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RESEARCH ARTICLE | *Control of Movement*

Grasping adjustments to haptic, visual, and visuo-haptic object perturbations are contingent on the sensory modality

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Camponogara I, Volcic R. Grasping adjustments to haptic, visual, and visuo-haptic object perturbations are contingent on the sensory modality. *J Neurophysiol* 122: 2614–2620, 2019. First published November 6, 2019; doi:10.1152/jn.00452.2019.—Haptics provides information about the size and position of a handheld object. However, it is still unknown how haptics contributes to action correction if a sudden perturbation causes a change in the configuration of the handheld object. In this study, we have occasionally perturbed the size of an object that was the target of a right-hand reach-to-grasp movement. In some cases, participants were holding the target object with their left hand, which provided haptic information about the object perturbation. We compared the corrective responses to perturbations in three different sensory conditions: visual (participants had full vision of the object, but haptic information from the left hand was prevented), haptic (object size was sensed by the left hand and vision was prevented), and visuo-haptic (both visual and haptic information were available throughout the movement). We found that haptic inputs evoked faster contralateral corrections than visual inputs, although actions in haptic and visual conditions were similar in movement duration. Strikingly, the corrective responses in the visuo-haptic condition were as fast as those found in the haptic condition, a result that is contrary to that predicted by simple summation of unisensory signals. These results suggest the existence of a haptomotor reflex that can trigger automatic and efficient grasping corrections of the contralateral hand that are faster than those initiated by the well-known visuomotor reflex and the tactile-motor reflex.

NEW & NOTEWORTHY We show that online grip aperture corrections during grasping actions are contingent on the sensory modality used to detect the object perturbation. We found that sensing perturbations with the contralateral hand only (haptics) leads to faster action corrections than when object perturbations are only visually sensed. Moreover, corrections following visuo-haptic perturbations were as fast as those to haptic perturbations. Thus a haptomotor reflex triggers faster automatic responses than the visuomotor reflex.

grip aperture correction; haptics; haptomotor reflex; multisensory integration; vision

INTRODUCTION

In everyday life, object manipulations are constantly performed also without the aid of vision. For instance, we can easily pass our smartphone from one hand to the other without ever looking at it. During these manipulations, we can effortlessly process many object properties (size, shape, position) through proprioceptive and tactile information (haptics) and mold the digits of the contralateral hand accordingly (Camponogara and Volcic 2019; Chieffi and Gentilucci 1993; Kritikos et al. 2002; Patchay et al. 2003, 2006; Pettypiece et al. 2009, 2010; Westwood and Goodale 2003). If the handheld object moves in an unexpected way, we are also able to perform a fast adjustment of the contralateral hand and still successfully grasp it. In such cases, the unexpected perturbation is sensed by the haptic inputs from the hand holding the object. Specifically, the simultaneous afferent tactile inputs from mechanoreceptors and proprioceptive inputs from the muscle spindles and tendons of the hand are integrated to signal a change in the object properties (Berryman et al. 2006; Johansson and Flanagan 2009) and trigger a correction of the contralateral hand. But how does this corrective process unfold? And, how do haptic corrections compare with the well-studied corrections to visual perturbations? Moreover, does the simultaneous availability of both visual and haptic inputs lead to a multisensory advantage with even faster corrections?

A considerable number of studies have shown that reaching and grasping corrections following visually sensed changes in target position or target size occur in ~150 ms (Bock and Jüngling 1999; Castiello et al. 1993, 1998; Gentilucci et al. 1992; Hesse and Franz 2009; Paulignan et al. 1991; Roy et al. 2006; van de Kamp et al. 2009). For example, in the van de Kamp et al. (2009) study, the target object could suddenly change its physical size while participants were moving their hand toward it. Even though the size perturbations were unexpected, participants rapidly and automatically corrected their grasp aperture on the fly on the basis of the new visual size.

