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The Influence of Arm Posture on the Uznadze Haptic Aftereffect

Verso running head : FRISCO, DANEYKO, MARAVITA, AND ZAVAGNO

Recto running head : ARM POSTURE INFLUENCE ON THE UZNADZE AFTEREFFECT

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Data of the experiments are available at the Open Science Framework at https://osf.io/ugahb/? view_only=d4f3b6861ddf417495da2854f1618789. The experiments' design and their analysis reported were not preregistered.

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ABSTRACT

The role of arm posture in the Uznadze haptic aftereffect is investigated: two identical test stimuli (i.e., spheres, TS) clenched simultaneously appear haptically different in size after hands have been adapted to two spheres (adapting stimuli, AS) differing in size: the hand adapted to a small AS feels TS bigger than the hand adapted to a big AS. In two experiments, participants evaluated the haptic impressions of two TS after adaptation by finding their match on a visual scale. In Experiment 1, all tasks were carried out with arms either uncrossed or crossed or crossed. In Experiment 2, only the matching task was performed with arms either uncrossed or crossed while adaptation was conducted by continuously changing arm posture from uncrossed to crossed and vice versa. The illusion occurred irrespectively of arm posture; however, its magnitude was smaller when adaptation was carried out in the classical condition of uncrossed arms. Results are discussed in light of two functional mechanisms: low-level somatotopic mapping (i.e., stimuli conformation) and high-level level factors (i.e., arm posture) that could modulate the haptic perception.

Public Significance Statement

Does proprioceptive information regarding the position of the hands affect size haptic processing? This study shows that the position of the hands in external space does not affect the direction of the Uznadze haptic illusion, but it can influence its magnitude. Hence, the work provides further understanding regarding the role of the egocentric spatial location of body parts (i.e., arms) on the construction of haptic experiences of size through bimanual processing. Furthermore, the results presented support the use of the crossmodal method employed by Daneyko et al. (2020) for measuring the magnitude of the Uznadze illusion under different types of manipulation.

KEYWORDS

- Uznadze haptic aftereffect
- haptic-visual crossmodal matching
- body perception
- crossed arms
- haptic illusion

Haptic feedback is critical to properly interact with objects: by grasping an object we acquire information about its three-dimensional structure such as its shape, size, and texture. A coherent representation of an object is created by combining different kinds of somatosensory sensations and information (i.e., input from receptors in the skin is integrated with proprioceptive afferent signals; Berryman et al., 2006; Van Doorn et al., 2010; Yau et al., 2016).

Like most perceptual experiences, haptic perception is also susceptible to perceptual adaptation. An example of haptic adaptation is the Uznadze aftereffect (1930, 1966), which is based on the double synchronous adaptation of the two hands to stimuli which differ in size (Homskaya et al., 1995). Adaptation is usually obtained by a procedure in which a participant either clenches simultaneously and out of sight two adapting stimuli (AS) that differ in size (e.g., spheres, one per hand) for a fixed time duration (e.g., 30 s), or by placing an adaptation stimulus in the palm of each hand and asking the participant

to clench and to open fists repeatedly for about 10–15 times. Immediately after the adaptation sequences have been terminated, two physically equal test stimuli (TS) are presented to participants in both hands simultaneously. Generally, participants perceive the test stimulus in the hand adapted to the smaller adaptation stimulus as bigger than the test stimulus clenched in the hand adapted to the bigger adaptation stimulus.

All experiments previously conducted on the Uznadze haptic aftereffect focused on measuring the direction and sometimes also the magnitude of the illusion without manipulating arm posture that is with uncrossed arms (Daneyko et al., 2020; Kappers & Bergmann Tiest, 2014; Uznadze, 1966). The postural manipulation of crossing arms allows to induce a strong conflict between somatotopic and external reference frames, and it implies a reweighting of tactile and proprioceptive signals. Changing arm posture can alter tactile sensations and delay the integration of tactile and proprioceptive cues, impairing performance in different tactile processing tasks (Eimer et al., 2003; Holmes et al., 2006; Matsumoto et al., 2004; Yamamoto & Kitazawa, 2001). For instance, not only the accuracy of judging the temporal order of touches on the two hands decreases when the arms are crossed (Yamamoto & Kitazawa, 2001), but this posture also seems to alterreduce the perception perceived intensity of nociceptive stimuli (Gallace et al., 2011; Sambo et al., 2013Sambo et al., 2 2011 013). Moreover, Pozeg et al. (2014) showed that crossing the arms can increase the effect of bodily illusions such as the illusory self-touch.

