Proprioceptive distance cues restore perfect size constancy in grasping but not perception when vision is limited

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Summary

Our brain integrates information from multiple modalities in the control of behavior. When information from one sensory source is compromised, information from another source can compensate for the loss. What is not clear is whether the nature of this multisensory integration and the re-weighting of different sources of sensory information is the same across different control systems. Here, we investigated whether proprioceptive distance information (position sense of body parts) can compensate for the loss of visual distance cues that support size constancy in perception (mediated by the ventral visual stream) [1, 2] vs. size constancy in grasping (mediated by the dorsal visual stream) [3-6], in which the real-world size of an object is computed despite changes in viewing distance. We found that there was perfect size constancy in both perception and grasping in a full-viewing condition (lights on, binocular viewing) and that size constancy in both tasks was dramatically disrupted in the restricted-viewing condition (lights off, monocular viewing of the same but luminescent object through a 1-mm pinhole). Importantly, in the restricted-viewing condition, proprioceptive cues about viewing distance originating from the non-grasping limb (Experiment 1) or the inclination of torso and/or the elbow angle of grasping limb (Experiment 2) compensated for the loss of visual distance cues to enable a complete restoration of size constancy in grasping but only a modest improvement of size constancy in perception. This suggests that the weighting of different sources of sensory information varies as a function of the control system being used.

Results and Discussion

Experiment 1: Proprioceptive distance cues originating from the non-grasping limb

We first measured size constancy (**Figures 1A and 1B**) in perception and in grasping in a full-viewing condition (**Figures 1C and 1D**) in which there were ample visual cues to object distance and in a restricted-viewing condition (**Figures 1C and 1D**) in which visual cues to distance were extremely limited. The target sphere was resting on top of a pedestal. The sphere but not the pedestal varied in diameter from trial to trial. The spheres were painted with luminescent paint so that they were visible in the dark. No proprioceptive cues to object distance were available (full-noPro or restricted-noPro).

Participants were asked to indicate the perceived size of the target sphere manually by opening their thumb and index finger a matching amount or to reach out and grasp the target sphere in ‘natural manner’ with their thumb and index finger. Although both the manual estimation and the grasping tasks involved the same effectors and similar movements, they are mediated by different control systems. Grasping is a visually-guided action that is mediated by visuomotor systems in the dorsal visual stream. The manual estimation task is essentially a magnitude estimation measure, which provides a readout of the visually perceived size of an object – and is mediated by the visual perceptual system in the ventral visual stream [7]. These two tasks have been used in many previous studies to reveal the double dissociation between perception and action in patients [8, 9] and in healthy participants [10-13]. The manual estimate of perceived size, rather than a two–alternative-forced choice task or a match-to-sample task, has typically been used to ensure that the same effectors are involved in both perceptual report and grasping [14]. The manual estimate (ME) was used as a perceptual report of the target's size on the perceptual trials, and the maximum grip aperture (MGA), which was achieved well before contact was made with the target, was used as a measure of grip scaling on the grasping trials (**Figure S1**). In both tasks, participants were unable to see their hand or the target during the execution of the movement, and therefore no online-adjustment based on visual feedback was possible (i.e., MGAs depended only on the programming of grasping). On manual estimation trials, the experimenter placed the sphere between participant's thumb and index finger at the end of each trial so that participants had the same haptic feedback about the size of the target on manual estimation trials as they did on grasping trials.

Consistent with previous studies [3, 6, 15], we found that, in the full-viewing condition, participants showed perfect size constancy in both the perceptual (manual estimation) task and the grasping task (main effect of distance, both F (1,13) < 2.11, $p > 0.17$; **Figure 2A, full-noPro**). This suggests that vision is sufficient to support perfect size constancy in both perception and grasping. In the restricted-viewing condition, size constancy in both perceptual and grasping tasks was largely disrupted (main effect of distance, both $F(1,13) > 46.80$, $p < 0.01$; **Figure 2A, restricted-noPro**) although both MEs and MGAs still scaled with the size of the object (main effect of object size, both $F(1,13) > 52.88$; $p < 0.01$), suggesting that size constancy in both tasks relies on distance information.