Studies on action corrections in response to tactile-only or visuo-proprioceptive perturbations are instead limited to reaching movements. For instance, in Pruszynski et al. (2016), participants reached with their right hand for a small target attached to the end of a rod that could unexpectedly rotate. In the tactile condition, the perturbation was sensed by the deformation of the skin of the left-hand thumb caused by the change in rod orientation. In the visual condition, the change in rod orientation was only visually sensed. Correction latencies were obtained by analyzing the changes in both the muscle activation (electromyography, EMG) and the kinematics of the reaching arm following the perturbation. They found that both tactile and visual inputs trigger corrective responses of the contralateral hand ~90 ms (EMG) and 110 ms (kinematic

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measure) after the onset of the perturbation, showing that the tactile-motor reflex is as rapid as the visuomotor reflex. Similarly, studies on bimanual coordination have also shown that visuo-proprioceptive perturbations lead to rapid arm trajectory adjustments of the contralateral arm, in as short as 55–90 and 130–150 ms for the EMG and the kinematic measures, respectively (Dimitriou et al. 2012; Mutha and Sainburg 2009). Movement adjustments to visual perturbations (based on kinematic measures) have instead been found to generally occur in 150–300 ms (for a review, see Sarlegna and Mutha 2015). However, we should be wary of comparing the rapidity of corrections among studies, because of the inherent differences among experimental procedures and among methods to determine the latency of online movement adjustments.

Thus, although it is evident that haptic inputs (proprioceptive and tactile) can successfully trigger appropriate corrective responses of the contralateral hand during reaching movements (Pruszynski et al. 2016) and in bimanual coordination tasks (Dimitriou et al. 2012; Manson et al. 2019; Mutha and Sainburg 2009; Omrani et al. 2013), it is still unclear *1*) whether haptic inputs can guide fast grip aperture adjustments, *2*) how haptically triggered grasping corrections compare with those triggered by visual inputs, and *3*) how the corrections elicited by the simultaneous combination of haptic and visual inputs compare with those triggered by each input separately.

Studies on grasping behavior have consistently reported that grasping performance is better under visual than under haptic guidance. For instance, actions under visual guidance are faster and exhibit a smaller grip aperture haptically guided movements (Camponogara and Volcic 2019; Chieffi and Gentilucci 1993; Pettypiece et al. 2010). In addition, it has been shown that the simultaneous availability of visual and haptic information leads to even faster movements and smaller grip apertures compared with the visual condition (Camponogara and Volcic 2019), supporting the idea that multisensory inputs are integrated during action planning and execution, resulting in optimized grasping movements. Whether visual (and visuo-haptic) inputs are also prioritized over haptic inputs when they signal unanticipated target perturbations is, however, still unknown.

To determine whether corrections of grasping actions are differentially affected by the available sensory information, we asked participants to perform reach-to-grasp actions toward an object that could unexpectedly change its size. We compared three different sensory conditions. In the haptic condition, participants were holding the object with the left hand and sensed the size change by means of both tactile and proprioceptive inputs. In the visual condition, the change was detected only by means of visual information. Finally, in the visuo-haptic condition, the object perturbation was sensed by the combination of both haptic and visual inputs. In all three conditions, the grasping action was performed with the right hand. To estimate how the different sensory conditions affect the ability to correct movements online, we computed the correction latencies by comparing the grip apertures in unperturbed (no object size change) and perturbed (object size change) trials.

If the findings by Pruszynski et al. (2016) on reaching movement corrections generalize for grasping movement corrections, we should find equally fast adjustments to haptic-only and visual-only perturbations. On the other hand, if the concurrent availability of both tactile and proprioceptive inputs during haptic perturbations is exploited, we should find that haptic perturbations trigger faster adjustments than visual perturbations. Moreover, based on the fact that the multisensory signals generally lead to behavioral benefits (Forster et al. 2002; Girard et al. 2011; Hagmann and Russo 2016; Raab 1962; Wada 2010), we might expect even faster corrective responses when both haptic and visual inputs are available compared with when corrections are triggered by either one of the two modalities.