Two similar models have been suggested to explain the relation between body and tactile processing (Longo et al., 2010; Medina & Coslett, 2010). Such models are based on three types of body representation that are crucial for interactions between the tactile representation, the body, external space, and action. The first representation is related to skin surface that links to somatotopic coordinates (i.e., "primary somatosensory representations" or "superficial schema"); the second is concerned with body size and shape representation (i.e., "body form representation" or "body model"); the third is a dynamic representation of the position of the body in space (i.e., "postural representations of the body" or "postural schema"). According to Medina and Coslett (2010), the processing of the position of tactile stimuli relies on the somatotopic representation related to the stimulus position on the skin. Subsequently, the processing moves further to a high-order representation where the tactile information is combined with the information about the hand's position in external space.

With respect to the Uznadze haptic illusion, this hypothesis suggests that crossed arms might create a conflict between the somatotopic and the high-level representations that should result in different perceptual experiences with respect to the situation when the arms are kept uncrossed, parallel in front of the body (Shore et al., 2002). However, few studies have focused on the effect of arm posture on haptic processing. Crucially, research on the "width effect" (kinesthetic figural aftereffects; Köhler & Dinnerstein, 1947) for which, after a period of tactile adaptation to a bar with a specific width, the perception of the width of a new bar change. This haptic illusion appears to be more somatosensory in nature and unrelated to the arms' position in space (Cameron & Wertheimer, 1965; Walker & Shea, 1974). A similar result also emerged in more recent works investigating the effects of postural changes in two different aftereffects: the tactile distance aftereffect (Calzolari et al., 2017) and the tilt aftereffect (Hidaka et al., 2022). In these works, the authors found that the two effects did not transfer across hands, suggesting that both tactile aftereffects occurred hand-centered and not in the external reference frame.

The aim of the present study is to investigate the role of arm posture (i.e., proprioceptive cues regarding the position of the arms in space) in the occurrence of the Uznadze haptic aftereffect. Specifically, we aimed to verify whether Uznadze's classic haptic aftereffect is the "product" of a relatively earlier (i.e., somatosensory processing based on somatotopic coordinates) rather than later (i.e., egocentric coding of hand position in external space) stage of information processing. To this purpose, two experiments are described in which the direction and the magnitude of the illusion were measured by employing the "see what you feel" method (Daneyko et al., 2020). This method makes use of an actual 3D scale visually presented to participants whose task is to find on it the objects that match in size those they are clenching out of sight. The two experiments are similar except for the position of the arms, which were either uncrossed (standard posture) or crossed throughout Experiment 1, or which switched continuously from uncrossed to crossed during the adaptation phase in Experiment 2.

A modulation of the magnitude of the haptic size aftereffect due to different arm postures (or even a modification of the direction of the illusion) would suggest that the aftereffect critically relies on the representation of hands in egocentric external space and not only on somatotopic mapping of somatosensory stimuli. A lack of significant differences in the occurrence of the illusion with respect to arm posture would instead support the hypothesis that the aftereffect is driven by an early stage of processing, mainly relaying on somatotopic representations. In both cases, we would be able to provide further understanding of the construction of haptic experiences through bimanual processing and the role of egocentric

Experiment 1

In Experiment 1, we investigated whether inducing the illusion with arms crossed would modulate the haptic aftereffect compared to the standard uncrossed position. If proprioceptive information relative to the crossed arm posture influences the haptic illusion, we expect to find a difference in the magnitude of the haptic effect between the two types of arm postures. This result would mean that higher-order representations of body and space may also affect the haptic aftereffect. Alternatively, if the strength of the effect is independent of the arms localization in external space, then we should not find a difference in the illusion's magnitude, thus suggesting that the haptic illusion would basically result from low-level somatosensory processing.

