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Haptic Touch Modulates Size Adaptation Aftereffects on the Hand

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When we interact with objects using our hands, we derive their size through our skin. Prolonged exposure to an object leads to a perceptual size aftereffect: adapting to a larger/smaller object makes a subsequently perceived object to appear smaller/larger than its actual size. This phenomenon has been described as haptic as tactile sensations with kinesthetic feedback are involved. However, the exact role of different haptic components in generating this aftereffect remains largely underexplored. Here, we investigated how different aspects of haptic touch influence size perception. After adaptation to a large sphere with one hand and a small sphere with the other, participants touched two test spheres of equal or different sizes and judged which one felt larger. Similar haptic size adaption aftereffects were observed (a) when participants repeatedly grasped on and off the adapters, (b) when they simply continued to grasp the adapters without further hand movements, and (c) when the adapters were grasped without involving the fingers. All these conditions produced stronger aftereffects than a condition where the palms were simply resting on the adapter. Our findings suggest that the inclusion of grasp markedly increased the aftereffects, highlighting the pivotal role of haptic interactions in determining perceptual size adaptation.

Public Significance Statement

Prolonged touch of a small or large object can alter how we perceive objects' size that we subsequently touch. This effect allowed us to assess the underlying mechanisms of tactile size perception. We show that not only tactile size itself, but also the manner in which the ball is touched contributes to this effect. These results suggest that the way we interact with objects serve as cues for tactile size perception. Our findings provide insight into the fundamental processes underlying our ability to explore the world using our hands.

Keywords: tactile size, size adaptation aftereffects, haptic touch, hand, Uznadze illusion

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When we close our eyes and touch an object with one hand, we can easily estimate the size of that object (Gibson, 1962). We can also easily compare the size of objects between the hands and judge which of the two objects is larger. If the physical size of the two objects remains fixed, it is reasonable to assume that our perception of both sizes should always be consistent with physical inputs. However, previous studies have shown that object size perception depends on the perceptual history: prolonged tactile exposure to an object such as touching a sphere for a few seconds modulates the subsequent perception of a second object. More specifically, adaptation to a larger object makes a subsequent perceived object feel smaller than it is, and vice versa. This phenomenon is known as the haptic size adaptation aftereffect or the Uznadze illusion (Kappers & Bergmann Tiest, 2013, 2014; Maravita, 1997; Uznadze, 1966).

In addition to reflecting adaptative aspects of our perception, perceptual aftereffects are a useful behavioral tool for investigating underlying perceptual and neural processing. The existence of perceptual aftereffects in one stimulus dimension suggests the existence of perceptual and neural processes specific to that stimulus dimension in the brain, even at the level of the peripheral system, such as in the retina (Solomon & Kohn, 2014). By utilizing visual size adaptation aftereffects (Blakemore & Campbell, 1969; Blakemore & Sutton, 1969), studies investigating vision have demonstrated orientation selectivity (Blakemore & Nachmias, 1971), interocular transfer (Murch, 1972), and object's feature selectivity such as shape (Bruno et al., 2018) focusing on whether adaptation aftereffects transfer between different stimulus properties. Similarly, research on tactile distance (Calzolari et al., 2017) and tilt/orientation (Hidaka et al., 2022) aftereffects has shown selectivity for low-level perceptual properties such as hand orientation (rotated or not), hand laterality (left/right), hand region (distal/proximal), and skin surface (dorsum/palm).

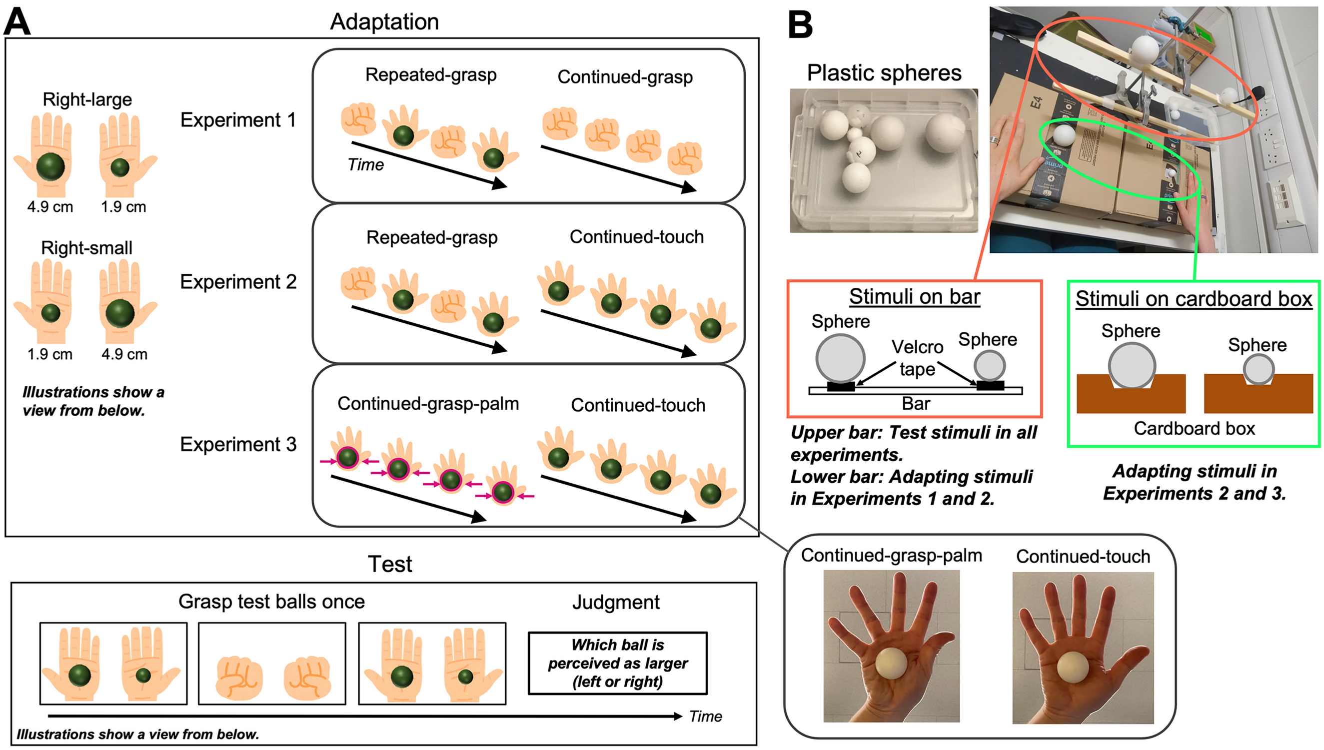
One unique aspect of the somatosensory system is that touch can actively interact with the surrounding environment by moving a body part: when we touch an object with our hands, we can move the hand to grasp and hold the object in a variety of ways as we can gather more information about its shape and size (Lederman & Klatzky, 1987). Haptic size adaptation aftereffects have been demonstrated with haptic touch, characterized by the combination of tactile sensation (touch) with kinesthetic feedback (body movement; Kappers & Bergmann Tiest, 2013, 2014; Maravita, 1997; Uznadze, 1966). Originally, the haptic size adaptation aftereffect was demonstrated with free haptic exploration (Uznadze, 1966). Participants repeatedly squeezed a large and a small sphere in each hand for 10–15 times. Afterward, they were presented with new test stimuli having an intermediate size of the adapted ones. Adaptation aftereffects occurred such that the stimulus held on the hand that was adapted to the smaller (or larger) stimuli was perceived larger (or smaller) than their veridical size. A similar dynamic adaptation procedure was tested on a patient with tactile extinction due to lesions in the posterior parts of the right parietal lobe, showing that the size adaptation aftereffect was experienced even when the size of the objects was not consciously perceived (Maravita, 1997). In contrast, other studies removed the exploration component as participants were asked to grasp the objects from the top without moving the hands but keeping the hand configuration still, during the adaptation and test phases (Kappers & Bergmann Tiest, 2013, 2014). They showed clear adaptation aftereffects with these static haptic touches.