Proprioception restored perfect size constancy in grasping but not in perception when vision was limited

To investigate if proprioceptive information about object distance can compensate for the loss of visual distance cues and thus restore size constancy in perception or in grasping, we moved participants' left hand to the position of the pedestal before each trial and asked them to hold the pedestal throughout that trial while estimating the size of the sphere or grasping it with their right hand (withPro, **Figure 1C)**. Thus, the left hand could provide static proprioceptive information about the distance of the sphere which was positioned on top of the pedestal. The same pedestal was used throughout the experiment so that participants could not predict the size of the objects from its diameter. Note that the right hand could provide proprioceptive distance feedback on grasping trials after contact was made with the sphere (**Figure S1**) but because the distance (and size) of the sphere varied from trial to trial, that information could not be used for the programming of the grasping movement on the next trial.

On restricted-viewing trials, the availability of reliable proprioceptive distance cues [16, 17] resulted in only a modest improvement in size constancy on manual estimation trials (interaction between proprioceptive condition (withPro vs. noPro) and distance: F (1, 13) = 6.30; $p = 0.03$, **Figure 2A**). Nevertheless, this improvement was far from perfect and participants continued to give larger manual estimations for closer objects (main effect of Distance: F (1, 13) = 49.89; $p < 0.01$; **Figure 2A, restricted-withPro**), suggesting that proprioceptive cues are not sufficient to fully restore perceptual size constancy when vision is restricted.

In striking contrast to what happened with manual estimation, size constancy for grasping was completely restored in the restricted-viewing condition when participants held the pedestal (interaction between proprioceptive condition and distance condition: (F (1, 13) = 22.79; $p <$

0.01; **Figure 2A, restricted-withPro**), and there was no longer an effect of distance on grip aperture; $F(1, 13) = 2.32$; $p = 0.15$). In other words, the proprioceptive cues from the limb holding the pedestal under the sphere were sufficient to scale the grasping hand to the physical size of the object regardless of viewing distance. Further analysis showed that size constancy was restored immediately after proprioceptive distance cues became available during grasping **(Figure S2**). This suggests that the difference in performance between grasping and perception cannot be attributed to the possibility that participants learned more quickly to incorporate proprioceptive cues into the computation of size constancy for grasping than they did for perceptual judgements.

Comparison between the contribution of proprioception to size constancy in perception and size constancy in grasping when vision was limited

To measure the contribution of proprioception directly, we first calculated a size constancy disruption index (DI) for each task in each condition, which was defined as the difference in ME or MGA between the near and far distance conditions averaged across object sizes. To compare the DIs between the two tasks, we had taken into account the fact that the slopes for MGAs as a function of object size are typically shallower than those for MEs. In other words, a "1 mm" difference in MGA is actually a "larger" difference than a "1 mm" difference in ME. Thus, DI was corrected for the difference in the slopes [18].

Figure 2B shows the corrected DI for each task. The DI in grasping was smaller than the DI in estimation in the restricted-noPro condition ($t(13) = 3.10$, $p < 0.01$). But what is more important is that the reduction in the DI by the availability of proprioceptive distance cues (restricted-withPro vs. restricted-noPro) was larger for grasping than for estimation. This is reflected in **Figure 2C** in which we defined the contribution of proprioception in the restricted viewing condition as the difference in DI between the restricted-noPro and the restricted-withPro conditions. The contribution of proprioception was significant for both the estimation and the grasping tasks (both $t(13) > 3.75$, $p < 0.01$), but was significantly greater for grasping than for manual estimations ($t(13) = 2.69$, $p = 0.02$).

We also examined the contribution of vision to size constancy in perception and action when no proprioceptive distance information was available. The contribution of vision was defined as the difference in DI between the full-noPro and the restricted-noPro conditions. We found that vision made a large contribution to both tasks (both $t(13) > 7.52$, $p < 0.001$; **Figure 2D**) and there was no significant difference between the contribution of vision to these two tasks ($t(1, 13) = 0.61$, $p = 0.55$).

