trial and return to their default state (< 6 ms) 3 s after she released the start button.

Experiment 2

The targets for size estimation and grasping were four Styrofoam spheres (*targets*) with diameters (*target sizes*) of 3.8, 5, 6.3, and 7.6 cm. Each was coated with phospholuminescent paint. Participants, including M.C., also wore a glove coated in phospholuminescent paint so that her hand would be visible in the dark for both the manual estimation and grasping tasks. For experiment 2, the grasping and manual estimation tasks were administered to M.C. at Heriot-Watt University, and the movements of her right hand were recorded by a magnetoelectric system (TRAKSTAR, Ascension Technologies). The hand movements made by the controls for the grasping task were recorded by an OPTOTRAK 3020 recording system. For the manual estimation task, the experimenter used a marker to indicate dots on the index finger and thumb of the right hand of the controls for a basis for measurement using a precision caliper.

Initial Assessment

The targets for size and distance estimation in the Initial Assessment were five black filled circles (3.8, 5.3, 6.9, 8.4, 10.3 cm). For size estimation, a marker was used to indicate dots on the index finger and thumb of the right hand of all participants, including M.C., for a basis for measurement using precision calipers.

Procedure

Experiment 1

In the first of two test sessions, M.C. (43 years of age at the time of testing) reached out to pick up target blocks across their sagittal (near-far) dimension (*target size*). In the second test session, held two days after the first, M.C. provided manual estimations of the target size by matching it to size of the aperture made between the tips of her index finger and thumb.

For both test sessions, M.C. sat comfortably at a table with a top surface painted matte black. Throughout the experiment, M.C. placed her chin in the chin rest and was positioned at the table such that her midline was aligned with a button that was located on the surface of the table. The button was positioned 10 cm from the table edge closest to her and served as the starting location for her right hand. M.C. was asked to pinch the tips of her thumb and index finger together and to use them to depress the start button before and after she performed the designated task on each trial. M.C.'s kept her left hand on her lap below the table.

Three IREDs were attached to M.C.'s hand and, for the grasping task, she was provided the PLATO goggles to wear. M.C. was informed before the outset of the experiment that the goggles would clear at the start of the trial. She was asked to use this event as an imperative to locate the target visually and reach out to pick up the target across its near-far dimension. The room lighting conditions were normal. Before the start of a given trial, an experimenter placed onto the table one of the four targets at one of three possible distances (8, 16, or 24 cm) from the start button along M.C.'s mid-sagittal plane.

For the first set of trials administered in the grasping task, viewing distance was not varied; the four targets were centered at the 16-cm location such that their near-far dimension corresponded to their lengths (5, 5.5, 6.2, and 7.1-cm *target sizes*). In total, each target was presented eight times across 32 trials. One additional trial was included so that the trial order could be constructed with a *null* lag-1 autocorrelation with respect to target size. Thus, any observed scaling of M.C.'s grip aperture to target size could not be attributed to an artifact of a compensatory strategy by which her grip aperture is based on the felt size of the target grasped on the immediately preceding trial, because a target on any given trial was preceded by any one of the other targets (or none at all for the first trial) with equal probability (see Table S1 for the results of these trial sets).

We varied target distance in a crucial second and fourth set of grasping trials. In each one of these two sets of trials, the 12 unique combinations of four target and three distances were presented six times each for a total of 72 trials per set (144 trials total across the two sets). Note that these second and fourth sets of trials were introduced immediately after their respective preceding trial sets (the first and third, sets, respectively) and, therefore, these sets did not require an additional trial to construct a null lag-1 autocorrelated trial order for target size.

The additional set of trials for the crucial case in which viewpoint distance was manipulated was administered for two reasons. First, additional trials would help compensate for the possibility that M.C.'s grasps would be noisier than the controls. Second, should M.C.'s grasps scale to target size in the first set of these crucial trials, a second test would offer an opportunity to replicate. Following the first two sets of trials, M.C. was invited to take a break for several minutes. After this break, a third set of trials was administered, in which we tested a different range of target sizes by presenting the targets such that, for all except the square shape whose width and length are necessarily identical, their near-far dimension was aligned with their widths (3.5, 5, 5.5, and 6.2-cm *target sizes*). The four targets were presented at a fixed 16-cm distance eight times each. As was done for the first set of trials, one additional trial was included to construct a null lag-1 autocorrelation with respect to target size. Thus, the total number of trials was 33, akin the first set of trials.