While these size adaptation aftereffects are generally described as "haptic," the specific contributions of different haptic components, that is, tactile sensations experienced with kinesthetic feedback when physically interacting with objects or surfaces, have not been tested. Perceptual aftereffects have been demonstrated for curvature in touch (Vogels et al., 1996) that may be related to size perception, particularly for spherical objects: prolonged touch of convex or concave spherical surfaces makes a subsequent percept of a flat surface concave or convex. A study investigated different features of haptic touch that might modulate tactile curvature adaptation aftereffects (Vogels et al., 1997). They compared the magnitudes of the adaptation aftereffects between static (i.e., placing the palmar side of the hand on the surface without moving the hand) and dynamic (i.e., the hand was free to move over the surface) touches and found no differences in the two conditions. This study suggests that similar mechanisms of haptic curvature processing exist between adaptations by dynamic and static touch (Pont et al., 1999). Interestingly, however, it has also been observed that the curvature adaptation aftereffect appeared without actual stimulation (i.e., no touch): the mere curvature configuration of the hand, where the fingers were bent as if touching a curved surface for 10 s induced similar adaptation aftereffects (Vogels et al., 1997). Putatively, the effect comes from the adaptation to the pattern of musculature in a particular hand configuration. This would suggest that haptic components of touch, such as hand shape and movement, can provide additional perceptual cues during adaptation and modulate resulting somatosensory aftereffects.

Here we investigated size adaptation aftereffects on the hand surface using spheres, with blindfolded participants as in previous studies (Cummins, 1976; Daneyko et al., 2020; Frisco et al., 2023; Kappers & Bergmann Tiest, 2013, 2014; Maravita, 1997; Uznadze, 1966). To explore the role of haptic components in eliciting haptic size adaptation aftereffects, we varied the amount of haptic components involved in touching the adapting spheres. Specifically, we manipulated the touching area, the presence or absence of muscle contraction, and whether the grasp was continuous (hands kept closed) or repetitive (hands repeatedly opened and closed). Given that each haptic component might provide unique perceptual cues, we expected that an adapting condition incorporating more haptic components would yield a larger magnitude size adaptation aftereffects.

Experiment 1 compared the magnitude of size adaptation aftereffects after adaptations by dynamic and static touch to the size of spheres (Figure 1A). In the former case, spheres were repeatedly grasped (repeated-grasp condition), whereas in the latter case, spheres were simply continued to be grasped without further movement (continued-grasp condition). The two conditions were similar in terms of hand configurations (as it was proportional to the object size) and muscle contractions typically involved in grasping spheres. The key difference between these conditions was the presence or absence of hand movements. Experiment 2 compared the repeated-grasp condition to a new condition, where participants simply rested their palms on the spheres (i.e., no grasping involved), keeping their fingers spread wide (continued-touch condition). These two conditions differed in several haptic components, including the amount of muscle contraction, the touched area involved (both fingers and palm vs. palm surface only), and the presence versus absence of hand movements. Hence, in Experiment 3, we focused on one haptic component, that is, the amount of muscle contraction associated with grasping, while keeping constant the other two components (i.e., the area of touch and the presence/absence of hand movements). In particular, Experiment 3 contrasted the continued-touch condition, where the hands were resting on the adapting spheres with a continued-grasp-palm condition, where the

Figure 1
Experimental Materials and Procedure



Note. (A) Schematic illustrations of adaptation and test phases. Note that the illustrations show a view from below to help clarify hand shapes with stimuli. The photo images of the continued-grasp-palm and continued-touch conditions are provided for illustration purposes. (B) Panels show photo images and schematic illustrations of stimuli and apparatus. The lower panel illustrates a relative position of the adaptation and test stimuli. See the online article for the color version of this figure.

hands were grasping the spheres, in both cases without the involvement of the fingers.

We found that adaptation aftereffects occurred for all conditions, including the continued-touch condition, where haptic input was significantly minimized. However, adaptation aftereffects were more pronounced for the conditions where haptic components were largely present (the repeated-grasp, continued-grasp, and continued-grasp-palm conditions). Furthermore, we observed that simply holding the spheres with the palm, which involves muscle contraction, resulted in a similar magnitude of adaptation aftereffect as observed in other conditions that entailed, in addition, repeated grasping with both the hand and fingers.