Method

Participants

Participants were 40 Italian healthy volunteers (30 females, $M_{age} = 23$), enrolled from the University of Milano-Bicocca, and were compensated with course credits. Participants were randomly assigned to one of two groups, which were differentiated for how arms were positioned throughout the experiment (uncrossed or crossed). All participants were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971) before the start of the experiment. None of the participants were familiar with the Uznadze haptic size aftereffect and were unaware of the experiment's purpose. Before taking part in the study, the experimental protocol was explained in detail and all participants gave written informed consent to participation. Data collection was performed in 2021, when the access to the laboratory was authorized by the University of Milano-Bicocca. The experiment was approved by the Ethics Committee of the Department of Psychology of the University of Milano-Bicocca and conducted in accordance with the Declaration of Helsinki (World Medical Organization, 1996).

A prior power analysis was performed for sample size estimation for a within-between interaction in a repeated measured analysis of variance (ANOVA) comparing the strength of the Uznadze aftereffect according to the type of adaptation performed (small vs. big) and arm posture (crossed vs. uncrossed). The sample size was calculated using the software G*Power 3.1 (Faul et al., 2007). We decided to **[AQ5]**set $\alpha = .05$, $1-\beta = .85$, and r = .5 as the correlation among repeated measures, the last of which is the default value considered to be conservative (Brysbaert, 2019). We chose as the smallest effect of interest a medium effect size of 0.5 (Cohen's *d*, corresponding to an f = 0.25) since there are no previous studies that conducted the Uznadze aftereffect with arms crossed. The analysis indicated the necessary sample size of 38 participants.

Materials

To assess the Uznadze haptic illusion, we employed a crossmodal matching method dubbed "see what you feel": the method entails that participants have to find the best match of the spheres they are clenching out of sight on a visual scale made of actual spheres that differ from each other in diameter (for a detailed description, see Daneyko et al., 2020). The visual scale consisted of 12 spheres mounted on a wooden base (80 cm in length) at regular spatial intervals (Figure 1A). The spheres were organized in growing size order from left to right (diameter from 2.2 to 4.7 cm) and each sphere was denoted below by a letter (from N to A). The TS corresponded to sphere E on the visual scale (3.9 cm in diameter); the small AS corresponded to sphere I on the scale (2.9 cm); the big AS corresponded to sphere C on the scale (4.3 cm).

Experimental Design and Procedure

Participants were randomly assigned to two groups: one group performed all phases with crossed arms, the other with uncrossed arms (Figure 1B). For all participants, the illusion was induced through the simultaneous stimulation of the two hands. Moreover, the hand with which a participant was asked to start all matching tasks and the position of the small adapting sphere were counterbalanced across participants. In line with a previous study (Daneyko et al., 2020), the experiment consisted of three phases: a Pre-Test (Phase 1), an Adaptation (Phase 2), and a Test Phase (Phase 3). Participants sat in front of a table and with palms facing upward placed their arms under the tabletop in an empty compartment open on both sides. In this way, hands were out of sight during the experiment. The visual scale was placed on the table at a distance of 30 cm from the participant's torso, at a comfortable height that allowed for a top and frontal view. In Phase 1, participants were requested to indicate on the visual scale placed in front of them which sphere matched in size the one they were grasping: a TS was therefore placed in one of the hands, and the participant sought for its match on the visual scale. Pre-Test matching was carried out two times for TS and for both AS, switching from one hand to the other after matches for the three spheres were made (but always starting with TS). In Phase 2, an AS was placed in each of a participant's palms. Participants were asked to clench their hands tightly and then to open them again; the spheres were

thus removed and immediately repositioned in the participant's palms, who had to clench again. This sequence was repeated 15 times, with the small and big adapting spheres always placed, respectively, in the same hand. On the 16th episode, the two AS were substituted by the two TS without any warning (i.e., Phase 3). Participants were thus requested to find on the visual scale a match for the size of each TS they were clenching in their hands. The hand with which Phase 3 started was counterbalanced across all participants. The total duration of the experimental session was approximately 30 min.

Transparency and Openness

Data of the experiments are available at the Open Science Framework athttps://osf.io/ugahb/? view_only=d4f3b6861ddf417495da2854f1618789. The experiments' design and their analysis reported were not preregistered.