For the manual estimation task, M.C. was asked to keep her eyes closed in-between trials. M.C. did not wear goggles, because it was not known how long it would take her to estimate target size nor was it known how long she would require a view of both her hand and the target. At the outset of each trial, the experimenter asked M.C. to open her eyes, which served as her cue to provide a manual estimate of the target's size. She was asked to do this without reaching toward the target and to keep the tips of her thumb and index finger on the surface of the table for stability. The experimenter emphasized she could take as long as she felt she needed to faithfully indicate the target's size. When M.C. was satisfied with her estimate, the experimenter initiated data collection (see Quantification and Analysis Details).

The order of the conditions in the manual estimation test session was the same as the order used in the grasp test session, except that only one block of trials in which both target size and distance were manipulated was administered. Only one block was administered for three reasons: first, a prior investigation conducted ~4 years prior had shown that M.C.'s estimates did not scale with target size when presented at a fixed distance; second, in an initial assessment using target circles presented outside peripersonal space, M.C.'s estimates did not scale with the real size of target discs (see Table S2); and third, test session time constraints required a prioritization of experimental conditions.

The control participants were tested using the same targets, distances, tasks, and designs that were administered to M.C. with two exceptions: first, they did not require the additional set of crucial trials in which both target size and distance were manipulated; and second, both grasping and manual estimation tasks occurred in the same test session. The results of the sets of grasping and manual estimation trials in which target position remained the same are reported in Table S1.

Experiment 2

In an additional test session, conducted approximately two years after the first, M.C. (45 years of age at the time of testing) grasped or estimated the size of four glow-in-the-dark Styrofoam spheres (*targets*) with diameters (*target sizes*) of 3.8, 5, 6.3, and 7.6 cm. M.C. sat comfortably in front of a table with her chin in a chin rest for both tasks. The targets were presented at M.C.'s eye level at different viewpoint distances (16, 21, 26.5, and 32 cm). Crucially, these viewpoint distances were selected such that when the spheres were presented at these distances in order of their increasing diameter, their retinal image-sizes were matched to subtend ~13.5 degrees of visual angle. Furthermore, the targets were photo charged before each trial so that they would glow in the dark with the room lights turned off. In each set of trials, the targets were presented four times each in a pseudorandom order for a total of 20 trials per set. It was not known how long M.C. would take to perform the task, and therefore data collection was manually initiated and terminated each trial. M.C. did not wear goggles for any of the tasks, but she was asked to open her eyes at the outset of the trial and to close them again upon completion of the trial. M.C. was asked to choose a comfortable starting position on the table for her right hand. She chose a position to the right of her midline. M.C.'s left hand lay on her lap below the table.

The first two sets of trials were designed to test the influence of retinal image size on M.C.'s estimates. Thus, in the first set of trials, M.C. estimated the sizes of the spheres when each one was presented at the far (32 cm) distance in a pseudorandom order. In the second set of manual estimation trials, M.C. estimated the sizes of the spheres when each was presented at the near (16 cm) distance. In the third set of trials, M.C. reached out with her right hand to grasp the targets, which were positioned so that their retinal image sizes were matched. In the fourth set of trials, the targets were positioned again so that their retinal images sizes were matched. In this set of trials, M.C. used her left index finger to touch the side of the sphere, before providing an estimate of the sphere's size with her right hand. She was asked to keep the tip of her left index finger on the side of the object while providing a manual estimate of the target's size with her right hand. M.C. did not wear a glow-in-the-dark glove on her left hand. She was instructed to take as long as she preferred to perform the manual estimation tasks and to verbally indicate when she was satisfied with her estimate.

Touching the sphere with the index finger of the left hand was designed to provide M.C. both kinesthetic and proprioceptive sources of information about the target's distance. This was done in order to approximate the availability of these sources of information when she reached out to grasp the targets. The concern was to guard against the possibility that reaching for the target and/or touching the target would provide a kinesthetic and/or proprioceptive cue to target distance that could be exploited in a strategic way to inform grasp aperture on-the-fly. If such sources could be exploited in this way, then M.C. should be able to provide reliable estimates of target size.

