Tool-Sensed Object Information Effectively Supports Vision for Multisensory Grasping

Ivan Camponogara[1, 2], Alessandro Farnè[3, 4], and Robert Volcic[2, 5, 6]

[1] Department of Psychology, College of Natural and Health Sciences, Zayed University
[2] Division of Science, New York University Abu Dhabi
[3] Integrative Multisensory Perception Action and Cognition Team, Lyon Neuroscience Research Center, Institut national de la santé et de la recherche médicale, Centre national de la recherche scientifique, University of Lyon 1
[4] Neuro-immersion, Hospices Civils de Lyon, Bron, France
[5] Center for Artificial Intelligence and Robotics, New York University Abu Dhabi
[6] Center for Brain and Health, New York University Abu Dhabi

Tools enable humans to extend their sensing abilities beyond the natural limits of their hands, allowing them to sense objects as if they were using their hands directly. The similarities between direct hand interactions with objects (hand-based sensing) and the ability to extend sensory information processing beyond the hand (tool-mediated sensing) entail the existence of comparable processes for integrating tool- and hand-sensed information with vision, raising the question of whether tools support vision in bimanual object manipulations. Here, we investigated participants' performance while grasping objects either held with a tool or with their hand and compared these conditions with visually guided grasping (Experiment 1). By measuring reaction time, peak velocity, and peak of grip aperture, we found that actions were initiated earlier and performed with a smaller peak grip aperture when the object was seen and held with the tool or the contralateral hand compared to when it was only seen. Thus, tool-mediated sensing effectively supports vision in multisensory grasping and, even more intriguingly, resembles hand-based sensing. We excluded that results were due to the force exerted on the tool's handle (Experiment 2). Additionally, as for hand-based sensing, we found evidence that the tool supports vision by mainly providing object positional information (Experiment 3). Thus, integrating the tool-sensed position of the object with vision is sufficient to promote a multisensory advantage in grasping. Our findings indicate that multisensory integration mechanisms significantly improve grasping actions and fine-tune contralateral hand movements even when object information is only indirectly sensed through a tool.

Public Significance Statement
Tools allow extending the hands' sensing capabilities beyond their anatomical limits. Here, we show that object information sensed through a tool can guide bimanual object manipulations as effectively as when directly sensed by the hand. Both tool-based and hand-mediated sensing provide relevant object positional information that is merged with vision to improve action performance. Our findings provide evidence about the interchangeable use of tools and hands for skilled actions and open new perspectives for prosthetic applications and rehabilitative plans.

Evolutionary speaking, tool use is a developmental milestone that allows different species to expand their motor repertoire and facilitate the interactions with objects otherwise unreachable, thus enhancing the chances of survival (Biro et al., 2013). Humans can use tools, such as a grabber, as an extension of the hand to manipulate objects located within and beyond their natural reaching capabilities (Bell & Macuga, 2022; Canzoneri et al., 2013; Cardinali, Brozzoli, Finos, et al., 2016; Cardinali et al., 2009, 2012; Costantini et al., 2011; Farnè, Bonifazi, & Làdavas, 2005; Farnè, Iriki, & Làdavas, 2005; Farnè & Làdavas, 2000; Gentilucci et al., 2004; Martel et al., 2019, 2021; Miller et al., 2017; Sposito et al., 2012) to the same degree as a natural hand grasp at both the kinematic (Gentilucci et al., 2004; Itaguchi & Fukuzawa, 2014) and neural levels (Gallivan et al., 2013; Jacobs et al., 2010; Johnson-Frey, 2004; Maravita & Iriki, 2004), suggesting common motor and neural control mechanisms for tool- and hand-mediated object manipulations.

Tools do not only expand our motor capabilities but they also allow humans to broaden their hand's inner haptic (proprioceptive and tactile) sensory abilities beyond its anatomical limits (Arbib et al., 2009; Burton, 1993; Gibson, 1966; Kilteni & Ehrsson, 2017; Klatzky & Lederman, 1999; Saig et al., 2012; Solomon & Turvey, 1988; Yamamoto et al., 2005; Yamamoto & Kitazawa, 2001) to an almost indistinguishable extent from hand-based sensing (Kilteni & Ehrsson, 2017; Miller et al., 2019, 2018; Takahashi et al., 2009; Takahashi & Watt, 2014, 2017). For instance, humans can easily localize objects' location using a rod by encoding the vibratory patterns elicited by the impact of a held rod with the object (Miller et al., 2019, 2018).

Concurrently, tools, such as pliers, can be used to detect the size of an object by decoding the distance between the digits holding the pliers (Takahashi et al., 2009; Takahashi & Watt, 2014, 2017). The striking similarity between tool-mediated and hand-based sensing entails a comparable integration process of tool- and hand-sensed information with vision. When a tool-held object is also simultaneously seen, the tool-sensed information integrates with vision in a hapticlike manner (Holmes et al., 2007; Takahashi et al., 2009; Takahashi & Watt, 2014, 2017), mimicking the same multisensory integration process occurring when the object is sensed by the hand (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Soto-Faraco et al., 2004). Additionally, it has been proposed that tool-mediated and hand-based sensing abilities share a common neural mechanism governing both sensing modalities (Miller et al., 2019). Thus, tools are incredible means to expand motor and sensory human capabilities, resembling handlike interactions with surrounding objects.

The stunning resemblance between the hand and the tool at the kinematic, perceptual, and neural levels raises the intriguing question of whether tools could also support bimanual object manipulations. In everyday life, we often interact with objects we already hold in our hand (e.g., passing our smartphone from one hand to the other). In this case, the haptic information stemming from hand-based sensing is sufficient to define the main features of an object, such as its size and position, and to guide the contralateral hand (Camponogara & Volcic, 2019a, 2019b, 2021, 2022) or tool grasping (Martel et al., 2019). However, when the object is concurrently felt and seen, the integration of redundant haptic and visual sensory information leads to superior grasping performance compared to when either vision- or haptic-only inputs are available (Camponogara & Volcic, 2019a, 2019b, 2021, 2022; Pettypiece et al., 2010). Specifically, actions in multisensory conditions (visuo-haptic) are performed faster and with

a smaller grip aperture compared to those in unisensory (haptic or visual) conditions (Camponogara & Volcic, 2019a, 2019b, 2021, 2022). Concurrently, the similar scaling of the maximum grip aperture according to the object size in visuo-haptic and visual conditions suggests that vision plays the primary role for the final hand shaping around the object (Camponogara & Volcic, 2021). By modulating the availability of haptic size during multisensory grasping, we additionally showed that within this multisensory–motor integration process, haptics plays a major role in providing positional information (Camponogara & Volcic, 2021, 2022). Thus, it is well-established that haptic inputs from the hand holding the object actively support vision in planning and executing accurate grasps. Yet, whether tool-mediated sensing also supports vision for multisensory grasping remains unknown.

Here, we filled this gap by examining the grasping performance toward seen and tool- or hand-held objects. In Experiment 1, we investigated whether tool-mediated sensing (sensing the to-be-grasped object with a grabber) could support vision in guiding contralateral hand grasping by comparing action performance toward objects that could only be seen (visual condition [V]) or toward seen and tool-held objects (visuo-tool condition [VT]). The level of multisensory advantage provided by the tool was further investigated by comparing these conditions with a condition in which objects were simultaneously seen and held by the hand (visuo-haptic condition [VH]). If tool-sensed information is irrelevant, we should see an unvaried grasping performance either with or without the additional support of the tool (i.e., similar performance in visuo-tool and visual conditions). In contrast, if tool-mediated sensing supports vision, we expect a superior grasping performance when tool-sensed information is available. Concurrently, if tool-mediated sensing and hand-based sensing support vision in equivalent ways (i.e., same multisensory advantage), we expect grasping actions to be similar in visuo-haptic and visuo-tool conditions. In Experiment 2, to exclude that the improvements in grasping kinematics were a mere effect of the force exerted by the hand clenching the tool, a phenomenon known as motor overflow (Addamo et al., 2007), we compared grasping performance with the tool either directly grasping the object (by exerting force to close the gripper) or simply touching it (without the need to exert any clenching force). If motor overflow plays a role, we expect any tool-mediated sensing advantage to disappear when the object is only touched and not held by the tool. Last, in Experiment 3, we investigated which tool-sensed information (object size or its position) is used in visuo-tool grasping. According to our previous works on visuo-haptic grasping (Camponogara & Volcic, 2021, 2022), we hypothesized that the tool supports vision by providing mainly positional object information.

Transparency and Openness

All data and data analysis scripts are available at Open Science Framework at https://osf.io/dtwfm/.

Experiment 1

Method

Participants

Twenty-two right-handed participants participated in this experiment (age = 20.2 ± 1.6 years). Power calculations based

on our previous studies (Camponogara & Volcic, 2021, 2022) and using the method proposed by Vasishth et al. (2018) showed that 20 participants were sufficient to detect a difference between conditions of the considered variables (reaction time ≈ 17 ms; peak velocity ≈ 25 mm/s; peak grip aperture ≈ 2 mm) with a power higher than 0.8 and an α level of .05. Two participants were excluded from the analysis because of technical issues during the experiment. All had normal or corrected-to-normal vision and no known history of neurological disorders. All of the participants were naïve to the purpose of the experiment and were provided with a subsistence allowance. The experiment was undertaken with the understanding and informed written consent of each participant, and the experimental procedures were approved by the institutional review board of New York University Abu Dhabi.