Method

Transparency and Openness

We report how we determined our sample size, all manipulations, and all measures in the study. Data were collected in 2018–2019 and were analyzed using JASP, Version 0.18 (JASP Team, 2023). We used G*Power 3.1 software (Faul et al., 2009) for sample size estimation.

Participants, Apparatus, and Stimuli

Sixty healthy participants took part in each experiment (20 in each). We excluded one participant's data from Experiments 2 and 3 (see the Analysis section for details). There were 20, 19, and 19 participants in Experiment 1, 12 women, $M_{\text{age}} = 28.9$ years, $SD = 8.3$, $M_{\text{handedness score}}$ according to the Edinburgh Inventory (Oldfield, 1971) = 70.11, all but one (−66.77) right-handed, range = 2.94–100, in Experiment 2 (11 women, $M_{\text{age}} = 32.2$ years, $SD = 11.5$, $M_{\text{handedness score}} = 79.40$, all right-handed, range = 5.88–100), and Experiment 3 (16 women, $M_{\text{age}} = 28.15$ years, $SD = 9.6$, $M_{\text{handedness score}} = 77.05$, all right-handed, range = 58.33–100). The sample size was determined for each experiment based on a previous study that compared the magnitudes of haptic size adaptation aftereffects across conditions that differed in terms of the congruency of the stimuli shapes between adaptation and test phases ($N = 16$; Kappers & Bergmann Tiest, 2014). In the study by Kappers and Bergmann Tiest (2014), the difference in haptic size adaptation aftereffects had an effect size of Cohen's $dz = 1.65$ (estimated from the result of a paired sample t test, $t(15) = 6.6$, in their comparison). A power analysis using G*Power with this effect size, α of .05, and power of 0.8 for a two-tailed, paired t test indicated that six participants were needed. First, we considered that the estimated sample size was relatively small and that it would be necessary to avoid a situation where we found no effects of conditions, which could be due to lack of power. Second, our ABBA experimental design resulted in four combinations. We therefore decided to collect data with five times this number (20 data in total), also considering the possibility that some participants' data would not fit a psychometric function well. Participants reported no abnormalities in sensory perception and were naïve to the purpose of the study. They were paid or given course credits for their participation and gave written informed consent. All procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London (Reference 171887; Title: *Building body representations: An investigation of the formation and maintenance of body representations*). The study was conducted in accordance with the principles of the Declaration of Helsinki.

The tactile stimuli were six ready-made plastic spheres, the diameters of which were 1.9, 3.1, 3.4, 3.7, 4.4, and 4.9 cm. The plastic spheres were set on two horizontal bars made of foam board (Experiment 1) or wood (Experiments 2 and 3) with Velcro tape (Figure 1B). The two bars were placed in front of the participant and were parallel to the participants' torso, and were 40 cm in length and around 1.1 cm thick. One bar was stacked on top of the other at a distance of approximately 10 cm using a metallic stand. Each bar held two spheres 10 cm apart from each side of the bar and 20 cm from each other (Figure 1B, red [dark gray] box). The bottom bar holds the two adapting spheres, one for the left hand and another for the right hand, while the top bar holds the test spheres. Participants could easily move their hands up and down to grasp the spheres from the adapting to the test phase (Figure 1B, bottom panel). In Experiments 2 and 3, the spheres were also placed on two cardboard boxes (approximately 45 cm × 16cm) in the continued-touch and continued-grasp-palm conditions. The center of each sphere was recessed in a square shape (approximately 4 × 4 cm or 2 × 2 cm) in 4 or 2 cm in depth to sustain the spheres such that the top surfaces of the large and small adapter spheres (see the Procedures section) were approximately at the same level while the height of the spheres differed as the difference in size (Figure 1B, green [light gray] box). The positions of the cardboard boxes were replaced depending on whether the right or the left hand was stimulated with the large or small sphere.

The experiments were presented using a PC (Dell Latitude E7440) and implemented with a custom MATLAB (MathWorks, Natick, Massachusetts, United States) script with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for sound presentations.

Procedures

Experiment 1

We compared the continued-grasp condition, with the repeated-touch condition within-participants. Participants sat on a chair in front of a table. Participants were instructed to visually check the positions of the bars on which the adapting and test spheres were placed and to practice moving their hands and arms between the bars before the experiment began. They were then blindfolded throughout the experiment. Each trial started with the adaptation phase that lasted 10 s in which participants were verbally asked by the researcher to touch the two adapting stimuli. The two adaptation spheres were always the largest and the smallest spheres (1.9 and 4.9 cm in diameter; Figure 1A) and placed on the left and right sides of the lower bar. While their elbows resting on the table, participants were asked to touch the spheres from the top with their palms facing down. Participants were asked to touch the adapting stimuli in two separate conditions of adaptation presented in four blocks, either while opening and closing their hands repeatedly (repeated-grasp) or while continuing to grasp the stimuli (continued-grasp). A pure tone of 2,000 Hz with 50-ms duration was presented via headphones (Sennheiser HD 439 Audio Headphones) as a cue for hand movements. In the repeated-grasp condition, we asked participants to start closing their hands at the onset of the sound and then open the hands before the onset of the next sound. The sound was presented in 2 s intervals so that participants repeatedly grasped the adapting stimuli five times during the adaptation phase. The sound was also presented in the continued-grasp condition, but participants were only required to listen to the sound and release the grasping position at the end of the sound presentation. Longer periods of adaptation (60 s, approximately) were present on the first trial and after a break, at the middle of each condition, to induce and reinforce reliable adaptation aftereffects and to diminish any possible residual adaptation from the previous condition.

On each trial, the test phase started right after the 10 s (or 60 s) adaptation phase. Following the termination of the sound presentation, participants moved their hands to the upper bar to grasp the two testing spheres. The testing spheres were placed at the same distance from each other as the adapter spheres (Figure 1B). A combination of spheres for the test stimuli was placed by the experimenter during the adaptation phase. There were five pairs of test stimuli (left–right) with four medium-sized spheres: 3.1–4.4, 4.4–3.1, 3.1–3.7, 3.7–3.1, and 3.4–3.4 cm. Participants were told to grasp the test spheres with the whole hand only once for around 1 s. After lifting their hand from the test spheres, participants verbally reported which of the two spheres ("left" or "right") was perceived as larger. Participants' responses were recorded by the experimenter via key presses on the PC keyboard.