METHODS

Participants. Twenty students from the New York University Abu Dhabi took part in this study (10 men, mean age 19.4 ± 0.9 yr). All had normal or corrected-to-normal vision and no known history of neurological disorders. All of the participants were naive to the purpose of the experiment and were provided with a subsistence allowance. The experiment was undertaken with the understanding and written informed consent of each participant. Experimental procedures were approved by the Institutional Review Board of New York University Abu Dhabi.

Apparatus. The stimulus inspired by van de Kamp and Zaal (2007) consisted of a custom-made wooden rectangular cuboid (5 cm × 4 cm × 3 cm), raised above the tabletop on a 10-cm pedestal. The two sides along its sagittal axis could slide out to change the size of the stimulus (see Fig. 1*B*) and were moved by two mini-pneumatic cylinders embedded in the object (model QP2A012A010, Camozzi; 4 cm long, 2.5 cm wide, 1-cm stroke). These pneumatic cylinders were linked to two solenoid valves (5/2 way 4V210-06; AirTac), which were connected to an air compressor. The solenoid valves were controlled by an Arduino Uno via MATLAB (MathWorks, Inc., Natick, MA). A command sent from MATLAB to Arduino activated the selected solenoid valve, which released the compressor's air into the piston, and the selected side slid out. The expandable side of the object was 5 cm wide when both sides were retracted and 6 cm wide when one of the two sides was slid out. The object was located at a distance of 50 cm along the frontal axis of the table from the home position (a 0.5-cm-high rubber bump with a diameter of 0.9 cm attached to the table; Fig. 1*B*).

A pair of occlusion goggles was used to prevent vision of the workspace in the haptic condition and between trials (Red Scientific, Salt Lake City, UT). A pure tone of 1,000 Hz, 100 ms in length, was

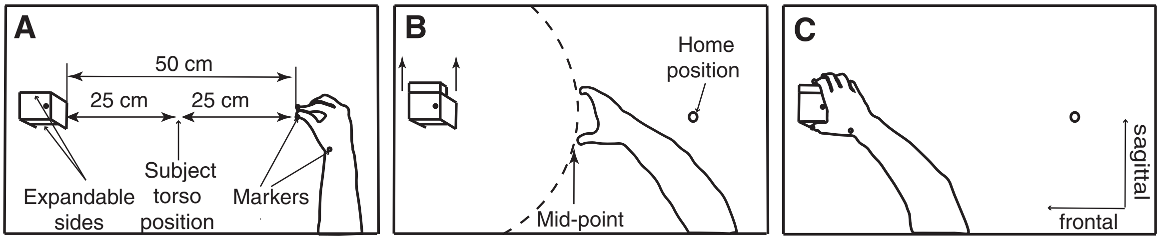

Fig. 1. Experimental paradigm. *A*: participants started each trial with the right hand on the home position. *B*: in the perturbation trials, one side of the cube slid out (index side out is represented) as soon as the hand reached the midpoint. *C*: participants had to adjust the grip aperture to successfully grasp the object.

used to signal the start of the trial, whereas another one of 600 Hz with the same length and intensity was used to signal its end.

Index, thumb, and wrist movements were acquired online at 200 Hz with an accuracy of 0.1 mm and resolution of 0.01 mm by using an Optotrak Certus system (Northern Digital Inc., Waterloo, ON, Canada). Markers were attached on the first phalanx of the thumb and index digit onto the lateral and medial fingernail top sides, respectively. An additional marker was attached on the styloid process of the radius. The Optotrak system and the occlusion goggles were controlled by a custom MATLAB program.

To monitor the distance between the hand and the object, we placed an additional marker on the top of the object. The perturbations were triggered when the hand was 25 cm from the object, that is, at the midpoint between the home position and the object (see Fig. 1*B*). The time latency from when participants reached this threshold to the onset of the actual expansion of the cube was always 20 ms. The perturbation onset is thus defined by taking into account this latency. The full expansion of the object took another 35 ms.