The controls were tested in the same task order and condition order in which M.C. had been tested. To determine if touching the targets with the left index finger could improve sensitivity to target size, however, we administered an additional set of manual estimation trials in which the retinal image sizes of the targets were matched but the participants were not permitted to touch the targets with their left hand. In the control participants this did result in a small but significant improvement in performance ($\overline{b}$ = 0.22, $t(7)$ = 5.07, $p < 0.002$).

To minimize testing time for the controls, all of whom were taking time off of work to participate, each target was presented three times in a pseudorandom order for a total of 12 trials for the grasping task. For the manual estimations, each target was presented twice in a pseudorandom order for a total of 10 trials for each of the four trial sets. Both the grasping and manual estimation tasks were performed in a darkened room in which all sources of light were blocked out. The room lights were turned on between trials in order to recharge the phospholuminescent targets and the glove. The results of the set of manual estimation trials in which the target position remained the same are reported in Table S1.

Initial Assessment

In an initial session in which we explored M.C.'s perceptual deficits, we asked M.C. to estimate the diameters (*sizes*) of five black filled circles (3.8, 5.3, 6.9, 8.4, 10.3 cm) presented on white plastic backgrounds face-on at her eye-level and at varying viewing distances outside her reachable space (53, 74, 97, 118, 144.5 cm) such that their retinal image sizes were either matched or varied systematically. Throughout testing, M.C. sat comfortably at a table with her chin in a chin rest and kept her eyes closed between trials. Her left hand rested on her lap below the table throughout testing. While M.C.'s eyes were closed, the experimenter positioned one of the five circles at one of the five viewing distances. After this brief pre-trial setup phase, the experimenter asked M.C. to open her eyes after which she localized the target and estimated its diameter (i.e., *target size*). M.C. announced her satisfaction with her estimate, after which the experimenter used a precision caliper to measure the distance between colored marks placed on the ends of M.C.'s index finger and thumb. The room lighting conditions were normal.

In the first set of trials each circle was presented at a unique distance such that their retinal image sizes were equivalent and subtended ~4° of visual angle across trials. The five unique combinations of size and distance were presented four times each in a pseudorandom order for a total of 20 trials. Three additional sets of trials were administered to test the influence of varied retinal image size on her manual estimates. In the second set of trials, the largest circle was presented at each of the five viewing distances four times each in pseudorandom order (20 trials total). In a third block of trials, the five circles were presented four times each in pseudorandom order at the closest viewing distance (20 trials total). In a final set of trials, the five circles were presented, one per trial, four times each in pseudorandom order at the farthest viewing distance (20 trials total). The room lighting conditions were typical.

We also tested M.C.'s judgments about target viewpoint distance. Thus, the trials and sets of trials were repeated in the same order as before, but rather than providing a manual estimate, M.C. provided a verbal estimate of the distance at which the circle was presented using an integer rating scale ranging from 1 to 10.

QUANTIFICATION AND STATISTICAL DETAILS

Data Recording

Experiment 1

Finger and wrist movements for the grasping and manual estimation tasks were recorded by an OPTOTRAK 3020 that sampled the positions of three infrared emitting diodes (IREDs) attached to M.C.'s right index finger, thumb, and wrist at 100 Hz. The resultant data were resampled offline to 200 Hz to match the controls, although resampling made no material difference to M.C.'s results (or our findings). It was not known how long M.C. would take to complete her grasping movements, and so data collection was set to 6 s and was initiated at the start of the trial when the goggles cleared. The manual estimation task was designed so that M.C.'s manual estimates would be stable at the start of data collection (see Procedure), and, therefore, only a brief (1 s) recording duration was required. For the controls, both the grasping and manual estimation tasks were sampled for 3 s at 200 Hz.

Experiment 2

M.C.'s finger and wrist movements for the grasping and manual estimation tasks were recorded by the TRAKSTAR at 80 Hz. The finger and wrist movements of the controls for the grasping task were recorded by the OPTOTRAK 3020 at 200 Hz for 3 s. For the manual estimation task for the controls, precision calipers were used to measure the manual estimate aperture when the lights were turned on after the goggles returned to their translucent state.

Initial Assessment

For both M.C. and controls, the experimenter used a precision caliper to measure the distance between colored marks placed on the ends of the index finger and thumb.

Data Processing and Statistical Analysis

Experiment 1

The positional data were low-pass Butterworth filtered at 20 Hz. At each sample frame of each trial, *grip aperture* was computed as the 3D distance between the IREDs positioned at the tips of the index finger and thumb; grip aperture velocity was computed as the inter-sample change in the aperture over the time from one sample frame to the next; and the 3D speed of each marker was computed as the 3D displacement over the time from one sample frame to the next.