Apparatus

The set of stimuli consisted of three 150-mm high, 3D-printed cylinders with diameters of 30, 40, and 50 mm positioned at 350 mm from the participants' position. The tool consisted of a 55-cm long claw grabber, whose gripper closed by applying pressure on its handle (Figure 1a). A 5-mm high rubber bump with a diameter of 9 mm was attached just in front of the participants, 300 mm to the right. This bump was marking the start positions for the right hand. A pair of occlusion goggles (Red Scientific, Salt Lake City, Utah, United States) was used to prevent vision of the workspace between trials. A pure tone of 1,000 Hz, 100 ms duration was used to signal the start of the trial, while a tone of 600 Hz of the same duration was used to signal its end. Index, thumb, and wrist movements were acquired online at 200 Hz with submillimeter resolution using an Optotrak Certus system (Northern Digital Inc., Waterloo, Ontario, Canada). The position of the tip of each digit was calculated during the system calibration phase with respect to two rigid bodies defined by three infrared-emitting diodes attached on each distal phalanx (Nicolini et al., 2014). An additional marker was attached to the styloid process of the radius to monitor the movement of the arm. The Optotrak system was controlled by the MOtion Tracking with Optotrak and Matlab toolbox (Derzsi & Volcic, 2018).

Procedure

Participants sat comfortably at the table with their torsos touching its edge. All the trials started with the participants' thumb and index digit of the right hand positioned on the start positions, the left hand on the side, either free close in a fist on the table's edge at a comfortable distance or with the tool, and the shutter goggles closed. Before each trial, one of the objects was positioned in front of the participant. In the V condition, the goggles turned transparent, and participants had only visual information about the object. In the VT condition, once the goggles turned transparent, the experimenter signaled the participants to move the tool's gripper to the object and close it on the object's base.

In the VH condition, once the goggles turned transparent, the experimenter signaled the participants to hold the object with their left-hand index and thumb at its base (i.e., sense its size and position through tactile and proprioceptive inputs). Thus, participants had both visual and haptic information about the object (Figure 1b). Hence, while in VH, the object size and position were sensed through haptics, in VT these properties were sensed through the tool

Figure 1
Experiment 1
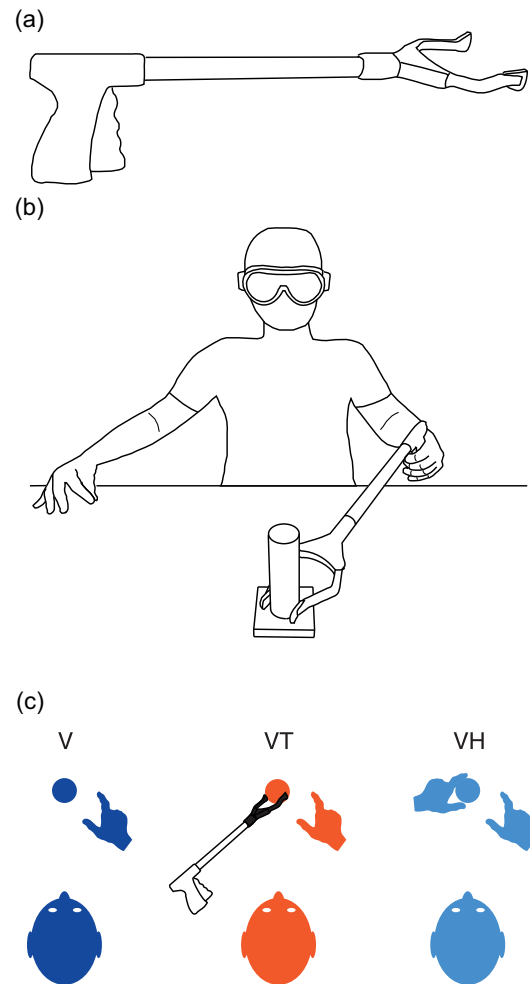
Note. Experiment 1 setup and procedure. (a) The tool used in the experiment was a grabber of 55-cm length. The gripper was closed by pressing the handle. (b) Experimental setup. Participant's sat at the edge of the table with the occlusion goggles on. Grasping actions were always performed with the right hand, and the tool was operated with the left hand. The picture represents the starting position in the VT condition. (c) Representation of the task in each condition (top view). In the V condition, participants had to perform a visually guided reach-to-grasp movement. In the VT condition, objects were concurrently held with the tool, whereas in the VH condition, objects were held with the left hand. V = visual; VT = visuo-tool; VH = visuo-haptic. See the online article for the color version of this figure.

(Figure 1c). After a variable period (1–1.5 s), the start tone was delivered, and participants had to reach for and grasp the object with their right hand. Movements were performed at a natural speed, and no speed constraints were imposed. After 3 s, the end sound was delivered, and participants had to move their right and left hands/tool back to the start positions, and then the goggles turned opaque. Another object was selected, and the next trial was ready to start. The order of conditions was randomized across participants, while object sizes were randomized within each condition. We ran

15 repetitions for each object size, which led to a total of 135 trials per participant (45 for each condition). During the experiment, trials were discarded and reperformed when: the participant did not start the movement when the start sound was delivered, or the participant did not complete the grasping before the end sound, or the movement started before the start sound was delivered, or the markers were not visible for 15% of the time. Before the experiment, a training session was performed in which 10 trials were run in each condition to accustom the participants to the task.

Data Analysis

Kinematic data were analyzed in R (R Core Team, 2020). 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 wrist. Movement onset was defined as the moment of the lowest, nonrepeating wrist acceleration value prior to the continuously increasing wrist acceleration values (Volcic & Domini, 2016), while 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 moment being the end of the movement decreased over time to capture the first instance in which the above criteria were met. We removed from the analysis trials in which: the movement initiated before the start tone (10 trials in total); the reaction time was lower than 50 ms or exceeded 900 ms, which correspond to the 1st and 99th quantiles (11 trials in total); the end of the movement was not captured correctly; or in which the missing marker samples could not be reconstructed using interpolation (six trials in total). The exclusion of these trials (63 trials, 2.3% in total) left us with 2,637 trials.

We focused our analyses on three dependent variables: the response time (RT), defined as the time from the start tone to the movement onset; the peak velocity of the hand movement (PV), defined as the highest wrist velocity along the movement; and the peak grip aperture (PGA), defined as the maximum Euclidean distance between the thumb and the index finger. We analyzed the data using Bayesian linear mixed-effects models, estimated using the brms package (Bürkner, 2017), which implements Bayesian multilevel models in R using the probabilistic programming language Stan (Carpenter et al., 2017). The models included as fixed effects (predictors) the categorical variable condition (V, VH, and VT) in combination with the continuous variable size. This latter was centered before being entered into the models. Thus, the estimates of the condition parameters ($\beta_{Condition}$) correspond to the average performance of each condition. The estimates of the parameter size (β_{Size}) correspond instead to the change in the dependent variables as a function of the object size. All models included independent random (group-level) effects for subjects. Models were fitted considering weakly informative prior distributions for each parameter to provide information about their plausible scale. For all the considered variables, we used weakly informative Gaussian priors for the condition and size fixed-effect predictors based on our previous studies (Camponogara & Volcic, 2019a, 2019b, 2021, 2022; RT $\beta_{Condition}$: $M = 250$ and $SD = 50$,

β_{Size}: $M = 0$ and $SD = 5$; PV $\beta_{Condition}$: $M = 1,100$ and $SD = 300$, β_{Size}: $M = 0$ and $SD = 5$; PGA $\beta_{Condition}$: $M = 75$ and $SD = 10$, β_{Size}: $M = 0.7$ and $SD = 0.5$). For group-level standard deviations and sigmas, we used default regularizing priors (Student's t distributions). Finally, we set a prior over the correlation matrix that assumes that smaller correlations are slightly more likely than larger ones (Lewandowski–Kurowicka–Joe prior set to two).

For each model, we ran four Markov chains simultaneously, each for 12,000 iterations (1,000 warm-up samples to tune the Markov chain Monte Carlo sampler) with the δ parameter set to 0.9 for a total of 44,000 postwarm-up samples. Chain convergence was assessed using the $\hat{R}$ statistic (all values equal to one) and visual inspection of the chain traces. Additionally, the predictive accuracy of the fitted models was estimated with leave-one-out cross-validation by using the Pareto smoothed importance sampling. All Pareto k values were below 0.5.

The posterior distributions we have obtained represent the probabilities of the parameters conditional on the priors, model, and data, and they represent our belief that the "true" parameter lies within some interval with a given probability. We summarize these posterior distributions by computing the medians and the 95% highest density intervals (HDIs). The 95% HDI specifies the interval that includes, with a 95% probability, the true value of a specific parameter. To evaluate the differences between parameters of two conditions, we have simply subtracted the posterior distributions of $\beta_{Condition}$ and β_{Size} weights between specific conditions. The resulting distributions are denoted as the credible difference distributions and are again summarized by computing the medians and the 95% HDIs.

For statistical inferences about the β_{Size}, we assessed the overlap of the 95% HDI with 0. A 95% HDI that does not span 0 indicates that the predictor has an effect on the dependent variable. For statistical inferences about the differences of the model parameters, $\beta_{Condition}$ and β_{Size}, between conditions, we applied an analogous approach. A 95% HDI of the credible difference distribution that does not span 0 is taken as evidence that the model parameters in the two conditions differ from each other. To assess the strength of evidence, we computed the Bayes factor for each comparison. The reported Bayes factor values (BF_{10}) that are higher than 3 provide evidence in support of a difference between conditions, whereas values below $\frac{1}{3}$ provide evidence in support of an absence of a difference between conditions (Lee & Wagenmakers, 2014).

Results and Discussion

We found that movements were released earlier (RT) and performed with a narrower PGA in the visuo-tool compared to the visual condition (Figure 2, panels a, and g), suggesting a successful integration of tool-mediated and visual sensory information. Interestingly, the RT and peak of grip aperture in the visual-tool condition were similar to the visuo-haptic condition. Corroborating our previous results (Camponogara & Volcic, 2019a, 2019b, 2021, 2022), we found a faster action with a narrower PGA in the visuo-haptic compared to the visual condition.