Results

To measure the effect of adaptation on the test spheres (Phase 3), we subtracted Pre-Test from Test estimations, deriving the value ΔT (ΔT = Test-Pre-Test). ΔT is a measure of the visually perceived distance between Test (visual evaluation of the size of TS after adaptation) and Pre-Test (visual evaluation of TS before adaptation) estimations. For each participant, there were two ΔT values, one corresponding to the size impression after adaptation to the small sphere (ΔT_{small}) and the other corresponding to the size impression after adaptation to the big sphere (ΔT_{big}). Data were inspected for outliers in each group: points that fell outside ±2.5 *SD* from the participants' means for the two types of ΔT values were discarded. Thus, two participants were removed from the sample (N = 38). We tested for normality distribution, examining skewness and kurtosis and using the Shapiro–Wilk test. The variables' distributions were essentially symmetric and ascribable to a normal distribution, as shown by a normal range of skewness and kurtosis (all values < |1|, except for ΔT_{small} Crossed group kurtosis = -1.29). While according to the Shapiro–Wilk test, only the left-hand Pre-Test data and ΔT_{big} for the Uncrossed group were not normally distributed (p < .05). Thus, we decided to use parametric tests, also considering the general robustness of parametric tests to normality violations (Knief & Forstmeier, 2021).

First, to verify the presence of any difference in the Pre-Test estimations (Phase 1), we compared the actual size of the TS (3.9 cm) and its visually evaluated size using one sample *t* tests for each *hand*. The analysis showed significant differences for both hands, left hand: t(37) = -5.90, p < .001, Cohen's d = -0.96; right hand: t(37) = -6.77, p < .001, Cohen's d = -1.10. Mean matching values are significantly underestimated compared to the actual size (left hand: M = 3.60 cm; SE = 0.04 cm). Moreover, a paired sample *t* test did not show significant differences between the two *arm postures* in the visual estimations during Phase 1 (p > .9). Finally, an independent *t* test conducted to compare the size estimations between the two *hands* showed no statistical difference (p > .8). All results are in line with those reported by Daneyko et al. (2020). Results for the size estimations of the two AS are reported in the online supplemental materials and are in line with those reported here for the test sphere.

Then, an ANOVA for repeated measures was carried out on the new variable ΔT data with *adaptation* (AS_{small}, AS_{big}) as the within-subject variable, and *arms* (crossed, uncrossed) as between-subjects variable. Adaptation determined a significant main effect: F(1, 36) = 90.47, p < .001, $\eta_p^2 = .71$, Cohen's d = 1.83. The effect of *arms* was not significant (p > .2); instead, the interaction *adaptation* × *arms* produced a significant effect: F(1, 36) = 6.04, p < .05, $\eta_p^2 = 0.14$, Cohen's d = 0.35. Regardless of arm posture, TS was perceived bigger after adaptation to AS_{small} (M = 0.41 cm, SE = 0.05 cm, CI: [0.31, 0.51]) and smaller after adaptation to AS_{big} (M = -0.15 cm, SE = 0.05 cm, CI: [-0.26, -0.05]). However, arm posture affected the evaluations of TS differently in relation to the different adaptation spheres: adaptation to AS_{big} with arms crossed leads to a stronger effect, while the difference in size estimation for TS with arms crossed or uncrossed is only mildly affected by arm posture after adaptation to AS_{small} (Figure 2A).

The aforementioned differences should also lead to a difference in the overall magnitude of the illusion, expressed for each participant as the absolute difference between ΔT_{small} and ΔT_{big} (Magnitude). On such data, an independent *t* test was conducted with *arms* as between factors. A significant main effect on the overall size of the illusion emerged: *t*(36) = 2.34, *p* < .005, Cohen's *d* = 0.76. Figure 2B shows that the perceived difference between the two TS was greater with arms crossed (*M* = 0.71 cm, *SE* = 0.09 cm) than with arms uncrossed (*M* = 0.45 cm, *SE* = 0.07 cm). Analyses were performed using Jamovi (Version 1.6.23.0, The Jamovi Project, 2022) and R software (R Development Core Team, 2016).

Discussion

During the visual evaluation of the test spheres before adaptation (Phase 1), we found a difference between the estimated and the actual size of the TS. Specifically, participants tend to choose a smaller visual sphere to match the size haptically felt (i.e., underestimation of the size compared to the actual sphere dimension). This visual estimation bias was also reported in an earlier study using the same crossmodal method to assess the magnitude of the illusion (Daneyko et al., 2020). Thus, it could reflect a general transduction mechanism of tactile to visual information that characterized this crossmodal matching method. However, we cannot determine if this difference was due to an underestimation of the tactile stimulus size or an overestimation of the visual stimuli dimension on the scale. Crucially, with reference to Phase 3, in both groups of participants, the direction of the aftereffect illusion was not affected by arm posture: the test sphere appeared always bigger in the hand previously adapted to a small sphere and smaller in the hand adapted to a big sphere (Daneyko et al., 2020; Kappers & Bergmann Tiest, 2014 Uznadze, 1966). These results suggest a main role of somatotopic mapping rather than spatial egocentric mapping of hands, in determining the adaptation aftereffect. However, we also found that the magnitude of the illusion is enhanced by maintaining the arms crossed throughout the entire experiment; this hints at the possibility that proprioceptive information (i.e., high-level factor) may also play a role.