The experiment consisted of two conditions of adaptation (repeated- and continued-grasp) presented in four blocks (ABBA design, order counterbalanced across participants). The position of the adapting stimuli (i.e., the large stimulus presented either at the left or right side) varied every two blocks (AB and BA) and were counterbalanced across participants. The order of presentation of the five test stimuli pairs was random. Participants completed 160 trials: 2 (conditions) × 2 (adapting stimuli position) × 5 (test stimuli presentations) × 8 (repetitions). The experimenter visually checked whether the participants correctly followed the instructions for touching the adapting and test stimuli during the experiment. We provided verbal instructions with the correct way of touching the spheres if any deviations were observed.

Experiment 2

We compared the continued-touch condition against the repeated-grasp condition in a within-participants design. In the continued-touch condition, participants were asked to place their palms on the adapting stimuli with their hands opened and relaxed on the cardboard box. Participants' hands rested on the top of the spheres, touching them with a concave hand posture. No hand movements were involved. In addition, muscle contractions associated with grasping the adapting stimuli were highly reduced or not involved, as participants' hands and arms were placed on top of the spheres as relaxed as possible. Except for this, the procedures were identical to those in Experiment 1.

Experiment 3

We introduced the continued-grasp-palm condition together with the continued-touch condition and compared them in a within-participant design. In the continued-grasp-palm condition, participants were asked to keep holding the adapting stimuli on the cardboard box with their palms. Thus, in the continued-grasp-palm condition, hand positions involved muscle contractions to maintain the grasp on the palm, yet there was no complete hand configuration that involved contacting the fingers with the adapting stimuli or performing opening and closing hand movements. Although we did not measure directly muscular contraction through electromyography (EMG) or track hand movements, we visually monitored adherence to instructions by observing the contraction of the participants' thumb and little fingers along the mediolateral axis of the hand, which served as an indicator of grasping force exertion. Except for this, the procedures were identical to those in Experiments 1 and 2.

Analysis

In each experiment, the proportion of trials in which the stimulus presented to the participants' right hand was judged as larger was analyzed as a function of the ratio of the test stimuli (Figures 2, 3, and 4). The data were plotted logarithmically to produce a symmetrical and evenly spaced distribution of the combinations of the testing spheres (± 0.15, ± 0.08, and 0.00 in the common logarithm, the positive values mean the right-hand stimuli were larger). We fitted a cumulative Gaussian function to each participant's data with Bayesian inference and estimated each participant's point of subjective equality (PSE) with the psignifit package in MATLAB (Schütt et al., 2016). All participants showed good fitting results (mean R^2 values were above .97 for all the experiments). We exclude data from one participant in Experiment 2, whose estimated PSE in the right-large adaptation of the continued-touch condition was outside the test stimulus range because the right-large response proportions were less than 0.5 for all test stimuli. Also, one participant's data were excluded from Experiment 3, in which the estimated PSE in the right-small adaptation of the continued-grasp-palm condition was outside the test stimulus range because the right-large response proportions were greater than 0.5 for all test stimuli. We then estimated the magnitudes of the adaptation aftereffects by subtracting the PSE associated with adaptation to the right-small sphere from the PSE associated with adaptation the right-large sphere (Figures 2, 3, and 4).

For each experiment, we performed a one-tailed, one-sample t test against 0 (note that since statistical tests are performed on the common logarithm of PSEs, the value of 0 corresponds to a raw ratio of 1, that is, where the stimuli were in fact identical in size) for each condition with Bonferroni correction (α level $= .05/2$) to check whether an adaptation aftereffect occurred in each condition. Then, we performed a two-tailed, paired t test to directly compare the two conditions. A mixed-designed analysis of variance (ANOVA) was also performed for the comparisons of the data between Experiments 2 and 3. These statistical tests were performed using JASP. We reported Bayes factors (BFs) for these analyses as estimations of the extent to which the null or alternative hypothesis was supported. We calculated Bayes factors for Student t tests with the Cauchy prior (0, 0.707), which is a default in JASP. We also estimated Bayes factors for the ANOVA with the default JASP multivariate Cauchy prior (r scale fixed effects $= .5$, r scale random effects $= 1$, and r scale covariates $= .354$) by comparing the null and all models (i.e., main and interaction effects).

Results

Experiment 1: Repeated- and Continued-Grasp Conditions

We estimated PSEs for the repeated-grasp (i.e., the adapters were grasped by opening and closing the hands) and continued-grasp (i.e., the adapters were grasped with hands closed with no further hand movements) conditions from the psychometric functions (Figure 2A). The magnitudes of the adaptation aftereffects were then estimated by subtracting the PSE for the right-smaller adaptation from the PSE for the right-larger adaptation (Figure 2B). We observed significant aftereffects both in the repeated-grasp, $t(19) = 12.62$, $p < .001$, $dz = 2.82$, $BF_{10} = 8.40 \times 10^7$, and continued-grasp, $t(19) = 12.34$, $p < .001$, $dz = 2.76$, $BF_{10} = 5.83 \times 10^7$, conditions. The aftereffect magnitudes did not differ between the conditions, $t(19) = 1.37$, $p = .19$, $dz = 0.31$, $BF_{01} = 1.92$.