The RT was modulated according to the available sensory information (Figure 2, Panels a and b), with an advantage when the object was concurrently seen and held by the tool (VT) or the hand (VH) compared to when it was only seen (V). The comparisons between conditions are represented in Figure 2, Panel c. The RT was

Figure 2

Summary of Experiment 1 Results
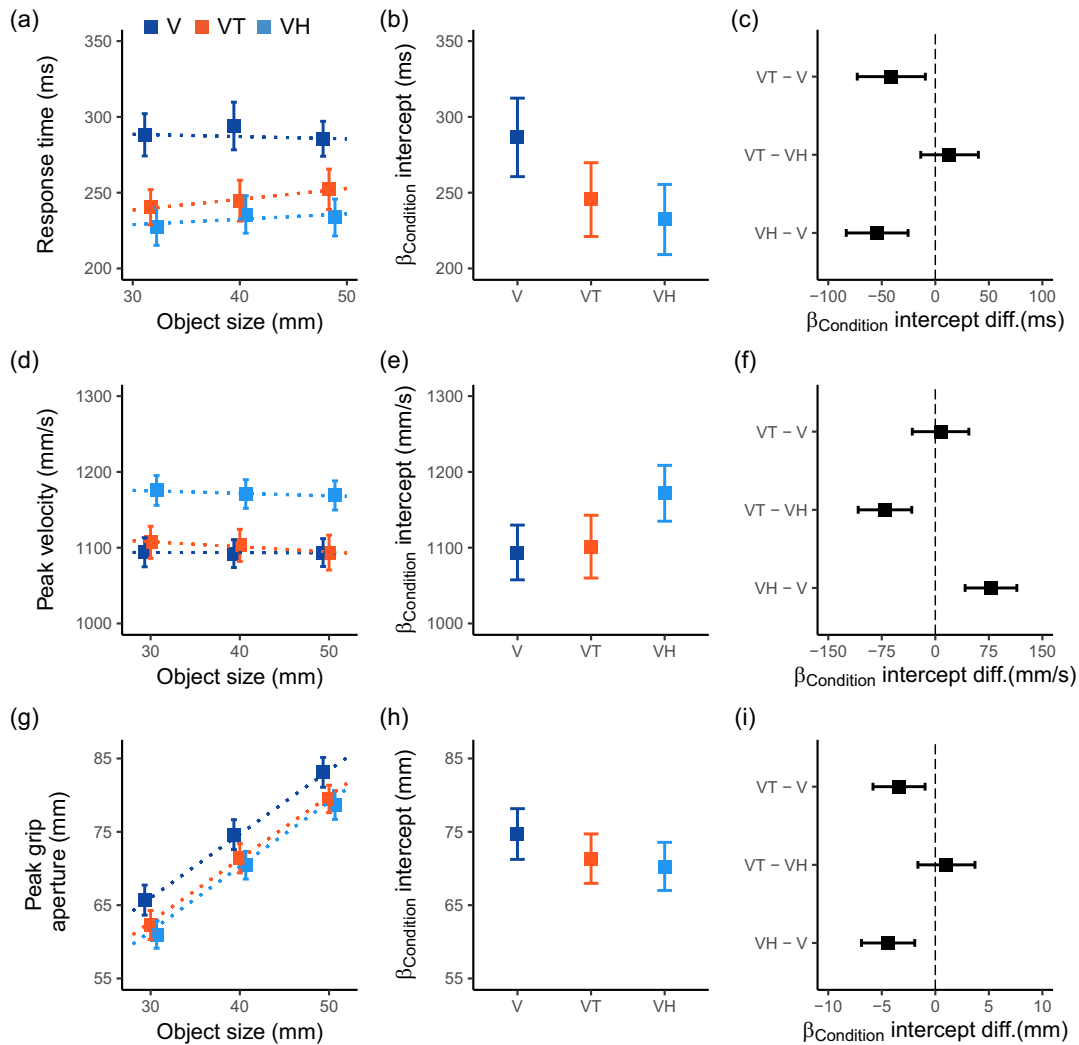
Note. Top row: response time; middle row: peak velocity; bottom row: peak grip aperture results. Panel a: median; Panels d and g: data averaged as a function of the object size; Panels b, e, and h: posterior β weights of the Bayesian linear mixed-effects regression model for the predictor condition; Panels c, f, and i: credible difference distributions between conditions for the predictor condition. In Panels a, d, and g, the error bars represent the standard error of the mean. The dotted lines show the Bayesian mixed-effects regression model fits. In Panels b, c, e, f, h, and i, the error bars represent the 95% HDIs of the distributions. V = visual; VT = visuo-tool; VH = visuo-haptic; HDI = highest density interval; diff. = difference. See the online article for the color version of this figure.

credibly lower in VT compared to V ($BF_{10} = 5.42$) and in VH compared to V ($BF_{10} = 63.23$), with no differences between VT and VH ($BF_{10} = 0.30$). The RT was not affected by changes in object size in any of the conditions, with slope values ranging between -0.13 and 0.59 corresponding to minimal variations in RT between the smallest and the largest object (~3 ms to ~12 ms difference equivalent to ~1%–6% of the average RT).

The PV was modulated according to the available sensory information as well, but actions were equally fast when the object was only seen or both seen and held with the tool (Figure 2, Panels e and f). We replicated our previous finding by showing a credibly higher PV ($BF_{10} = 36.90$) in VH compared to V (Camponogara &

Volcic, 2019b, 2021, 2022). The PV was similar between V and VT ($BF_{10} = 0.04$), whereas it was also credibly higher in VH compared to VT ($BF_{10} = 12.02$). Additionally, it was not affected by a change in the object size in V and VH and showed only a minimal variation in VT. Results showed a slope value in VT of -0.67 (95% HDI $[-1.23, -0.10]$), which corresponds to a change of ~14 mm/s from the largest to the smallest objects (equivalent to ~1% of the average PV).

The PGA was also clearly affected by the available sensory inputs (Figure 2, Panels h and i). The PGA was smaller in VT compared to V ($BF_{10} = 3.07$) and similar between VT and VH conditions ($BF_{10} = 0.12$). These patterns of results were remarkably consistent

across participants (Figure 3), suggesting that position and size information sensed from the tool can be effectively used to aid vision and improve grasping performance. PGA was credibly smaller in the VH condition compared to the V condition (BF_{10} = 15.47), confirming that the simultaneous availability of visual and haptic inputs leads to a multisensory advantage (Camponogara & Volcic, 2019b, 2021, 2022).

Thus, tool-sensed object information was effectively integrated with vision to support grasping performance. Tool-mediated sensing may have occurred by translating the haptic information from the hand holding the tool in positional and size information. Specifically, a change in the object size required modulation of the clenching force exerted on the handle to close the tool's gripper

on the object. This force modulation was also associated with a concurrent change of the distance between the thumb and the other four fingers, a cue that may have been used to infer the object size (Berryman et al., 2006; Takahashi et al., 2009; Takahashi & Watt, 2014). Concurrently, the pattern of somatosensory inputs generated by the impact of the tool's gripper with the object (Miller et al., 2019, 2018) and the haptic inputs stemming from the inertia generated by the active placement of the tool's gripper on the object (Chan, 1994; Solomon et al., 1989; Solomon & Turvey, 1988) may have been used to infer the tool's length and, consequently, the object's position. However, the faster action initiation and the smaller PGA observed when vision was complemented with tool-sensed information may have been alternatively aroused from the

Figure 3
Scatterplots of Paired Observations in Experiment 1
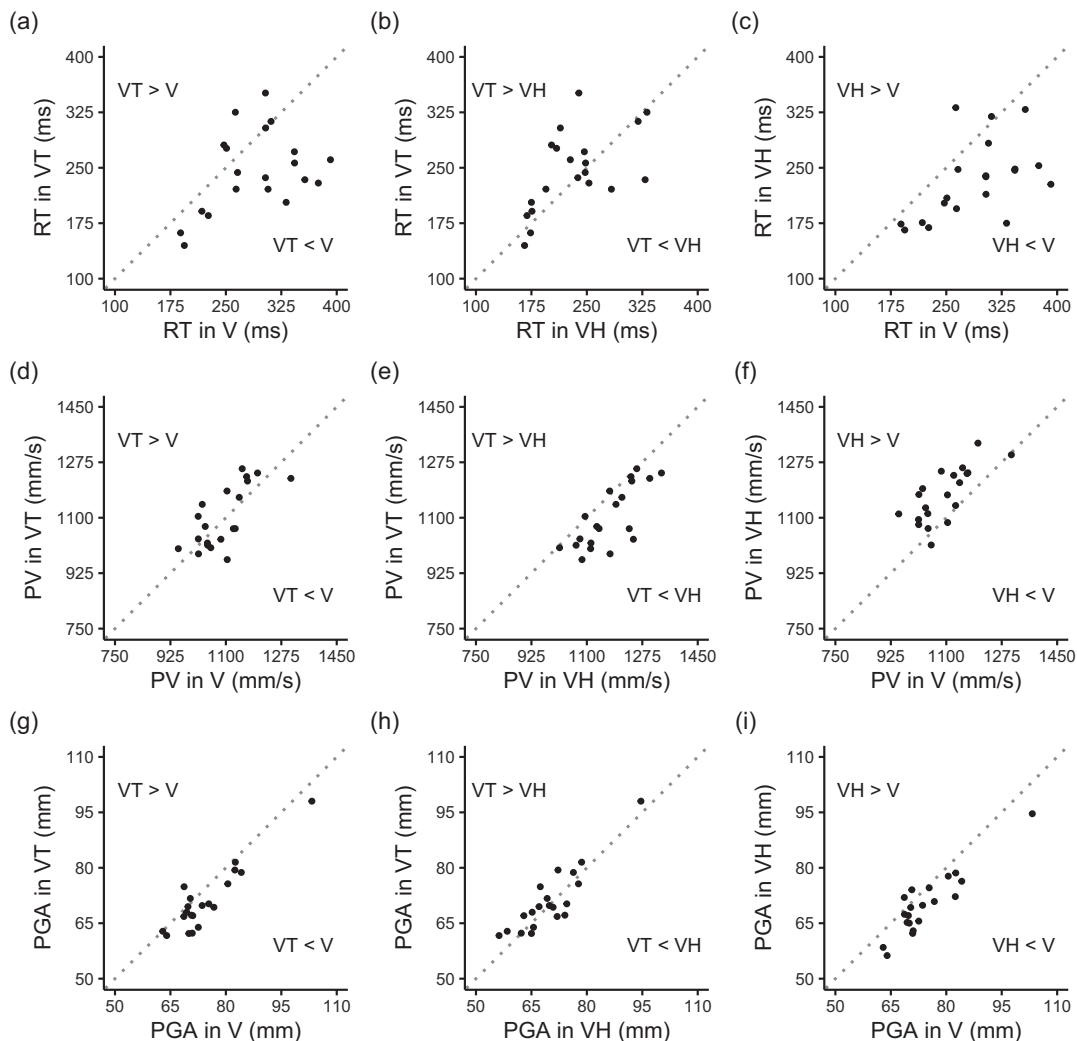
Note. Each point represents the average response time (top row, RT), average peak velocity (middle row, PV), and average peak of grip aperture (bottom row, PGA) of a single participant for a pair of conditions: first column, Panels a, d, and g—VT and V; second column, Panels b, e, h—VT and VH; third column, Panels c, f, and i—VH and V. The diagonal reference line of no effect has slope 1 and intercept 0. Points above the diagonal line indicate that the variable of the condition represented on the ordinate axis is larger than the variable represented on the abscissa. V = visual; VT = visuo-tool; VH = visuo-haptic; RT = reaction time; PV = peak velocity; PGA = peak grip aperture.