A discussion of these findings would be too speculative at this stage, but we can hypothesize that sensorimotor control of bimanual grasping in the opposite hemispace may require more effortful control during the task as the crossed arm position is an uncommon posture for grasping and object manipulation. Overall, it could be hypothesized that two concurrent factors determine the *fixed-set* that, according to Uznadze (19696 [AQ6]), would induce the adaptation aftereffect. On the one hand, there is the somatotopic coding, which is anatomically determined and, therefore, unchangeable. On the other, there is the spatial mapping of the hand, which depends on the current posture of the arms in peripersonal space. When arm posture is kept constant during the adaptation phase, the aftereffect occurs regardless of the position of the hands. In Experiment 2, this hypothesis is tested by systematically interfering with the spatial location of the hands in external space (i.e., with the spatial component of the *fixed-set*) by crossing and uncrossing hands on each trial during adaptation.

Experiment 2

In Experiment 2, a mixed adaptation procedure was used in which participants repeatedly switched arm posture from crossed to uncrossed and vice versa. Once the adaptation phase was completed, participants judged the size of the test sphere in the crossed or uncrossed posture, depending on their group settings. We hypothesized that such manipulation during the adaptation phase might disrupt the stability between the spatial and the somatotopic component of the fixed-set, thus affecting the overall magnitude of the aftereffect.

Method

Participants

Participants included in Experiment 2 were 40 Italian healthy volunteers (28 females, $M_{age} = 23$), enrolled from the University of Milano-Bicocca and compensated with course credits. As in the previous experiment, participants were tested to be right-handed and performed the same protocol. Given that the variables investigated are the same as the Experiment 1, but the type of arm posture manipulation in Experiment 2 is different from that in Experiment 1, and it has never been studied, we performed the same power analysis as in Experiment 1. We thus set $\alpha = .05$, $1-\beta = .85$, r = .5, and the medium effect size of 0.5 (Cohen's *d*, effect size f = 0.25). As before, the suggested sample was 38 participants.

Materials, Experimental Design, and Procedure

Experimental stimuli and procedures were the same as in Experiment 1 except for the following main difference: the position of the arms varied continuously during adaptation, from crossed to uncrossed and vice versa (see Figure 3). For instance, in the uncrossed-arms group, participants carried out Pre-Test (Phase 1) and Test matching (Phase 3) with uncrossed arms, they however started the adaptation sequence (Phase 2) with crossed arms and switched back and forth from crossed to uncrossed during the 15 steps adaptation sequence, ending the sequence with crossed arms to then carry out test matching (with uncrossed arms (Figure 3, top row). The crossed-arms group conducted the experiment in the exact opposite way.

Results

As in Experiment 1, the dependent variables ΔT_{small} and ΔT_{big} were calculated and inspected for outliers: three participants were discarded from the analysis (N = 37). Data were essentially normally distributed as assessed by the Shapiro–Wilk test (all ps > .05) and the normal range of skewness and kurtosis (all values < |1|, except for the kurtosis of ΔT_{small} Crossed group = 1.82 and ΔT_{big} Uncrossed group = 1.38).

Thus, we first considered the TS Pre-Test matching values (Phase 1). One sample *t* tests conducted for the two *hands* separately revealed a significant difference between the actual size of the TS (3.9 cm) and its visually evaluated size, left hand: t(36) = -6.89, p < .001, Cohen's d = -1.13; right hand: t(36) = -5.09, p < .001, Cohen's d = -0.837. As in Experiment 1,

mean matching values are significantly underestimated compared to the actual size (left hand: M = 3.55 cm, SE = 0.05 cm; right hand: M = 3.61 cm, SE = 0.06 cm). The results for the size estimations of the two AS also showed an underestimation (see the online supplemental materials) in line with those reported in Experiment 1 and in the previous work by Daneyko et al. (2020).