Procedure. Participants sat comfortably in front of the table, with the center of their torso positioned between the object, located on their left side, and the home position, located on their right side (Fig. 1*A*). For all sensory conditions, participants were then required to perform a precision grip with their right hand along the sagittal axis of the stimulus (Fig. 2). In the haptic (H) condition, vision was prevented (goggles closed), but participants were allowed to touch the object along its sagittal axis with the left, nongrasping hand. In the visual (V) condition, participants were allowed to see the object and the surrounding workspace (goggles open) but were not allowed to touch the object with their left nongrasping hand. In the visuo-haptic (VH) condition, participants were allowed to both see and touch the object.

All the trials started with the participants' thumb and index digit of the right hand positioned on the home position (Fig. 1*A*), the left hand positioned on the left side of the object (at a subjective comfortable distance), and the shutter goggles closed. Before each trial the object was set to the appropriate size (5 cm), and *1*) in the H condition, the experimenter signaled to the participants to touch the object with their left hand (i.e., sense its size and position by means of touch and proprioception) while shutter goggles remained closed. Participants then moved their left hand slowly toward the object and had to firmly

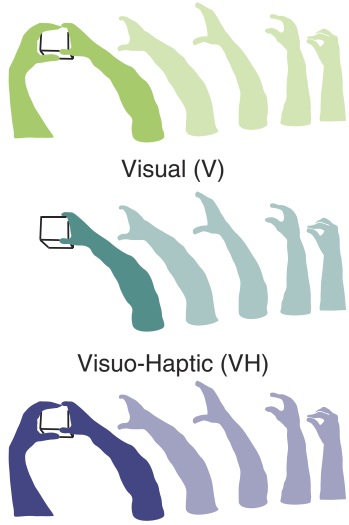

Fig. 2. Experimental conditions. Participants had to grasp the object with their right hand. *Top*: in the haptic (H) condition, vision was prevented and participants were feeling the object with the left, nongrasping hand. *Middle*: in the visual (V) condition, participants were only allowed to see the object. *Bottom*: in the visuo-haptic (VH) condition, participants were allowed to both see and feel the object.

enclose it between the index and the thumb fingers. The right hand was stationary at the home position. *2*) In the V condition, the goggles turned transparent to enable the participant to see the object, or *3*) in the VH condition, the participants had to enclose the object with their left hand as in the H condition, and the goggles turned transparent.

After a variable period, the start tone was delivered, and participants had to perform a reaching and grasping action at their natural speed toward the object (Fig. 1*C*). No reaction time constrains were imposed. After 3 s, the end sound was delivered, and, only in the H condition, the goggles were made transparent. Participants had to move their right hand back to the home position and the left one to the object's side, and then the goggles turned opaque.

In 50% of the trials, participants grasped the object that was presented throughout the duration of the trial (unperturbed condition). In the other 50% of the trials, the object changed its size during the movement (perturbed condition; see Fig. 1*B*). The object changed its shape by sliding out either the index or the thumb side (25% of trials for each side). This perturbation was triggered when the grasping hand reached the midpoint between the home position and the object (Fig. 1*B*).

Each sensory condition was recorded in a separate block of trials. The order of these blocks was randomized across participants. We ran 40 trials for each sensory condition for a total of 120 trials per participant. Before the experiment, a training session was performed to accustom the participants with the task (10 trials for each sensory condition).

Data analysis. Kinematic data were analyzed in R (R Core Team 2018). The raw data were smoothed and differentiated with a third-order Savitzky-Golay filter with a window size of 21 points. These filtered data were then used to compute velocities and accelerations in three-dimensional space for each digit and the wrist. Movement onset was defined as the frame of the lowest, nonrepeating wrist acceleration value before a 50-ms sequence of continuously increasing wrist acceleration values (Volcic and Domini 2016, 2018), whereas the end of the grasping movement was defined on the basis of the Multiple Sources of Information method (Schot et al. 2010). We used the criteria that the grip aperture is close to the size of the object, that the grip aperture is decreasing, that the second derivative of the grip aperture is positive, and that the velocities of the wrist, thumb, and index finger are low. Moreover, the probability of a frame being the end of the movement decreased over time to capture the first frame in which the above criteria were met (Volcic and Domini 2016, 2018).