influence of the clenching force exerted on the tool's handle. Studies on bimanual interactions showed that exerting force with one limb generates a mirrored involuntary movement of the homologous muscles in the contralateral limb, a phenomenon that is known as "motor overflow" (see Addamo et al., 2007, for a review). Even though its origin is still under debate, several studies claim that the motor overflow stems from a facilitatory effect of the movement-related cortical regions onto the homologous contralateral areas in the opposite hemisphere (Hoy et al., 2004). Thus, exerting a clenching force on the tool's handle might have promoted a preactivation of the cortical areas involved in the contralateral limb control (i.e., the grasping limb), which enabled a faster release of the motor plan with a concurrent reduction of the overall grip aperture. To test whether the results in the VT condition were due to the motor overflow, a second experiment was performed where we manipulated the clenching force exerted on the handle by asking participants to either close or not the tool's gripper on the to-be-grasped object. If actions are affected by the motor overflow, we expected the right-hand reach-to-grasp actions to be released earlier (i.e., shorter RT) and with a smaller grip aperture when the gripper is closed than when it is not.

Experiment 2

Method

Participants

Nineteen right-handed new participants took part in Experiment 2 (age = 20.9 ± 2.9 years). All had normal or corrected-to-normal vision and no known history of neurological disorders. All of the participants were naïve to the purpose of the experiment and were provided with a subsistence allowance. The experiment was undertaken with the understanding and informed written consent of each participant, and the experimental procedures were approved by the institutional review board of New York University Abu Dhabi.

Apparatus

The experimental setup was the same as in Experiment 1, except that a new set of stimuli was used, which consisted of three cylinders of 60-mm height supported by a 60-mm high cylindrical post of 10-mm diameter (Figure 4a). The upper part of these stimuli was identical to the first set of stimuli and thus varied in diameter across trials. The post supporting the upper part had instead a fixed diameter. Thus, enclosing the gripper on the post led to a constant clenching force level on the handle across the different object sizes.

Procedure

The procedure was the same as for the visuo-tool condition of Experiment 1. In a visuo-tool-closed condition (VTC), participants closed the tool's gripper around the post supporting the object (Figure 4b), whereas in the visuo-tool-open condition the gripper was kept open, with the left tip in contact with the object's post (Figure 4c). The order of the conditions was randomized across participants. Object sizes were randomized within each condition, and 15 trials were performed for each object size and condition, which led to a total of 90 trials per participant. During the experiment trials were discarded and reperformed when: the participant did not start the movement when the start sound was delivered, or the participant did not complete the grasping before the end sound, or the movement started before the start sound was delivered, or the markers were not visible for 15% of the time. Before each condition, participants underwent a training session of 10 trials to get accustomed with the task.

Figure 4
Experiment 2 Setup and Procedure
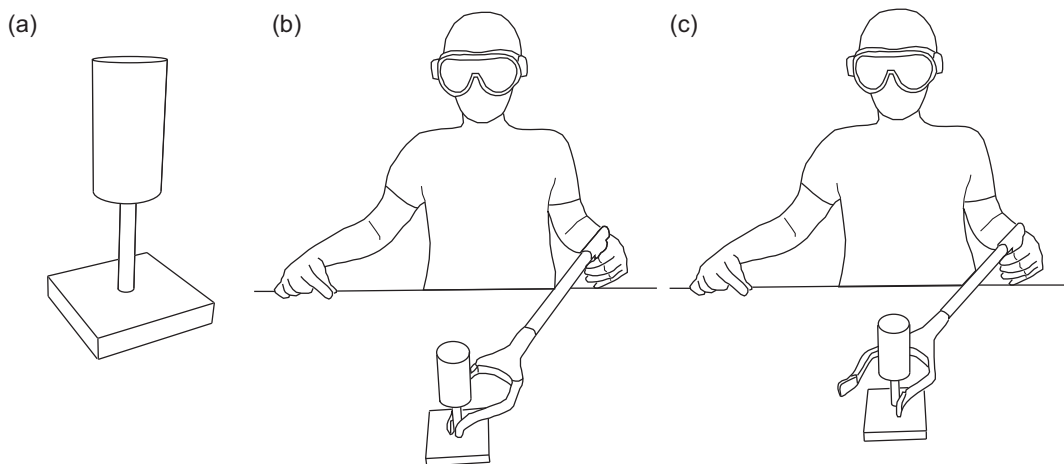
Note. (a) Example of a stimulus used in Experiment 2. (b) Representation of the task in the visuo-tool-closed condition. Participants closed the tool's gripper on the post supporting the to-be grasped object. (c) Representation of the task in the visuo-tool-open condition. Participants kept the tool's gripper open, with the left tip of the gripper touching the post supporting the object.

Data Analysis

The raw data processing and the statistical analyses were identical to those of Experiment 1. We removed from the analysis trials in which: the movement initiated before the start tone (seven trials in total), the reaction time was lower than 50 ms or exceeded 900 ms (five trials in total), the end or start of the movement was not captured correctly, or in which the missing marker samples could not be reconstructed using interpolation (26 trials in total). The exclusion of these trials (38 trials, 2.2% in total) left us with 1,672 trials for the final analysis. As in Experiment 1, we focused our analyses on RT, PV, and PGA. The $\hat{R}$ statistic and visual inspection

of the chain traces confirmed successful chains convergence. All Pareto k values were below 0.5. As in Experiment 1, we report the posterior distribution of the $\beta_{Condition}$ and β_{Size} for each condition and contrast the different conditions by computing the differences between the posterior distributions for each predictor.

Results and Discussion

Movements were almost indistinguishable between the two conditions, with a slightly higher velocity when the tool's gripper was closed compared to when it was open (Figure 5).

Figure 5

Summary of Experiment 2 Results
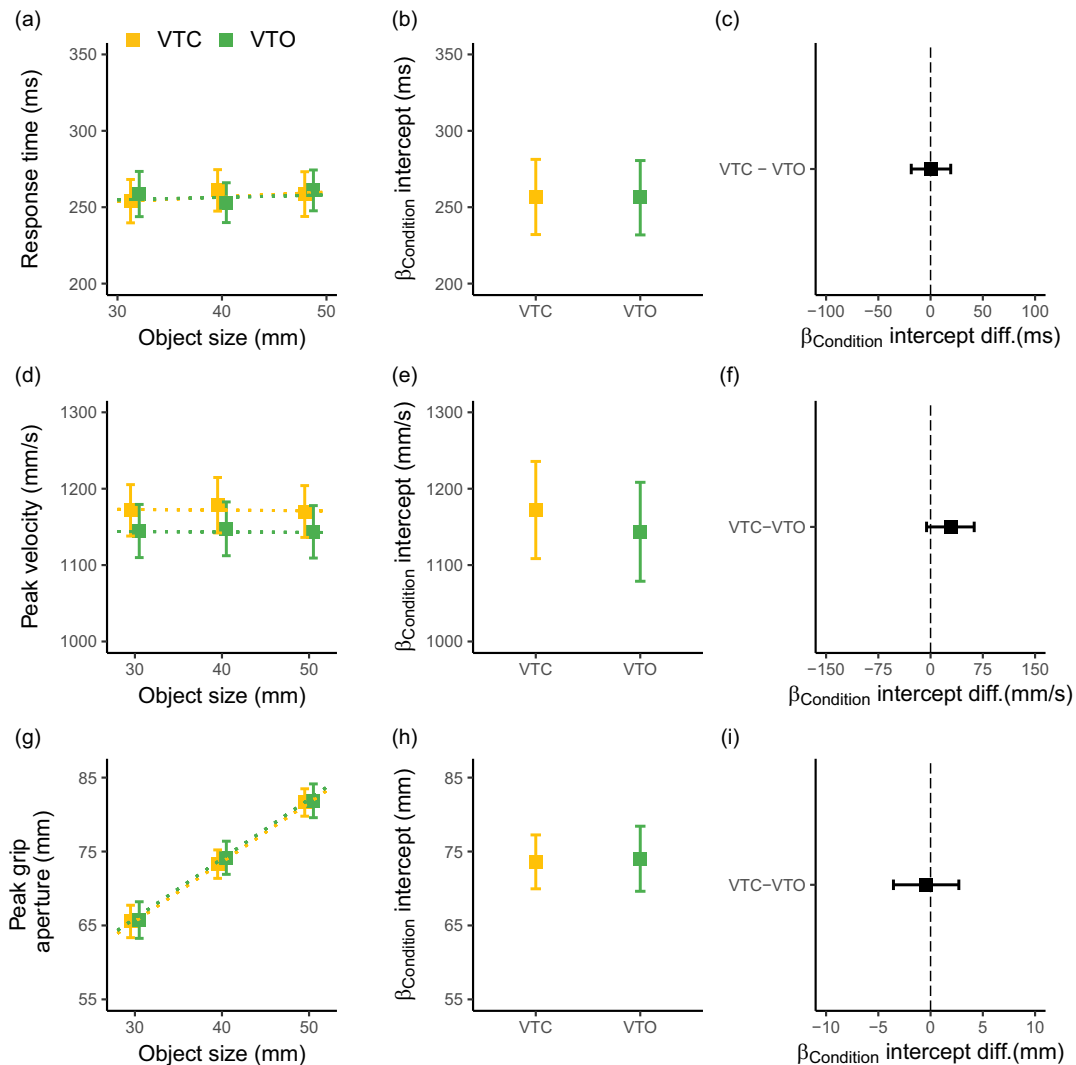
Note. Top row: reaction time; middle row: peak velocity; bottom row: peak grip aperture results. Panels a, d, and g: data averaged as a function of the object size; Panels b, e, and h: posterior β weights of the Bayesian linear mixed-effects regression model for the predictor condition; Panels c, f, and i: credible difference distributions between conditions for the predictor condition. In Panels a, d, and g, the error bars represent the standard error of the mean. The dotted lines show the Bayesian mixed-effects regression model fits. In Panels b, c, e, f, h, and i, the error bars represent the 95% HDIs of the distributions. HDI = highest density interval. VTC = visuo-tool-closed; VTO = visuo-tool-open; diff. = difference. See the online article for the color version of this figure.