Overall, these results suggest that perceptual size constancy depends mainly on visual distance cues, and proprioceptive cues from holding the pedestal cannot fully replace the role of vision in the computation of size constancy for perception. Size constancy in grasping also depends on visual distance cues, but unlike perceptual size constancy, proprioceptive distance cues can completely restore size constancy for grasping when vision is limited.

Experiment 2: Proprioceptive distance cues originating from the inclination of torso and/or the elbow angle of grasping limb

One might argue that the haptic distance feedback on grasping trials from the right hand, unavailable during estimation trials, may play a role in the restoration of size constancy in grasping. This is unlikely, however. First, when participants held the pedestal (i.e., withPro), the proprioceptive information from the left hand could already provide reliable information about object distance [16, 17, 19] at the beginning of each trial before the target sphere was visible. Second, as addressed above, distance feedback on grasping trials was only available at the "contact" stage, which always occurred well after MGA was achieved (**Figure S1**), and therefore could not influence MGA on the current trial. Finally, the distance feedback on the current trial (n) could not provide distance information for the next trial (n+1) because the distance of the target sphere varied randomly from trial to trial.

Nevertheless, to rule out any potential contribution of distance feedback on grasping trials, we conducted Experiment 2 in which the position of the target was fixed across viewing distance conditions, and was always at the same distance as the start position of the right hand for both grasping and manual estimation tasks (**Figure 1D**). Therefore, when participants grasped objects, they were always moving their hand straight to the left, and as a result, the grasping hand could not provide any additional distance information. To manipulate the viewing distance, participants were required to lean forward or backward (**Figure 1D**), so that viewing distance information could be derived from the proprioceptive information from the angle of inclination of their torso and/or the angle of the right elbow. The same full- and restricted-viewing conditions were tested (full-withPro and restricted-withPro).

Unsurprisingly, we found that, in the full-viewing condition (with proprioception), there was perfect size constancy for both tasks (main effect of distance, both F (1, 17) < 0.39, p > 0.54; **Figure 3A**). Importantly, and consistent with Experiment 1, in the restricted-viewing condition, only size constancy in grasping was completely restored (main effect of distance, F (1, 17) = 0.58; p = 0.46) by the proprioceptive cues from their torso and/or right elbow. In the manual estimation task, participants still perceived objects as larger when they were closer (main effect of distance, F (1, 17) = 8.40; p = 0.01). These findings suggest that the proprioceptive distance cues originating from the torso and/or right limb, like those from the non-grasping (left) limb in Experiment 1, enable perfect size constancy in grasping but not in perception. In addition, because the position of the target sphere and the position of the start position of the grasping hand did not change with viewing distance, the results cannot be attributed to the additional distance feedback available on grasping trials.

As in Experiment 1, we calculated the contribution of vision to both tasks. The contribution of vision was significant for perceptual report (t(17) = 2.77, p = 0.01; **Figure 3C**), but close to 0 for grasping (t(17) = 0.18, p = 0.86) when proprioception was available. The contribution of vision to perception was also marginally larger for estimation than it was for grasping (t(17) = 2.07, p = 0.05). These results converge on those from Experiment 1 and show that when proprioceptive distance cues are available, size constancy in perception continues to rely on visual distance cues, while size constancy in grasping no longer needs visual cues.

One reason why proprioceptive inputs are not as readily incorporated into the perceptual experience of size is that, in everyday life, the need for accurate perception of size extends to objects well beyond peripersonal space, where proprioception can play no role and visual cues to distance are essential. In contrast, the need to compute the real size of goal objects for grasping, which always takes place in peripersonal space, makes it likely that proprioceptive information would make a significant contribution.