Trials in which the end of the movement was not captured correctly or in which the missing marker samples could not be reconstructed using interpolation were discarded from further analysis. Data from four participants have been excluded because of a high proportion of discarded trials (more than 5 trials excluded for a combination of sensory condition and perturbation). From the data of the remaining 16 participants, 104 trials (5.4%) were discarded, which left us with a total of 1,816 trials.

Two separate analyses were performed. In a first analysis (kinematic variables analysis), we computed the maximum grip aperture (MGA) and the movement duration (the time from the beginning to the end of the movement; Fig. 3). These two variables were analyzed with a repeated-measures ANOVA by considering the sensory conditions (H, V, VH) and the perturbation (perturbed and unperturbed trials) as the main factors. Bonferroni corrections were used for the pairwise comparisons.

The second analysis (grip aperture correction analysis) was focused on the compensatory adjustments of the grip aperture following the perturbation by comparing the grip aperture in the unperturbed and perturbed conditions for each sensory condition (Fig. 4, *top* row) for each time frame from perturbation onset to 300 ms after the perturbation onset. Grip apertures were averaged for each subject, each unperturbed/perturbed condition, each sensory condition, and each time frame (5-ms resolution) of the 300-ms-long time window. On each time frame, a paired t test was

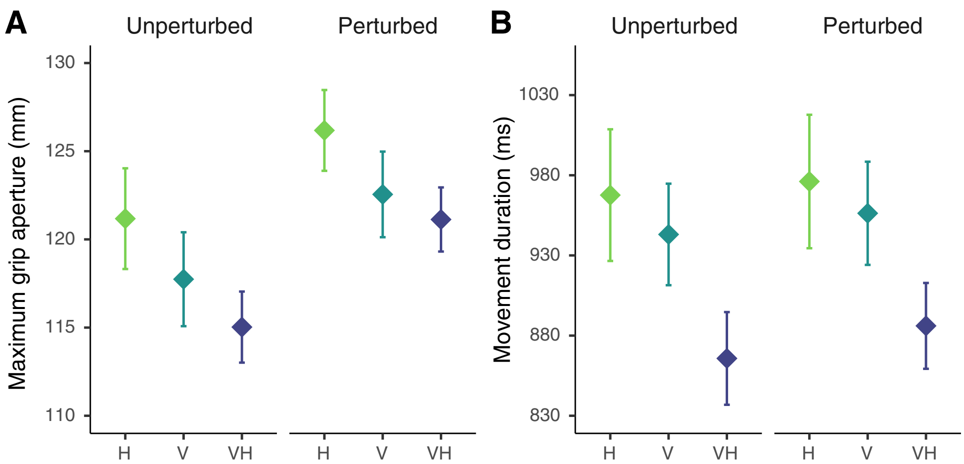

Fig. 3. Kinematic variables. Graphs show mean maximum grip aperture (*A*) and movement duration (*B*) from the beginning to the end of the trial for haptic (H), visual (V), and visuo-haptic (VH) conditions. Error bars are SE.

then used to compare the grip aperture between the perturbed and unperturbed conditions in each sensory condition. The correction latency was defined as the first point in time where the lower boundary of the 95% confidence interval (CI; obtained from the *t* tests) was positive and stayed positive for at least five consecutive time frames. To estimate the sampling distributions of the correction latencies for each sensory condition, we used the bootstrapping method in which 10,000 random samples of trials (with replacement) were chosen to create new data sets with the same properties of the original data set (number of participants and number of trials per participant). Correction latencies were then computed on each iteration using the above-specified method (*t* test at each time frame followed by the confidence interval method to extract the point in time when the perturbed grip apertures started to differ from the unperturbed grip apertures).