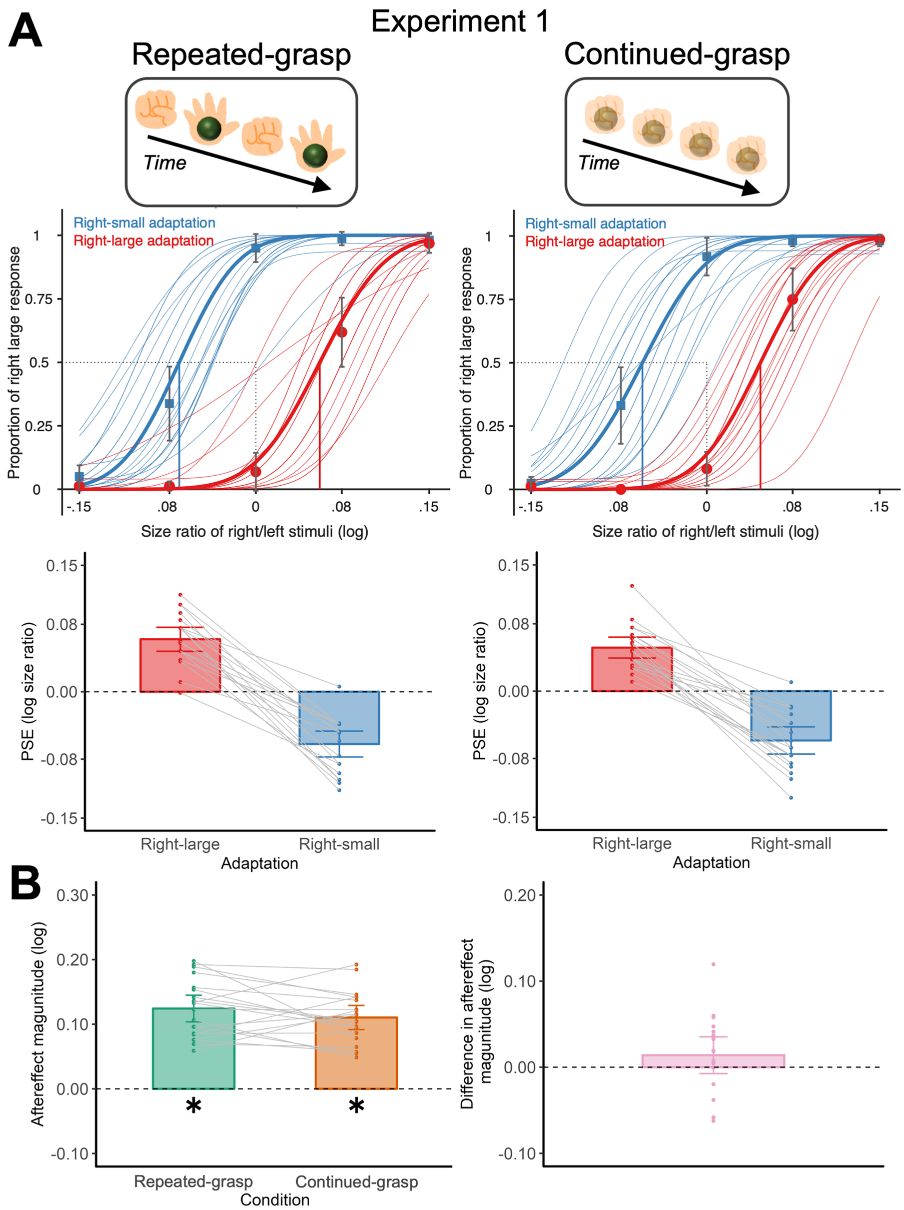
Experiment 2: Repeated-Grasp and Continued-Touch Conditions

Experiment 1 compared a condition rich in haptic components (the repeated-grasp condition), characterized by continuous grasping actions that in principle generated extensive proprioceptive and kinesthetic feedback, against a condition that offered more restricted haptic feedback. This was achieved by eliminating the repeated grasping actions and focusing solely on the act of grasping itself (the continued-grasp condition). In Experiment 2 we reduced haptic feedback further, by asking participants to simply lay on the adapting spheres without exerting any force (the continued-touch condition) for the duration of the adaptation (Figure 3). The aim of this condition was to minimize the influence of haptic components while maintaining the natural curvature of the hand that is typically associated with grasping the spheres. This continued-touch condition was then compared with the repeated-grasp condition, where the adapters were repeatedly grasped with hand movements. We found that the adaptation aftereffects were substantially reduced for the continued-touch condition: The magnitude of the adaptation aftereffects was significantly larger in the repeated-grasp condition than in the continued-touch condition, $t(18) = 14.58$, $p < .001$, $dz = 3.34$, $BF_{10} = 3.91 \times 10^8$ (Figure 3A and 3B). However, we observed significant aftereffects in both the repeated-grasp, $t(18) = 22.39$, $p < .001$, $dz = 5.14$, $BF_{10} = 3.81 \times 10^{11}$, and continued-touch, $t(18) = 4.27$, $p < .001$, $dz = 0.98$, conditions, with the latter also showing very strong evidence in support of the effect ($BF_{10} = 72.03$).

Experiment 3: Continued-Grasp-Palm and Continued-Touch Conditions

The results of Experiment 2 showed that the magnitude of adaptation aftereffects in the continued-touch condition was smaller than the repeated-grasp condition. The difference in the amount of the haptic feedback (the presence vs. absence of hand movements and the addition of muscular contraction) is a plausible explanation. However, the area of the skin surface touching the stimuli was also different between these conditions: participants touched the adapting stimuli with palms and fingers in the repeated-grasp condition, whereas only with the palms during the continued-touch condition. To isolate the impact of the haptic feedback in the form of muscle contraction associated with grasping spheres, we asked participants to just lay the hand on the adapting stimuli (continued-touch condition as in Experiment 2) or to keep grasping it only with their palms (continued-grasp-palm condition) in order to control for the touched area in Experiment 3 (Figure 4A and 4B). Significant aftereffect magnitudes were observed in both the continued-grasp-palm, $t(18) = 10.27$, $p < .001$, $dz = 2.36$, $BF_{10} = 2.02 \times 10^6$, and continued-touch,