The observation that proprioceptive signals to distance contribute more to size constancy in grasping than to size constancy in perception is probably related to differences in the neural circuits mediating the two tasks. The neural circuits mediating grasping, which include the anterior intraparietal sulcus (AIP) and premotor cortex [20, 21], not only receive inputs from the visual cortex but are also densely interconnected with the somatosensory cortex. The premotor cortex has been shown to code limb position on the basis of both proprioceptive and visual signals [22]. Moreover, monkey neurophysiology suggests that AIP processes size, shape, and orientation information about the goal object for grasping [23]. All of these properties make the premotor-parietal circuitry mediating grasping well-poised for combining proprioceptive and visual cues. In contrast, there is no clear evidence for strong direct connections between the premotor cortex and visual areas in the occipito-temporal cortex nor is there any evidence for bimodal neurons coding both visual and proprioceptive information in this region. Nevertheless, there was some improvement in perceptual size constancy when proprioceptive distance information was available suggesting that the computations carried out by ventral-stream visual structures can be modulated by proprioceptive input.

We found that the role of visual distance cues in the computation of size constancy in grasping can be fully compensated by proprioceptive distance cues; but this does not mean that proprioceptive distance cues can replace the role of visual cues in all aspects. For example, the MGAs in general were still larger in the restricted-withPro condition than they were in the full-noPro condition probably because there was more uncertainty when vision was limited.

Although proprioception did not restore perfect size constancy in perception, it did result in a moderate improvement, which is consistent with earlier work showing size constancy in perception was enhanced by an observer’s movement [24], and previous work showing perceived size was influenced by the position of the hand on which the stimulus was projected [25, 26]. Gosselin-Kessiby et al., [27, 28] showed that proprioceptive information from one hand can be used by the other hand in both an orientation-matching task and a letter-posting task, with a result that is consistent with our observation that proprioceptive information can be transferred between hands.

Previous studies examining the integration of visual and proprioceptive position information have shown that the weighting of each sensory cue depends on its reliability [29-31]. Our finding that, even though the same visual and proprioceptive distance cues were theoretically available for grasping and perceptual report, these cues were incorporated differently in the two tasks reveals an important caveat for current models of multisensory integration: the nature of the task and its underlying neural substrate have to be taken into account when determining the relative weighting of different cues.

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Author Contributions

J.C., I.S., and M.A.G. designed the study. J.C. collected and analyzed the data. J.C., I.S., and M.A.G. wrote the paper.

Declaration of Interests

The authors declare no competing interests.

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Figure legends

Figure 1. The setup and design of Experiments 1 and 2. A. To measure size constancy, the main experimental conditions included two object sizes and two viewing distances. Other sizes and distance conditions were also introduced to increase the unpredictability of size and distance (see STAR methods for details). **B**. Predicted patterns of results for Perfect and Disrupted size constancy (not actual data). If there is perfect size constancy, the perceived size or the grip aperture should be constant regardless of viewing distance (PERFECT). But if size constancy is disrupted due to the lack of distance information, people will tend to report the size of the sphere or scale their grasp according to the visual angle the object subtends on the retina. Thus, the perceived size or the grip aperture should be larger for the near than for the far viewing distance [3, 32] (DISRUPTED). **C**. The design and setup of Experiment 1 in which distance was manipulated by moving the sphere and pedestal together to different positions. Participants viewed the target sphere and the workspace in a full-viewing and a restricted-viewing condition while placing their left hand on the table or on their lap throughout the experiment so that no proprioceptive cues about the distance of the object were provided (full-noPro and restricted-noPro). Only the target sphere, which was glowing in the dark, was visible in the restricted-viewing condition. In the withPro condition, participant's left hand held the pedestal on which the target sphere was resting so that proprioceptive information about object distance was provided from the left hand. Full-withPro, rather than restricted-withPro, is shown for demonstration purposes. **D**. The design of Experiment 2 in which the viewing distance was manipulated by moving the chinrest and hence the observer's head to different positions. The positions of the target sphere, the start position of the grasping hand, and the participants' chair were fixed across viewing distance conditions. Therefore, the inclination of torso and/or the elbow angle of grasping limb provided proprioceptive information about the viewing distance of the object. Experiment 2 also included the full-viewing and restricted-viewing conditions but proprioceptive information was always available (full-withPro and restricted-withPro). In both experiments, the grasping distances were constant (distance from the start position of the hand to the target object) despite the changes in viewing distance, to minimize the influence of biomechanical constraints that would differ as a function of grasping distance [33-35]. In each distance condition, participants' head position was fixed with a chinrest as shown by the smiling persons in **C** and **D**.