The sampling distributions of the correction latencies were then used to calculate the median correction latency with its 95% percentile bootstrap confidence interval for each sensory condition (Fig. 5*A*). Moreover, the correction latency differences between each pair of sensory conditions (H-V, H-VH, V-VH) were calculated to obtain the sampling distributions of the differences from which the median correction latency differences with their 95% percentile bootstrap confidence intervals were obtained (Fig. 5*B*). The correction latencies were considered to be significantly different between sensory conditions if their confidence intervals did not overlap with zero.

RESULTS

Kinematic variables. The analysis performed on the MGA showed a main effect for the factor condition [$F(2,30) = 11.096$, $P = 0.0002$, $\eta_p^2 = 0.44$] and perturbation [$F(1,15) = 87.74$, $P < 0.0001$, $\eta_p^2 = 0.85$] but no interaction effect. The post hoc test for the factor condition showed a larger MGA in H (124 ± 1.86 mm) compared with VH (118 ± 1.44 mm; $P = 0.002$) and V (120 ± 1.82 mm; $P = 0.02$), whereas no difference between V and VH was found. The difference in MGA between V and VH previously reported (Camponogara and Volcic 2019) was now probably masked by the mixture of unperturbed and perturbed trials. It is, in fact, known that grasping actions can be directly affected by increased uncertainty and by preceding actions (Bozzacchi et al. 2016; Volcic and Domini 2018; Whitwell et al. 2008). With regard to the factor perturbation, MGA was larger in the perturbed than in the unperturbed trials (perturbed: 123 ± 1.28 mm, unperturbed: 118 ± 1.48 mm). The analysis performed on the movement duration showed a main effect for the factor condition ($F(2,30) = 13.086$, $P < 0.0001$, $\eta_p^2 = 0.46$]. No effect of perturbation and no interaction were found. The post hoc test showed a longer movement duration in H (972 ± 28.8 ms) compared with VH (876 ± 19.5 ms; $P = 0.001$) and in V

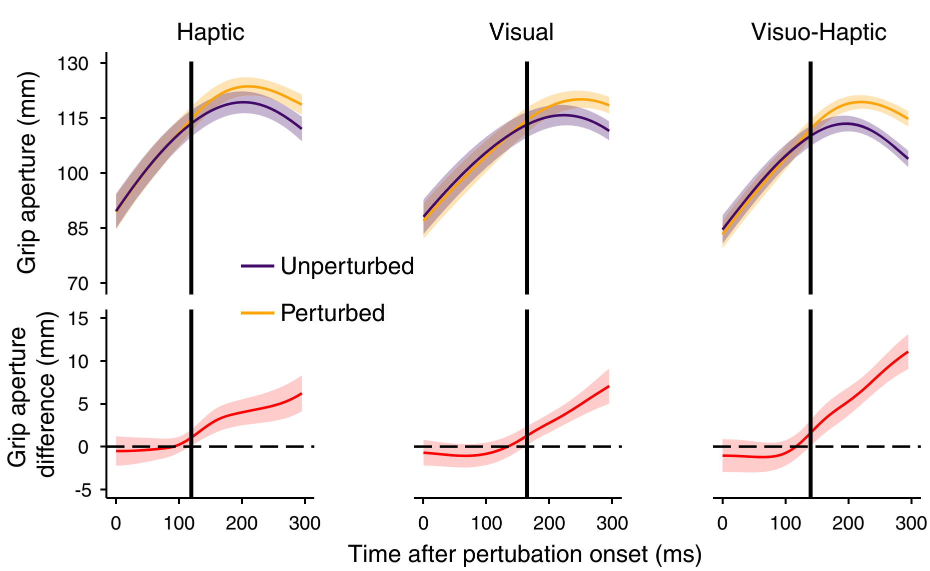

Fig. 4. Correction latency calculation. *Top*: average grip aperture in the haptic, visual, and visuo-haptic conditions in the perturbed (orange) and unperturbed (purple) conditions within a 300-ms time window after the perturbation onset. Shaded bands are SE. *Bottom*: grip aperture difference profiles representing the difference between perturbed and unperturbed conditions. Shaded bands represent the 95% confidence intervals of the difference. *Time 0* on the abscissa of each graph corresponds to the moment at which the perturbation occurred in the perturbed condition. Vertical black lines represent the time at which the grip aperture corrections were detected, i.e., when the grip aperture in the perturbed condition started to deviate from the grip aperture in the unperturbed condition.