Figure 2
Results of Experiment 1

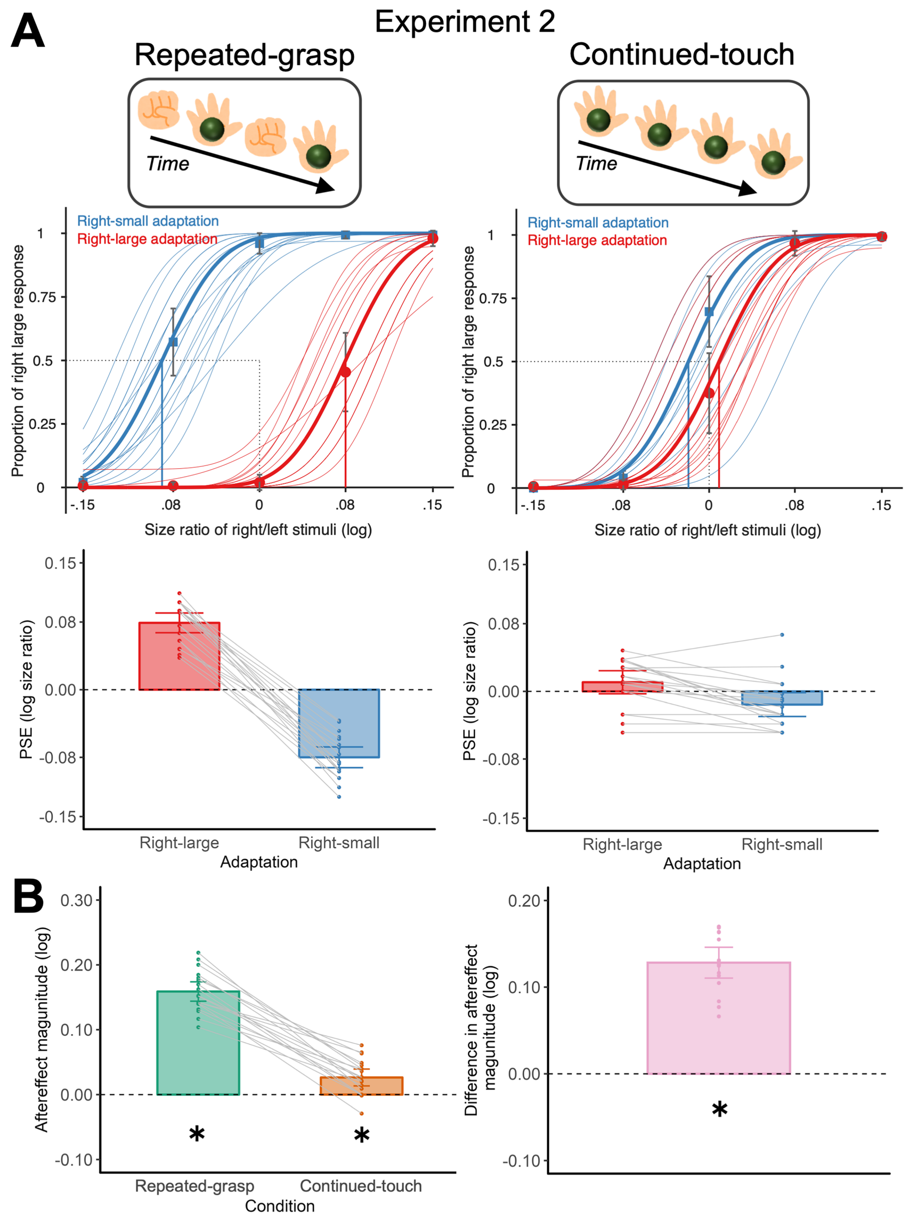


Note. (A) Psychometric functions and estimated PSEs in the log size ratio of testing stimuli as a proportion of responses "right was larger." Blue (light gray) and red (dark gray) colors indicate whether the larger adapting sphere was touched with the participant's right (red [dark gray]) or left (blue [light gray]) hand. In the top panels, a log size ratio of the *x*-axis equal to 0 indicates that the two testing spheres had the same size; positive/negative log ratios indicate that the right sphere was larger/smaller than the left one. The thin lines represent the curves fitted with the individual data. The curves fitted with the averaged data are shown as thick lines for illustration purposes only. (B) Magnitudes of adaptation aftereffects in the log size ratio (left) and the differences in the magnitudes between the conditions (right). Error bars denote 95% confidence intervals ($N = 20$). PSE = point of subjective equality. See the online article for the color version of this figure.
$^* p < .001$.

$t(18) = 5.34$, $p < .001$, $dz = 1.23$, $BF_{10} = 574.38$, conditions. We further observed that the magnitude of the aftereffect was significantly larger for the continued-grasp-palm condition than the continued-touch condition, $t(18) = 7.78$, $p < .001$, $dz = 1.78$, $BF_{10} = 44{,}979.84$.

Moreover, a post hoc 2×2 mixed-design ANOVA with the between participants factor of experiment (Experiments 2 and 3) and within-participants factor of condition (repeated-grasp [Experiment 2] or continued-grasp-palm [Experiment 3] against continued-touch)