For the grasps, the principal measure on each trial was peak grip aperture (PGA), which was defined as the largest grip aperture during the forward reach component of the grasp response, prior to finger-contact with the object. To isolate the forward reach component, the start of the reach was operationally defined as the first sample frame in which the velocity of the thumb or index finger IRED exceeded a threshold of 5 cm/s for 150 ms; The search for the end of the forward reach began on the sample frame 100-150 ms after the start of the reach and was defined as the first sample frame in which the velocity of the thumb or index finger IREDs fell below 5 cm/s. The peak grip aperture closing velocity was defined as the minimum grip aperture velocity between the PGA and the end of the forward reach. The stable phase of the grasp, when the hand is holding the object, was defined as the first sample frame in which the grip aperture velocity fell within ± 1 cm/s for a minimum of 100 ms. The peak hand velocity (PHV) tends to occur before the hand starts to close down on the object. PHV was defined as the maximum speed achieved by the wrist IRED during the forward reach. The wrist IRED was used to define the onset of the reach to compute the time to achieve PGA as well as the time to achieve a stable grip on the object.

Each trial was visually screened for instances in which the landmarks were noticeably erroneous. For one of the ten control participants, the velocity threshold for terminating the forward movement was raised for 11 trials. Of the 210 grasping trials administered to M.C., 16 (7.6%) were removed due to missing data that overlapped with the PGA. One control participant noticeably fumbled grasping the target on three trials and those three trials were rejected. For the illustration of M.C.'s grip aperture profile in the bottom right panel of Figure 2 in the main text, her grip aperture was extracted beginning at the start of the wrist movement and terminating at the point at which a stable grasp of the object was achieved. This window was interpolated to 100 time points for each trial of trial-sets two and four (the sets in which target distance varied). The resultant standardized profiles were grouped according to target size and averaged across all distances. Missing data, while rare, tended to occur towards the beginning of the reach and were interpolated using linear and cubic-spline fits. The trials in which peak grip aperture were rejected for the analysis were also rejected for the illustration. No additional analysis was performed on these profiles.

For the controls, the beginning of the manual estimation movement was defined as the first sample frame in which the IRED of the index finger or thumb exceeded 2 cm/s. Note that the threshold is lower (than the threshold used for grasps) because the hand remains stationary and the fingers do not move as quickly (or as ballistically) as the hand does when reaching out to pick up an object. The manual estimate (ME) of target size was defined as the aperture between the index finger and thumb during the first frame of the stable phase of the finger-opening response did not achieve an aperture velocity of more than ± 0.5 cm/s for 250 ms following the beginning of the movement. On occasion, the threshold and/or duration criterion was marginally adjusted to ensure that the plateau phase, under the assumption that participants were most satisfied with their estimate following subtle fine-tuning adjustments to their manual estimate aperture.

M.C.'s manual estimate aperture was steady at the time of recording. Nevertheless, on 12 of 138 trials, M.C. closed her fingers before data collection had finished. This ruled-out computing a straight-forward average of the manual estimate aperture across all sample frames within a given trial. Thus, we isolated a window within each trial during the plateau phase of M.C.'s response by selecting a sample frame as starting point for a search to find the first and last sample frame in which the criterion described above

was satisfied. The resultant temporal window of stable grip aperture was averaged to derive M.C.'s ME. This window was also used to standardize M.C.'s MEs to 100 interpolated points for each trial to construct bottom left panel of Figure 2 in the main text. The interpolated MEs were grouped by target size and averaged across all distances. The bottom left panel of Figure 2 shows the interpolated manual estimates averaged as a function of target size, and shows, among other things, that the manual estimate aperture isolated across the temporal window defined above is stable. No additional anlaysis was performed on these profiles. One trial of 138 (.7%) administered to M.C. was removed due to too many missing data points.