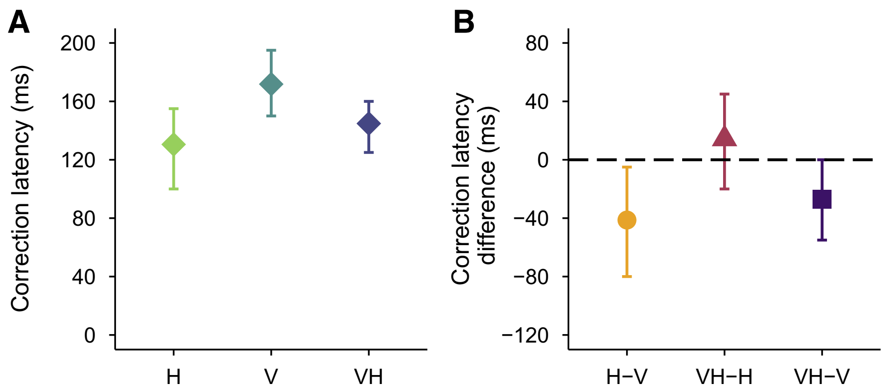

Fig. 5. Correction latency. *A*: medians and 95% confidence intervals for the correction latencies distributions for each sensory condition (H, haptic; V, visual; VH, visuo-haptic). *B*: medians and 95% confidence intervals for the differences between correction latencies distributions.

(950 ± 22.2 ms) compared with VH (P = 0.0001). No differences were found between H and V.

Grip aperture corrections. When the object did not change size, participants made smooth grasping movements toward the object irrespective of the available sensory information (see unperturbed conditions in Fig. 4, *top* row). When the object was suddenly perturbed, participants made the appropriate grip aperture corrections to shape the hand around the larger object (see perturbed conditions in Fig. 4, *top* row). Participants took 130 ms (95% CI: 100, 155) in the H sensory condition, 171 ms (95% CI: 150, 195) in the V sensory condition, and 144 ms (95% CI: 125, 160) in the VH sensory condition to initiate the grip aperture correction (Fig. 5*A*). The paired differences revealed that when haptic information was available, corrections were generally faster by ~30 ms (Fig. 5*B*). Correction latencies were shorter in H compared with V (−41 ms; 95% CI: −80, −5), equal for H and VH modalities (14 ms; 95% CI: −20, 45), and shorter in VH compared with V sensory condition (−26 ms; 95% CI: −55, 0). This time-domain analysis was further confirmed by an analysis in which the correction latencies were extracted from the space-normalized trajectories (Volcic and Domini 2016). This analysis showed the same pattern of results: correction latencies were shorter in H (120 ms; 95% CI: 89, 144) and VH (130 ms, 95% CI: 115, 142) compared with V (165 ms; 95% CI: 138, 189).

DISCUSSION

In this study we investigated whether grip aperture corrections are contingent on the sensory modality used to detect an object's size perturbation. We showed that, as for vision, haptic inputs can guide very fast grip aperture adjustments. However, we found that haptically triggered corrections were faster compared with those triggered by visual inputs. Interestingly, the simultaneous availability of haptic and visual inputs generated corrections as fast as those to haptic inputs only, but faster compared with those triggered by visual inputs only.

When perturbations are only haptically sensed, tactile and proprioceptive inputs from mechanoreceptors, muscle spindles, and tendons of the hand are sufficient to detect a change in the object properties (Berryman et al. 2006; Johansson and Flanagan 2009) and trigger a fast corrective adjustment of the contralateral hand. These adjustments occur ~130 ms after the perturbation onset and thus indicate the existence of a rapid haptomotor reflex similar to the visuomotor reflex that follows visual perturbations (Hesse and Franz 2009; Roy et al. 2006; Sarlegna and Mutha 2015; van de Kamp et al. 2009). Thus, as for vision, haptic information can be used to successfully update the ongoing action.