Figure 2. Results from Experiment 1. A. The manual estimates (ME) of the perceived size and the maximum grip aperture (MGA) of the small and large objects at the near or far distances in three conditions: full-noPro, restricted-noPro and restricted-withPro. *** indicate that the main effect of distance was significant at $p < 0.001$. Error bars represent within-subjects 95% confidence intervals [36]. Note: differences in the slopes between near and far distances for ME in the restricted-noPro and restricted-withPro conditions probably arose because of a floor effect for the small object; that is, participants may have been reluctant to give estimates of the size of the sphere that were smaller than smallest sphere in the set. This account may also apply to the slopes of the MEs in **Figure 3**. **B**. Size constancy disruption index (DI) for each task corrected for the different slopes of MEs and MGAs as a function of object size to allow for comparisons across tasks. A positive index indicates disruption of size constancy, and thus ME or MGA of the same object was larger at the near than at the far viewing distance. An index of 0 indicates perfect size constancy (i.e., $ME_{near} = ME_{far}$ or $MGA_{near} = MGA_{far}$). **C**. Contribution of proprioceptive distance cues in the restricted-viewing condition, which was defined by the

difference in DI between the restricted-noPro and the restricted-withPro conditions. **D**. Contribution of vision in the noPro condition, which was defined by the difference in DI between the restricted-noPro and the full-noPro conditions. In **B**, **C** and **D**, ** or *** above a vertical bar indicate the value was significantly different from 0 at $p<0.01$ or $p<0.001$, respectively. * , **, or *** above a horizontal line indicate the difference between two bars was significantly different at $p < 0.05$ $p < 0.01$ or $p<0.001$ levels. Error bars in **B**, **C** and **D** represent 95% confidence intervals.

Figure 3. Results from Experiment 2. A. The manual estimates (MEs) and the maximum grip apertures (MGAs) of the small and large objects at the near or far distances in the full-withPro and restricted-withPro conditions. In this Experiment, participants always had proprioceptive distance cues from the inclination of the body and the angle of right elbow. ** indicate that the main effect of distance was significant at $p< 0.01$. Error bars represent within-subjects 95% confidence intervals [36]. **B**. Size constancy disruption index (DI) corrected for the different slopes of MEs and MGAs as a function of object size for each condition and each task. **C**. Contribution of vision. Note that unlike **Figure 2D**, here the contribution of vision was estimated when proprioceptive information was available (i.e., withPro condition) because proprioception was always provided in Experiment 2. In **B** and **C**, * or ** above a vertical bar indicate the value was significantly different from 0 at $p < 0.05$ or $p < 0.01$ level, respectively. Error bars in **B** and **C** represent 95% confidence intervals.

STAR★Methods

Key Resources Table

REAGENT or	SOURCE	IDENTIF
Software and Algorithms		
MATLAB R2014a	https://www.mathworks.com/products/matlab.html	N/A
Psychtoolbox 3	http://psychtoolbox.org/	N/A
IBM SPSS 24	https://www.ibm.com/analytics/us/en/technology/spss/	N/A

Contact for Reagent and Resource Sharing

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact Juan Chen (jchen737@uwo.ca).

Experimental Model and Subject Details

Participants

Fourteen participants (five males, nine females) took part in Experiment 1. Eighteen new participants (eight males, ten females) took part in Experiment 2. All were right-handed and had normal or corrected-to-normal vision with contact lenses. Their ages ranged between 18 and 25 years (M = 21.4, SD = 2.2). Participants gave informed consent and the experiments were approved by the University of Western Ontario Ethics Review Board.