Linear regression was used to compute the unstandardized regression coefficients, *b*, corresponding to the slope of the linear functions relating PGA and ME to target size for each set of trials and for each participant. Target distance was included in the regression analysis for trial sets in which both target size and distance were varied independently. Note that these slopes reflect the average increment in the response (PGA or ME) per incremental increase in target size or, where applicable, target distance. As such, the coefficients track unique sensitivity to target size or, where applicable, target distance. The sensitivity of PGA to target size is sometimes referred to as *grip scaling*, which is the term adopted here. Furthermore, the manual estimates are considered measures of *size perception*. Two-tailed t tests were performed on M.C.'s slopes and on the mean of the control slopes to test for significant differences from zero (i.e., no relationship) and, where appropriate, differences from one (i.e., unitary relationship). One-tailed independent-samples t tests were used to test for a neurological deficit (i.e., whether or not M.C. performed worse than the controls) and two-tailed independent-samples t tests for differential (i.e., across tasks) dissociation [50–54]. Alpha was set to 0.05 for each test.

Experiment 2

The data were processed and analyzed as described in Experiment 1 with minor or no variation and so the techniques are only briefly mentioned here. For caliper-based measurements of ME, the mean MEs for each target size were computed for each set of trials, and for each participant. M.C.'s movements were collected by the TRAKSTAR and were resampled to 200 Hz to match the sample rate for the controls. No material differences in her results were observed between the two sample rates. For one of the controls, two grasp trials were erroneously administered and were therefore rejected. Furthermore, one trial failed to record for a second control participant. For the illustration of M.C.'s grip aperture profile in Figure 3, M.C.'s grip aperture from movement start to the point at which a stable grip was achieved was interpolated across 100 points from movement start to the point at which a stable grip on the target object was achieved. This was done for each trial separately. Due to the small number of contributing trials (five) for each target size, the interpolated grip aperture was smoothed. The resultant profiles were grouped according to target size and then averaged within each of the 100 time points. No additional analysis was performed on these profiles.

Initial Assessment

The mean manual estimate (ME) for each combination of target size and viewing distance was computed for each participant. The slopes of the linear function relating the mean ME to target size in each trial set were computed separately for each participant using linear regression.

The mean verbal distance judgments for each target were computed for each participant. The slopes of the linear function relating the mean distance judgment to target distance were computed for each participant using linear regression. For each condition, one-tailed independent-samples t tests were used to test for neurological deficit with an alpha level set to 0.05 for each test (see Table S2 for details).

Update

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Correction

Grip Constancy but Not Perceptual Size Constancy Survives Lesions of Early Visual Cortex

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In the original Figure 3, the bottom two images were mislabeled as "7.1 cm 6.2 cm 5.5 cm 5 cm." They should read as follows: 7.6 cm 6.3 cm 5.0 cm 3.8 cm, respectively. This has been corrected online and appears below. The authors apologize for any confusion the error may have caused.