However, we showed that haptic perturbations trigger a faster movement correction of the contralateral hand compared with visually detected perturbations (H: ~130 ms; V: ~171 ms). Since the kinematic marker analysis showed a similar movement duration in both H and V conditions, it is unlikely that this difference is due to distinct temporal constraints between these conditions (Hesse and Franz 2009). It is more plausible that the haptic advantage is due to one or both of the following reasons. First, somatosensory, proprioceptive, and visual signals differ in terms of transmission latencies. The transmission latency for somatosensory and proprioceptive signals to travel from the periphery to the primary somatosensory area is shorter than the transmission latency for visual signals to travel from the retina to the primary visual cortex (somatosensory: ~30–60 ms; proprioceptive: ~60–100 ms; visual: ~75–100 ms) (Arnfred 2005; Mima et al. 1996; Walsh et al. 2005).

Second, the corrective responses to the haptic perturbation could have been triggered by either of two redundant signals (Todd 1912): the passive stretch of the fingers flexors' muscles and/or the increased pressure on the fingers' pads caused by the size change of the object. The availability of redundant proprioceptive and tactile inputs could also be the reason why our results differ from Pruszynski et al. (2016), who found equally fast movement corrections to tactile-only and visual-only perturbations. A further reason why we found faster corrections latencies in H compared with V condition, whereas Pruszynski et al. (2016) found no difference between tactile and visual conditions, could be due to biomechanical factors: redirecting the arm following a perturbation of the target position requires more effort compared with moving the index and thumb digits following a change in object size.

With regard to the comparison between the multisensory and unisensory conditions, we found that movement corrections in the VH condition were as fast as in the H condition and faster than in the V condition. This was surprising if we consider that multisensory inputs usually trigger faster responses compared with unisensory inputs (Forster et al. 2002; Girard et al. 2011; Hagmann and Russo 2016; Raab 1962; Wada 2010). It was even more surprising considering that grip aperture correction latencies tend to be faster when the time available for action correction is limited (Hesse and Franz 2009). Thus, even though the movement duration was shorter in the VH condition than in the unisensory conditions, the action corrections in VH were as fast as those in the H condition. A possible reason for the lack of a multisensory advantage could be due to haptics being the more appropriate modality for detecting a change in object size, and hence there was no reason to incorporate also the visual information (Welch and Warren 1980).

Although our study does not assess the underlying neural structures involved in grasping corrections, the ~30-ms delay of the visual corrections compared with the haptic and visuo-haptic corrections might suggest that these responses are mediated by different networks. Whereas the visual pathways are mainly located at the cortical level (Desmurget et al. 1999; Mutha et al. 2011; Pisella et al. 2000), the somatosensory pathways for reflexive responses are predominantly located at the spinal level (Allison et al. 1983; Mima et al. 1996; Walsh et al. 2005). Therefore, the haptomotor reflex might have benefited from the overlap and linear summation of the spinal and cortical sensorimotor integration processes to trigger faster action corrections than the visuomotor reflex (Pruszynski et al. 2008, 2011a,b; Weiler et al. 2019). In fact, it was recently suggested that the fine-tuning of corrective responses following an external arm perturbation partially occurs at the level of the spinal cord (Weiler et al. 2019). However, the specific interactions between the cortical and spinal neuronal circuitry during movement corrections following mechanic limb perturbations remain poorly understood.

In sum, our results show that haptically detected changes lead to successful motor adjustments of the contralateral hand via the haptomotor reflex. This reflex is substantially faster than the well-known visuomotor reflex and thus plays a pre-eminent role even when both haptic and visual information about the object perturbation are simultaneously available.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

I.C. and R.V. conceived and designed research; I.C. performed experiments; I.C. analyzed data; I.C. and R.V. interpreted results of experiments; I.C. prepared figures; I.C. and R.V. drafted manuscript; I.C. and R.V. edited and revised manuscript; I.C. and R.V. approved final version of manuscript.

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