Method Details

Stimuli, Apparatus

The stimuli in both experiments were white 3D-printed hollow spheres with diameters of 12.5 mm, 25 mm, 37.5 mm, 50 mm, and 62.5 mm. Only trials with the 25 mm and 50 mm spheres were included in the analysis. The other diameters were occasionally presented to increase the variability of the sizes so that participants kept adjusting their grip aperture according to the size of the sphere. The spheres were painted with white luminescent paint and therefore were visible in the dark (although they appeared to be slightly green). Each sphere rested on a small moveable black stand, which varied with the size of the sphere (30 mm height at most), to ensure that the center of all spheres was always along the same line of fixation. The stands were black and therefore participants could not see them in the dark. The stand itself was placed on top of a black pedestal (115 mm height; the same pedestal was used in all conditions) in Experiment 1 and directly on the table in Experiment 2 (**Figures 1C and 1D**).

In both experiments, participants wore liquid crystal goggles (PLATO goggles; Translucent Technologies, Toronto, ON, Canada) throughout the experiments to control for the visibility of the display and their moving hand. In the restricted-viewing condition (see below), they also wore a pair of glasses with a 1-mm hole in the center of the right lens. The PLATO goggles were worn over the pinhole glasses. A start button was located at 15 cm from the edge of the tabletop facing the participants. The 3D positions of the thumb and index finger of the right hand were tracked with an OPTOTRAK system (Northern Digital, Waterloo, ON, Canada) in which the infrared light emitting diodes (IREDs) were attached to the right corner of the thumbnail and the left corner of the index finger. The sample rate was 200 Hz. The OPTOTRAK was calibrated at the beginning of each testing session.

Procedure and design

In Experiment 1, participants were seated in front of a black table with their chin on a chinrest. The target spheres, together with the pedestal underneath it, were placed at 20 cm (i.e., near), 30 cm (i.e., middle) or 40 cm (i.e., far) of viewing distance (**Figure 1C**). The 30-cm viewing condition was used on only a small number of trials to make target position less predictable. Data from this condition were not used in the analysis. Previous studies [33-35] which manipulated the grasping distance (the distance from the start position of the grasping hand to the target) have observed that the grip aperture decreased or increased with the increase of grasping distance even in the full-viewing condition. To eliminate the confound of biomechanical effects, we kept grasping distance constant (the distance on the table was 17.3 cm) despite of changes in viewing distances.

At the beginning of each trial, the goggles were closed. Participants held down the start button with their thumb and index fingers pinched together. The experimenter placed the target sphere, together with the pedestal, at a specific location and then turned on the goggles. On grasping trials, they were required to reach out and pick up the target sphere in a ‘natural manner’ with their thumb and index finger as soon as the goggles were opened. The OPTOTRAK was triggered when the goggles were opened to record the movement for 3 s. On perceptual trials, participants were required to indicate as accurately as they could the *perceived* size of the target sphere by opening their thumb and index finger a matching amount (no time limitation). When participants signalled that they were satisfied with their manual estimate of the sphere's size, the experimenter triggered the OPTOTRAK to record the data for 800 ms. In both tasks the goggles closed as soon as the participants released the start button (i.e., open loop) so that they were not able to see the target or their hand during the execution of the grasping or estimation task, preventing any online adjustment based on visual feedback. In other words, the grip aperture (or manual estimate) was determined only by the programming of the grasp (or manual estimate) based on size and distance information that was available before the hand was moved. In addition, in the manual estimation task, the target sphere was placed in their right hand right after they had made their estimate so that they received the same haptic feedback about the size of the sphere as they did on grasping trials. Therefore, any difference in results between MEs and MGAs could not be attributed to the difference in haptic size feedback between the two tasks.