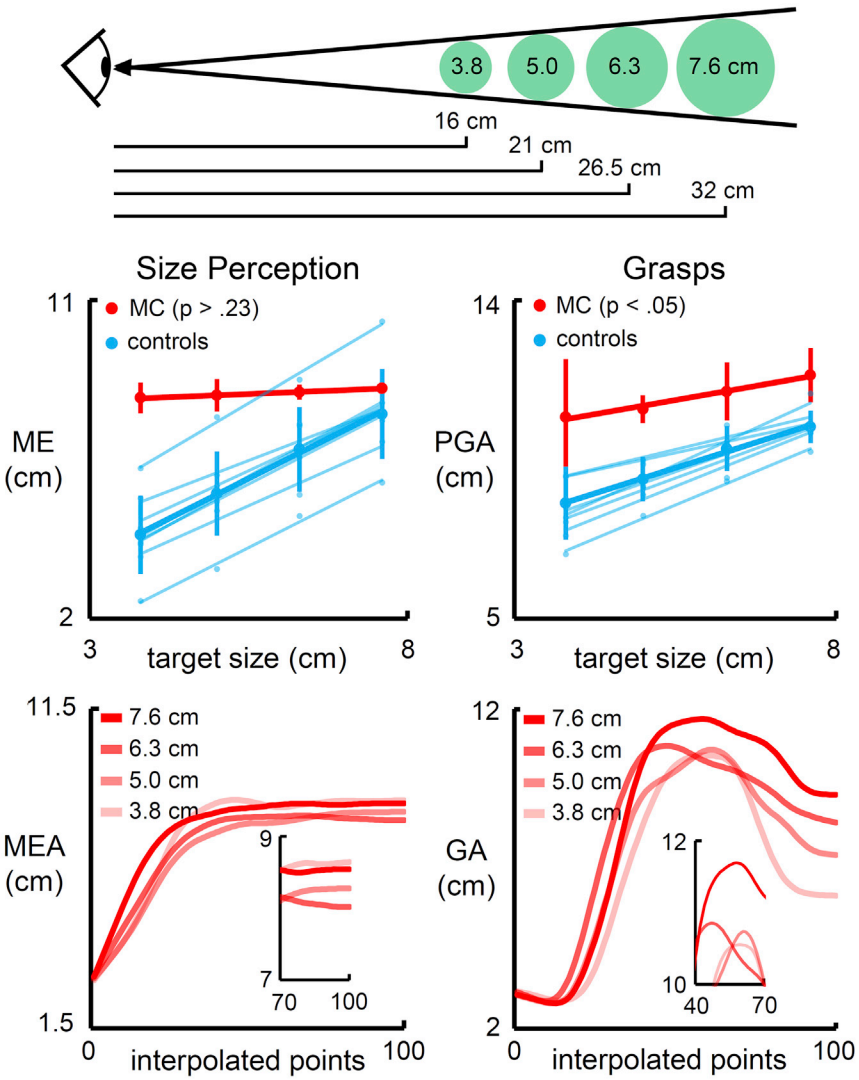

Figure 3. Main Results from Experiment 2 (corrected)

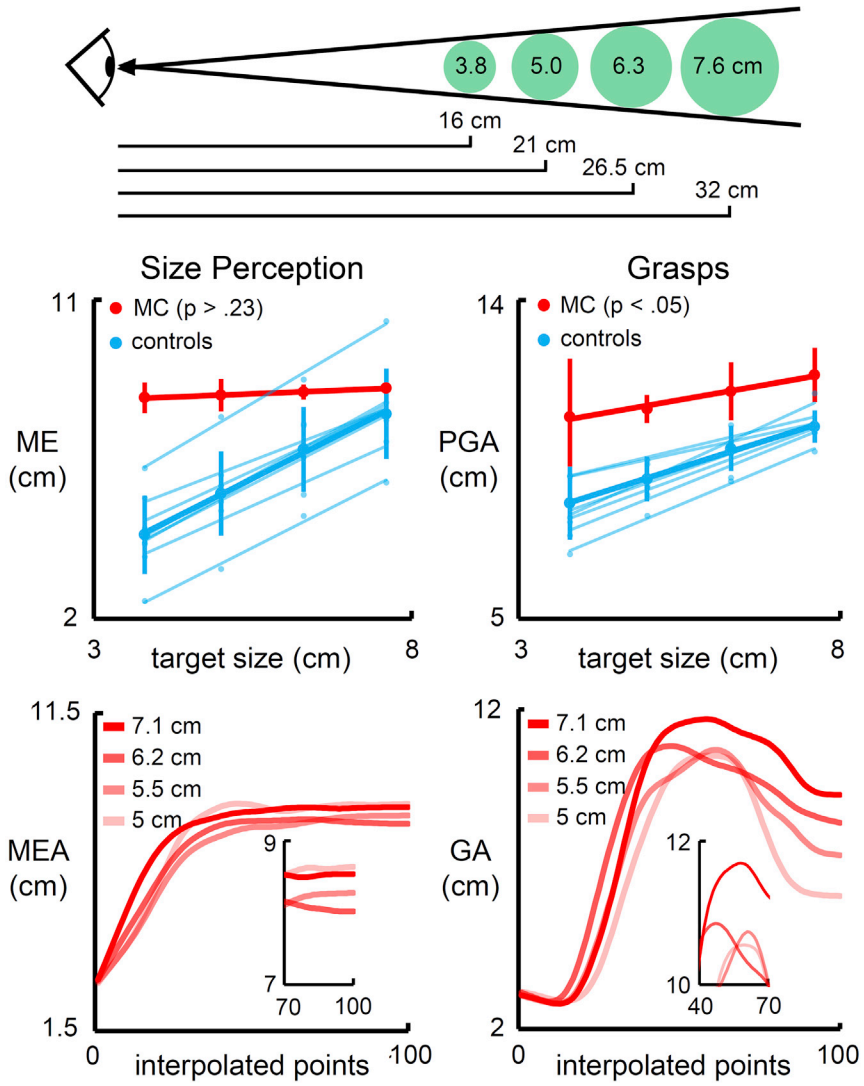

Figure 3. Main Results from Experiment 2 (original)