An independent *t* test was conducted on TS's Pre-Test values for each *hand*, comparing the two *arms* (crossed, uncrossed), but no significant difference emerged (p > .7). Finally, we also compared the Pre-Test matching values between the two *hands* using a paired sample *t* test: results confirmed that means are statistically undistinguishable (p > .1).

An ANOVA for repeated measures was conducted with*adaptation* (AS_{small} and AS_{big}) as within-subjects variable, and test matching *arms* (crossed, uncrossed) as between-subject variable. Only *adaptation* determined a significant main effect: *F*(1, 35) = 75.54, *p* < .001, $\eta_p^2 = 0.68$, Cohen's *d* = 1.92. As in Experiment 1, TS is perceived bigger (*M* = 0.27 cm, *SE* = 0.05 cm, CI: [0.16, 0.37]) in the hand adapted to AS_{small} and smaller in the hand adapted to AS_{big} (*M* = -0.38 cm, *SE* = 0.06 cm, CI: [-0.51, -0.25]), regardless of arm posture during test matching. Factor *arms* and its interaction with *adaptation* did not determine significant effects (*p* > .9).

As for Experiment 1, we calculated the absolute difference between ΔT_{small} and ΔT_{big} (Mm agnitude) for each participant to test the overall size of the illusion. We performed an independent *t* test on such data with *arms* during test matching as between variable; mean magnitudes are not statistically distinguishable, t(35) = -0.02, p = .985, Cohen's d = 0.006; see the online supplemental materials for means' tables of Experiment 2 and comparisons between the two experiments.

Thus, to test the absence of a difference in the effect between the two arm postures, we also performed a Bayesian independent *t* test. The Bayesian analysis showed a Bayes factor (B_{b_1}) of $3.134\% \pm 0.004\%$ in favor of the null hypothesis of no differences in the aftereffect magnitude between the crossed and uncrossed postures. This analysis indicates that the null hypothesis is 3.134 times moderately better at explaining the data than the alternative hypothesis of a difference between the two arm postures.

Discussion

Results for Pre-Test matching show again an underestimation of the spheres size prior to adaptation, which is in line with results from Experiment 1 and those reported by Daneyko et al. (2020). Given the consistency of such finding, the visual estimation bias of a haptic sensation appears to be a general feature of the "see what you feel" method (Daneyko et al., 2023Daneyko, Maravita, & Zavagno, in preparation [AQ7]). The mixed adaptation, in which arm position changed back and forth from crossed to uncrossed, did not affect the outcome of the illusion; nor was this affected by test matching arm posture. This result allows to speculate that the instability of the spatial component of the fixed-set is efficiently compensated by the fast recoding of sensory representation of the body in egocentric space (Lloyd et al., 2003), thus, not affecting the illusion.

Finally, the size estimations of all spheres involved in Experiments 1 and 2 Phase 1, and the size estimations of TS by the uncrossed-arms group in Experiment 1 Phase 3 are in line with those reported by Daneyko et al. (2020). Thus, this evidence would support the use of the "see what you feel" method for measuring the magnitude of the Uznadze haptic illusion since the results are consistent across experiments.

General Discussion

In this study, we aimed to investigate whether proprioceptive information about the position of one's hands in space could modulate the Uznadze haptic aftereffect. To this purpose, we conducted an experiment in which Pre-Test matching, adaptation, and Test matching were always carried out either with arms uncrossed (i.e., parallel) or crossed (Experiment 1). We found that the direction of the illusion was not affected by arm posture, with a TS clenched in the hand adapted to a small AS haptically perceived as bigger than a TS clenched in the hand adapted to a big AS. However, an effect of arm posture on the magnitude of the illusion also emerged, which resulted statistically bigger for crossed arms. Crossing arms induces a conflict between the somatotopic and body-centered frames of reference (Shore et al., 2002; Yamamoto & Kitazawa, 2001). Consequently, a remapping of coordinates is necessary to process and compare the objects features properly. We thus hypothesize that the sensorimotor control of bimanual grasping in the opposite hemispace would require more effortful control, which may enhance the adaptation and/or size-matching processes underlying the illusion.