Actions initiated approximately ~260 ms following the start tone for both conditions, with no differences between conditions ($BF_{10} =$ 0.12) and no modulation of the RT according to the object size (slope values of 0.26 and 0.13 for the VTC and visuo-tool-open conditions, respectively). The PV was similar between conditions ($BF_{10} = 0.18$), as well as the PGA and the PGA scaling ($BF_{10} =$ 0.11). As seen in the Experiment 1, these patterns of results were consistent across participants (Figure 6).

Taken together, our results support that action performance toward a seen and a tool-held object in Experiment 1 resulted from the concurrent use of tool and vision. It is also interesting to notice that by grabbing the post supporting the object, only positional and not size information could be sensed through the tool. Even though the tool-sensed size was prevented, results were comparable to those found in the VT condition of Experiment 1, where both position and size were available. This suggests that, in both experiments, the tool may have supported vision by mainly providing relevant positional information, which was integrated with visual position and size to enable superior grasping performance. If this is the case, the tool may have played an equivalent role of haptics in visuo-haptic grasping. Previous studies showed that haptic object position is indeed sufficient to produce the typical multisensory advantage characterizing actions toward seen and held objects (Camponogara & Volcic, 2021, 2022). To further investigate whether the tool-sensed positional information is sufficient to promote a grasping advantage, we ran a third experiment where we manipulated the availability of tool-sensed object size information. If the tool-sensed size is crucial for the grasping performance, preventing access to haptic object size will increase the peak of the grip aperture and reduce the grip aperture scaling compared to when the object size is available. In contrast, if the position is sufficient to provide an advantage, we expect a comparable performance, either with or without the concurrent presence of size information. According to our previous results with hand-held and seen objects, in either case, we expect no change in the RT and PV since in both conditions, positional information is constantly provided (Camponogara & Volcic, 2021).

Experiment 3

Method

Participants

Twenty-one right-handed new participants took part in Experiment 3 (age = 21.3 ± 2.77). One participant was excluded from the analysis because of technical issues during the experiment. All had normal or corrected-to-normal vision and no known history of neurological disorders. All of the participants were naïve to the purpose of the experiment and were provided with a subsistence allowance. The experiment was undertaken with the understanding and informed written consent of each participant, and the experimental procedures were approved by the institutional review board of New York University Abu Dhabi.

Apparatus

We made use of the same experimental setups and sets of objects already used in Experiments 1 and 2. To recap, the first set of objects consisted in three cylinders whose diameter of 30, 40, and 50 mm was constant along their whole height (150 mm). The second sets of objects consisted of three cylinders of 75-mm height supported by a 75-mm high cylindrical post of 10-mm diameter (Figure 7a). The upper part of these stimuli was identical to the first set of stimuli and, thus, varied in diameter across trials. The post supporting the upper part had a fixed diameter instead.

Procedure

We chose the VT and the VTC conditions of Experiments 1 and 2, respectively. In the VT condition, participants were presented with the first sets of objects, thus having access to both tool-sensed position and size information (Figure 7b). In the VTC condition, the second set of objects was presented; thus, the tool could be used only to sense object positional information (Figure 7c). The order of the conditions was randomized across participants, whereas the object sizes were randomized within each condition. Fifteen trials were

Figure 6
Scatterplots of Paired Observations in Experiment 2
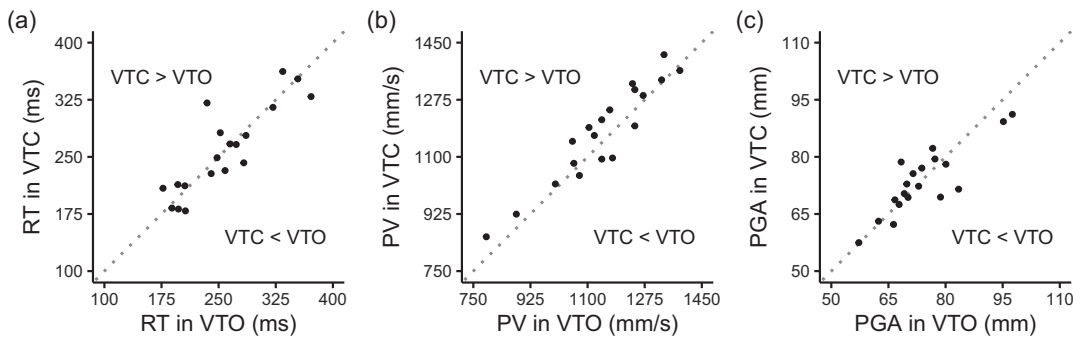
Note. Each point represents the average response time (RT, a), average peak velocity (PV, b), and average peak of grip aperture (PGA, c) of a single participant for a pair of conditions. The diagonal reference line of no effect has slope 1 and intercept 0. Points above the diagonal line indicate that the variable of the condition represented on the ordinate axis is larger than the variable represented on the abscissa. VTC = visuo-tool-closed; VTO = visuo-tool-open.

Figure 7
Experiment 3 Setup and Procedure

(a)   (b)   (c)
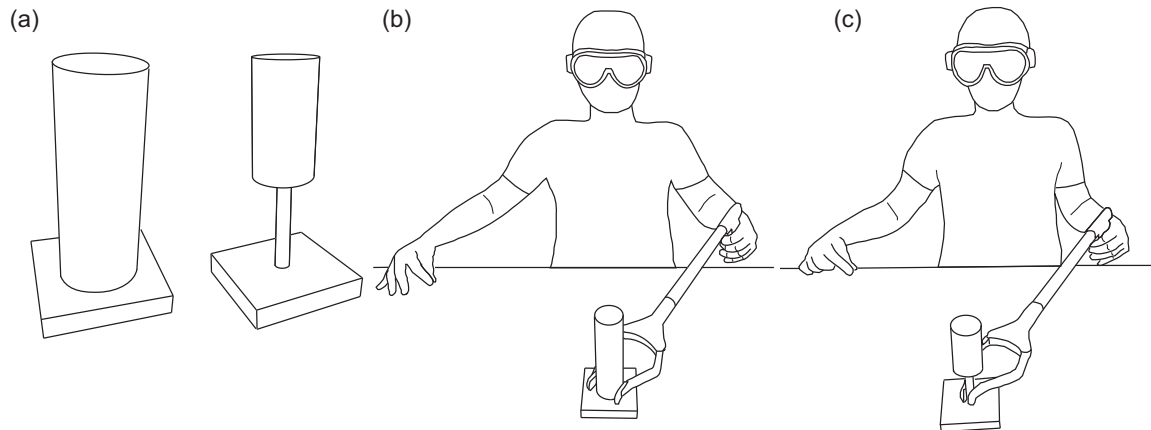
Note. (a) Example of the sets of objects used in Experiment 3. (b) Representation of the task in the visuo-tool condition. Participants closed the tool's gripper on the base of the object, thus sensing both position and size information through the tool. (c) Representation of the task in the visuo-tool-closed condition. Participants closed the tool's gripper on the post supporting the to-be grasped object, thus sensing only position information through the tool.

performed for each object size and condition, which led to a total of 45 trials per condition (90 per participant). During the experiment, trials were discarded and reperformed when: the participant did not start the movement when the start sound was delivered or the participant did not complete the grasping before the end sound, or the movement started before the start sound was delivered, or the markers were not visible for 15% of the time. Before each condition, participants underwent a training session of 10 trials to get accustomed to the task.

Data Analysis

The raw data processing and the statistical analyses were identical to those of Experiments 1 and 2. We removed from the analysis trials in which: the movement initiated before the start tone (two trials in total), the reaction time was lower than 50 ms or exceeded 900 ms (three trials in total), the end or start of the movement was not captured correctly (12 trials in total), or in which the missing marker samples could not be reconstructed using interpolation (26 trials in total). The exclusion of these trials (43 trials, 2.38% in total) left us with 1,757 trials for the final analysis. As in Experiments 1 and 2, we focused our analyses on RT, PV, and PGA. The $\hat{R}$ statistic and visual inspection of the chain traces confirmed successful chain convergence. All Pareto k values were below 0.5. We reported the posterior distribution of the $\beta_{Condition}$ and β_{Size} for each condition and contrasted the different conditions by computing the differences between the posterior distributions for each predictor.