Figure 3
Results of Experiment 2

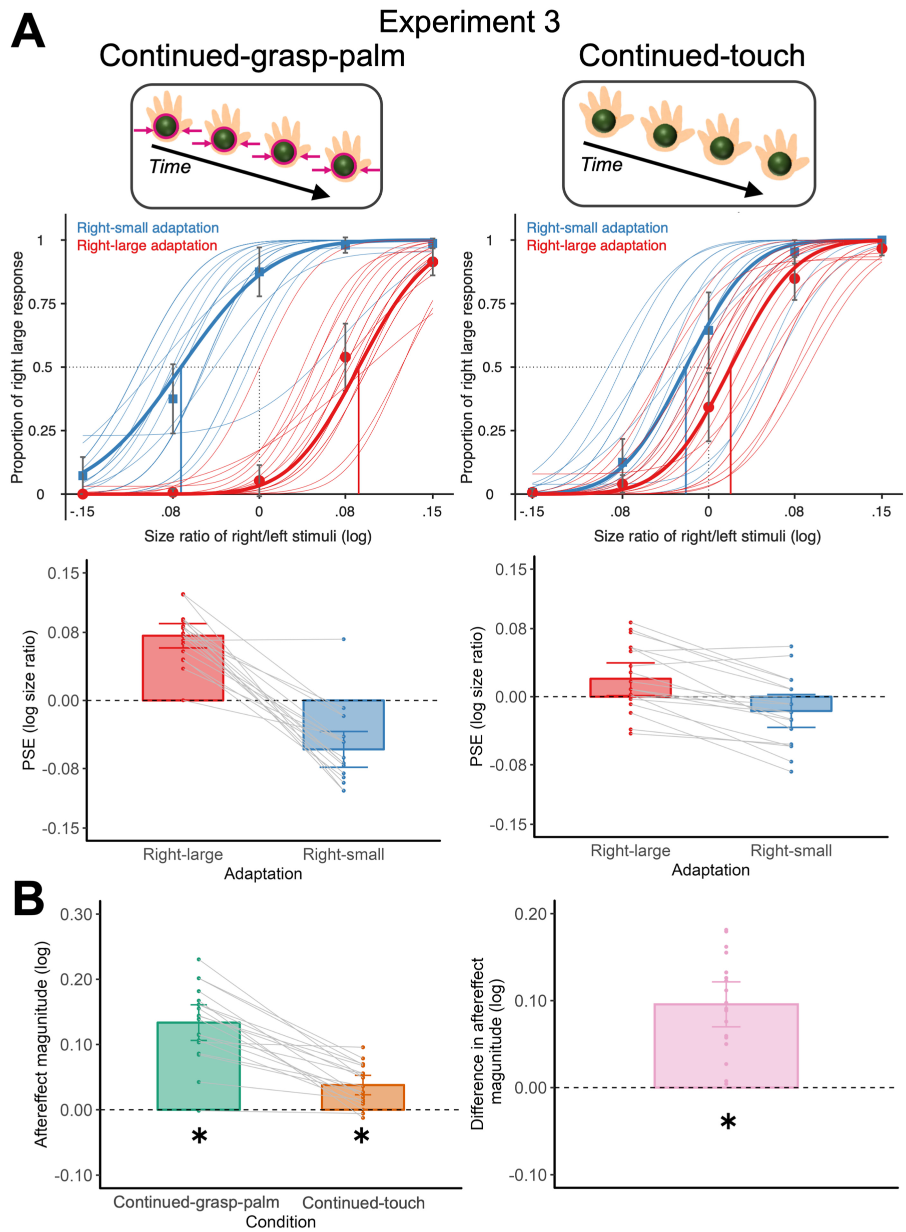


Note. (A) Psychometric functions and estimated PSEs in the log size ratio of test stimuli. In the top panels, the thin lines represent the curves fitted with the individual data. The curves fitted with the averaged data are shown as thick lines for illustration purposes only. (B) Magnitudes of adaptation aftereffects in the log size ratio (left) and the differences in the magnitudes between the conditions (right). Error bars denote 95% confidence intervals ($N = 19$). PSE = point of subjective equality. See the online article for the color version of this figure.
* $p < .001$.

showed no significant main effect of experiment, $F(1, 36) = 0.51$, $p = .48$, $\eta_p^2 = .003$, $BF_{10} = 0.28$. There was a significant main effect of the condition, $F(1, 36) = 222.55$, $p < .001$, $\eta_p^2 = .69$, $BF_{10} = 2.35 \times 10^{19}$. Also, we found a significant interaction experiment by condition, $F(1, 36) = 5.79$, $p = .02$, $\eta_p^2 = .02$, $BF_{10} = 8.45 \times 10^{18}$. Post hoc pairwise comparisons with Bonferroni correction showed the consistent tendencies of the main effect of the adaptation, as there were no significant differences between the repeated-grasp and continued-grasp-palm conditions ($t = 2.04$, $p = .27$, $dz = 0.66$) or between the continued-touch conditions ($t = -0.92$, $p = 1.00$, $dz = -0.30$) across the experiments.

These results suggest that muscle contraction of the hand due to grasping the adapters is sufficient to induce stronger haptic size adaptation aftereffects. Moreover, at least in the current experimental

Figure 4
Results of Experiment 3



Note. (A) Psychometric functions and estimated PSEs in the log size ratio of test stimuli. In the top panels, the thin lines represent the curves fitted with the individual data. The curves fitted with the averaged data are shown as thick lines for illustration purposes only. (B) Magnitudes of adaptation aftereffects in the log size ratio (left) and the differences in the magnitudes between the conditions (right). Error bars denote 95% confidence intervals ($N = 19$). PSE = point of subjective equality. See the online article for the color version of this figure.
* $p < .001$.

situation, the amount of skin touching the adapting stimulus may not be a determinant factor in the magnitudes of the aftereffect.

Discussion

The current study investigated whether and how different haptic components (i.e., the touching area, the presence or absence of muscle contraction, and whether the grasp is continuous or repetitive) modulate size adaptation aftereffects. We observed that adaptation aftereffects were present across all conditions. Importantly, the aftereffects were more pronounced in conditions with significant haptic interaction (i.e., the repeated-grasp condition in Experiments 1 and 2, the continued-grasp condition in Experiment 1, and the continued-grasp-palm condition in Experiment 3) compared to the continued-touch condition in Experiments 2 and 3, where the input was predominantly tactile, significantly minimizing the haptic feedback.

Generally, stronger adaptation inputs (e.g., longer presentations of adapting stimuli) induce aftereffects of greater magnitude (e.g., Blakemore & Campbell, 1969). However, adding haptic components did not lead to the anticipated larger aftereffects. Indeed, we observed no statistically significant difference between merely holding the sphere with the palm (continued-grasp-palm condition) and engaging in active hand movements (repeated-grasp condition), indicating that increasing kinesthetic and proprioceptive feedback as well as introducing fingers did not enhance the adaptation aftereffect. This suggests that muscle contraction alone, along with the resultant proprioceptive feedback of the applied force and hand shapes, is sufficient to elicit a significant and large aftereffect. This occurs without the necessity of repetitive movements or finger involvement, highlighting the significant role of static muscle contraction and proprioception in driving haptic size adaptation aftereffects.