Participants performed the two tasks described above in either a full-viewing condition (light on, binocular viewing, **Figure 1C**) or a restricted-viewing condition (light off, monocular viewing through a 1-mm hole with their right eye [32]; only the glowing target sphere was visible in this condition). In the full-viewing condition, a number of distance cues to size constancy were available, including binocular disparity, pictorial cues, vergence, and accommodation. In the restricted-viewing condition, all binocular cues, most pictorial cues, and blur were removed; moreover, accommodation could not provide valid distance information in this condition [32]. In the full-viewing condition, the procedure of grasping and estimation trials was exactly the same as described above. In the restricted-viewing condition, in addition to the general procedure, the experimenter briefly turned on the light to position the target sphere for that trial, placed the sphere that had just been used into a light-filled box (covered with black cloth so that participants could not see it) to re-charge the luminescent paint on the sphere, and then turned off all lights (including the computer monitor) before turning on the goggles for the participant. Only the glowing target sphere was visible in the restricted-viewing condition.

To test whether or not proprioceptive information about object distance would restore size constancy in the restricted-viewing condition, at the beginning of each trial in Experiment 1, we moved participants' left hand to the position of the pedestal on which the sphere was resting, and asked them to hold the pedestal with that hand throughout the trial (the full-withPro condition is illustrated in **Figure 1C**. But note that in the restricted-withPro condition, only the glowing sphere was visible. In noPro conditions (full-noPro or restricted-noPro), participants' left hand was placed on the table or on their lap (i.e. not at the same position as the target sphere), and therefore could not provide information about the distance of the object) while they were performing the same estimation and grasping tasks.

To rule out any potential contribution of the distance feedback from the grasping hand on grasping trials and to test the contribution of another source of proprioceptive distance information, we conducted Experiment 2 in which the position of the target was fixed across viewing distance conditions, and was always at the same distance as the start position of the right hand for both the grasping and the manual estimation tasks (**Figure 1D**). Therefore, when participants grasped objects, they were always moving their hand straight to the left (grasping distance: 14.5 cm), orthogonal to the plane between the target object and the eyes, and as a result, grasping the object could not provide any additional distance information.

To manipulate viewing distance, the chinrest, which was fixed on the drawer of the table, was moved to different distances (20 cm or 40 cm) from the target object for both tasks. The chair where participants were seated was fixed in position so that participants had to lean forward (Near, **Figure 1D**) or backward (Far, **Figure 1D**) to ensure that their head was stabilized on the chinrest. As a result, viewing distance information could be derived from the proprioceptive information from the angle of inclination of their torso and/or the angle of the right elbow. Participants' left hand was placed on their lap. The same full- and restricted-viewing conditions (full-withPro and restricted-withPro) were tested. No "noPro" conditions were tested because Experiment 1 has already shown clearly that both size constancy in grasping and in estimation would be disrupted in the restricted viewing condition when no proprioception was available.

In Experiment 1, task (grasping or manual estimation and sensory conditions (full-noPro, restricted-noPro, and restricted-withPro) were manipulated in separate blocks. There were 6 blocks in total, one block for each combination of task and sensory condition. The order of the blocks was randomized across participants. In each block, distance and size were randomized on a trial-by-trial basis so they were unpredictable. Each of the four size-distance combinations (**Figure 1A**) included in the analysis had 8 repetitions. The remaining sizes were presented once at each of the 2 main distance conditions, and all five sizes was presented once at the middle distance.

In Experiment 2, task (grasping or manual estimation) and sensory condition (full-withPro and restricted-withPro) were manipulated in separate blocks. There were four blocks in total, one block for each combination of task and sensory condition. The order of the blocks was randomized across participants. Within each of these 4 blocks, the trials with the same viewing distance was blocked to avoid dizziness induced by frequent movements of their body and head. The order of the two viewing distances was randomized across participants. The size was also randomized but on a trial-by-trial basis. There were 8 repetitions for each of the 25-mm and 50-mm sizes, and 2 repetitions for the remaining 3 sizes in each distance block.