Results and Discussion

Results showed identical movements either with or without the concurrent availability of object size information (Figure 8), and resembled those obtained in the VT and VTC conditions in Experiments 1 and 2, respectively.

The action plan was released ∼260 ms following the start tone (no difference in RT between conditions, $BF_{10} = 0.16$), with no

modulation according to the object size (slope values of −0.36 and 0.62 for the VT and VTC conditions, respectively). The PV was identical in both conditions ($BF_{10} = 0.04$), again with no modulation according to the object size (slope values of −0.54 and −0.18 for the VT and VTC conditions, respectively). Interestingly, the PGA and its scaling were indistinguishable between conditions as well ($BF_{10} = 0.51$), confirming the main role of the tool-sensed position within the sensory integration process. These patterns of results were very consistent across participants (Figure 9).

Thus, as seen for visuo-haptic grasping (Camponogara & Volcic, 2021, 2022), results showed that the tool also supports vision by providing mainly positional information. This further corroborates the hypothesis that tools can extend the sensory capacity beyond the body and sensory inputs from the tool can be used as those coming from our own limb (Miller et al., 2019, 2023, 2018). Here, we extended such findings by showing that this tool-sensed information can be actively used to guide a contralateral hand's grasping.

General Discussion

In this study, we demonstrated that tool-mediated sensing can guide skilled bimanual object manipulations: In the first experiment, we demonstrated that humans can successfully integrate tool-mediated object information with vision to guide contralateral hand grasping. Actions assisted by tool-mediated sensing initiated as early as those assisted by hand-based sensing and were performed with the same peak grip aperture. Both types of action outperformed grasping actions based only on visual information. In a second experiment, we excluded that grasping performance based on tool-mediated sensing was affected by the clenching force exerted on the tool's handle, suggesting a genuine combination of tool-sensed information with vision. Even more intriguingly, in a third experiment, we found that the underpinning mechanisms of tool-mediated sensing resemble those of hand-based sensing in multisensory grasping. As for the real hand, the tool supports vision mainly by providing information about

Figure 8
*Summary of Experiment 3 Results*
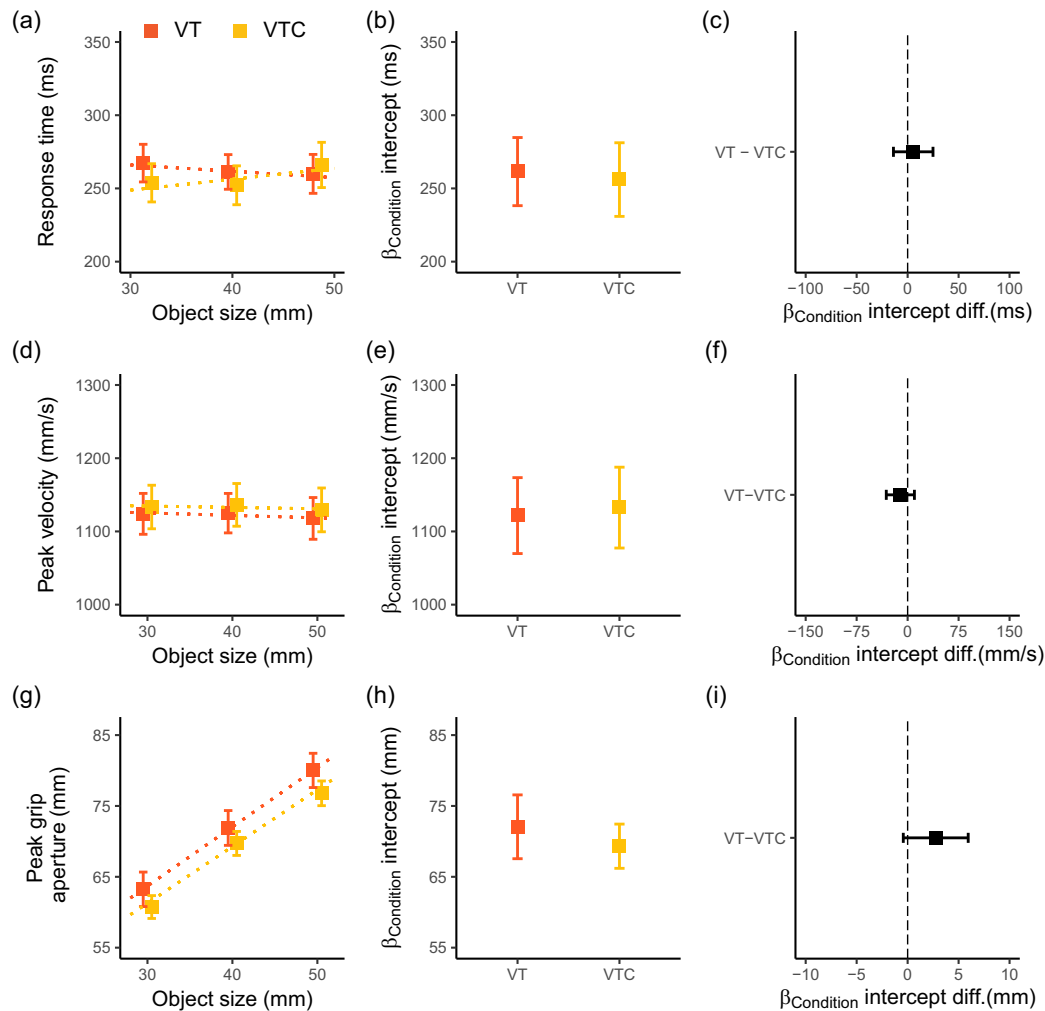
Note. Top row: response time; middle row: peak velocity; bottom row: peak grip aperture results. Panels a, d, and g: data averaged as a function of the object size; Panels b, e, and h: posterior β weights of the Bayesian linear mixed-effects regression model for the predictor condition; Panels c, f, i: credible difference distributions between conditions for the predictor condition. In Panels a, d, and g, the error bars represent the standard error of the mean. The dotted lines show the Bayesian mixed-effects regression model fits. In Panels b, c, e, f, h, and i, the error bars represent the 95% HDIs of the distributions. VT = visuo-tool; VTC = visuo-tool-closed; HDI = highest density interval; diff. = difference. See the online article for the color version of this figure.

the object's position (Camponogara, 2023; Camponogara & Volcic, 2019b, 2021, 2022). This similarity suggests an effective translation of haptic information from the hand operating the tool into object-relevant information for multisensory grasping performance.

The object localization may have occurred by two concurrent processes, consisting of encoding the pattern of somatosensory inputs elicited by the tool's impact with the object (Miller et al., 2019, 2018) and/or the haptically experienced inertia stemming from the active tool movement, which may have been used to infer the tool's length and, thus, the object position at the end of it (Chan, 1994; Solomon et al., 1989; Solomon & Turvey, 1988). Patients deprived of proprioception, indeed, show reduced or even absent

effects of action performance when using a tool: The usually observed change in hand kinematics after tool use (Cardinali et al., 2009) fades away when proprioceptive inputs are prevented (Cardinali, Brozzoli, Luauté, et al., 2016). A reduction in action performance following tool use is also observed when the haptically experienced inertia is prevented by passive tool movements, that is, when the tool is moved by the experimenter (Farnè, Iriki, & Làdavas, 2005; Hihara et al., 2003; Iriki et al., 1996; Maravita et al., 2002; Obayashi et al., 2000). Thus, the inherent somatosensory and haptic stimulation characterizing the tool's active placement on the object may have played a key role in establishing the tool's length and, consequently, the object's location.

Figure 9

Scatterplots of Paired Observations in Experiment 3
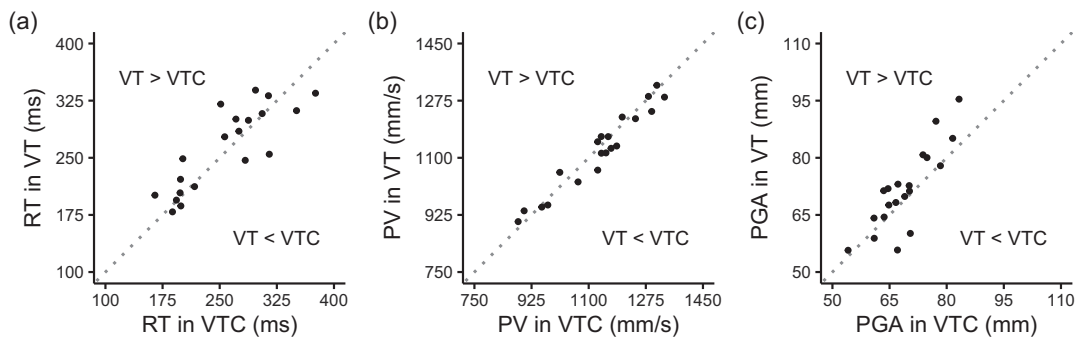
Note. Each point represents the average reaction time (RT, a), average peak velocity (PV, b), and average peak of grip aperture (PGA, c) of a single participant for a pair of conditions. The diagonal reference line of no effect has slope 1 and intercept 0. Points above the diagonal line indicate that the variable of the condition represented on the ordinate axis is larger than the variable represented on the abscissa. VT = visuo-tool; VTC = visuo-tool-closed.