The smaller but reliable amount of adaptation aftereffect observed in the continued-touch condition, where participants simply rested their hands on the spheres, suggests that proprioceptive information alone, provided by maintaining the hand in a curved position, plays a pivotal role in size adaptation. This phenomenon could be partially attributed to tactile curvature adaptation aftereffects which might influence size perception (Vogels et al., 1997). It is known that holding a hand in a curved position leads to a subsequent perception of a flat surface as having the opposite curvature, even in the absence of direct contact with the object during adaptation (Vogels et al., 1997). It is important to note, however, that our study did not include EMG measurements. Consequently, we cannot definitively rule out the possibility of muscle contraction occurring in our continued-touch condition might have contributed to the observed aftereffect. Beyond proprioception, local tactile cues may also play a role, either independently or in conjunction with proprioceptive feedback, in driving the adaptation aftereffect observed in the continued-touch condition. Such cues include the amount of curvature computed through touch (Pont et al., 1999; Vogels et al., 1996, 1997), the distance between stimulated points on the skin (Calzolari et al., 2017), the orientation of the touched surface (Hidaka et al., 2022), or the perceived height of the object (Glowania et al., 2020; van Dam et al., 2016) among others.

Future studies are thus necessary to evaluate the critical contributing factors of the aftereffect associated with changes in tactile and haptic components produced when simply maintaining a grasp without tactile input, or when laying on the adapting object with precise image-based or physical measurements. In addition, involvements of attention should also be considered. Attention to tactile stimuli can induce better behavioral performance in tactile discrimination and produce stronger neural activity in early somatosensory cortices (SI and SII; Burton et al., 1999). In principle, the involvement of haptic components beyond purely touching the object may enhance and maintain top-down modulations like attention to the stimuli during adaptation.

Since the current study always presented adaptation and test stimuli to both hands and asked participants to compare the size of the test stimuli between hands, we should also consider the role of interlateral interactions of tactile size information (Tamè et al., 2019). These interactions might emphasize perceived differences in tactile size between the hands during adaptation. Such perceived differences might be more pronounced when haptic information is actively engaged, as opposed to scenarios involving mostly passive touch (as in our continued-touch condition). This concept aligns with recent research showing that adaptation in crossed-arm positions leads to a larger amount of size adaptation aftereffects than adaptation in standard, uncrossed-arm positions (Frisco et al., 2023). Additionally, the transfer of tactile curvature adaptation aftereffects across hands is minimal (van der Horst, Duijndam, et al., 2008) or nonexistent (Vogels et al., 1997) when adaptation and test stimuli are experienced through static touch. In contrast, a complete interlateral transfer is observed when tactile stimuli are presented dynamically with both active and passive movements (van der Horst, Willebrands, & Kappers, 2008).

We would like to note that although in Experiment 3 we aimed to isolate the effect of muscle contraction by ensuring that the palm area touched the spheres equally in both the continued-grasp-palm and continued-touch conditions, it is possible that there was a slightly larger contact area in the former condition. However, it may be unlikely that the effects of contact area had a significant influence on the magnitude of the aftereffect in our experiments because the aftereffect magnitudes were comparable between the repeated-grasp condition (involving both palm and fingers) and the continued-grasp-palm condition (involving only the palm), which also differ in the contact area.

Although we can assume that the haptic size adaptation aftereffects and the specific way of interacting with the adaptors introduced in our study are general and universal (Lederman & Klatzky, 2009), there are several constraints to the generalizability of our results. We included only a limited range of haptic components with a limited type of touch. Additionally, our focus was narrowed to a specific body area, that is, the hand surface, using only one type of tactile stimulus. Future studies need to validate our findings across a broader array of haptic components, body/skin areas, and stimulus types. In particular, we often use our fingers, the part of the body with one of the highest sensory/perceptual sensitivity (Lederman & Klatzky, 2009), to grasp objects in everyday life. Future research is needed to investigate the effects of haptic touch when using the fingers, taking into account different aspects of finger movements, such as finger aperture during grasping, finger position, and dynamics of movement, which affect size perception (Schot et al., 2017; Uccelli & Bruno, 2024; Uccelli et al., 2019). It will be also important to examine dissociations between perception and finger grasping aperture/finger position (Smeets et al., 2023; Westwood & Goodale, 2003).

As for stimulus types, most previous studies of the haptic size adaptation aftereffect have consistently used spheres (Cummins, 1976; Daneyko et al., 2020; Frisco et al., 2023; Kappers & Bergmann Tiest, 2013, 2014; Maravita, 1997; Uznadze, 1966), perhaps because spheres fit well on the focused body part, namely, the hand surface. However, exploring different stimuli may prove valuable, particularly when attempting to distinguish the potential influence of curvature on the haptic size adaptation aftereffect. Research using both tactile (Kappers & Bergmann Tiest, 2014) and visual (Bruno et al., 2018) stimuli have shown that size adaptation aftereffects are stronger when the shapes are consistent between adapting and test stimuli. Future studies should investigate the possible interaction between the effects of haptic touch and stimulus shape consistency, using an adaptation transfer paradigm.

In addition, it may be worthwhile to test whether differences in participants' hand size, together with the associated differences in touched area and hand surface extension, interact with the magnitude of tactile adaptation aftereffects, especially considering that the size of our hand, particularly the dominant hand, might serve as a standard reference point for size perception (Linkenauger et al., 2014, 2010). Future studies are also necessary to investigate how haptic components and related somatosensory processes contribute to size adaptation aftereffects using brain imaging techniques and EMG. Finally, it will be interesting to investigate commonalities and differences in perception of tactile distance (Calzolari et al., 2017; Jeschke et al., 2023) and size adaptation aftereffects, given the former might simply be considered as the distance between two distal spots in two-dimensional space while the latter also includes three-dimensional information such as volume.

In conclusion, this study provides insights into the modulation of size adaptation aftereffects by various haptic components, such as the area of touch, the presence of muscle contraction, and the nature of the grasp. We have shown that adaptation aftereffects were present in all our conditions, with more pronounced effects observed in conditions involving active haptic engagement compared to the one relying mostly on passive touch. Contrary to our expectation of a stronger adaptation aftereffect with more haptic components, a comparable magnitude of the aftereffect was observed for conditions involving active haptic engagement regardless of the complexity of haptic interactions, suggesting that basic proprioceptive feedback from muscle contraction is sufficient to induce notable perceptual changes. This underscores the primary role of proprioception and static muscle contraction in mediating haptic size adaptation effects, independent of the complexity of tactile engagement. Nevertheless, our study also underscores the necessity of employing a broader range of stimuli, investigates additional body parts, and applies more accurate methods for isolating and measuring each haptic component.

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