All participants were given about 30 min of training on both tasks before taking part in the real experiment. At the beginning of the restricted-viewing block, participants were asked to adjust the pinhole glasses to make sure that they could see the largest sphere in its entirety in darkness and to keep still throughout the block.

Quantification and statistical analysis

The distance between the two IREDs was calculated. The maximum grip aperture (MGA), which is a commonly used kinematic measure of how well participants scale their grip to the size of the object [5, 15, 21], was extracted for each grasping trial. The manual estimate (ME) was the first value of distance between the two fingers on each trial when participants informed the experimenter that they were indicating the perceived size of the sphere. The distance between the IREDs when participants' fingers were pinched together (**Figure S1**) was subtracted from the extracted MGAs or MEs. There was occasional signal loss during grasping or manual estimation because the target object might have occluded the IREDs or the IREDs were rotated so that they were out of view. Overall, 11.6% of grasping trials and 3.35% of estimation trials were discarded because of signal loss.

In the restricted-viewing condition, when participants were not holding the pedestal of the target sphere (i.e., restricted-noPro condition), they failed to reach the correct position on approximately half the trials (i.e., incorrect trials) due to the lack of distance information. Nonetheless, a preliminary analysis showed that the MGAs on incorrect trials were also scaled to object size at each distance (F (1, 13) = 22.52, p < 0.01), and whether or not the participant reached correctly towards the sphere did not have a significant main effect on MGAs (F (1, 13) = 0.31, p = 0.59). This is not surprising given that the size information of the object was evident (the target object was glowing in the dark) although the distance information was extremely limited. Indeed, it was reported that even a patient with complete loss of proprioceptive sensation in the fingers and wrist of both arms could scale her grip aperture to the size of the object [6] suggesting that people can scale their grip aperture to the size of the object no matter whether they could "feel" the object at the "contact" stage (**Figure S1**). For this reason, we included both correct and incorrect trials in the analysis.

Repeated-measures ANOVAs with size (25 mm vs. 50 mm) and distance (near vs. far) as main factors were conducted to test the main effect of distance separately for each combination of task and sensory condition (full-noPro, restricted-noPro and restricted-withPro in Experiment 1, and full-withPro and restricted-withPro in Experiment 2) to examine if there was perfect size constancy (i.e., main effect of distance is NOT significant; **Figure 1B**) or the size constancy was disrupted (i.e., main effect of distance is significant; **Figure 1B**).

The size constancy disruption index (i.e., DI) was defined as $(ME_{near} - ME_{far})_{\text{Averaged Across Sizes}}$ for manual estimation and $(PGA_{near} - PGA_{far})_{\text{Averaged Across Sizes}}$ for grasping. The disruption was then divided by the slope for PGA or ME as a function of physical size (the slope was averaged across distances) to correct the effect of slopes. The corrected DI was used to calculate the contribution of vision and proprioception to size constancy in each task. These calculations were performed individually and were then subjected to one-sample t-test (compare with 0) or paired t-tests for group analysis.

Data and software availability

Individual datasets are available upon request.

Legends for supplementary figures

Figure S1. **The profile of grip aperture for objects of different sizes (blue, small; red, large).** The thin lines show profiles of individual trials. The thick lines show the average of trials from the same size condition. At the beginning of grasping trials, the fingers were pinched together. The fingers then began to open, reaching maximum grip aperture (MGA), and then closed down on the object (Contact), lifted it up, and finally put it down (Release). Note that the MGA always occurs well before participants contact the target.

Figure S2. The results of the first 2 trials and last 2 trials in the restricted-noPro and restricted-withPro conditions for both the estimation (A) and grasping (B) tasks in Experiment 1. S means small and L means large. In both the restricted-noPro and restricted-withPro conditions for both tasks, the main effect of order (i.e., first 2 trial versus last 2 trials) was not significant (in all cases, F (1,13) < 0.32, p > 0.581). This suggests that differences in performance between grasping and manual estimation when proprioceptive cues were available cannot be attributed to differences in learning over the course of the experiment.