However, the similarities in PV between V and VT and the highest PV in VH suggest that somatosensory inputs from the hand holding the tool may not be sufficient to provide a full multisensory advantage akin to when the hand is directly contacting the object. This may be due to the different ways haptic information is used. In VH, vision could be supported by the continuous haptic information signaling the arm extension, thus benefiting from a constant flow of haptic inputs during the contralateral hand grasping. In contrast, in the VT condition, vision was supported by haptic information stemming from the contact of the tool with the object when clenching it, and the object position was likely inferred only through haptic encoding before grasping it with the contralateral hand (Miller et al., 2018, 2019, 2023). This may have played a fundamental difference in action performance and, thus, reduced the PV in the VT condition. It is also worth noting that the arm postures in VH and VT were considerably different. In the VT condition, the arm holding the tool was bent and close to the participant's body (Figure 1b), whereas in the VH condition, the arm holding the object was extended. This difference in arm posture may also have played a role in guiding the contralateral hand grasping.

Even though our results suggest that the tool supports vision by providing mainly positional information, it may be that, in specific visual conditions, the tool-sensed size also plays a role. In haptic-based multisensory grasping (i.e., grasping a seen hand-held object), the haptic size plays only a marginal role in optimal visual conditions (Camponogara & Volcic, 2019b, 2021), whereas it provides a significant contribution to action performance in conditions of visual uncertainty (Camponogara & Volcic, 2022). Thus, introducing visual uncertainty when grasping a tool-held object may lead to a gradual use of the tool-sensed size gathered through the haptically sensed distance between the thumb and the other digits holding the tool's handle. A second factor, other than optimal vision, that may have prevented the use of tool-sensed size is the unequal mapping between the hand controlling the handle and the aperture of the gripper. When the hand was semiopen or semiclosed, the gripper was either completely open or closed, respectively. This unequal mapping may have prevented the use of the haptic distance between the digits holding the handle to infer the object size (Takahashi et al., 2009; Takahashi & Watt, 2014, 2017).

The tool-mediated and hand-based sensing advantage may alternatively be explained by other factors. First, because object position was not varied it might have been easily memorized. However, if this was the case, a memory effect should have benefited not only the actions guided by tool-mediated and hand-based sensing, but also those based solely on visual information. Second, participants may have taken advantage of the close proximity of the tool's grabber or their hand to the object to visually compare their sizes with the object's size, or distance information may have been enriched by the view of the grabber or their arm. In this case, the similar performance between VH and VT could be simply due to a visual comparison between a known (tool/hand/arm) with an unknown (object) size and distance. It is worth considering, however, that previous studies showed that seeing the arm and the hand holding the object in multisensory conditions has no impact on object size estimation (Volcic & Alalami, 2017). Furthermore, ad hoc experiments should be conducted to either confirm or exclude this hypothesis.

The successful use of tool-sensed information for action execution hints at common neural structures that govern both tool-mediated and hand-based multisensory grasping. Indeed, the primary motor and somatosensory cortices and the posterior parietal cortex have been shown to play a role in both tool-mediated and hand-based sensing (Gallivan et al., 2013; Jacobs et al., 2010; Johnson-Frey, 2004; Maravita & Iriki, 2004; Miller et al., 2019). These neural structures are also involved in the sensory–motor transformation process of grasping and reaching movements toward visual and haptic targets (Bernier & Grafton, 2010; Buneo et al., 2002; Cohen & Andersen, 2002). Thus, transforming haptic information about the tool (i.e., length of the tool, size of the handle) into object positional and size information for action guidance may rely on the same neural circuits involved in processing haptic information (i.e., arm extension and digits separation) stemming from the direct contact of the hand with the object (Berryman et al., 2006; Proske & Gandevia, 2012).

The discovery that a tool can be used as a sensory device to guide a contralateral limb movement has strong practical relevance for prosthesis engineering and rehabilitation studies. It has been shown that the sense of touch could be restored in amputees through special prosthetic devices equipped with microelectrodes,

surgically implanted in the amputees' nerves. During object manipulation, the prosthetic hand movement activates the microelectrodes, which elicit the sensory nerves. The decoding of the nerves' activation pattern allows recognizing the size of the held objects to an almost comparable level as in control participants (D'Anna et al., 2019). Our study suggests that amputees could use the restored haptic information to develop and fine-tune bimanual object manipulation skills. Additionally, it also hints at the use of sensory stimulation and multisensory integration techniques to improve prosthesis compliance. Through bimanual object manipulations, prosthesis users could associate the visual with the felt object features (i.e., position and size) and improve prosthesis control. The overlap of neural structures involved in the tool- and hand-mediated sensing can also be successfully exploited to promote the restoration of motor functions following a stroke. By incorporating tasks that require the use of a tool or the hand to guide reaching and grasping movements with their affected hand, stroke patients could practice and improve their motor skills in more varied contexts. This type of interleaved training could promote generalized learning and help maintain the gains made during rehabilitation by improving hand dexterity and coordination.

In conclusion, our study demonstrates that humans can not only use tools as pure grasping or sensory devices, but they can integrate tool-sensed object information with vision to guide fine motor skills, such as precision grips.

References

Addamo, P. K., Farrow, M., Hoy, K. E., Bradshaw, J. L., & Georgiou-Karistianis, N. (2007). The effects of age and attention on motor overflow production—A review. *Brain Research Reviews*, *54*(1), 189–204. https://doi.org/10.1016/j.brainresrev.2007.01.004

Arbib, M. A., Bonaiuto, J. B., Jacobs, S., & Frey, S. H. (2009). Tool use and the distalization of the end-effector. *Psychological Research*, *73*(4), 441–462. https://doi.org/10.1007/s00426-009-0242-2

Bell, J. D., & Macuga, K. L. (2022). Are tools truly incorporated as an extension of the body representation?: Assessing the evidence for tool embodiment. *Psychonomic Bulletin & Review*, *29*(2), 343–368. https://doi.org/10.3758/s13423-021-02032-6

Bernier, P.-M., & Grafton, S. T. (2010). Human posterior parietal cortex flexibly determines reference frames for reaching based on sensory context. *Neuron*, *68*(4), 776–788. https://doi.org/10.1016/j.neuron.2010.11.002

Berryman, L. J., Yau, J. M., & Hsiao, S. S. (2006). Representation of object size in the somatosensory system. *Journal of Neurophysiology*, *96*(1), 27–39. https://doi.org/10.1152/jn.01190.2005

Biro, D., Haslam, M., & Rutz, C. (2013). Tool use as adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), Article 20120408. https://doi.org/10.1098/rstb.2012.0408

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632–636. https://doi.org/10.1038/416632a

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Burton, G. (1993). Non-neural extensions of haptic sensitivity. *Ecological Psychology*, *5*(2), 105–124. https://doi.org/10.1207/s15326969eco0502_1

Camponogara, I. (2023). The integration of action-oriented multisensory information from target and limb within the movement planning and execution. *Neuroscience & Biobehavioral Reviews*, *151*, Article 105228. https://doi.org/10.1016/j.neubiorev.2023.105228

Camponogara, I., & Volcic, R. (2019a). Grasping adjustments to haptic, visual, and visuo-haptic object perturbations are contingent on the sensory modality. *Journal of Neurophysiology*, *122*(6), 2614–2620. https://doi.org/10.1152/jn.00452.2019

Camponogara, I., & Volcic, R. (2019b). Grasping movements toward seen and handheld objects. *Scientific Reports*, *9*(1), Article 3665. https://doi.org/10.1038/s41598-018-38277-w

Camponogara, I., & Volcic, R. (2021). Integration of haptics and vision in human multisensory grasping. *Cortex*, *135*, 173–185. https://doi.org/10.1016/j.cortex.2020.11.012

Camponogara, I., & Volcic, R. (2022). Visual uncertainty unveils the distinct role of haptic cues in multisensory grasping. *ENeuro*, *9*(3), 1–12. https://doi.org/10.1523/ENEURO.0079-22.2022

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, *228*(1), 25–42. https://doi.org/10.1007/s00221-013-3532-2

Cardinali, L., Brozzoli, C., Finos, L., Roy, A., & Farnè, A. (2016). The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition*, *149*, 1–5. https://doi.org/10.1016/j.cognition.2016.01.001

Cardinali, L., Brozzoli, C., Luauté, J., Roy, A. C., & Farnè, A. (2016). Proprioception is necessary for body schema plasticity: Evidence from a deafferented patient. *Frontiers in Human Neuroscience*, *10*, Article 272. https://doi.org/10.3389/fnhum.2016.00272

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology*, *19*(12), R478–R479. https://doi.org/10.1016/j.cub.2009.05.009

Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A. C., & Farnè, A. (2012). Grab an object with a tool and change your body: Tool-use-dependent changes of body representation for action. *Experimental Brain Research*, *218*(2), 259–271. https://doi.org/10.1007/s00221-012-3028-5

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, 1–32. https://doi.org/10.18637/jss.v076.i01

Chan, T.-C. (1994). Haptic perception of partial-rod lengths with the rod held stationary or wielded. *Perception & Psychophysics*, *55*(5), 551–561. https://doi.org/10.3758/BF03205312

Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience*, *3*(7), 553–562. https://doi.org/10.1038/nrn873

Costantini, M., Ambrosini, E., Sinigaglia, C., & Gallese, V. (2011). Tool-use observation makes far objects ready-to-hand. *Neuropsychologia*, *49*(9), 2658–2663. https://doi.org/10.1016/j.neuropsychologia.2011.05.013

D'Anna, E., Valle, G., Mazzoni, A., Strauss, I., Iberite, F., Patton, J., Petrini, F. M., Raspopovic, S., Granata, G., Di Iorio, R., Controzzi, M., Cipriani, C., Stieglitz, T., Rossini, P. M., & Micera, S. (2019). A closed-loop hand prosthesis with simultaneous intraneural tactile and position feedback. *Science Robotics*, *4*(27), Article eaau8892. https://doi.org/10.1126/scirobotics.aau8892

Derzsi, Z., & Volcic, R. (2018). MOTOM toolbox: MOtion Tracking via Optotrak and Matlab. *Journal of Neuroscience Methods*, *308*, 129–134. https://doi.org/10.1016/j.jneumeth.2018.07.007

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. https://doi.org/10.1038/415429a

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–169. https://doi.org/10.1016/j.tics.2004.02.002

Farnè, A., Bonifazi, S., & Làdavas, E. (2005). The role played by tool-use and tool-length on the plastic elongation of peri-hand space: A single case study. *Cognitive Neuropsychology*, *22*(3–4), 408–418. https://doi.org/10.1080/02643290442000112

Farnè, A., Iriki, A., & Làdavas, E. (2005). Shaping multisensory action–space with tools: Evidence from patients with cross-modal extinction. *Neuropsychologia*, *43*(2), 238–248. https://doi.org/10.1016/j.neuropsychologia.2004.11.010

Farnè, A., & Làdavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, *11*(8), 1645–1649. https://doi.org/10.1097/00001756-200006050-00010

Gallivan, J. P., McLean, D. A., Valyear, K. F., & Culham, J. C. (2013). Decoding the neural mechanisms of human tool use. *eLife*, *2*, Article e00425. https://doi.org/10.7554/eLife.00425

Gentilucci, M., Roy, A. C., & Stefanini, S. (2004). Grasping an object naturally or with a tool: Are these tasks guided by a common motor representation? *Experimental Brain Research*, *157*(4), 496–506. https://doi.org/10.1007/s00221-004-1863-8

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Houghton Mifflin.