Is the stability of different aspects of the set-fixing condition, somatotopic or spatial mapping of hands in external egocentric space, critical for the aftereffect? Experiment 2 was designed to answer such question by employing mixed arm postures during the adaptation phase. One group of participants carried out Pre-Test and Test matching with uncrossed arms, the other with crossed arms. Crucially, both groups were requested to switch continuously their arm posture between

the crossed to the uncrossed arm position during throughout the adaptation phase. Such manipulations did not affect the direction or the magnitude of the illusion. Therefore, even interfering with the stability of the spatial component, the aftereffect still occurs. This result indicates that, in the adaptation phase, the brain can quickly recode the location of arms in space, thus relying on the critical somatotopic coding to match the bimanual stimulation.

Moreover, such a result allows to speculate about the role played by arm posture. In our view, the continuous change of the arm posture can reduce the effect of adaptation found with arms crossed in Experiment 1, thus reducing the difference in the strength of the effect between the two groups in Experiment 2. Thus, the adaptation with the crossed arms would have an impact on the magnitude of the illusion only if the stability of the spatial component during adaptation is preserved. The findings of this experiment also suggest that posture during the Test Phase has a minor effect on the magnitude of the illusion. In other words, it is possible that test size estimations would be driven mainly by the characteristics and size of the stimuli manipulated in the hands during adaptation and not by the posture of the arms during the testing phase.

Given the results that emerged from the two experiments, we hypothesized that the illusion is mainly related to low-level somatosensory processing linked to somatotopical representations of the skin surface ("primary somatosensory representations" or "superficial schema"). This result is consistent with previous studies investigating the role of postural changes in different aftereffects for which the effects seem to be anchored specifically to the hand (Calzolari et al., 2017; Cameron & Wertheimer, 1965; Hidaka et al., 2022; Walker & Shea, 1974). Indeed, the brain would be able to quickly remap the position of the hand in space, suggesting the main role of somatosensory inputs and the characteristics of the manipulated stimuli in the occurrence of the illusion, as shown also by Kappers and Bergmann Tiest (2014). However, also the representation of the location of the body in the external space ("postural representations of the body" or "postural schema") seems to subsequently modulate the effect. It is possible that size coding with crossed arms would require additional cognitive processing, thus, increasing the haptic aftereffect.

These findings appear in line with several works that showed how hand laterality and hand position in external egocentric space could alter tactile processing (Eimer et al., 2003; Hidaka et al., 2022; Holmes et al., 2006; Kennett et al., 2001; Matsumoto et al., 2004; Yamamoto & Kitazawa, 2001). For instance, in the work of Hidaka et al. (2022), the authors considered that tactile orientation processing is linked to higher-level body representations. It seems that both somatotopic and postural representations could be involved in processing passive and active touch (Medina & Coslett, 2010).

Following the overall results of the present work, we hypothesized a General Model of Induction (Figure 4) to explain the neural mechanisms underlying the Uznadze aftereffect. The neural coding of the stimulus depends on the sensitivity of the cortical neurons to specific stimulus properties. In particular, the haptic perception of objects involves the integration of different information derived from cutaneous mechanoreceptors, proprioceptive and kinesthetic receptors located in muscles, tendons, and joints to extract information about the objects' surface, shape, temperature, and weight. Then, the information is somatotopically transmitted to the primary somatosensory cortex (SI), the secondary somatosensory cortex (SII) necessary for haptic integration and intraparietal sulcus (IPS), integrating the position of limbs in external space.

In the Test Phase, when participants grasped two identical spheres, they felt the two spheres different in size: the test sphere appears larger to the hand subject to less adaptation (i.e., small adapting sphere), while it seems smaller to the hand with greater adaptation (i.e., big adapting sphere). This process calls for a critical integration of bimanual information in the cortex. The comparison between the sensory information coming from each hand likely starts in SI, where some neurons holding bimanual receptive fields are found (Iwamura et al., 1994) and continues in SII, which receives information processed by SI of both sides of the brain and holds neurons with larger and bilateral receptive fields (Disbrow et al., 2003; Friedman et al., 1980; Iwamura, 2000; Pons et al., 1987). This area is not only related to sensory processing, but it also seems involved in multimodal integration and object manipulation and recognition (Binkofski et al., 1999; Fitzgerald et al., 2004). The crucial role of SII would be to compare sensory information from each hand (i.e., processed in SI) and the information relating to the arms' location in space (i.e., processed in IPS). Ishida et al. (2013) showed the role of SII in processing active touch: they found a population of neurons in SII that are selectively activated during active manipulation of objects, compared to passive touch in the absence of voluntary movement. The posterior parietal cortex then plays a crucial role in monitoring tactile afference in reference to the external egocentric space (Bolognini & Maravita, 2007).