Hihara, S., Obayashi, S., Tanaka, M., & Iriki, A. (2003). Rapid learning of sequential tool use by macaque monkeys. *Physiology & Behavior*, *78*(3), 427–434. https://doi.org/10.1016/s0031-9384(02)01006-5

Holmes, N. P., Sanabria, D., Calvert, G. A., & Spence, C. (2007). Tool-use: Capturing multisensory spatial attention or extending multisensory peripersonal space? *Cortex*, *43*(3), 469–489. https://doi.org/10.1016/s0010-9452(08)70471-4

Hoy, K. E., Fitzgerald, P. B., Bradshaw, J. L., Armatas, C. A., & Georgiou-Karistianis, N. (2004). Investigating the cortical origins of motor overflow. *Brain Research Reviews*, *46*(3), 315–327. https://doi.org/10.1016/j.brainresrev.2004.07.013

Itaguchi, Y., & Fukuzawa, K. (2014). Hand-use and tool-use in grasping control. *Experimental Brain Research*, *232*(11), 3613–3622. https://doi.org/10.1007/s00221-014-4053-3

Jacobs, S., Danielmeier, C., & Frey, S. H. (2010). Human anterior intraparietal and ventral premotor cortices support representations of grasping with the hand or a novel tool. *Journal of Cognitive Neuroscience*, *22*(11), 2594–2608. https://doi.org/10.1162/jocn.2009.21372

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, *8*(2), 71–78. https://doi.org/10.1016/j.tics.2003.12.002

Kilteni, K., & Ehrsson, H. H. (2017). Sensorimotor predictions and tool use: Hand-held tools attenuate self-touch. *Cognition*, *165*, 1–9. https://doi.org/10.1016/j.cognition.2017.04.005

Klatzky, R. L., & Lederman, S. J. (1999). Tactile roughness perception with a rigid link interposed between skin and surface. *Perception & Psychophysics*, *61*(4), 591–607. https://doi.org/10.3758/BF03205532

Lee, M. D., & Wagenmakers, E.-J. (2014). *Bayesian cognitive modeling: A practical course*. Cambridge University Press.

lriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport*, *7*(14), 2325–2330. https://doi.org/10.1097/00001756-199610020-00010

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, *8*(2), 79–86. https://doi.org/10.1016/j.tics.2003.12.008

Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, *83*(2), B25–B34. https://doi.org/10.1016/s0010-0277(02)00003-3

Martel, M., Cardinali, L., Bertonati, G., Jouffrais, C., Finos, L., Farnè, A., & Roy, A. (2019). Somatosensory-guided tool use modifies arm representation for action. *Scientific Reports*, *9*(1), Article 5517. https://doi.org/10.1038/s41598-019-41928-1

Martel, M., Finos, L., Koun, E., Farnè, A., & Roy, A. C. (2021). The long developmental trajectory of body representation plasticity following tool use. *Scientific Reports*, *11*(1), Article 559. https://doi.org/10.1038/s41598-020-79476-8

Miller, L. E., Cawley-Bennett, A., Longo, M. R., & Saygin, A. P. (2017). The recalibration of tactile perception during tool use is body-part specific.

Experimental Brain Research, *235*(10), 2917–2926. https://doi.org/10.1007/s00221-017-5028-y

Miller, L. E., Fabio, C., Ravenda, V., Bahmad, S., Koun, E., Salemme, R., Luauté, J., Bolognini, N., Hayward, V., & Farne, A. (2019). Somatosensory cortex efficiently processes touch located beyond the body. *Current Biology*, *29*(24), 4276–4283.e5. https://doi.org/10.1016/j.cub.2019.10.043

Miller, L. E., Jarto, F., & Medendorp, W. P. (2023). A horizon for haptic perception. *Journal of Neurophysiology*, *129*(4), 793–798. https://doi.org/10.1152/jn.00442.2022

Miller, L. E., Montroni, L., Koun, E., Salemme, R., Hayward, V., & Farnè, A. (2018). Sensing with tools extends somatosensory processing beyond the body. *Nature*, *561*(7722), 239–242. https://doi.org/10.1038/s41586-018-0460-0

Nicolini, C., Fantoni, C., Mancuso, G., Volcic, R., & Domini, F. (2014). A framework for the study of vision in active observers. In B. E. Rogowitz, T. N. Pappas, & H. de Ridder (Eds.), *Human vision and electronic imaging XIX* (Vol. 9014, pp. 297–307). Society of Photo-Optical Instrumentation Engineers. https://doi.org/10.1117/12.2045459

Obayashi, S., Tanaka, M., & Iriki, A. (2000). Subjective image of invisible hand coded by monkey intraparietal neurons. *NeuroReport*, *11*(16), 3499–3505. https://doi.org/10.1097/00001756-200011090-00020

Pettypiece, C. E., Goodale, M. A., & Culham, J. C. (2010). Integration of haptic and visual size cues in perception and action revealed through cross-modal conflict. *Experimental Brain Research*, *201*(4), 863–873. https://doi.org/10.1007/s00221-009-2101-1

Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, *92*(4), 1651–1697. https://doi.org/10.1152/physrev.00048.2011

R Core Team. (2020). *R: A language and environment for statistical computing* [Computer software]. https://www.R-project.org/

Saig, A., Gordon, G., Assa, E., Arieli, A., & Ahissar, E. (2012). Motor-sensory confluence in tactile perception. *The Journal of Neuroscience*, *32*(40), 14022–14032. https://doi.org/10.1523/JNEUROSCI.2432-12.2012

Schot, W. D., Brenner, E., & Smeets, J. B. J. (2010). Robust movement segmentation by combining multiple sources of information. *Journal of Neuroscience Methods*, *187*(2), 147–155. https://doi.org/10.1016/j.jneumeth.2010.01.004

Solomon, H. Y., & Turvey, M. T. (1988). Haptically perceiving the distances reachable with hand-held objects. *Journal of Experimental Psychology: Human Perception and Performance*, *14*(3), 404–427. https://doi.org/10.1037//0096-1523.14.3.404

Solomon, H. Y., Turvey, M. T., & Burton, G. (1989). Perceiving extents of rods by wielding: Haptic diagonalization and decomposition of the inertia tensor. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(1), 58–68. https://doi.org/10.1037/0096-1523.15.1.58

Soto-Faraco, S., Ronald, A., & Spence, C. (2004). Tactile selective attention and body posture: Assessing the multisensory contributions of vision and proprioception. *Perception & Psychophysics*, *66*(7), 1077–1094. https://doi.org/10.3758/bf03196837

Sposito, A., Bolognini, N., Vallar, G., & Maravita, A. (2012). Extension of perceived arm length following tool-use: Clues to plasticity of body metrics. *Neuropsychologia*, *50*(9), 2187–2194. https://doi.org/10.1016/j.cognition.2016.01.001

Takahashi, C., Diedrichsen, J., & Watt, S. J. (2009). Integration of vision and haptics during tool use. *Journal of Vision*, *9*(6), Article 3. https://doi.org/10.1167/9.6.3

Takahashi, C., & Watt, S. J. (2014). Visual-haptic integration with pliers and tongs: Signal "weights" take account of changes in haptic sensitivity caused by different tools. *Frontiers in Psychology*, *5*, Article 109. https://doi.org/10.3389/fpsyg.2014.00109

Takahashi, C., & Watt, S. J. (2017). Optimal visual–haptic integration with articulated tools. *Experimental Brain Research*, *235*(5), 1361–1373. https://doi.org/10.1007/s00221-017-4896-5

Vasishth, S., Mertzen, D., Jäger, L. A., & Gelman, A. (2018). The statistical significance filter leads to overoptimistic expectations of replicability. *Journal of Memory and Language*, *103*, 151–175. https://doi.org/10.1016/j.jml.2018.07.004

Volcic, R., & Alalami, N. (2017). The role of proprioception in visuo-haptic size perception. *Journal of Vision*, *17*(10), Article 360. https://doi.org/10.1167/17.10.360

Volcic, R., & Domini, F. (2016). On-line visual control of grasping movements. *Experimental Brain Research*, *234*(8), 2165–2177. https://doi.org/10.1007/s00221-016-4620-x

Yamamoto, S., & Kitazawa, S. (2001). Sensation at the tips of invisible tools. *Nature Neuroscience*, *4*(10), 979–980. https://doi.org/10.1038/nn721

Yamamoto, S., Moizumi, S., & Kitazawa, S. (2005). Referral of tactile sensation to the tips of L-shaped sticks. *Journal of Neurophysiology*, *93*(5), 2856–2863. https://doi.org/10.1152/jn.01015.2004