Thus, since the illusion aftereffect occurs with both postures and even when interfering with the spatial component of the fixed-set of the illusion during adaptation, our results support the role of a similar mechanism, possibly located in SI/SII, in generating the aftereffect. Nevertheless, the influence of body posture on the magnitude of the haptic perception would involve a processing that extends to the IPS for the ongoing remapping of body parts in space. However, further investigations are required to verify the causal role of different brain areas in the occurrence of the illusion and the modulation of its magnitude, as anatomical data were not collected in the present work.

Constraints on Generality

Our results demonstrate the influence of arm posture on the Uznadze haptic aftereffect in right-handed undergraduate students. Unpublished studies from our laboratory support the use of the "see what you feel" method to measure the haptic illusion also outside of laboratory settings. Consequently, we expect to obtain the same modulation of crossed arms in different testing contexts and with right-handed participants of different cultural backgrounds and ages. However, we have no evidence that arm posture modulation also occurs with left-handed participants. Data from left-handed participants are currently being collected only with the uncrossed arm posture. Finally, we expect the results **[AQ8]** to **be** generalisableze to situations were right-handed participants match the test spheres with the visual scale located in the peripersonal space, since an unpublished manipulation check for scale distance (Daneyko et al., 2023Daneyko, Maravita, & Zavagnc, in preparation) indicates that a visual scale located far away from the body influences the size evaluation of the test stimulus. We have no reason to believe that the results depend on other characteristics of the participants, materials, or context.

Conclusions

We investigated the role of arm posture (i.e., proprioceptive cues regarding the position of the arms in space) on haptic perception by using the established Uznadze haptic aftereffect. The present work allows to confirm and extend evidence on the illusion, showing that the aftereffect occurs both when a person maintains stably arms crossed or when the stability between the spatial and somatotopic components is compromised during the adaptation phase. Thus, somatotopic mapping would be the crucial component in the occurrence of the illusion. Moreover, the present study suggests that the position of the arms in space also affects the magnitude of the illusion if the crossed posture is maintained stably during the adaptation. Therefore, the effect seems to be determined primarily by low-level somatotopic mapping (i.e., characteristics and dimensions of the manipulated stimuli); yet also high-level factors (i.e., proprioceptive information regarding the arm position in space) could modulate the haptic perception.

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Figure 1

Experimental Materials and Procedure

Note. (A) Visual scale used for the matching test in both experiments. It is composed of 12 spheres, organized in growing size order from left to right (diameter from 2.2 to 4.7 cm) and denoted by a letter (from N to A). The TS corresponded to sphere E (3.9 cm); the small AS to sphere I (2.9 cm); the big AS to sphere C (4.3 cm). (B) Experimental procedure for Experiment 1. Based on the group they were assigned to (uncrossed vs. crossed arms), participants maintained the same arm posture during all phases of the experiment. TS = test stimuli; AS = adapting stimuli.



Figure 2

Results of Experiment 1

values indicate size overestimation, and negative values size underestimation. (B) Size of the illusion is calculated as the absolute difference between ΔT_{small} and ΔT_{big} (magnitude, cm) distinguished by arm posture. Error bars indicate confidence intervals (Cls) set at 95% level.



Figure 3

Procedure of Experiment 2

Note. During adaptation (i.e., Phase 2), arm posture changed continuously from crossed to uncrossed and vice versa. The position of the arms during Pre-Test (i.e., Phase 1) and test matching (i.e., Phase 3) were instead kept constant.



Figure 4

General Model of Induction

Note. In the adaptation phase, two spheres of different sizes are grasped simultaneously with the two hands. Due to the different dimensions of the AS, each hand is subject to a different amount of adaptation. Sensory information coming from the hands is transmitted somatotopically to SI (responsible for the haptic processing) and IPS (responsible for coding the arm position in space). Finally, SII works as a comparator between the sensory information coming from SI and arm position information from IPS. AS = adapting stimuli; IPS = intraparietal sulcus; SI = primary somatosensory cortex; SII = secondary somatosensory cortex.



Attachment Files

1 fig_4_HighRes_400.tif : Fig 4 High Resolution (to replace)